

Boreal and Tethyan late Aptian to late Albian ammonite zonation and palaeobiogeography

by

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(Figs. 1-5, Tabs. 1-3)

Abstract

The Tethyan region throughout the Aptian and Albian stretched from the western coastal region of northern South America and southern North America in the west to Australia in the east. It occupied much of the marine regions of Gondwanaland which was splitting apart at this time in response to the development of the early South Atlantic, Tethyan and Indian Ocean crust. Along the southern boundary of the European region stretching from Iberia in the west to Georgia in the east, phylloceratid, lycoceratid and desmoceratid Tethyan faunas interfinger or marginally mix with more highly ornamented shell forms characteristic of the European epicontinental shelf seas. In the Aptian a distinction between Tethyan and Boreal faunas is not so clear cut as it is in parts of the Albian and the ammonite zonal and subzonal scheme can be applied equally to both areas. Distinct provincialism occurs in the Albian where sonneratiinid and hoplitinid ammonites are confined to the European seas and this is reflected in the zonation. However, the incursion into the European seas in the Lower and Middle Albian by certain Tethyan ammonite stocks provides points of correlation between the two essentially separate faunal provinces at that time. The Upper Albian saw a much more general intermixing of provincial and more cosmopolitan ammonites in the European seas. A third ammonite faunal province included all of the Arctic regions of Alaska, Canada, the northern part of the United States, northern Greenland and Spitzbergen, together with northern Russia. Apart from an apparently continuous but restricted link with the North Pacific region, faunal links also occurred between the Arctic province and the European and even Tethyan provinces. These links between the Arctic and European seas were controlled by tectonic activity associated with the developing northern North Atlantic rather than the ecological barriers which seem to separate the European from the Tethyan seas.

The paper briefly but critically reviews the ammonite zonal and subzonal schemes for the late Aptian (so-called Gargasian and Clansayesian Substages) and the Lower Albian in the European Province, providing necessary revisions of the schemes and identifying, by means of mapped reconstructions, those links which are known to occur between the three ammonite faunal provinces. Five mapped reconstructions of outline palaeogeography are provided; late Upper Aptian, early Lower Albian, early Middle Albian, and early and late Upper Albian. It is concluded that marine links between the Atlantic and the north west European shelf seas occurred from time to time via the western approaches to the Channel.

1. Introduction

Brief reviews of the known ammonite faunal links between the Arctic, European and Tethyan ammonite faunal provinces in the Lower Albian (OWEN 1988a) and in the Middle and Upper Albian (OWEN 1973) have been presented elsewhere. In the present contribution, the intention is to review certain aspects

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of the Upper Aptian and Lower Albian ammonite zonal and subzonal schemes in order to assist the current debate on these schemes in the European and Tethyan provinces and to eliminate a number of misconceptions. The opportunity is also taken to present a series of palaeogeographic maps at five intervals of time in the late Upper Aptian, early Lower Albian and in the Middle and Upper Albian to illustrate the distribution of certain ammonite genera and possible dispersal routes between the Tethyan, European and Arctic seas.

When recognising meaningful ammonite zonal and subzonal schemes, it is essential to base conclusions regarding the succession of species strictly in accordance with stratigraphical sequence as opposed to theoretical concepts of the morphological development of ammonite stocks (eg AMEDRO 1992). All available stratigraphical sequences need to be taken into account within the ammonite faunal province and not simply those recognised in one area of special pleading. Whether one is looking at the late Aptian or early Albian, many of the older schemes reflect what is to be seen in the geographical area studied by the researchers concerned, with little regard to a more widely based overview. The sedimentological evidence of succession needs to be adhered to strictly. This is particularly so in the case of pebble faunas. If these are preserved in a bed which contains "indigenous" faunas which are, therefore, contemporaneous with the enclosing sediment, the age of the bed and the "indigenous" fauna is the later date of the interment of the pebble fauna and not the date or dates of the derived pebble material itself. Not least, it is essential to compare objectively the ammonites collected in one region with those contemporaneous congeneric and conspecific forms existing elsewhere within the faunal province.

It is obvious that there are many combinations of species of suitable range which could be included in any zonal scheme, whether that happens to be based on macropalaeontological or micropalaeontological/microphytological faunas and floras. However, there should be a significant faunal change at the lower boundary of the Zone and Subzone which is geographically widespread and perhaps of cosmopolitan extent, the species selected should be those which are characteristic and reasonably common, and changes to the schemes should only be made if the existing schemes prove to be wrong or not fully representative of the total time represented by a sediment sequence. There is no reason for supposing that zonal schemes based on different taxa should have common boundaries, but if they do, it suggests a physical event affecting the depositional environment as a whole.

It is important to realise that non-sequences exist in the Upper Aptian and Lower Albian sediments in England and France, together with polyphase derivation of fossils into phosphatic pebble assemblages. Locally these may involve sequences in which individual periods of time are well-represented by sediment, but which are not sufficiently continuous either in the geographical or the vertical senses to permit precise correlation with like sediment sequences elsewhere. Non-sequences, condensed horizons with polyphase-derived fossils and these isolated but locally well-developed sedimentary sequences may not easily be correlated with each other. The correctness of the interpretation of sedimentological events and the recognition of data gaps in the regional analysis, affect the accuracy of the critical interpretation of the ammonite sequence. To these problems must be added the relatively uncommon occurrence of ammonites in many sediment intervals in the Lower Greensand Formation, despite the great variety of genera and species present indicated by CASEY's Monograph (1960 -). Indeed, his Monograph is a tribute to his dedicated collecting of relatively uncommon ammonites and it is largely through his efforts that the relatively

sparse English late Aptian and early Albian ammonite faunas are now so well known and available for both taxonomic biostratigraphical and palaeobiogeographical comparison.

CASEY (1961; 492-9) has discussed the history of the development of the Aptian and Lower Albian ammonite zonal and subzonal schemes which had been erected essentially from the stratigraphical sequences in southern and western Europe. There is no need here to cover the same ground, except to point out that the scheme proposed by BREISTROFFER (1947) recognised the biostratigraphical significance of the admixture in the Upper Aptian of more Tethyan forms with those which are of more widespread occurrence in northern Europe. CASEY's scheme recognised an ammonite zonal and subzonal scheme for the Upper Aptian (including the Gargasian and Clansayesian substages) which differed from that proposed by BREISTROFFER (1947) and perhaps tended to emphasise the sequence seen in the Lower Greensand Formation of England rather than in Europe as a whole. CASEY's scheme was introduced with little discussion or precise description, the sedimentary sequences of individual sections being fitted into the scheme rather than providing a more definitive support of it. It remained unchanged during the publication of his superb Monograph of the Ammonoidea of the Lower Greensand (CASEY 1960 -).

Recently BOGDANOVA et al. (1989) published an outstanding review of the Russian Lower Cretaceous stratigraphy and faunal zonation which includes also a review of the various zonal and subzonal schemes which had been proposed internationally. This work forms a foundation for future studies but HANCOCK (1992) has reiterated the Aptian scheme proposed by CASEY (1961) and it is necessary here to discuss the stratigraphical basis of part of CASEY's scheme.

This paper terminates with a series of outline marine sediment distribution maps to illustrate the distribution of key genera and to aid the determination of reasons for ammonite faunal dispersal and endemism. These reconstructions are based on the geological match and ocean-floor spreading data maps published in the author's Atlas of Continental Displacement, 200 million years to the Present (OWEN 1983a). Most dispersal routes have envisaged connection between southern and northern Europe via connections to the south of the Anglo-Paris Basin and through the Polish Trough, a view to which the author has previously subscribed. There is now, however, good evidence for connections via the developing northern North Atlantic from the Tethyan region to both the north west European shelf seas and the Arctic region.

2. The ammonite zonal and subzonal scheme for the late Aptian and early Albian in western Europe.

The ammonite zonal and subzonal scheme for the Upper Aptian and Lower Albian proposed by CASEY (1961) was based essentially on the stratigraphical sequences seen in the Lower Greensand Formation of southern England. It is in need of revision (Tables 1 & 2) in the light of sequences seen elsewhere in Europe. In particular, a separate Zone of *Parahoplites nutfieldiensis* following upon that of *Chelonicerias (Epicheloniceras) martinoides* is not justified in the light of recent studies in southern Europe which have tended to support the reading of the succession by BREISTROFFER (1947). In the Tethyan region, *Chelonicerias (Epicheloniceras)* persists throughout the sediments which would normally be classified with the *martinoides* Zone of Casey, and through sediments containing *Parahoplites*. A return to a more historical reading of the zonal and subzonal classification is justified here.

