

Aspects of the distribution of Early Jurassic belemnites

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ABSTRACT - The first true belemnites are considered to be of Early Jurassic age. They evolved in Europe, and remained restricted to the European shelf seas up to the Toarcian. In the Toarcian, significant changes took place, with the development of a Tethyan belemnite fauna, and a Boreal fauna largely endemic to the Arctic Basin. Possible causes for the distribution patterns observed are discussed.

KEY WORDS: belemnites, biogeography, Early Jurassic, Toarcian.

INTRODUCTION

The palaeobiogeography of the belemnites has received much attention over the past two decades (eg Saks and Nal'nyaeva, 1970, 1975; Stevens, 1973a,b; Stoyanova-Vergilova, 1982; Mutterlose *et al.*, 1983; Doyle, 1987, 1992b; Mutterlose, 1988). However, few of these studies deal with the belemnites from inception; most concentrate on the details of patterns which emerged in the later Jurassic and Cretaceous, and as such the distribution of Early Jurassic belemnites remains relatively unknown. In view of this, and following my review of the biogeography of the Aulacocerida (Doyle, 1990a), the present paper is an attempt to discuss in some detail the distribution of the early belemnites.

In my view the earliest belemnites, excluding the Aulacocerida (?Devonian-Jurassic) in the presently accepted manner, are Jurassic in age, appearing in the Hettangian (Planorbis Zone) of Europe. A review of the evidence for this is presented below. A basic, largely accepted synthesis of Early Jurassic belemnite distribution is one of restriction to Europe prior to the

Toarcian (Stevens, 1973a). This is obviously difficult to test using a criterion of absence, but in view of the preservation potential of belemnites, and the known extent of Lower Jurassic rocks (eg Arkell, 1956) it seems unlikely that this distribution is wholly artificial.

Research on the earliest Jurassic (Hettangian-Pliensbachian) belemnites has been limited in recent years, and in consequence meaningful data is available only to generic level. The Toarcian was a period of change, and fortunately recent detailed research (eg Saks and Nal'nyaeva, 1970, 1975; Riegraf, 1980; Riegraf *et al.*, 1984; Doyle, 1985, 1990b, 1992a) allows meaningful comparisons at the specific level.

This paper probably generates more questions than can be readily explained; it aims at least to present uniform data for future interpretation, and to this end the classification here, the basis for the relevant part of the *Treatise on Invertebrate Palaeontology*, forms an appendix to the paper.

EARLY ORIGINS OF THE BELEMNITIDA

Even before Flower's (1945) paper on a Carboniferous belemnite from North America, there had been much debate on the origins of the Belemnitida. Ideas in the first half of this century were that the belemnites and aulacocerids were closely related (discussion in Jeletzky, 1966, p.12), with the former directly derived from the latter. After a detailed study of all available evidence, Jeletzky (1966) finally

separated the belemnites and the aulacocerids as different orders within the class Cephalopoda. He also concluded that belemnites and aulacocerids arose independently from orthoconic, echtochleate cephalopods such as the bactritids. A detailed critique of this hypothesis is beyond the scope of the present paper, but if this is so, the most conservative estimate of the earliest belemnites would be Permo-Triassic,

with extension into the Carboniferous and even Devonian possible (Jeletzky 1966, fig 2). Recent cladistic treatments of belemnite phylogeny (eg Engeser and Bandel, 1988), suggest that derivation from the Aulacocerida may be more appropriate, Doyle *et al.* (1994).

Accepting that aulacocerids are not true belemnites, records of Carboniferous belemnites do exist in the form of *Eobelemnites caneyensis* Flower and *Jeletzkyia douglassae* Johnson and Richardson. Most authorities agree that the only true specimen of *Eobelemnites* is indeed a belemnite phragmocone, indistinguishable from Jurassic examples (Flower, 1945; Jeletzky, 1966, p.166). However, as this specimen was not collected by the author of the species, and as evidence for its age rests only on the label attached to it as a museum specimen, its stratigraphical location must surely be treated as dubious and unsafe. *Jeletzkyia* is without doubt a Carboniferous cephalopod, but evidence for its belemnite affinities rest with its ten hook-bearing arms (Gordon, 1971). No phragmocone or rostrum has been observed in detail, and Saunders and Richardson (1979) argued for teuthid origins through the identification of so-called 'gladii' (since identified as fish scales by Riccardi and Sabattini, 1985) in the same strata. Arm hooks are known from Permian phragmoteuthids (Engeser and Clarke, 1988), and therefore, *Jeletzkyia* could just as easily be a phragmoteuthid, or even an aulacocerid for that matter, as no aulacocerid arm crowns have yet been recovered. Discounting both these records as equivocal, we are left with two other pre-Jurassic belemnite records, from the Permian and Triassic of China.

Chen and Sun (1982) described a new family from the Permian of south China, the Palaeobelemnopsidae, which they considered were ancestral, early belemnites. This family occurs with the aulacocerid *Stenoconites*, and has recently been reassigned to the Aulacocerida by Doyle (1990a) on phragmocone characteristics. Zhu and Bian (1984) described another new coleoid family from China, the Sinobelemnitidae. These are apparently Triassic in age, and are apparently true belemnites, as far as can be ascertained from the illustrations and descriptions. However, they are remarkable in being closer in morphology to Middle and Late Jurassic belemnites (Belemnopseidae) than to the Early Jurassic Belemnitidae. Certainly, very similar belemnites were described from the Late Jurassic-Early Cretaceous of Tibet by Yang and Wu (1964). These are the only serious contenders in the search for pre-Jurassic belemnites, but due to the aberrant nature of their morphology, further clarification of the stratigraphical data, and detailed study of their morphology, is needed.

Thus, the earliest belemnites are considered to be of Early Jurassic age (Planorbis Zone), and comprise simple, conical belemnites without grooves and with generalised lateral lines. These are here taken as the ancestral belemnite stock.

