

Fossil-Vergesellschaftungen Nr. 61*

Palaeobiogeography of the European Boreal Realm during Oxfordian (Upper Jurassic) times: a quantitative approach

By

Franz T. Fürsich, München and Richard M. Sykes, Sarawak

With 12 figures and 1 table in the text

FÜRSICH, F. T. & SYKES, R. M.: Palaeobiogeography of the European Boreal Realm during Oxfordian (Upper Jurassic) times: a quantitative approach. — N. Jb. Geol. Paläont. Abh. 155, 137—161, Stuttgart 1977.

Abstract: During Oxfordian times, the Boreal Realm consisted of a relatively stable Boreal Province with rather diverse benthos and a Subboreal Province whose complex geography, facies patterns, and shallow-water nature reflects an unstable ecosystem with erratically varying diversity values. Salinity and temperature gradients can be discounted as mechanisms of faunal provinciality, but environmental fluctuations in the Subboreal Province in connection with temporary physical or physiological barriers are thought to have hindered migration from the Tethys, thus generating faunal provinciality.

Key words: Oxfordian, boreal province, subboreal province, palaeotemperature, palaeosalinity, shelf environment, palaeogeography, palaeorelief, clastic rock, limestone, biogeography, brachiopod fauna, mollusc fauna, echinoderm fauna, Greenland (Milne Land), Scotland, London Basin, Paris Basin.

Zusammenfassung: Im Oxfordium (Unterer Malm) lässt sich die Boreale Region im Bereich des europäischen Schelfmeeres in eine Boreale Provinz im Norden und eine Subboreale Provinz im Süden unterteilen. Die Boreale Provinz charakterisiert einen stabilen Lebensraum mit einer hohen Faunendiversität des marinen Benthos, während in der Subborealen Provinz sich rasch ändernde Faziesmuster, eine komplexe Geographie und die vorwiegend sehr flachen Meeresbecken ein Ecosystem mit geringer Stabilität widerspiegeln, in dem Faunendiversität stark variierte.

Salinitäts- und Temperaturgradienten bieten keine Erklärung für die Existenz von Faunenprovinzen und -regionen in dieser Zeit. Vielmehr können Milieuschwankungen in der Subborealen Provinz zusammen mit zeitweilig wirksamen physischen oder physiologischen Barrieren Faunenwanderungen aus der Tethys stark eingeschränkt und somit eine Differenzierung in Faunenprovinzen bewirkt haben.

* Nr. 60 siehe BECKER G., *Senckenbergiana lethaea*, Frankfurt a. M., 1978.

Introduction

Provincialism within Jurassic marine faunas has been recognised since the now classic study of NEUMAYR (1883). Two faunal realms are usually distinguished, the so-called Boreal Realm occupies the northern part of the Northern Hemisphere, whilst the rest of the world belongs to the Tethyan Realm. The distinctness of these realms varied through time, as did their boundaries and the provinces recognized within them.

Whereas the existence of these realms and provinces is generally accepted, the controversy continues over the environmental factors which brought them into being and maintained them throughout the period. Explanations for the existence of the Boreal Realm have included salinity and temperature gradients, physical barriers, environmental fluctuations, and low resource stability (for summary see HALLAM 1975). A serious draw-back of most hypotheses is that they are not usually supported by any quantitative data. HALLAM (1972) recently redressed this position in an interesting, if only semi-quantitative study of diversity and density changes of Liassic molluscan and brachiopod faunas of the North Atlantic margin from Morocco to Greenland, relying partly on museum collections and information from the literature. The influence of several critical factors on faunal distribution patterns in particular facies has been neglected. Insufficiency of 'hard data' still represents a major handicap for evaluating the various hypotheses under current debate (HALLAM 1975, p. 209).

The aim of this study is to present quantitative data on faunal diversity in relation to facies and geography within the Boreal Realm, and to utilize it in testing the hypotheses already proposed. By way of conclusion, a tentative palaeobiogeographic model is proposed for the Boreal Realm.

The study area stretches from Normandy to East Greenland; within this area, all principal outcrops of Oxfordian sediments (excepting the basal Mariae Zone) were sampled bed by bed. Additional observations on sections in the Swabian Alb and the Swiss Jura provided comparative data from the Submediterranean Province of the Tethyan Realm, and a total in excess of 30 000 specimens were collected in this way and identified to the species level. Their relationship to substrate and facies was then determined (see details in FÜRSICH 1976a, b; SYKES 1975a) in order to understand the rôle these factors play in influencing faunal distribution.

One feature of the Boreal Realm is the low diversity of ammonite faunas. This observation has often been erroneously extrapolated to other groups of the fauna and has served as a focal argument in the discussion on the origin of the Realm. HALLAM (1972) showed however that diversity trends are quite different from group to group; diversity was, therefore, thought to play a key rôle in any interpretative analysis of the palaeobiogeographic

patterns we studied. Faunal diversity was measured using SANDERS' (1968) rarefaction method; in the case of ammonites, diversity was expressed by the number of genera and species respectively. The change in faunal composition of collections from different regions was analysed using SIMPSON's (1947) similarity coefficient.