The terminal Zone of the Aptian, referred to as the *Hypacanthoplites jacobi* Zone by CASEY (1961), needs considerable revision (RUFFEL & OWEN 1995). As will be shown below, CASEY's zonal and subzonal scheme does not reflect the succession seen either in England or the rest of Europe. As currently interpreted (eg CASEY 1960 -,421-4), the genus *Hypacanthoplites* (SPATH 1923a) is only separable from the slightly earlier genus *Acanthohoplites* (SINZOV 1907) by the possession of a tabular venter in the former and a rounded *Parahoplites* - like venter in the ancestral latter. In reality, it appears that there is a shell-form progression from the umbilical bullate, mid flank and ventro-lateral untuberculated genus *Parahoplites* (apparently a development of the earlier *martinioides* Subzone genus *Colombiceras*), through the mid-lateral tuberculated *Acanthoplites* to the mid-flank and ventro-lateral tuberculated *Hypacanthoplites*. All of these genera occur in both the European and Tethyan provinces where they are associated with *Diadochoceras* and in particular, *Eodouvilleiceras*, the link genus between the earlier *Chelonicerases* (*Epicheloniceras*) of the *martinioides* Zone and the later, Lower Albian, *Douvilleiceras* known to occur as early as the latter part of the *Leymeriella acuticostata* Subzone. Although the writer has followed BREISTROFFER (1947) in using the index *Diadochoceras nodosocostatum* for the last Zone of the Aptian Stage, it might well prove to be advantageous to employ the geographically widespread genus *Eodouvilleiceras* as a zonal index of this interval of time (eg. ETAYO SERNA 1979, KOTETISHVILI 1986). Whether one retains BREISTROFFER's older index or employs a new one, it is possible to recognise an earlier Subzone of *Nolanicerases nolani* and a later Subzone of *Hypacanthoplites jacobi*. *Hypacanthoplites continues* on into the early Lower Albian *Leymeriella schrammeni* and *L. acuticostata* Subzone of the *Leymeriella tardefurcata* Zone.

The Subzonal scheme of the *Leymeriella tardefurcata* Zone has been discussed elsewhere (eg. OWEN 1988a), but in recent years a major error in the interpretation of the *Douvilleiceras mammillatum* Superzone succession has arisen in the French literature (eg. DESTOMBES 1979, AMEDRO 1980, 1992). Unfortunately, their schemes has been used by other workers (eg. BARABOSCHKIN 1991) and it is necessary to discuss the problems again here. The writer has reviewed the ammonite sequence in the *Douvilleiceras mammillatum* Superzone (OWEN 1988b) in the European Province and described the detailed stratigraphy of deposits of this age in southern England and northern France (OWEN 1992). In the process, an attempt to correct the error in the interpretation of the ammonite succession has been made. However, as AMEDRO (1992) has asserted that the field evidence supports his interpretation of the succession (but see OWEN 1992), a brief discussion of the evidence against his conclusion is given here.

2.1 Upper Aptian (Gargasian) - Tab. 1.

There are, important non-sequences in the Upper Aptian of southern England, particularly affecting the time interval between CASEY's concept of the *Tropaeum* (*Epitropaeum*) *subarcticum* Subzone of the *Parahoplites nutfieldiensis* Zone and the end of the *Hypacanthoplites jacobi* Zone. To this fact has to be added the scattered nature of localities in which *Parahoplites* is present in the sediment sequence.

AS CASEY (1961;496) has indicated, the appearance of the Subgenus *Chelonicerases* (*Epicheloniceras*) forms a well definable lower limit to the Upper Aptian (Gargasian) in Europe as a whole and this appears to hold true throughout the Tethyan belt as well as in Europe. The employment of *Chelonicerases* (*Epicheloniceras*) *martinioides* CASEY as a zonal index is also useful as this species, or very closely related forms, are widespread in Europe and in the Alpine (Tethyan)

belt. In England, the sequence in the *martinioides* Zone is well represented by sediments, particularly in the Isle of Wight and the succession of Subzones recognized by Casey is reasonably well established. However, the sequence in sediments classified with the *Parahoplites nutfieldiensis* and *Hypacanthoplites jacobi* Zones in CASEY'S sense is imperfectly developed in England and France and problems arise when one attempts to apply his scheme to the much more fully developed lithological sequences in Germany, the Alpine belt and the Soviet Union.

CASEY recognised within his *Parahoplites nutfieldiensis* Zone, two Subzones; an earlier one characterised by *Tropaeum (Epitropaeum) subarcticum* and a later one characterised by *Parahoplites cunningtoni*. In reality, the faunal distinction between these two Subzones depends on whether *T. (E.) subarcticum* is present in the ammonite assemblage or not. In the Weald of south east England, ammonites are well represented in the Sandgate Fullers Earth Beds and in the equivalent Bargate Beds in which *T. (E.) subarcticum* is a highly characteristic albeit minority element in a fauna dominated by *Parahoplites*. This relationship is also found in contemporaneous deposits in northern Germany (eg. GAIDA, KEMPER & ZIMMERLE 1978) and in the Alpine zone of southern Europe. However, the *Parahoplites cunningtoni* Subzone is not well defined. Its 'type' area is in Wiltshire in central southern England where it is not underlain by other sediments containing *Parahoplites*. The ammonites in sediments classified with this 'Subzone' are not common (eg. CASEY 1961;514,551,563. 1965;400-416) and, bearing in mind that *T. (E.) subarcticum* is itself a minority element in the ammonite fauna, there is a strong possibility of collecting failure being the reason for its absence. Moreover, the specimens of *Parahoplites* in the Sandgate and Bargate Beds are preserved as partly phosphatised sandstone steinkerns, or as wholly unphosphatised sandstone casts with a variable amount of crushing and resulting partial reduction in the strength of the shell ornament. In contrast the phosphatised steinkerns of the *cunningtoni*-bearing beds are little distorted, or not at all, and the ornament is sharp. The differences in morphology are due essentially to these differences in preservation and the degree of steinkern compaction. Elsewhere in Europe and the tethyan belt, a separate *cunningtoni* Subzone cannot be recognized at present and it should be abandoned.

A problem now arises in respect of the zonal nomenclature; the Zone of *Parahoplites nutfieldiensis* being the equivalent time span of its single Subzone of *Tropaeum (E.) subarcticum*. In the Vocontienne Basin, identifications of the collections made by Dr. MICHEL DELAMETTE (eg. DELAMETTE 1988) show that species of *Chelonicerus (Epicheloniceras)* persist from the *Ch. (E.) buxtorfi* Subzone to co-exist with species of *Parahoplites* throughout the range of that genus. *Epicheloniceras* is not present in the following Zone of *Hypacanthoplites jacobi* where it is replaced by its descendant *Eodouvilleicerus*. Species of *Parahoplites* do persist into the earliest Subzone of the *jacobi* Zone, the *Nolanicerus nolani* Subzone, in the Vocontienne Basin, but they are a subordinate element to *N. nolani* and associated species of *Acanthohoplites*. It is best at this time to regard the *P. nutfieldiensis* time interval as a Subzone and the terminal one of the *Ch. (E.) martinioides* Zone; its end marking the termination of the Gargasian Substage of European authors. The Gargasian becomes synonymous, therefore, in its time span with the *martinioides* Zone.

With regard to the nomenclature of the *Parahoplites nutfieldiensis* Subzone, that species is the earliest one of that genus to be named. Several forms described as distinct species from elsewhere in Europe are not separable from the range of morphological variation seen in *P. nutfieldiensis*. This index name of *Parahoplites nutfieldiensis* is retained here in Table 1 for this time interval

following SPATH (1923b) and as such it represents the total range Subzone of that species. It is further recommended that the Substage name Gargasian be dropped from the nomenclature in favour of the simple grouping of Upper Aptian.