PATTERNS OF BELEMNITE DISTRIBUTION

Hettangian-Pliensbachian belemnites

Given the origins discussed above, the earliest apparent record is that of a group of very small, simple and conical rostra from the Planorbis Zone in Germany (Schwegler 1939). Riegraf (1980) erected the genus *Schwegleria* to house these species, although they are essentially *Nannobelus*-like, and this genus is retained here (text-fig. 1). Few belemnites of this age have been recorded elsewhere than southern Germany so that it is difficult to predict the initial distributions in the Hettangian.

Nannobelus is the most familiar Sinemurian to earliest Pliensbachian belemnite genus, identifiable by its simple conical form (text-fig. 1). It is common in the European region, including England (Phillips, 1865-1909), Germany (Werner, 1912), France (Dumortier, 1869), Bulgaria (Stoyanova-Vergilova, 1978) and Czechoslovakia (Činčurová, 1983), and is recorded from as far afield as North Africa (Coquand, 1862), Turkey (Doyle and Marriotti, 1991) and east Greenland (Rosenkrantz, 1934, Doyle, 1991). However, records of *Nannobelus* from rocks of this age in Tuscany (Savi and Meneghini, 1850) and from La Spezia are representative of conical-shelled aulacocerids of the genus *Moisisovicsteuthis*. At least four species flourished in Europe in the Sinemurian (eg Phillips, 1865-1909; Dumortier, 1869; Werner, 1912) but *N. acutus* itself appears to be longest lived, extending into the Lower Pliensbachian. *Coeloteuthis*, itself extending into the Lower Pliensbachian, is a distinctive genus of small, cup-like rostra (text-fig. 1) which has been recorded largely from Europe and the Tethyan borders (eg Bairstow, 1950; Schumann, 1974; Doyle and Marriotti, 1991). As discussed below, the Russian interpretation of the genera *Nannobelus* and *Coeloteuthis* (= *Clastoteuthis*) from the Toarcian (Saks and Nal'nyaeva, 1970) is based upon endemic homeomorphs (see below). Frebold and Little (1962) have recorded belemnites from the Sinemurian of Canada, but examination of the actual specimens indicate that they are representative *Atractites* (Aulacocerida). Isolated records are available for poorly preserved and equivocal Sinemurian belemnoids in Antarctica, Pakistan and Siberia (possibly aulacocerids) and Tibet. These cannot be positively identified, and although unlikely, could represent a relict of a former more widespread distribution (Doyle, 1987).

The early Pliensbachian saw the first appreciable increase in diversity and distribution of the belemnites. Thompson (1910) in an early review of belemnite distribution and diversity in Britain, recorded a peak of belemnite species diversity in the early Pliensbachian (Jamesoni Zone). Certainly generic diversity was boosted with the appearance of the genera *Passaloteuthis*, *Angeloteuthis*, *Pseudohastites* (*sensu stricto*), *Bairstowius* (= '*Pseudohastites*' *sensu* Lang, 1928, a genus typified by *Belemnites iunceus* Phillips, Jeletzky *in* Doyle *et al.*, 1994) and *Hastites* (text-fig. 1). The belemnites were still concentrated in Europe at this time (text-fig. 2); large, diverse faunas have been distinguished particularly in England, France and southern and northern Germany (eg Dumortier, 1869; Lang, 1928; Schwegler, 1962a, b). Similar faunas are known from Turkey (Anatolia), Bulgaria, Czechoslovakia, Sweden and East Greenland (Rosenkrantz, 1934; Troedsson, 1951; Činčurová, 1971, 1983; Stoyanova-Vergilova, 1978, 1982; Doyle, 1991; Doyle and Marriotti, 1991). A similar fauna has recently been obtained from Mount Kumaet, Sicily (N. Marriotti, personal communication, 1990). The taxonomic composition of these faunas is broadly similar, but with differing proportions of the genera *Nannobelus*, *Coeloteuthis*, '*Pseudohastites*', *Passaloteuthis* and *Hastites*, suggesting some incipient, local endemism, but much

more detailed collecting is required to prove this. By the late Pliensbachian, *Nannobelus* and *Coeloteuthis* were extinct, and *Passaloteuthis* was dominant, with new genera such as *Parapassaloteuthis* making their first appearance. In addition to *Hastites*, the short-lived hastitid genera *Gastrobelus* and *Pleurobelus* (text-fig. 1) also appeared, and during their brief period of existence extended across Europe to Portugal (Choffat, 1880), France and Germany (Dumortier, 1869; Schwegler, 1965) and Britain (Phillips, 1865-1909) (text-fig. 2).

Toarcian belemnites

The Toarcian was an important period of change in belemnite distribution. During the Tenuicostatum Zone, the Europe-wide (and reaching East Greenland) belemnite fauna, was Late Pliensbachian in aspect; it was composed primarily of the genus *Passaloteuthis* (eg Riegraf, 1980, table 1; Riegraf *et al.*, 1984; Doyle, 1990b), *Hastites sensu stricto* and the other hastitid genera *Gastrobelus* and *Pleurobelus* had become extinct in the Late Pliensbachian. The picture is one of a decline in the passaloteuthidin belemnites from a maximum in the Early Pliensbachian.

According to Lissajous (1927), the earliest *Acrocoelites*, the first of the megateuthin belemnites which were to dominate the Toarcian, appeared in the