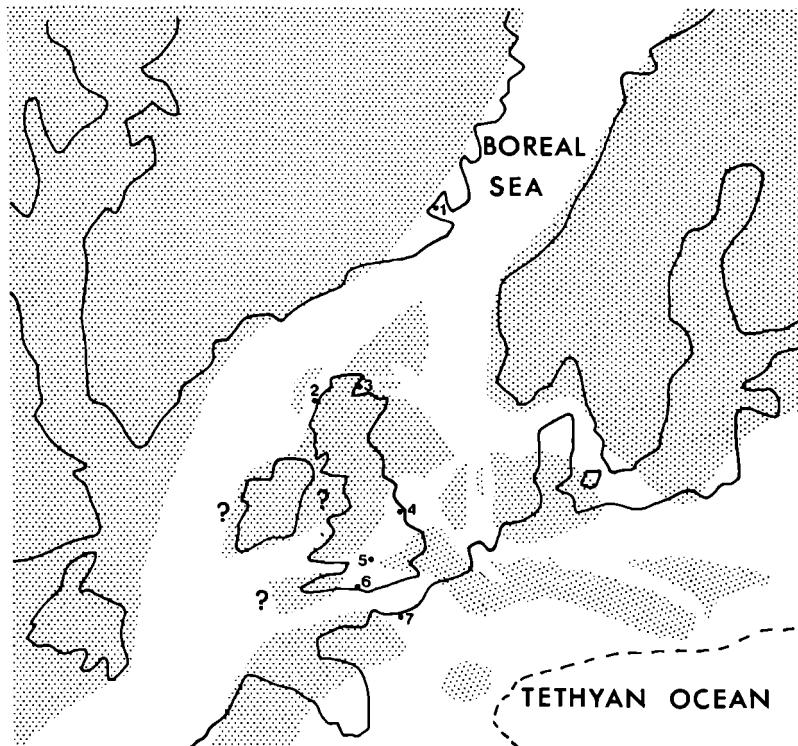


Fig. 1. Palaeogeographic sketch of the study area (mainly after ZIEGLER 1975). Numbers indicate areas of large-scale collecting.
1: Milne Land (East Greenland); 2: Skye (north-western Scotland); 3: Brora and Balintore (north-eastern Scotland); 4: Yorkshire; 5: Oxfordshire; 6: Dorset; 7: Normandy.

The Boreal Realm

Fig. 1 is a palaeogeographic map of the study area and adjacent regions during late Jurassic time. Between the southern European Tethyan Ocean (Mediterranean Province) and the land-locked Boreal Sea (Boreal Province) were a number of islands defining a series of marine basins (the Subboreal Province). These basins were usually interconnected although temporary

barriers — as in the Oxford area — occurred. Towards the south, the Subboreal Province was replaced by the Submediterranean Province which in turn graded into the Mediterranean Province.

The Boreal and Tethyan Realms were originally distinguished by the composition of their ammonite faunas and a further subdivision into provinces and subprovinces has been proposed (ARKELL 1956, CARIOU 1973). The boundaries of these provinces appear to have been gradational, whilst their location changed through time reflecting the southerly excursions of northern elements — the 'Boreal Spreads' of ARKELL (1956).