2.2 Upper Aptian (Clansayesian) – Tab. 1.

Tab. 1: Ammonite zonal and subzonal scheme for the Upper Aptian (Gargasian and Clansayesian substages) – European Province

ZONE	SUBZONE
<i>Diadochoceras nodosocostatum</i> (<i>H. jacobi</i> Zone of CASEY)	{ <i>Hypacanthoplites jacobi</i> (including those of <i>H. anglicus</i> & <i>H. rubricosus</i>) <i>Nolaniceras nolani</i>
<i>Chelonicerases (Epicheloniceras) martinioides</i>	{ <i>Parahoplites nutfieldiensis</i> (including those of <i>T. subarcticum</i> & <i>P. cunningtoni</i>) <i>Chelonicerases (Epicheloniceras) buxtorfi</i> <i>Chelonicerases (Epicheloniceras) gracile</i> <i>Chelonicerases (Epicheloniceras) debile</i>

There is an indication at the top of the Sandgate Beds Member of the Lower Greensand in the Sandgate area of Kent, of the representation of an interval later than that of *Parahoplites nutfieldiensis* and earlier than that of *Hypacanthoplites jacobi*, in which *Nolaniceras nolani* is present. Despite the extreme paucity of sediments of this age in England, elsewhere in Europe, in northern Germany, in the Soviet Union and in the southern European Alpine Zone, eastward to Iran (SEYED AMAMI 1980b) and south to Madagascar (eg. COLLIGNON 1978), this Subzone of *Nolaniceras nolani* is well represented and is of application to both the European and Tethyan regions. This time interval is as much characterised by species of *Acanthoplites* as it is of *Nolaniceras* and the *Acanthoplites aschiltaensis* Zone of SPATH (1923b) represents the same time period and I follow CASEY (1961) in abandoning its use. However, CASEY (1965, 418) when accepting the Subfamily grouping Acanthoplitinae (STOYANOW 1949), thought that while *Nolaniceras* and *Acanthoplites* (and *Diadochoceras*) were contemporaneous, which they are, they appear in the *nutfieldiensis* Zone, which they do not. There is no doubt from the sequence in the Vocontienne Basin (eg. DELAMETTE 1988) and elsewhere in the European province (eg. BOGDANOVA et al. 1989) that *Nolaniceras* and *Acanthoplites* are later than the *nutfieldiensis* time interval. Transitional forms of *Parahoplites* do occur in the earliest part of the *nolani* Subzone and the Subzone sees the appearance of the earliest forms of *Hypacanthoplites*. Indeed, the morphological sequence in this group of ammonites is *Colombiceras* (up to *buxtorfi* Subzone) – *Parahoplites* – *Acanthoplites* – *Hypacanthoplites* (the latter ranging on into the Lower Albian *acuticostata* Subzone of the *Leymeriella tardefurcata* Zone).

The true ammonite succession in the post-*nolani* Subzone *Hypacanthoplites jacobi* Zone sedimentary sequence in England is difficult to determine with any degree of accuracy. In the Folkestone area of Kent, the basal phosphatic nodule beds of the Folkestone Beds Member yield a remanié and possibly polyphase mixed ammonite pebble faunal assemblage embedded in arenaceous sediments. CASEY (1961, 529) recognised an earlier Subzone of *Hypacanthoplites rubricosus* based on the occurrence of ammonites preserved in lenticles of ferruginous stone in the basal part of his Bed 1, this assemblage being indigenous to the sediments

and not part of the pebble assemblage. If this is the case, the pebble fauna of *anglicus* Subzone age is earlier than the indigenous fauna of *rubricosus* Subzone age; the reverse of CASEY's scheme. He also regarded the Luccomb Plant Bed of the Sandrock Series near Shanklin, Isle of Wight, to belong to the *rubricosus* Subzone on the basis of poorly preserved phosphatised pebble ammonites. However, an indigenous partly crushed example of *Hypacanthoplites* from the Luccomb Plant Bed suggests that it is later in age and possibly even of early Lower Albian *schrammeni* or *acuticostata* Subzone age. The remainder of Bed 1 at Folkestone with its pebble fossil assemblage was classified by CASEY (1961) with a Subzone of *Hypacanthoplites anglicus*. These two occurrences of the '*rubricosus* Subzone' with their reworked and largely pebble faunas are totally insufficient upon which to base the concept of a Subzone and, moreover, this interval of time has not been recognised elsewhere in the European or Tethyan sequences. Indeed, this subzonal distinction cannot be made in East Kent at the Sandling Sandpit, a mere 8 km to the WNW of Folkestone. The concept of a Subzone of *Hypacanthoplites rubricosus* should be abandoned (RUFFEL & OWEN 1995).

In the case of the Subzone of *Hypacanthoplites anglicus*, which CASEY considered to succeed the '*rubricosus* Subzone', we can recognise the well-known and geographically widely distributed *Hypacanthoplites jacobi* fauna. Its representation by sediments in southern England is limited to Bed 1 of the Folkestone Beds Member at Folkestone, the less condensed sequence of Beds 1-9 at the Sandling Sandpit, Hythe (CASEY 1961, 533) and equivalent sediments in this region of Kent, a condensed sequence between Lewes and Willingdon in Sussex and within the Sandrock Member of the Lower Greensand Formation in the Isle of Wight. There is no doubt that the *jacobi* fauna forms a recognisable time interval throughout Europe and beyond, but there is no evidence that it can be subdivided and the interval of time is best regarded as a Subzone of *Hypacanthoplites jacobi*.

There is now a problem of the zonal nomenclature. A separate Subzone of *Nolaniceras nolani* and a separate Subzone of *Hypacanthoplites jacobi* can be recognised. However, although the ammonite faunas of the two Subzones are related sufficiently to permit them to be grouped together in a Zone which is faunistically distinct from the preceding *martinioides* Zone and the succeeding early Albian *tardefurcata* Zone, there is the problem of designating a suitable zonal index ammonite. *Hypacanthoplites* appears already in the *nolani* Subzone, but no species has a total range throughout both this and the *jacobi* Subzones. MULLER & SCHENK (1943) foreshadowed in their zonal arrangement the nomenclature adopted by CASEY (1961) using *Hypacanthoplites jacobi* as the zonal (and subzonal) index. If a typically Tethyan species, such as *Diadochoceras nodosocostatum* (D'ORBIGNY) employed by BREISTROFFER (1947), can be shown to be present in both Subzones, it would be suitable for use as a zonal index. At present, I know of it only from the *nolani* Subzone. If it is sufficiently widespread in the Tethyan belt, *Nodosohoplites multispinatus* (ANTHULA), reported by KOTISHVILI (1986) from both the *nolani* and *jacobi* Subzones (her Zones), might be a very suitable total range Zone index ammonite. Further research might show that a species of *Eodouvilleiceras* is more widespread in the wider Tethyan and southern provinces including the southern marginal area of the European shelf seas. But, even if *Nodosohoplites multispinatus* was provisionally adopted as the Zone index, it would not adversely affect the interpretation of the shelf European sequences, and the subzonal index *Hypacanthoplites anglicus* would be replaced by *Hypacanthoplites jacobi* and thus preserve the historical nomenclature.

The lack of justification for retaining a separate Gargasian Substage has been referred to above and the same applies to the Clansaysian Substage, both coinciding with ammonite Zones. There is also no reason for erecting separate ammonite zonal and subzonal schemes for the European and Tethyan regions throughout the Upper Aptian. Although the diversity within the ammonite populations is far higher in the Tethyan region and more restricted within Europe north of the Alpine Belt, the Subzones are recognisable in both regions.