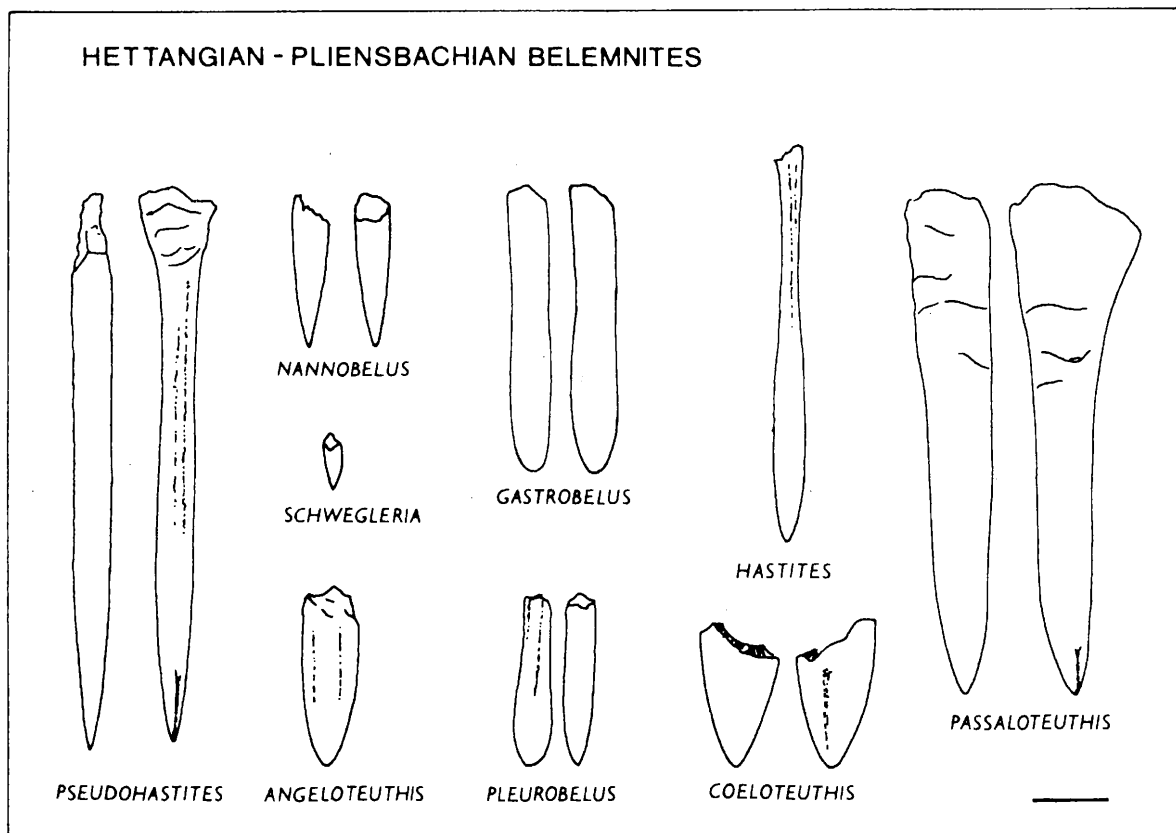


Fig. 1 - Representing Hettangian-Pliensbachian belemnites. Scale bar represents 2 cm.

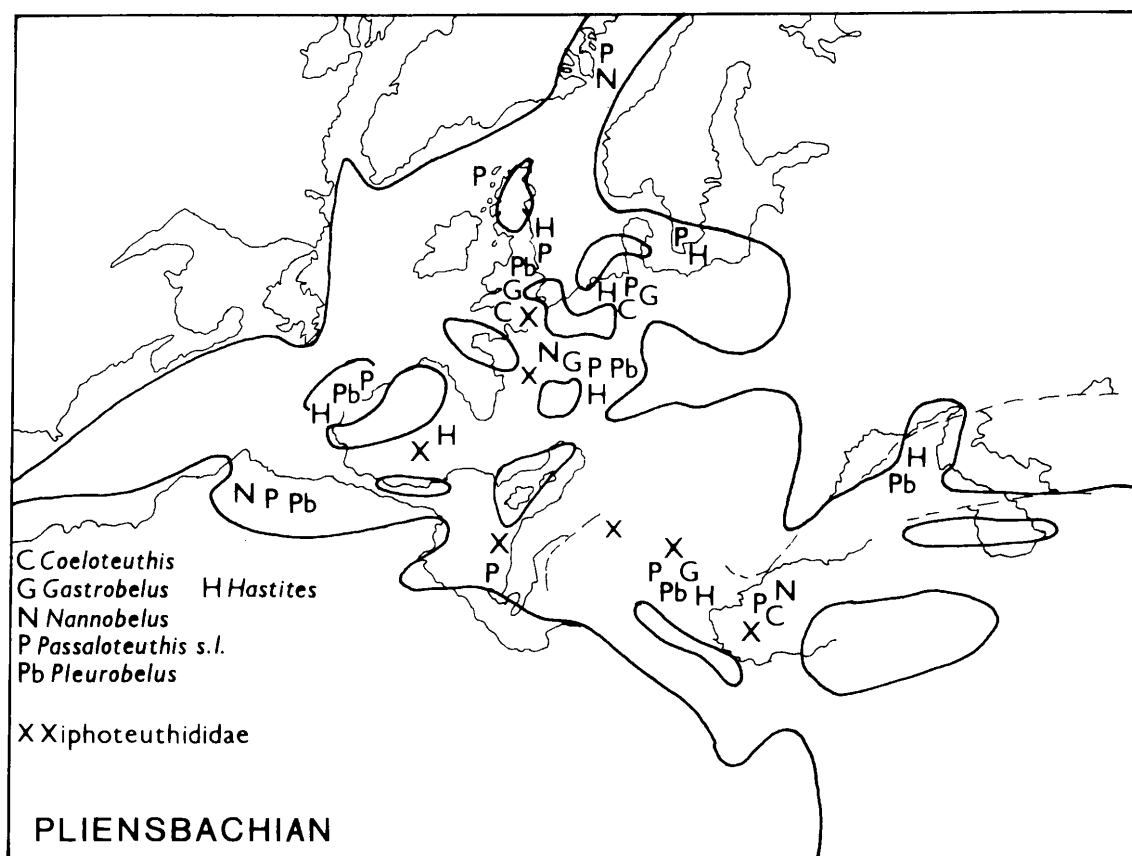


Fig. 2 - Distribution of Pliensbachian belemnites and aulacocerids (Xiphoteuthididae). Base map from Howarth (1981, fig. 13.7).