ammonite distribution

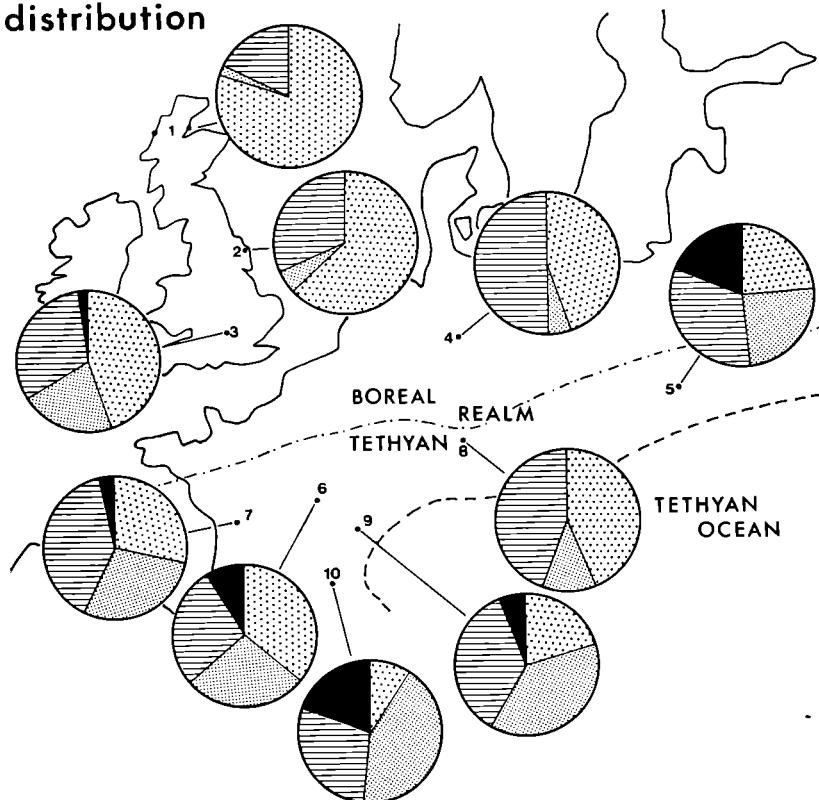


Fig. 2. Composition of Lower Oxfordian ammonite faunas. Spaced stippling: cardioceratids; dense stippling: oppeliids; ruling: perisphinctids and aspidoceratids; black: phylloceratids and lytoceratids; 1: Scotland; 2: Yorkshire; 3: Oxfordshire; 4: Saxony; 5: Southern Poland; 6: Eastern Paris Basin; 7: Western France (northern part of Aquitaine Basin); 8: Swabian Alb; 9: Swiss Jura; 10: Ardèche.

Based on data in ARKELL (1956; see also for earlier references); CALLOMON (1968; pers. comm.); ENAY (1966); GYGI (1969); KARVÉ-CORVINUS (1966); MALINOWSKA (1966, 1971); SCHMIDT-KÄLER (1962); WRIGHT (1972); ZEISS (1958, 1966) inter alia.

In order to clarify the extension of these provinces during the time interval studied quantitative data on the composition of early Oxfordian ammonite faunas are presented in Fig. 2. A distinct increase in cardioceratids northwards was matched by an equally noticeable decrease of oppeliids. The center of perisphinctid and aspidoceratid distribution is thought to have been in Western and Central Europe, whilst phylloceratids and lytoceratids were very rare or absent outside southern Europe. The boundary between the Boreal and Tethyan Realms can be regarded as corresponding to a faunal composition of 40 % Cardioceratidae and 20 % Oppeliidae, but without Phylloceratidae or Lytoceratidae. For the early Oxfordian, this boundary ran through southern Poland, southern Germany, and northern France. The true Boreal Province is distinguished from the Subboreal Province by the virtual absence of Oppeliidae; the boundary ran through Scotland.

ammonite diversity gradients

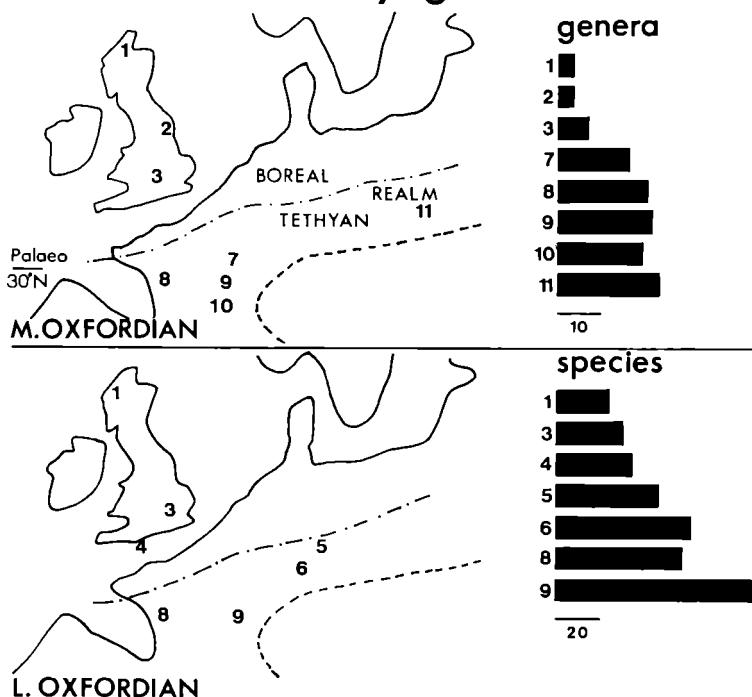


Fig. 3. Diversity gradients of Oxfordian ammonites across the Boreal/Tethyan Realm boundary.

1: Scotland; 2: Yorkshire; 3: Oxfordshire; 4: Dorset; 5: Franconian Jura; 6: Swabian Alb; 7: Eastern Paris Basin; 8: Western France; 9: Swiss Jura; 10: Ardèche; 11: Southern Poland. M. Oxf. = Mid Oxf.; L. Oxf. = Late Oxfordian. For source of data see Fig. 2.