2.3 Lower Albian (*Leymeriella tardefurcata* Zone) – Tab. 2.

A brief review of the classification of the Zone of *Leymeriella tardefurcata* was made by the writer in 1988 (OWEN 1988a) in which it was concluded that the Subzones recognised in it and the Zone itself could be applied to, or correlated with, the Tethyan region, the European shelf seas and the Arctic Province. I would propose, therefore, that CASEY's scheme (1961) based on the imperfectly known Folkestone Beds sequences in South East England be no longer used for the reasons given in that paper and a more detailed paper in preparation. In effect the proposal here (and OWEN 1988) is that we revert to the basic scheme recognised by SPATH (1941; 668), partially adopted by BREISTROFFER (1947), which, based on BRINKMANN (1937), recognises the morphological lineage sequence in *Leymeriella tardefurcata* from '*Proleymeriella schrammeni*' to *Leymeriella acuticostata* to *Leymeriella tardefurcata*. Both the form stages *Leymeriella schrammeni* and *L. acuticostata* characterise definite intervals of time, recognisable as Subzones. The form stage of *L. tardefurcata tardefurcata* appears in the *acuticostata* Subzone and continues on into the *regularis* Subzone, a subzonal interval well represented in both England and Russia (CASEY 1957, 1978; SAVELIEV 1973). The Zone of *Leymeriella tardefurcata* is essentially a total range Zone and to treat the three Subzones of the *tardefurcata* Zone as distinct Zones (eg. KEMPER 1975, 1982, SAVELIEV 1973) tends to obscure the geographically widespread and interprovincial value of the interval characterised by the total range of the genus *Leymeriella* (eg. SAYED-EMAMI 1980a). Moreover, to continue to use these Subzones in the Zone sense is out of step with the biozonation of the Cretaceous as a whole based on ammonites in which significant but relatively long-ranging

Tab. 2: Ammonite zonal and subzonal scheme for the Lower Albian – European Province.

SUPERZONE	ZONE	SUBZONE
<i>Douvilleiceras mammillatum</i>	<i>Otohoplites auritifomis</i>	<i>Pseudosonneratia (Isohoplites) steinmanni</i>
		<i>Otohoplites bulliensis</i>
		<i>Protohoplites (Hemisonneratia) puzosianus</i>
		<i>Otohoplites raulinianus</i>
	<i>Sonneratia chalensis</i>	<i>Cleoniceras floridum</i>
		<i>Sonneratia kitchini</i>
		<i>Sonneratia (Globosonneratia) perinflatum</i>
	<i>Leymeriella tardefurcata</i>	<i>Leymeriella regularis</i>
		<i>Leymeriella acuticostata</i>
		<i>Leymeriella schrammeni</i>

forms are used as zonal indices and the Subzones represent the shorter time-ranging, but characteristic forms co-existing with the zonal index. The *Leymeriella tardefurcata* Zone of BRINKMANN (1937), KEMPER (1979) and SAVELIEV (1973) refers to a single Subzone indexed by SPATH (1941) using *Leymeriella acuticostata* and which includes the *Pseudosonneratia sakalava* interval recognised by COLLIGNON (eg 1978) in Madagascar. As interpreted here, the *tardefurcata* Zone is a true total range zone and the usage of Russian workers of this index as a replacement for the *acuticostata* Subzone can only lead to error. There has been much debate and controversy on the stratigraphical position of the genus *Arcthoplites*. I have given good reasons why this genus is not of Middle Albian age (OWEN 1988a,b) but occurs in the basal part of the *acuticostata* Subzone. Apart from the polyphase condensed phosphatic nodule beds in the Moscow Basin, where *Arcthoplites* is found in a mixed fauna of Middle Albian, *dentatus* and *loricatus* Zones ammonites as well as early Lower Albian elements, nowhere else is *Arcthoplites* found in well developed *regularis* Subzone or *mammillatum* Superzone sediments in the Lower Albian nor in uncondensed Middle Albian sediments including other areas in the Soviet Union (eg. BARABOSCHKIN 1991).

2.4 Lower Albian (*Douvilleiceras mammillatum* SuperZone) – Tab. 2.

The ammonite zonation of the *Douvilleiceras mammillatum* Superzone has been discussed in some detail (OWEN 1988b). Although the *mammillatum* Superzone is cosmopolitan, provincialism becomes apparent at zonal and subzonal level. The two Zones and their Subzones recognised in the European sequences (Table 2) are restricted essentially to that region. Species of *Cleonoceras* can provide important correlative links between the Tethyan, European and Arctic provinces. *Paragonoceras*, *Tegoceras* and *Oxytropidoceras* can provide important correlative links between the European scheme and Tethys, but as yet no there is no accurate subdivision of the *mammillatum* Superzone outside the European region and that of COLLIGNON (eg.1978) is not acceptable as it includes *tardefurcata* Zone correlatives. *Tegoceras* and its direct descendant *Lyelliceras* (the occurrence of which marks the lower limit of the Middle Albian) are members of the family Lyelliceratidae and, therefore, are typically Tethyan genera as well as being represented in European province sequences. Also, species of *Oxytropidoceras* (Mojsisovicsiidae) and *Paragonoceras* (Engonoceratidae) migrated into the European shelf seas at intervals throughout the *mammillatum* Superzone, the former genus extending in time-range into the Middle Albian.

However, a disagreement has arisen in recent years concerning the relative positions in time of the Subzones of *Otohoplites raulinianus* and *Protohoplites (Hemisonneratia) puzosianus* Subzones of CASEY's scheme. DESTOMBES (1979) proposed a scheme in which the *puzosianus* Subzone is placed earlier than that of the appearance of the genus *Otohoplites* (in the *Otohoplites larcheri* Subzone of DESTOMBES 1979). This was based on the French sequences in which important non-sequences exist on the one hand, which were largely ignored, and on the other hand certain subzonal intervals are particularly well developed in terms of sediment and fauna. The writer (OWEN 1988a) has given evidence that the sequence at Folkestone, Kent and elsewhere in the northern and western Weald of south east England, shows unequivocally that *Otohoplites of the raulinianus* Subzone precedes the appearance of *Protohoplites* including its Subgenus *Hemisonneratia*. AMEDRO (1992) has again discussed the ammonite succession in his *Douvilleiceras mammillatum* Zone which appears to suggest that the French and English successions are out of step. They are not and the detailed stratigraphy of the sequence in the Weald and the Boulonnais (OWEN 1992), in which the superposition of faunas alone can be tested, supports CASEY's reading

of the sequence. Recently, new evidence is to hand that the *Otohoplites bulliensis* Subzone fauna, which is very well developed in the northern Pays de Bray and the Aube in France, occurs at the equivalent of the Sulphur Band of the Folkestone sequence near Newington and elsewhere in southern England (OWEN 1992).

3. Middle and Upper Albian ammonite zonal and subzonal scheme

(Tabs. 3, 4)

Tab. 3. Ammonite zonal and subzonal scheme for the Middle Albian in the European faunal province (from OWEN 1971)

ZONE	SUBZONE
<i>Euhoplites lautus</i>	{ <i>Anahoplites daviesi</i> <i>Euhoplites nitidus</i>
<i>Euhoplites loricatus</i>	{ <i>Euhoplites meandrinus</i> <i>Mojsisovicsia subdelaruei</i> <i>Dimorphoplites niobe</i> <i>Anahoplites intermedius</i>
<i>Hoplites dentatus</i>	{ <i>Hoplites spathi</i> <i>Lyelliceras lyelli</i>

The discussion of the Middle Albian and Upper Albian ammonite zonal and subzonal schemes have been presented elsewhere (OWEN 1971, 1984) and no major emendment of it is required in the writer's opinion. That of the Middle Albian shown in Tab. 3 applies only to the European shelf seas and reflects the succession of hoplitinids endemic to this region termed the hoplitinid faunal province. The scheme also reflects the temporary incursions of more cosmopolitan southern forms such as in the *Lyelliceras lyelli* and *Mojsisovicsia subdelaruei* Subzones.