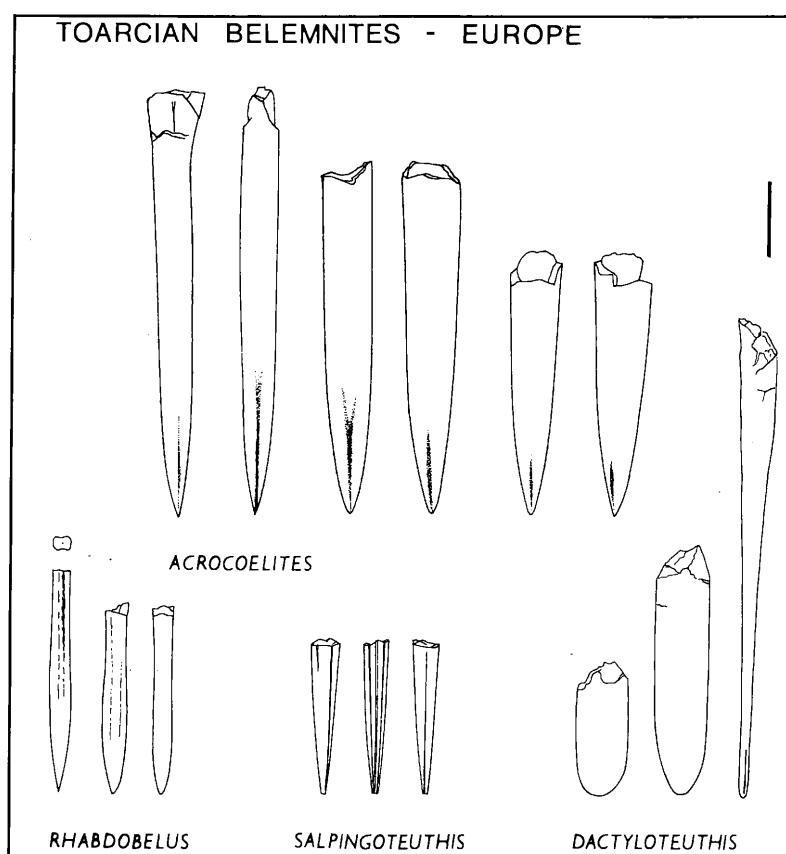


Fig. 3 - Representative Toarcian belemnites from Europe. Scale bar represents 2 cm.

Domerian of France. *Acrocoelites harleyi* Lissajous is *Passaloteuthis*-like in overall form but with an additional, ventrally situated, apical groove. This so-called tripartite morphology is characteristic of most of the Early Toarcian belemnites that were to follow (text-fig. 3). The first of these megateuthin belemnites to appear in Britain and the rest of northern Europe was *Acrocoelites trisulculosus* (Simpson) (= *A. rauli* (Werner) of authors). This belemnite resembles the published photographs of *A. harleyi* in its cylindrical form, and was abundant within the Falciferum Zone of Europe (eg Činčurová, 1971, 1983 (= *Salpingoteuthis carpaticus* Činčurová); Riegraf *et al.*, 1984). Diversity was very low at this time; only this and the related species *A. ilminsterensis* (Phillips) flourished coincidental with the spread of black-shale facies over much of Europe (Hallam, 1986, 1987) in the Exaratum Subzone. Before the cessation of anoxia in the European basin the belemnite diversities increased markedly with new genera such as *Youngibelus* Riegraf, and *Simpsonibelus* Doyle appearing in Europe. The diversity probably reached a maximum in the late Bifrons Zone (eg Činčurová, 1971, 1983; Stoyanova-Vergilova, 1978, 1982; Riegraf, 1980; Riegraf *et al.*, 1984; Doyle, 1990b, 1992a), but with new taxa appearing to the close of the Toarcian.

Up to the Bifrons Zone, the European belemnite fauna had been remarkably uniform in composition. Despite the regional differences and apparent endemism recorded by Činčurová (1971, 1983) and Stoyanova-Vergilova (1982), detailed study of these published records reveals the identity of these faunas with those of France, Germany, Britain and East Greenland. However, definite endemism is apparent in Europe in the Variabilis Zone with the appearance of the genera *Dactyloteuthis*, *Rhabdobelus* and *Salpingoteuthis* (text-figs. 3,4). Although it could be argued from origination data that *Acrocoelites* was originally southern ('Tethyan') in aspect if it evolved from *A. harleyi* or similar, these three genera can be said to show essentially a Tethyan- restricted distribution at this time.

Dactyloteuthis, in its restricted sense (Doyle, 1992a) is an extremely common component of the Late Toarcian fauna of continental Europe (text-fig. 4). *D. digitalis* (Blainville) and related taxa are widely distributed from Portugal (Choffat, 1880) to France, Germany and Czechoslovakia (d'Orbigny, 1842; Kolb, 1942; Riegraf, 1980; Činčurová, 1971, 1983). The northern-most range of *Dactyloteuthis* is Britain; *D. digitalis* (Blainville) is uncommon in southern England, but to date has never been recorded from the