A further characteristic of the Boreal Realm was the low diversity of ammonite faunas. Due to their high evolutionary rate and rarity in many "Corallian" faunas only generalised diversity data in terms of raw numbers of genera and species are presented (Fig. 3). There is, of course, no sharp drop in diversity across the boundary between the two realms stressing its gradational nature. However, in the mid Oxfordian the number of genera in the South of France was about four to five-times higher than in Yorkshire and Scotland, and the same trend is visible in the distribution of late Oxfordian ammonite species. Thus, in mid and late Oxfordian times low diversity Boreal ammonite faunas were clearly separated from higher diversity Tethyan assemblages.

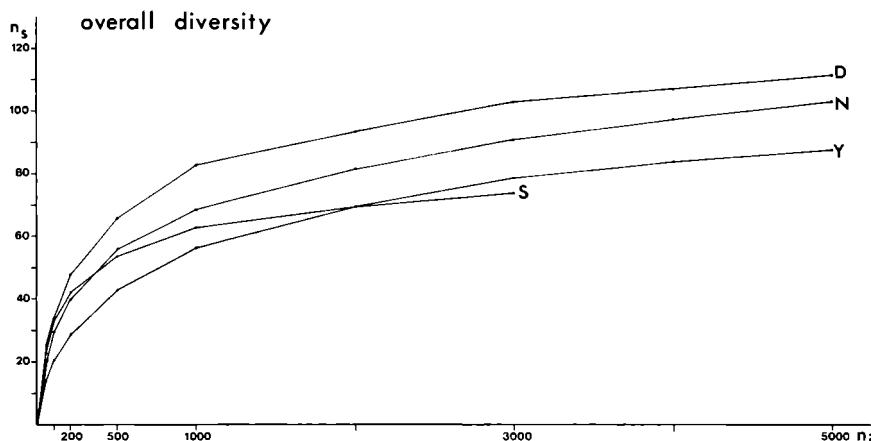


Fig. 4. Rarefaction curves for bivalves from the main study areas indicate a northward decrease in diversity.

D: Dorset; N: Normandy; Y: Yorkshire; S: Scotland.

Diversity variation with respect to facies

HALLAM (1972) presented data on the regional variation in diversity of benthic macroinvertebrate groups (bivalves, gastropods, brachiopods) in the Pliensbachian—Toarcian, but did not differentiate between facies types or compare diversities within and between facies. In the case of bivalves for

Fig. 5. Faunal changes in the Oxfordian of Staffin (north-western Scotland). With only slight changes in facies (the sequence represents a mid-outer shelf to transition zone sequence), faunal composition and associations change markedly.

1: clay; 2: silt; 3: fine-grained sandstone; a: cephalopods; b: bivalves; c: gastropods and scaphopods.

1: *Oxytoma*; 2: *Dacromya* (paralleled by *Mesosaccella*); 3: *Palaeonucula* (similar distribution: *Trautscholdia*); 4: *Grammatodon*; 5: *Pinna* (similar distribution: *Gryphaea*, *Camptonectes*, *Corbulomima*, *Thracia*, and *Pholadomya*).