Tab. 4 Ammonite zonal and subzonal scheme for the Upper Albian in the European faunal province (modified from OWEN eg 1991)

ZONE	SUBZONE
<i>Stoliczkaia (Stoliczkaia) dispar</i>	{ No formal name <i>Mortoniceras (Durnovarites) perinflatum</i> <i>Mortoniceras (Mortoniceras) rostratum</i>
<i>Mortoniceras (Mortoniceras) inflatum</i>	{ <i>Callihoplites auritus</i> (early part & a later interval with <i>Mortoniceras (Cantabrigites) minor</i>) <i>Hysterocheras varicosum</i> <i>Hysterocheras orbigny</i> <i>Dipoloceras cristatum</i>

The zonal and subzonal scheme for the Upper Albian (Tab. 4) marks the principal change in the ammonite faunas of the European shelf seas, where the endemic hoplitinids coexisted with the more cosmopolitan mortoniceratids,

brancoceratids and, eventually, *Stoliczkaia*. There are two intervals of time which require re-assessment in the subzonal sense. The first of these is the *Calihoplites auritus* Subzone. GALLOIS & MORTER (1982) demonstrated that the latter part of the *auritus* Subzone contained an ammonite fauna in which elements characteristic of earlier, *inflatum* Zone, date were associated with elements reflecting the early part of the *Stoliczkaia dispar* Zone. This interval is poorly seen in East Anglia in the United Kingdom, but is much more fully developed elsewhere in Europe. Characteristic ammonites of this interval include *Mortoniaceras (Cantabrigites) minor* SPATH, but not the other species assigned to that subgenus which are of *dispar* Zone age.

The second interval relates to the terminal part of the *Stoliczkaia dispar* Zone. It is clear from sequences stretching in geographical extent from the United Kingdom to southern Europe and eastward to Transcaspiia, that a recognisable subzonal time interval intervenes between the *perinflatum* Subzone and the beginning of the Cenomanian.

4. Late Aptian and Albian palaeogeography

(Figs. 1-5).

The boundaries between ammonite Zones and Subzones reflect events ranging from distinct taxonomic changes in time to changes in physical geography. It is constructive to examine the distribution of ammonites in the Boreal Region in the late Aptian and the Albian against marine sediment distribution maps (which most so-called palaeogeographic maps happen to be). They help to explain in some instances why provincial faunas have been isolated from each other. Whether the barriers were the physical separation of sea-ways totally preventing dispersal, whether sea-ways existed but provided a selective barrier to the dispersal of certain families but not others, whether climatic and thus sea-water temperatures were factors, or the distribution of relatively shallow shelf seas and deep water zones controlled dispersal, can all be made much clearer on a palaeogeographic reconstruction which accords with the geological and geophysical data for the periods of time concerned. The writer has provided map reconstructions of the *tardefurcata* Zone (OWEN 1988a, ARHUS 1991) and the earliest Upper Albian (*Dipoloceras cristatum* Subzone (OWEN 1973 & see JELETZKY 1980), elsewhere, but the opportunity is taken here to amend these earlier reconstructions and to provide a set from the late Aptian to the end of the Albian.

There are inherent problems in all of these reconstructions. From the sedimentological point of view, the absence of marine sediments does not necessarily mean that the area concerned was a positive land area. In shallow seas, subject to tidal flow or of a depth in which storm waves can remobilise sea-floor sediment at relatively frequent intervals, a bare rock surface stripped of all but mobile sediments normally exists. In the geological column, such an erosion surface might be deemed emergent (eg. OWEN 1983a), when in fact a seaway existed. Occasionally, pockets of sediment are preserved in cobble-scoured pot-holes in a hard rock surface. A classic example of this is to be seen at the well known Kassenberg locality in the Ruhr where Cenomanian sediments are preserved in erosional depressions in the surface of Carboniferous sediments. Hitherto, most dispersal routes from the Tethyan region into northern Europe have been regarded as occurring across the Anglo- Paris Basin or along the Polish Trough. In some instances this is correct, but there is increasing evidence that an important dispersal route for the Tethyan elements into the north west European shelf seas occurred through the western approaches to the English Channel from a growing northern North Atlantic.

The base-map used here conforms fully with the geological and geophysical data which determines precisely the fit of the continents and oceanic crust together in the middle part of the Cretaceous and are derived from the writer's Atlas (OWEN 1983b). Similar base reconstructions by ROWLEY & LOTTES (1988),

Late Upper Aptian

180°

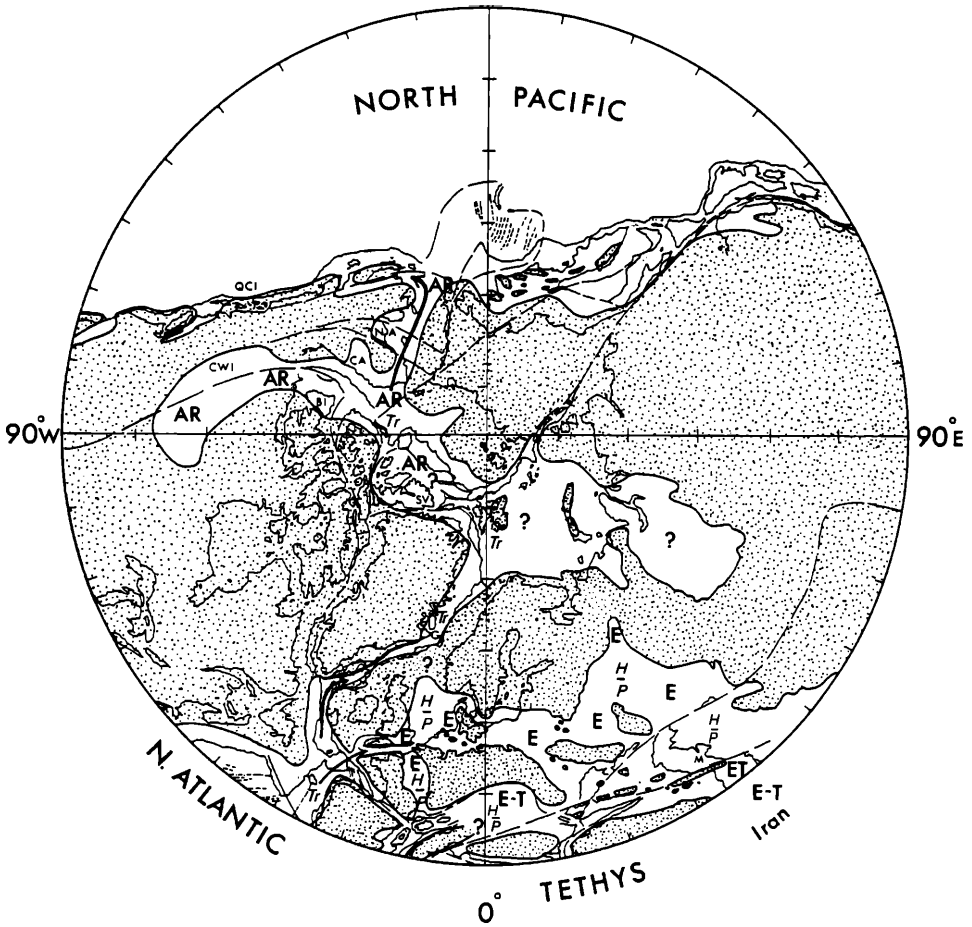


Fig. 1: Tentative palaeogeographic map of the Boreal Region in the late Aptian *Parahoplites nutfieldi* Subzone [*Chelonicer* (*Epicheloniceras*) *martinioides* Zone] to the end of the *Hypacanthoplites jacobi* Subzone to illustrate areas of marine sedimentation (unstippled areas), likely dispersal routes (arrowed) and faunal realms. AR = Arctic shelf seas with connection to the Pacific, and the Atlantic via Greenland; E = European shelf seas; E-T = seas with a mixed ammonite fauna of shelf and deep open water aspect. P = generalised distribution of *Parahoplites* in the *nutfieldi* Subzone, H = generalised distribution of *Nolaniceras* and *Hypacanthoplites* in the *jacobi* Zone. Tr = dispersal of *Lytoceras* and *Tropaeum* into the European and Arctic shelf seas from the North Atlantic extension of the Tethyan faunal province. Bars separating faunal symbols represent zonal/subzonal boundaries.

Modern localities in Text-Figs 1-5: QCI Queen Charlotte Islands, C-T = Chitina Valley & Talketna Mountains, NA = North Alaska, CA = Central Alaska, CWI = Canadian Western Interior, BI = Banks Island, SV = Sverdrup Basin, P = Peary Land, S = Spitzbergen, G = East Greenland, M = Mangyschlak. Azimuthal equidistant projection; for source of base map see text.

which assume an Earth of modern dimensions, are based on a faulty computer program which fails to correct for changes in the circumferential distortion on the plane surface (the 'map') as North America is moved progressively northward towards the pole in order to close the Arctic Ocean for which there is no pre-Cretaceous evidence of existence.