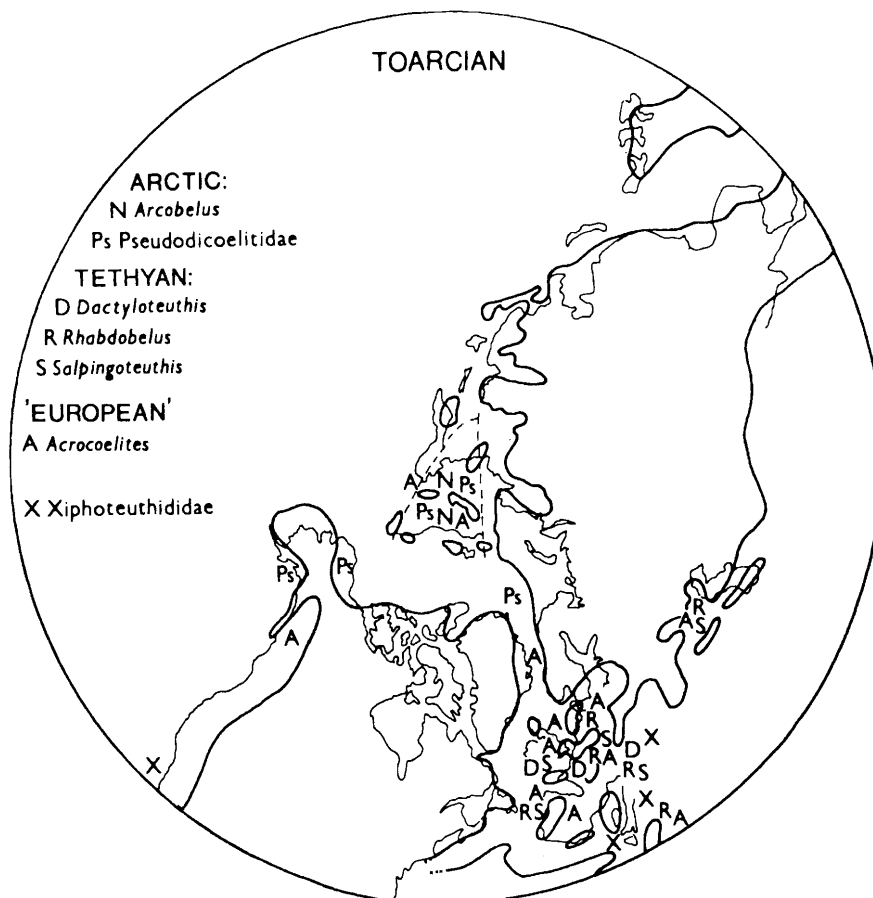


Fig. 4 - Distribution of Toarcian belemnites and aulacocerids (Xiphoteuthididae). Base map from Howarth (1981, fig. 13.8).

Yorkshire and Minch basins. In contrast, *D. crossotela* (Blake) (= *Belemnites meta* Blainville *pars* of authors) is found in the Upper Toarcian rocks of Yorkshire, southern England and Raasay (Inner Hebrides) (Doyle, 1992a). The specimens of *Dactyloteuthis* recorded by Saks and Nal'nyaeva (1975) from Siberia are probably aberrant and do not belong to this genus. This complex distribution pattern is mirrored somewhat by the range of *Salpingoteuthis*. Again common in Europe, and recorded from Portugal (Choffat, 1880), Germany and France (d'Orbigny, 1842; Riegraf, 1980) and the Caucasus (Krimhol'z, 1931), it extends into Britain, reaching only as far north as the English Midlands (Doyle, 1992a). Finally, *Rhabdobelus*, a distinctive hastitid genus, had a similar distribution in Europe (eg d'Orbigny, 1842; Kolb, 1942; Riegraf, 1980), the Caucasus (Krimhol'z, 1931) and Turkey (new data), but this time has not been recorded from Britain at all (text-fig. 4). All these forms are coeval with a continuing, Europe-wide fauna of *Acrocoelites* and its allies, but represent the first indication of an exclusively southern, or Tethyan, belemnite fauna (Doyle, 1987).

More significant is the passaloteuthid colonisation of Siberia, Svalbard and North America for the first time in the Early Toarcian (?Falciferum Zone) (text-

fig. 4). Prior to this event, East Greenland had marked the farthest northern belemnite penetration, maintaining a European aspect, as far as can be determined from the collections made by Rosenkrantz (1934) now in the Geologisk Museum, Copenhagen (Doyle, 1992a). The Siberian fauna contains a strong element of the genus *Acrocoelites*, with some European species, most notably *Acrocoelites trisulculosus* (Simpson), the first *Acrocoelites* to appear in northern Europe, but in the main the fauna is dominated by endemic genera. Saks and Nal'nyaeva (1970) identified several Early Pliensbachian genera from the Toarcian of Siberia, *Nannobelus* and *Clastoteuthis* for example, which are distinct from their namesakes are actually endemic homeomorphs evolved in the Siberian basin. These are here accommodated in the *Arcobelus*, promoted to full generic rank. Other taxa, such as *Passaloteuthis*, *Hastites* and *Catateuthis* (= ?*Pseudohastites* s.s.) text-fig. 5) are recorded reaching much beyond their stratigraphic range in Europe (Saks and Nal'nyaeva, 1970) and retain differences which suggest generic autonomy from their older European counterparts. Finally, a range of other distinct and endemic taxa, such as the Pseudodicoelitidae (*Lenobelus* and *Pseudodicoelites*), *Sachsibelus* and other hastitids indicate the overall endemic nature of the Siberian

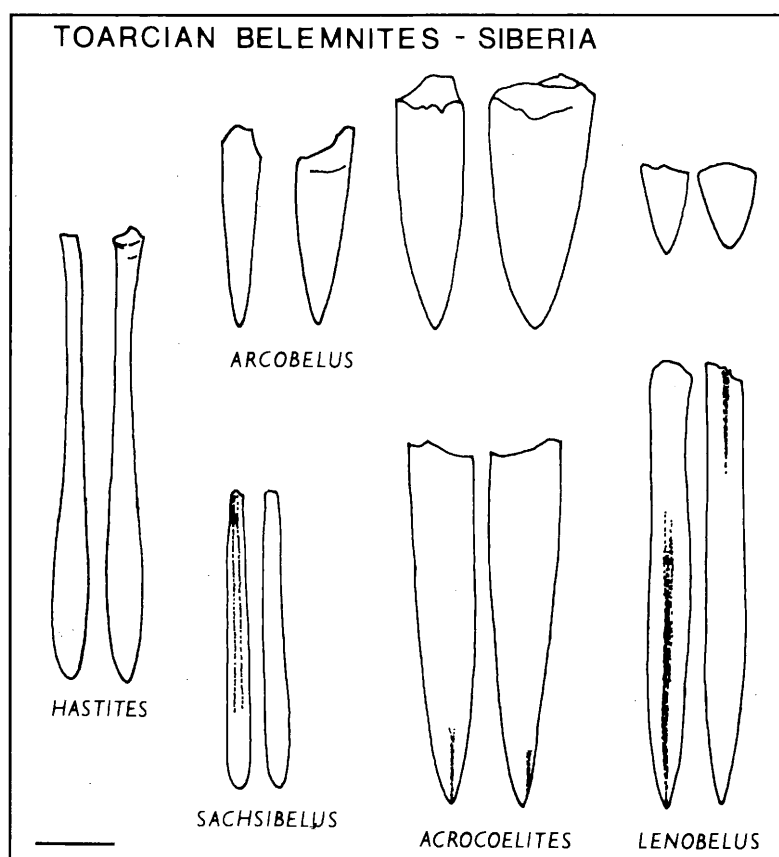


Fig. 5 - Representative Toarcian belemnites from Siberia and the Arctic Basin. Scale bar represents 2 cm.