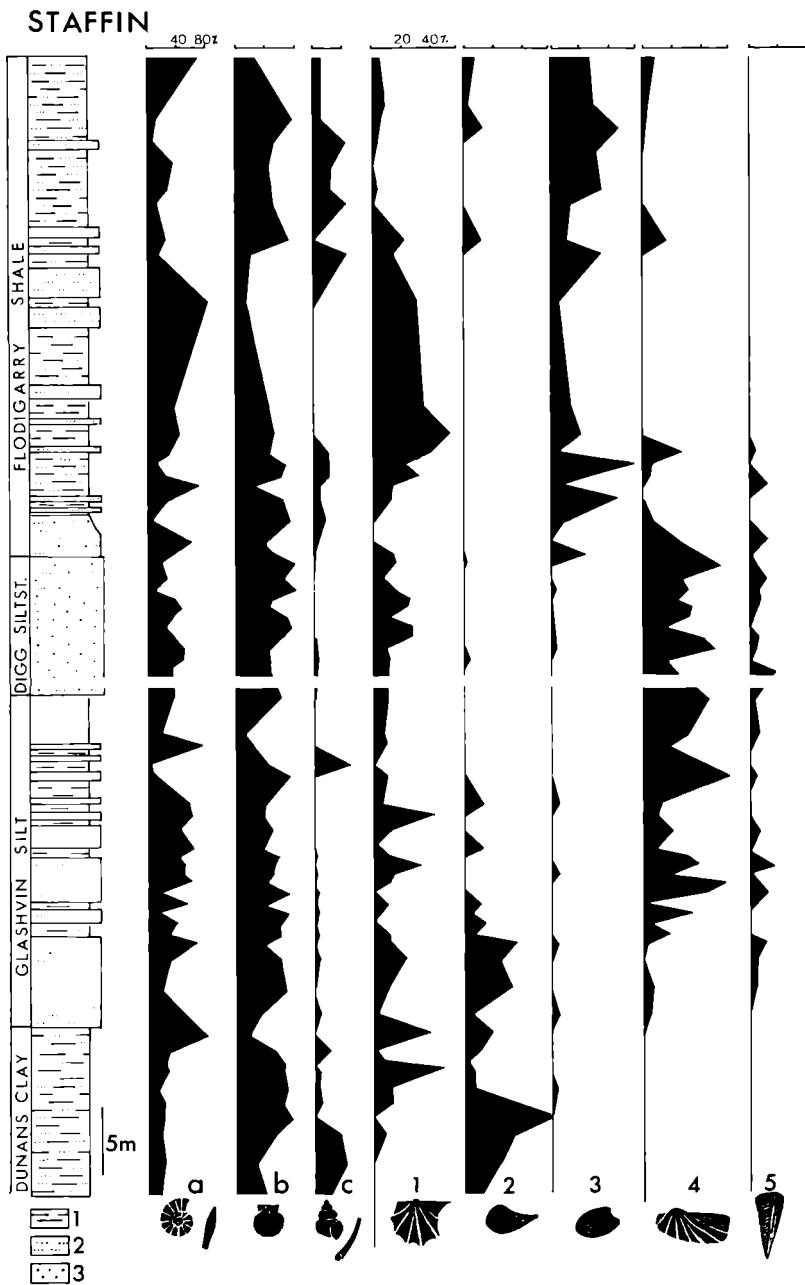


Fig. 5 (Legend see p. 142)

example, diversity generally increased northwards (HALLAM 1972, figs. 3—5). For direct comparison, Oxfordian bivalve data have been treated in the same manner (although on the species level) and indicate a clear decrease in diversity northwards (Fig. 4). However the distribution of benthic faunas and especially bivalves is clearly controlled by facies and environment. The influence of substrate, for instance, has been clearly demonstrated in Recent sediments by numerous authors (e. g. BUCHANAN 1958, SANDERS 1958, RHOADS & YOUNG 1970). In the fossil record similar relationships exist (e. g. BRETSKY 1969, SCOTT 1974, FÜRSCHE 1976b). This is also clear from a detailed study of the Staffin Shale Formation (SYKES 1975b) in northwestern Scotland (Fig. 5); even slight changes in substrate and facies resulted in a major change of faunal composition. The presence of several faunal associations in a given section naturally results in a higher faunal diversity when these data are lumped together. Cumulative diversities of various regions thus only partly reflect the diversity of the ecosystem. To overcome this problem, diversities have been computed for the following ten facies types:

- (1) condensed sandstones and limestones
- (2) condensed ferruginous sediments
- (3) reefs, reef debris
- (4) clays
- (5) silts and siltstones
- (6) fine-grained sands and sandstones
- (7) medium to coarse-grained sands and sandstones
- (8) oolites
- (9) marls and argillaceous limestones
- (10) pelletal, oolitic, shelly, or sandy limestones.

These facies types reflect both the original nature of the substrate and also certain environmental conditions. Their distribution in the central part of the study area during the Oxfordian is shown in Fig. 6.

It is now possible to compare the rarified diversity curves from different facies types within one area in order to establish the degree of facies control (Fig. 7). Whereas in Yorkshire and Dorset clear differences in diversity are apparent, the curves are all closely grouped in Normandy. Also the rarefaction curves from two facies may differ as in the case of facies 6 and 7 in Yorkshire and Normandy.

Discussion

The northwards decrease of the overall benthic diversity (Fig. 4) seems to be a result of the decrease in habitat diversity in the same direction (Fig. 6; see also SCOTT 1975). The more monotonous facies (only clastics) of Scotland provide a lower number of habitats and niches than the complex