4.1 Late Upper Aptian – Fig. 1.

The map represents the approximate marine areas and connections in the *nutfieldiensis* Subzone through to the end of the *jacobi* Subzone. It is very provisional, but probably close to reality. The distribution of key ammonites is indicated in accordance with the text figure explanation. The general view at present is that the late Aptian, *nutfieldiensis* Subzone, marks an interval of higher sea-level but this appears to be based on the wider distribution of sediments of this age in southern England. However, if one compares the distribution of late Aptian sediments in the Boreal region and even in northern France with those seen in the Lower Albian, this alleged rise in sea-level appears doubtful. The apparent increase in sedimentary representation in England in the *nutfieldiensis* Subzone in comparison with earlier and later Aptian sediments is perhaps due to epeirogenic warping of the southern region of the British Isles associated with continued rifting in the graben between East Greenland and the European margin (AINSWORTH et al 1987). The occurrence of *Lytoceras* and *Tropaeum* in East Greenland (FREBOLD 1935) and *Tropaeum* in Spitzbergen (NAGY 1970) and the absence of a *Parahoplites* fauna in both areas, suggests a dispersal route of these more Tethyan groups from southerly regions of the opening North Atlantic via the narrow strait between Greenland and the north west European margin (AINSWORTH et al 1987). A connection from the Atlantic through the western approaches to the English Channel and then across into northern Germany is further supported by the distribution of *Tropaeum* in southern England and northern Germany. There is no definitive evidence of a sea-way and faunal dispersal route from southern France through to northern Europe via the Paris Basin in the late Aptian. Equally, the distribution of *Lytoceras* and *Tropaeum* and the absence of *Parahoplites*, in Greenland or Spitzbergen suggests that no connection existed during the late Aptian between the northern European region and the Arctic region via the North Sea or central Russia. The Aptian faunas of the inner regions of the Arctic Province suggest a greater affinity with the Pacific Province rather than with the Atlantic.

With the exception of the more conservative lytoceratid, phylloceratid and desmoceratid ammonites which clearly favoured the deeper, more open and probably warmer waters of the Tethyan region, the distribution of ammonite faunas in the European shelf seas during the late Aptian, shows no significant provincial differences to that of the Tethyan region. *Chelonicer* and its descendant *Douvilleicer*, *Colombicer*, *Parahoplites*, *Acanthoplites*, *Nolanicer* and *Hypacanthoplites* are widely distributed outside of the European shelf seas from Madagascar and Iran (SEYED-EMAMI 1980b) to the Americas (eg. ETAYO-SERNA 1979, RENZ, 1982, STOYANOW 1949, YOUNG 1974,)

4.2. Early Lower Albian (*Leymeriella tardefurcata* Zone) – Fig. 2.

The Subfamily *Leymeriellinae* (*Lyelliceratidae*) gave rise to the genera grouped in the *Lyelliceratinae* and probably to the genus *Oxytropidoceras* of the *Mojsisovicsiidae*. Both families are typically Tethyan in origin and incursions into the European and Arctic regions were not continuous throughout the Albian, although they were widespread when they occurred. The writer has discussed the distribution of ammonites in the Boreal region during the *tardefur-*

cata Zone (OWEN 1988a) and there is nothing to add to that account. It is useful, however, to compare the palaeogeographic reconstruction given in that account and reproduced here in Fig. 2, with that of the late Aptian reconstruction in Fig. 1 and the early Middle Albian reconstruction in Fig. 3. The marine dispersal route via the Rockall Trough to the Arctic which can be implied from the late Aptian faunal distributions, clearly no longer existed in the Lower Albian. The distribution of ammonites suggests in the Lower Albian, *tardefurcata*, *chalensis* and *auritifformis* Zones, a distinct connection between the North Sea region and through northern Russia to the Arctic Province. The distribution of *tardefurcata*

Early Lower Albian
tardefurcata Zone

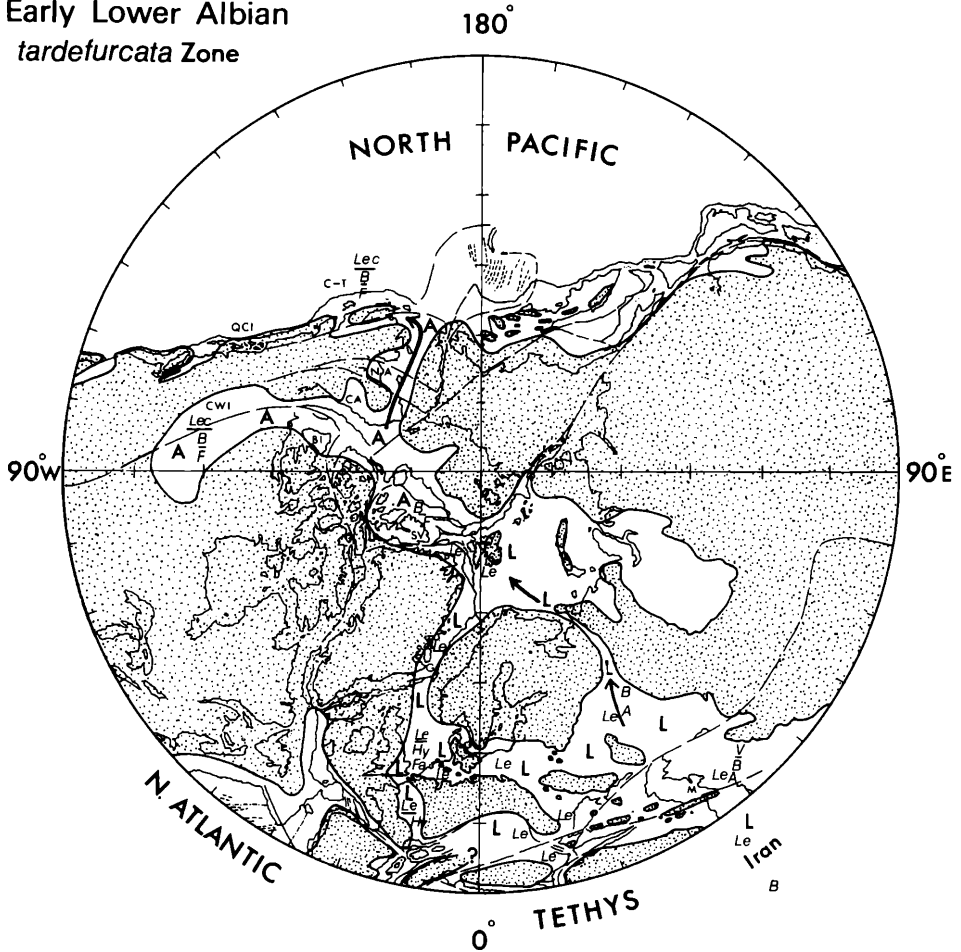


Fig. 2: Palaeogeographic map of the Boreal Region in the *Leymeriella tardefurcata* Zone (early Lower Albian) to illustrate areas of marine sedimentation (unstippled areas), likely dispersion routes across Europe from the Tethys to the North Pacific (arrowed) and ammonite faunal provinces (L = leymeriellinid, A = Arctic). Significant ammonite occurrences are shown with bars representing subzonal boundaries (Lec = *Leconteites*, B = *Bellidiscus/Subarcthoplites*, F = *Freboldiceras* of possible *schrammeni* Subzone age, Le = *Leymeriella*, Hy = *Hypacanthoplites* of lower and middle *tardefurcata* Zone age in the Anglo-Paris Basin, Fa = *Farnhamia*, V = *Vnigrigeras*, A = *Arcthoplites* in the European province only; it is ubiquitous in the Arctic province). Locality symbols and map projection as in the explanation to Text Fig. 1.

Zone sediments in southern England (OWEN 1992) and northern France suggests that no route via the Western Approaches to the English Channel existed during this period of time, a reading supported by the restricted fauna of *acuticostata* Subzone age seen in the English sequence.