BRITAIN	n= 34					
FRANCE	D 75 J 60 S 79	n= 19				
GERMANY	D 55 J 37 S 81	D 57 J 44 S 89	n= 41			
CZECH.	D 68 J 52 S 76	D 31 J 18 S 37	D 75 J 60 S 96	n= 26		
BULGARIA	D 59 J 42 S 52	D 29 J 17 S 31	D 53 J 36 S 94	D 52 J 20 S 44	n= 16	
SIBERIA	D 8 J 4 S 12	D 9 J 5 S 21	D 9 J 5 S 12	D 6 J 3 S 12	D 2 J 1 S 6	n= 71
	BRITAIN	FRANCE	GERMANY	CZECH.	BULGARIA	SIBERIA

Fig. 6 - Correlation coefficients calculated for Europe and Siberia in the Toarcian. There is a broad correlation between European countries and a notable endemism for Siberia. Coefficients: D = Dice coefficient; J: Jaccard coefficient; S; Simpson coefficient.

fauna (text-figs. 4,5). The Pseudodicoelitimidae are the most widespread, and take as their distribution the Arctic basin, occurring in Siberia (Saks and Nal'nyaeva, 1975), Arctic Canada (Jeletzky, 1980) and Svalbard (Doyle and Kelly, 1988). It is clear that the Arctic Basin was a major endemic centre at this time (text-fig. 6), with only *Acrocoelites* in common with Europe. *Acrocoelites* species with identity with European species are also found in the Fernie Formation (Hall, 1984; Doyle, 1987) of Alberta, North America.

Toarcian belemnites are also recorded from South America, Tibet, New Caledonia and New Zealand (Moricke, 1895; Stevens, 1965; Wu, 1982; Challinor and Grant-Mackie, 1989). These records are too isolated to be significant but represent the first firm records of true belemnites in the Southern Hemisphere.

DISTRIBUTION PATTERNS IN COEVAL CEPHALOPODS

Early Jurassic aulacocerids

The distribution of Early Jurassic aulacocerids, more specifically the family Xiphoteuthididae has been reviewed by Doyle (1990a). The Aulacocerida were widespread in the Late Triassic, and continued to be so in the Early Jurassic with xiphoteuthids recorded from the Hettangian to Toarcian rocks of North and South America, the Tethyan borders and

northern Europe, penetrating into northwest Europe (references in Doyle, 1990a). Xiphoteuthids are also recorded from Early Jurassic rocks in New Zealand (Toarcian) and New Caledonia (Sinemurian) (Stevens, 1965; Challinor and Grant-Mackie, 1989).

Early Jurassic ammonites

The distribution of Early Jurassic ammonites has been reviewed by Donovan (1967) and Howarth (1973), and more recently by Smith and Tipper (1986). A detailed evaluation is therefore outside the scope of the paper, but the most relevant results are reproduced here. From their appearance in the Hettangian ammonites have been widespread in distribution, and as such do not mirror the distribution of coeval belemnites. Some Boreal and Tethyan stocks have been recognised, but maximum Boreal and Tethyan differentiation appeared in the Late Pliensbachian (text-fig. 7). This pattern was notably reversed in the Toarcian when the pattern was one of maximum cosmopolitanism (Howarth, 1973; Smith and Tipper, 1986). This contrasts strongly with the endemism developing in the belemnites at this time (text fig. 8).

CONTROLS ON DISTRIBUTION

The causes of Mesozoic provinciality have been much discussed, the most relevant recent review being that of Doyle (1987), who, in common with Hallam

(1975), Fursich and Sykes (1977) and Smith and Tipper (1986) considered that the factor of environmental control governed by the palaeogeography and relative hostility of the 'European archipelago' of islands was paramount.

Prior to the Toarcian, belemnites were limited to the European shelf seas. Other cephalopods, including coleoids (Aulacocerida) had a much more widespread distribution, being present across the globe. The reason for such differences is difficult to explain; if other cephalopods, including the possible poor swimmers (enclosed body-chamber) such as aulacocerids could disperse, why not the belemnites? Species of present-day cephalopods exhibit similarly restricted distributions (Jefferts, 1988), but given the diversity of belemnites in the Early Pliensbachian it is difficult to understand why belemnites were unable to disperse beyond Europe. One suggestion could be that belemnites were unable to compete with the already widespread Aulacocerida. Although the role of competition is difficult to judge in the fossil record, it is unlikely that this factor was important in delimiting the belemnites; if anything, the aulacocerids would probably not have been able to

AMMONITE GENERA

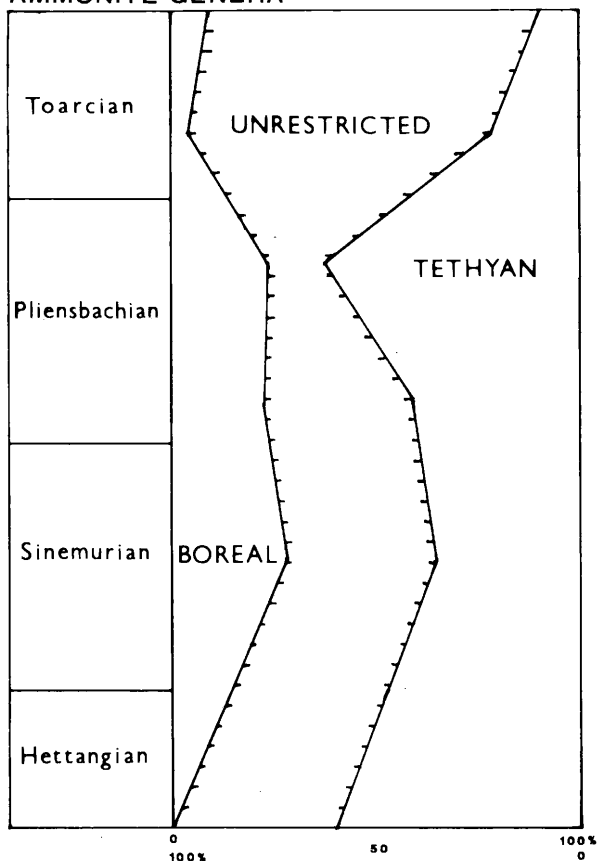


Fig. 7 - Ammonite endemism and diversity in Europe, adapted from Smith and Tipper (1986, fig. 1).