Facies distribution

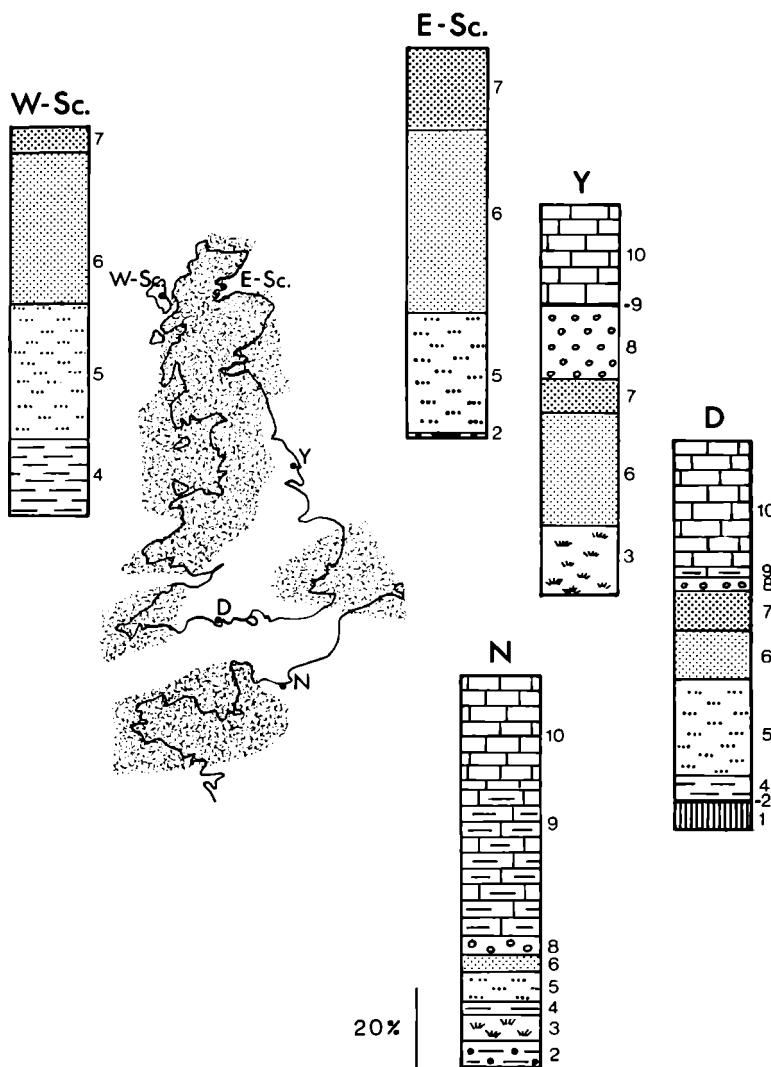


Fig. 6. Distribution of facies within the Oxfordian of Normandy (N), Dorset (D), Yorkshire (Y), and Scotland (S). Note the dominance of clastics in Scotland compared to the predominantly carbonate sequence in Normandy. Numbers denote facies types (see p. 144).