4.3. Early Middle Albian (*Hoplites dentatus* Zone) – Text Fig. 3.

The rise in sea-level which occurred progressively during the *mammillatum* Superzone (OWEN 1992) would have been sufficient to have re-opened the English Channel connection between north west Europe and the Atlantic. There

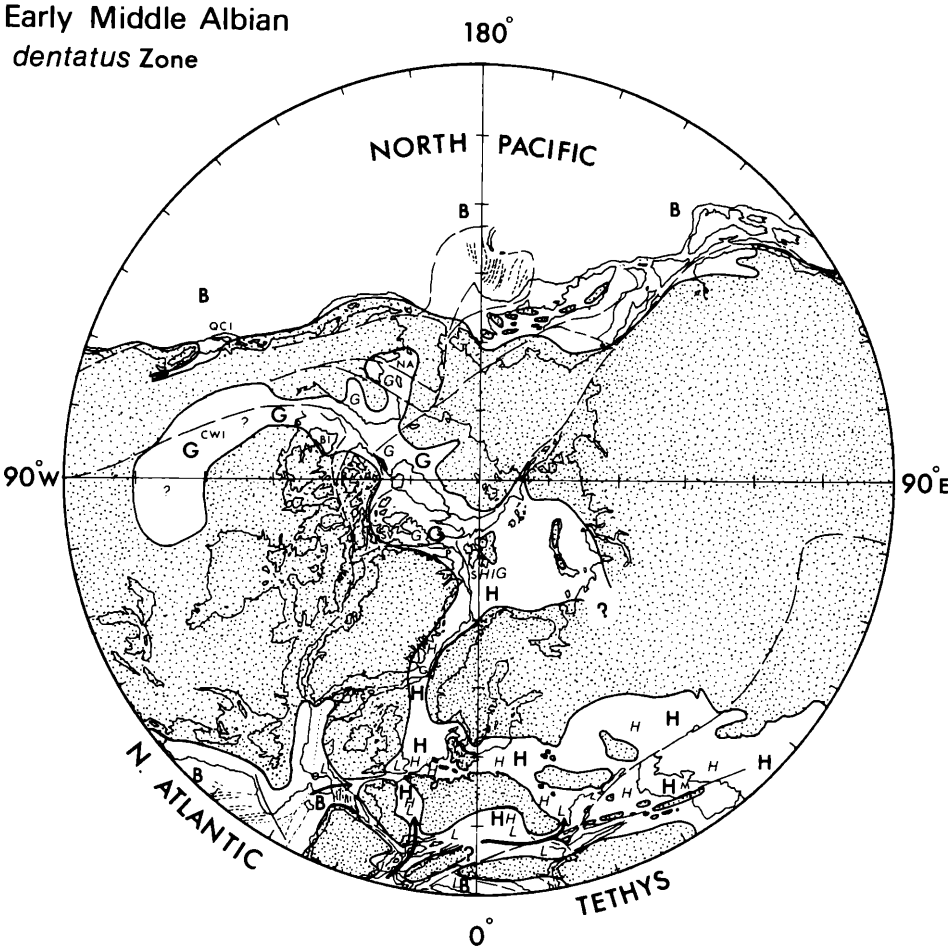


Fig. 3: Palaeogeographic map of the Boreal Region in the *Hoplites dentatus* Zone (early Middle Albian) to illustrate areas of marine sedimentation (unstippled areas), ammonite faunal provinces (H = Hoplitinid, the European shelf seas, B = Brancoceratinid, the Tethyan, Gondwanan and Pacific regions, and G = Gastroplitid, the Arctic - North American shelf seas) and faunal dispersal routes indicated by arrows. Dispersal of Tethyan elements into north west Europe was probably via the developing North Atlantic as well as the southern region of France. The region of East Greenland and Spitzbergen has a mixed fauna of European endemic hoplitinids and Arctic region endemic gastroplitids. Significant ammonite occurrences are shown L = *Lyelliceras*, *Brancoceras* and *Oxytropidoceras* fauna, H = *Hoplites*, G = *Grycia*. Locality symbols and map projection as in the explanation to Text Fig. 1.

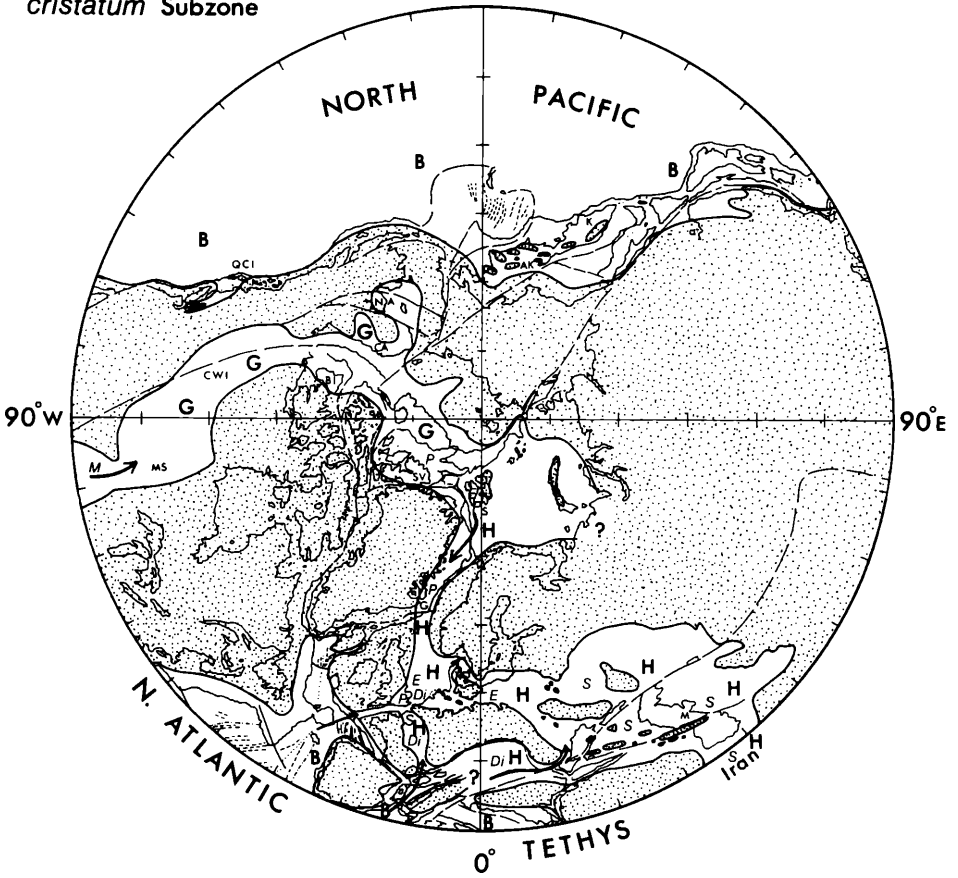


Fig. 4: Palaeogeographic map of the Boreal Region in the *Dipoloceras cristatum* Subzone (earliest Upper Albian), a period of widespread rift-faulting, to illustrate areas of marine sedimentation (unstippled areas), ammonite faunal provinces as in Text Fig. 3. Dispersal of Arctic and Tethyan elements via the Greenland - Norwegian strait and from the Tethyan region via the growing North Atlantic and southern Europe into the European shelf seas is indicated by arrows. *P* = *Pseudogastrolites*, *E* = *Euhoplites*, *Di* = *Dipoloceras*. Mixing of *Euhoplites* and gastrolitids occur in the region extending from South East England to Spitzbergen. Locality symbols and map projection as in the explanation to Text Fig. 1.

seems to be little doubt that an open sea connection existed between the Anglo-Paris Basin and the northern margins of the Tethyan Belt in the *Lyelliceras lyelli* Subzone, but the sharp cut-off between the hoplitinid and Tethyan faunas at the southern margin of Europe is a puzzle. One would expect a distinct zone of drifted shells providing a broad area of mixed faunas, but that appears not to be the case at the southern margin of Europe. A connection through the English Channel from the Atlantic, both in the *lyelli* Subzone and later, in the *spathi* Subzone, could be the cause of the admixture of endemic hoplitinids and the more cosmopolitan elements of Tethyan origin seen in the southern England sequence and perhaps northern France. In the remainder of Europe, including Transcaspiya, the more cosmopolitan Tethyan elements are notable for their absence in the *dentatus* Zone sediments.