BELEMNITE GENERA

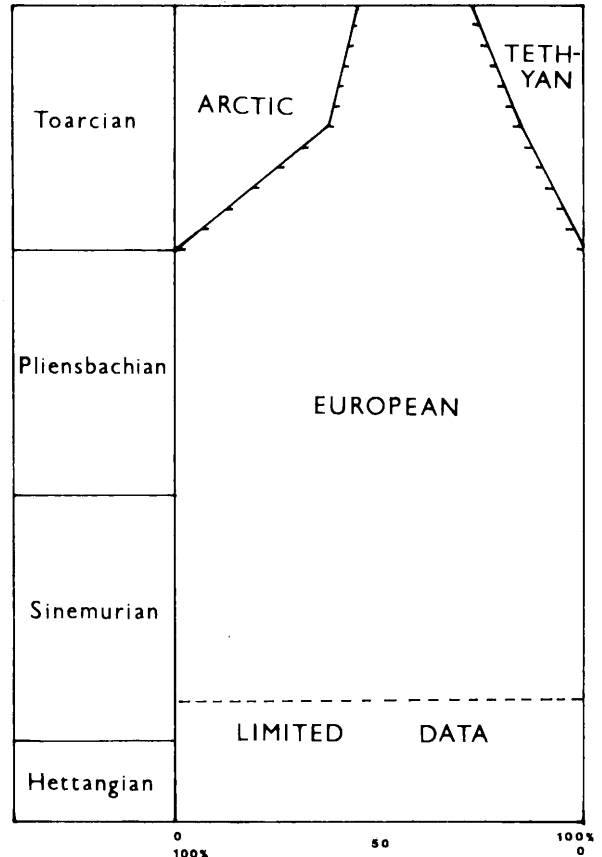


Fig. 8 - Belemnite endemism and diversity in Europe and the Arctic Basin.

compete with what would have been faster swimming belemnites. This is supported by the decline of the Aulacocerida in the Toarcian and the coincidental increase in diversity and distribution of the belemnites.

What of climatic control? Recently, Brandt (1986) has suggested that, contrary to the accepted view of an equable Jurassic climate (eg Hallam, 1975), there is evidence of polar ice in the Jurassic, with consequent glacioeustatic controls of sea level due to climatic changes. In particular, Brandt pointed to the Toarcian as a possible period of 'greenhouse state' characterised by high sea level, high temperature and anoxic bottom waters. This could explain the decrease in endemism encountered in the Toarcian ammonites (text fig. 6), and suggest that temperature zonation was a considerable factor. However, although the belemnites were able to make their first migrations northwards at this time, the pattern is one of increasing endemism (text fig. 7), with northern ('Arctic') and southern ('Tethyan') belemnite faunas for the first time, suggesting that climatic control was not the sole factor.

However, eustatic changes may have been significant. Hallam (1986, 1987) has discussed the

effect of eustasy in the European shelf sea area during the Early Jurassic. He charted a gradual rise in diversity amongst many fossil groups in the earliest Jurassic, with an extinction in the Toarcian. Rather than climatic control, Hallam suggested that the initial increase in diversity was due to a transgressive phase, and that the extinction in the Toarcian was coincidental with the spread of anoxia in Europe. Although there is a corresponding increase in diversity in the belemnites up to the Pliensbachian, and a fall in diversity in the Toarcian too, in many cases a single species in the Falcifer Zone, it is difficult to envisage why this alone should have delimited the belemnites to Europe. It may be that the ameliorating effect of a transgressive sea rise on the unstable habitats of an archipelago of islands would allow greater dispersal of more eurytopic species (c.f. Doyle, 1987).

Synopsis

It is my view that climatic control was not paramount in delimiting the Early Jurassic belemnite distributions; it explains neither the restriction of the

belemnites to Europe coincident with widespread distributions of ammonites and aulacocerids, nor the contemporaneous increase in cosmopolitanism amongst ammonites and the increase in endemism amongst belemnites. This disparity could be explained, however, by the restriction of belemnites to niches in the European Archipelago prior to the main Toarcian transgression. The transgression would allow amelioration of local hostile conditions, and the exploitation of new niches. Certainly the first recoloniser of northern Europe after the demise of the belemnite belemnites, *Acrocoelites trisulculosus* (Simpson), was able to penetrate far north to be one of only six belemnite species common to both Europe and Siberia. After the Arctic Basin had been colonised, the relatively unstable European Archipelago, and stable Arctic Basin, developed separate, diverse endemic stocks, with only what must have been eurytopic species of *Acrocoelites* bridging the two. It is probable that precisely this mechanism of control continued into the later Jurassic and Cretaceous (Doyle, 1987).

TAXONOMIC APPENDIX

The following is an attempt to present a classification for the Early Jurassic belemnites which will form a basis for the classification to be employed in the belemnite part of the *Treatise on Invertebrate Palaeontology*. This is necessary because interpretations by western and eastern European workers have often widely differed, leading to the recognition of sometimes erroneous patterns of endemism. Most important is the recognition that the genera *Clastoteuthis*, *Nannobelus* and *Brachybelus* as interpreted by Soviet workers (Saks & Nal'nyaeva, 1970) are unrelated to their western European counterparts, and following Jeletzky (in MS) these are separated in the genus *Arcobelus*, promoted from subgeneric rank. Another problem area is the widespread misinterpretation of the genera *Salpingoteuthis* and *Mesoteuthis*, which often have species of the genus *Acrocoelites* assigned to them. This has been rectified by Doyle (1990b, 1991), and these genera are restricted to an interpretation closer to their nominated type species.