REGIONAL VARIATION IN DIVERSITY

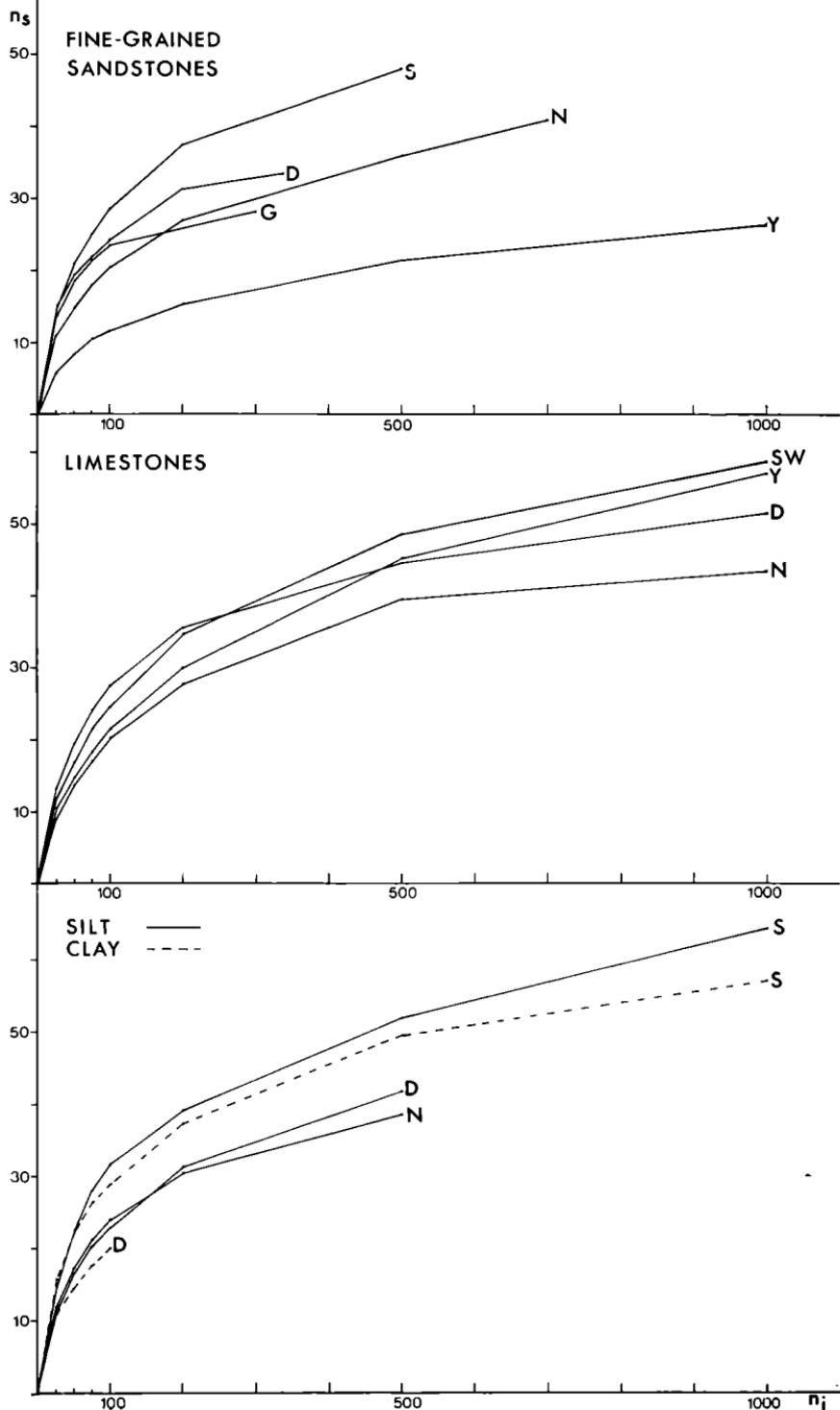


Fig. 7 (Legend see p. 147)

depositional system of intertonguing clastics and carbonates in southern England and Normandy.

Whilst there are obvious differences in diversity between various facies types, the absence of a simple pattern may be attributed to three principal factors:

a) The presence of onshore-offshore gradients.

A seaward increase in diversity in Recent environments has been demonstrated in transitions from lagoon to open marine clastic shelf (PARKER 1959, DRISCOLL & BRANDON 1973), and surf zone to shallow subtidal shelf (JOHNSON 1970). A similar pattern was established for Carboniferous shelf associations by STEVENS (1971). Using rarified diversity curves the same trend is again apparent in Upper Jurassic clastic shelf to shoreface facies in Scotland (FÜRSICH & SYKES in press), whereas further south the paucity of preserved environments and the complex facies patterns preclude elucidation of such gradients (FÜRSICH 1976a).

b) A corollary of SANDER's (1968) time-stability hypothesis is that if in a given basin the same facies (or broad environmental conditions) are maintained for long periods of time, diversity should increase as the communities become biologically accommodated. Thus different diversities in identical facies in different areas may be a reflection of their long-term stability.

c) Sediments only reflect part of a given environment. Several factors which have a strong influence on faunal diversity, e. g. seasonal variation in salinity or temperature cannot be deduced directly from the sediment type. Thus identical facies may in fact represent somewhat different environments with in consequence, differences in faunal diversity.

These three factors represent a clear limitation of the approach used in this paper. Despite this, the importance of facies in influencing faunal diversity can be unequivocally demonstrated.

Regional diversity variation within selected facies

Diversity is related to facies which reflects a number of variables including substrate, turbulence, and depth of deposition. If these variables can be kept reasonably constant by considering only a single facies, then the remaining variation in diversity may give a clue to the presence or absence of regional environmental gradients such as temperature and salinity. Fig. 8 shows the diversity patterns of some widespread facies types within the study area for the total preserved macroinvertebrate fauna. No diversity gradient is visible in the fine-grained sandstone facies, or in pelletal

Fig. 7. Rarefaction curves of bivalve faunas for various facies in different regions illustrate the influence of facies on diversity without producing a clear pattern. Numbers denote facies types (see p. 144).