There is definite evidence of the connection between the European hopliti-
nid ammonite faunal province and the Arctic Province in Spitzbergen at the
northern outlet of the Greenland – Norwegian graben strait. NAGY (1970) has il-
lustrated the coexistence in Spitzbergen of *Hoplites* and the Arctic Province ge-
nus *Grycia* in the *dentatus* Zone. This connection is a continuation of provincial
faunal mixing between the Arctic and Europe known, not only in the *tardefur-*
cata Zone, but perhaps in the *Cleoniceras floridum* Subzone of the *Sonneratia*
chalensis Zone in Arctic Canada and in the *Otohoplites auritifformis* Zone in
Spitzbergen. Any boundaries here are likely to be water temperature controlled
(eg. KEMPER & SCHMITZ 1981, KEMPER 1987).

4.4. Early Upper Albian (*Dipoloceras cristatum* Subzone) – Fig. 4.

During the bulk of the Middle Albian, there seems to have been only spora-
dic dispersal of Tethyan elements into the European shelf seas, the notable ex-
ception being the influx into southern England and northern France of Tethyan
forms such as *Lyelliceras* and *Brancoeras* in the *lyelli* Subzone, *Oxytropido-*
ceras in the *spathi* Subzone, *Eubrancoeras* and *desmoceratids* in the *interme-*
dus Subzone and *Mojsisovicsia* in the *subdelaruei* and *nitidus* Subzones. A
connection from the Atlantic through the Western Approaches and English
Channel again seems likely. However, the *Dipoloceras cristatum* Subzone was a
period of considerable and geographically widespread tectonic activity (OWEN
1971, 1973) and this seems to have permitted not only a general invasion of the
European shelf seas by mortoniceratid Tethyan ammonite faunas but also the
influx of *Paragastrolites* (*Gastrolites cantianus* SPATH) from the Arctic (OWEN
1973).

4.5. Late Upper Albian (*Stoliczkaia dispar* Zone) – Text Fig. 5.

There is no evidence of any marine connection between the Arctic seas and
the Tethyan region via the northern Atlantic, or between the European shelf
seas via the North Sea region or northern Russia after the *cristatum* Subzone.
Sea-way connections between the Atlantic and the Anglo-Paris Basin certainly
would have existed in the English Channel region and in southern Europe. Much
of the condensation of *dispar* Zone sediments in northern Europe marked the
commencement of a major transgression at the beginning of the Cenomanian as
much in response to epeirogenic movements, rather than a reduction in sea-level
as normally advocated.

5. Summary and conclusions.

An attempt has been made here to critically review the Upper Aptian am-
monite zonal and subzonal scheme developed for the western European sequen-
ces. The scheme recognised by CASEY (1961) needed revision on account of a cri-
tical analysis of the sedimentary sequence seen in southern England, upon
which the scheme is largely based, and the nature of the sequences in this inter-
val of time seen elsewhere in Europe. Problems also relate to the superposition
of Subzones in the *auritifformis* Zone of the Lower Albian *Douvilleiceras mam-*
millatum Superzone and these are touched on here. No revision of the Middle
and Upper Albian zonal and subzonal schemes appear to be necessary at this
time.

The palaeogeographical reconstructions at periods of time from the late
Upper Aptian to the end of the Albian, given here, illustrate approximately the
configuration of the European shelf seas and their inferred connections with

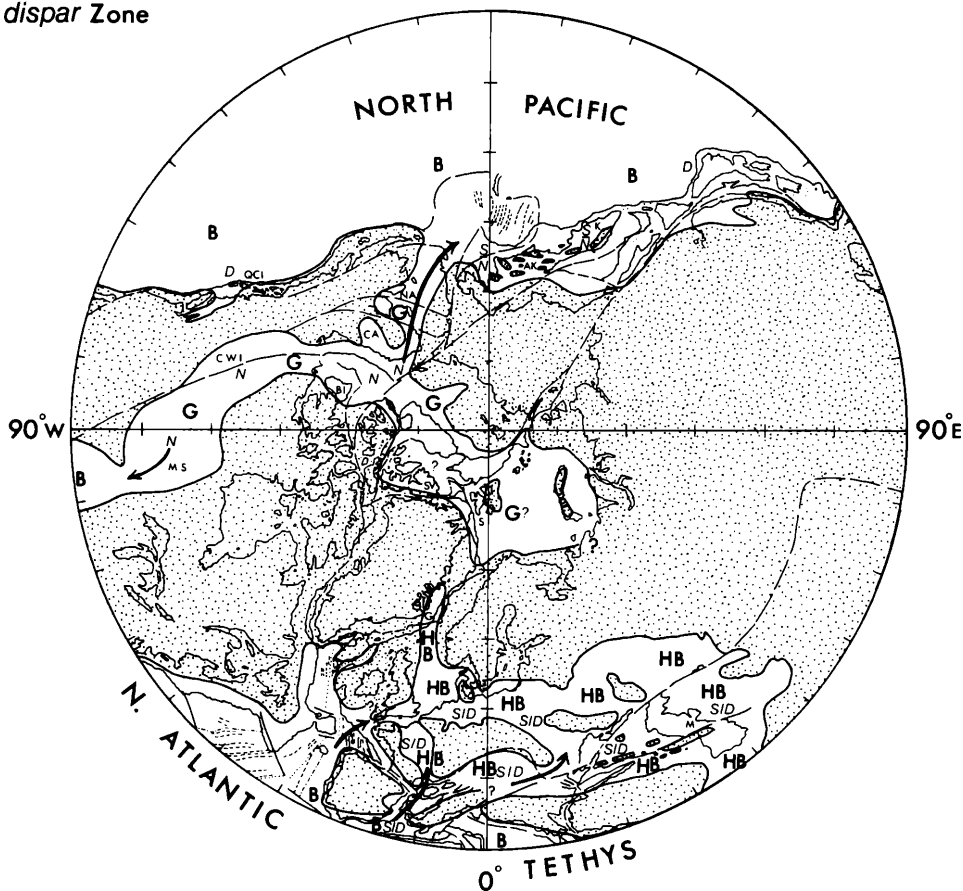


Fig. 5: Palaeogeographic map of the Boreal Region in the *Stoliczkaia dispar* Zone (latest Upper Albian) to illustrate areas of marine sedimentation (unstippled areas), ammonite faunal provinces as in Text Fig 3 with HB indicating the mixture of the hoplitinid faunas endemic to Europe and the coexisting more cosmopolitan Mortoniceratinae and Stoliczkaia characteristic of Upper Albian time. Although isolated from Europe, the Arctic regions were connected via the Maury Sea (MS) to the North American interior, and to the North Pacific. S/D = *Stoliczkaia* – *Durnovarites* association, D = *Durnovarites* occurrences in the Pacific realm, N = *Neogastropiles* fauna. Locality symbols and map projection as in the explanation to Text Fig. 1.

the Tethyan Belt and with the seas of the Arctic Province. Hitherto, the writer has tended to discount marine connections from the Atlantic to southern England and northern France through the Western Approaches and western part of the English Channel. However, the nature of *intermedius* Subzone sedimentation in south west England, which was clearly below storm wave erosive depth, together with depth deep sea drilling in the Western Approaches (eg. IPOD hole 398D RENZ 1979, OWEN 1984) and the results of the search for oil in this region requires a change of view. In fact, as in the case of earlier Aptian occurrences of faunas more closely allied to those occurring in Iberia (eg. CASEY

1961), such sea-connections at certain times, or the lack of them at others, help in the explanation of Tethyan faunal admixture. Hitherto it has been assumed that the dispersal of more southerly, Tethyan, species and genera into north west Europe from the southern European marginal regions was solely through the Paris Basin region (eg OWEN 1971). This has always been difficult to prove from the late Aptian sedimentary history of northern France. In the Middle Albian, because of a major hiatus which involves all post-*intermedius* Subzone sediments in the Paris Basin region, the inference that this was the sole dispersion route was also highly subjective. Moreover, if connections were solely via southern Europe, why were the Tethyan elements so conspicuously absent from the *dentatus* Zone onward in the Middle Albian and early in the Upper Albian in the northern and eastern parts of Europe, including Mangenschlak?

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