In the following scheme, the genus is followed by the type species [*] and junior synonyms. Belemnite genera of later Jurassic age are included for completeness, in parentheses.

Order Belemnitida Zittel, 1895

Suborder Belemnitina Zittel, 1895	<i>Coeloteuthis</i> Lissajous, 1906 [* <i>Belemnites excavatus</i> Phillips, 1866] (= <i>Clastoteuthis</i> Lang, 1928; non <i>Clastoteuthis sensu</i> Saks & Nal'nyaeva, 1970, see below)
Family Passaloteuthididae Naef, 1922 (=Polyteuthidae Stolley, 1919)	<i>Angeloteuthis</i> Lang, 1928 [* <i>Angeloteuthis gabriel</i> Lang, 1928]
Subfamily Passaloteuthidinae Naef, 1922 (=1922, Coeloteuthinae Naef, 1922)	<i>Passaloteuthis</i> Lissajous, 1915 [* <i>Belemnites bruguierianus</i> d'Orbigny, 1842] (= <i>Holcoteuthis</i> Stolley, 1919; <i>Belemnites</i> Lamarck, 1799 <i>sensu</i> Jeletzky, 1966 and Schumann, 1974)
<i>Schwegleria</i> Riegraf, 1980 [* <i>Belemnites feifeli</i> Schwegler, 1939]	<i>Pseudohastites</i> Naef, 1922 [* <i>Belemnites scabrosus</i> Simpson, 1855] (non <i>Pseudohastites sensu</i> Lang, 1928, see below) (= ? <i>Catateuthis</i> Nal'nyaeva, 1967; <i>Propassaloteuthis</i> Riegraf, 1980)
<i>Nannobelus</i> Pavlow, 1914 [* <i>Belemnites acutus</i> Miller, 1826] (= <i>Prototeuthis</i> Lemoine, 1915; non <i>Nannobelus sensu</i> Saks & Nal'nyaeva, 1970)	

Parapassaloteuthis Riegraf, 1980 [**Belemnites zieten* Werner, 1912]
Orthobelus Nal'nyaeva, 1970 [**Orthobelus obscurus* Nal'nyaeva, 1970]

Subfamily Megateuthidinae Saks & Nal'nyaeva, 1967
 (=Acrocoelitinae Riegraf, 1980)

Acrocoelites Lissajous, 1915 [**Belemnites oxycorus* Zieten, 1831] (=Mesoteuthis sensu Saks & Nal'nyaeva, 1975, Činčurová, 1971, 1983 and Stoyanova-Vergilova, 1978, 1982. Subgenera *Odontobelus* Naef, 1922 [**Belemnites pyramidalis* Zieten, 1831]; *Toarcibelus* Riegraf, 1980 [**Belemnites quenstedti* Oppel, 1856]
Youngibelus Riegraf, 1980 [**Belemnites tubularis* Young & Bird, 1822]
Simpsonibelus Doyle, 1991 [**Belemnites expansus* Simpson, 1855]
Dactyloteuthis Bayle, 1878 [**Belemnites irregularis* Schloteim, 1813] (=Cuspoteuthis Abel, 19160
Brevibelus Doyle, 1991 [**Belemnites breviformis* Voltz, 1830] (nom nov for *Brachybelus* Naef, 1922, junior homonym of *Brachybelus* Stal, 1869 (Insecta); non *Brachybelus sensu* Saks & Nal'nyaeva, 1970 see below)
Arcobelus Saks, 1967 [**Dactyloteuthis dolosa* Voronets, 1962] (=Clastoteuthis, Nannobelus and *Brachybelus sensu* Saks & Nal'nyaeva, 1970)
Megateuthis Bayle, 1878 [**Belemnites giganteus* Schlotheim, 1820] (=Mesoteuthis Lissajous, 1915; *Mucroteuthis* Abel, 1916)
 (=Paramegateuthis Gustomesov, 1956)
 (=Homaloteuthis Stolley, 1919)
 (=Holcobelus Stolley, 1927)

Family Salpingoteuthididae Doyle, 1991

Salpingoteuthis Lissajous, 1915 [**Belemnites trisulcatus* Blainville, 1827] (=Orbignybelus Gustomesov, 1977; *Hartmanibelus* Gustomesov, 1977; non

Salpingoteuthis sensu Činčurová, 1971, =Acrocoelites)

Family Hastitidae Naef, 1922

Subfamily Hastitinae Naef, 1922

Hastites Mayer-Eymar, 1883 [**Belemnites clavatus* Schloteim, 1820] (=Rhopalobelus Pavlow, 1914)
Gastrobilus Naef, 1922 [**Belemnites ventroplanus* Voltz, 1830]
Pleurobelus Naef, 1922 [**Belemnites compressus* Stahl, 1824]
Sachsibelus Gustomesov, 1966 [**Sachsibelus minus* Gustomesov, 1966]
Bairstowius Jeletzky, in Doyle et al 1994 [**Belemnites junceus* Phillips, 1867]

Subfamily Rhabdobelinae Nal'nyaeva, 1967

Rhabdobelus Naef, 1922 [**Belemnites exilis* d'Orbigny, 1842]. Subgenus: *Neoclavibelus* Riegraf, 1980 [**Belemnites neumarktensis* Oppel, 1856]
Parahastites Nal'nyaeva, 1967 [**Parahastites marchaensis* Nal'nyaeva, 1967]

Suborder Belemnitina Zittel, 1895 or Belemnopseina Jeletzky, 1965

Family Pseudodicoelitidae Saks & Nal'nyaeva, 1967

This family retains characteristics of both suborders (eg Doyle and Kelly, 1988), and further detailed work is needed for a definitive assignment.

Lenobelus Gustomesov, 1966 [**Lenobelus lenensis* Gustomesov, 1966] (*Sibiriobelus* Gustomesov, 1977)
Pseudodicoelites Saks, 1967 [**Dicoelites bidgievi* Saks, 1961]

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