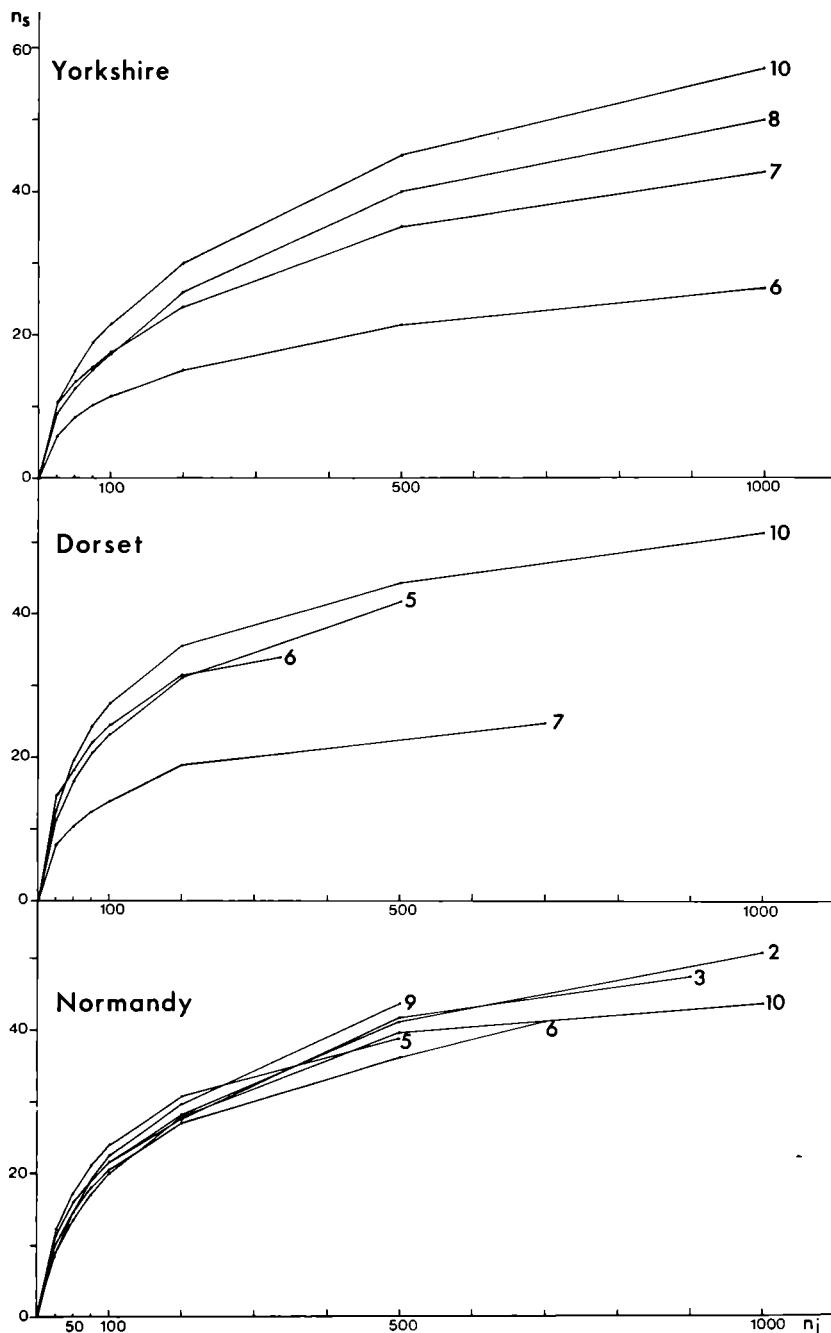


Fig. 8 (Legende see p. 149)

shelly, oolitic or sandy limestones. In clays and silts however a distinct reduction in diversity southwards from Scotland to Normandy is apparent.

Discussion

The lack of a regular latitudinal diversity gradient argues against a regional temperature or salinity gradient as the principal factor controlling faunal diversity. According to these models (e. g. HALLAM 1969, 1971, GORDON 1974, 1975) diversity should decrease northwards due to decreasing salinity or lowered temperatures. It follows then that other factors influenced diversity patterns to a considerable extent masking any affects of the two parameters mentioned above. These 'other factors' were probably

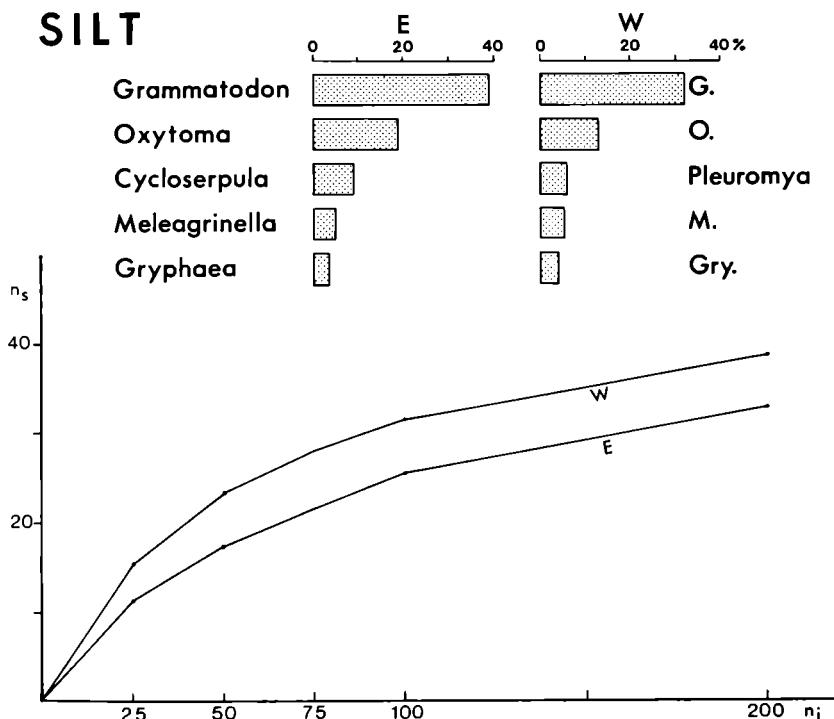


Fig. 9. Within the same facies and at the same latitude, rarefaction curves from north-eastern (E) and north-western (W) Scotland indicate different diversity values for the two regions, despite a very similar faunal composition. This emphasises the influence of basin configurations and other local factors on diversity.

Fig. 8. Rarefaction curves of macroinvertebrate faunas in four widely distributed facies types do not show any latitudinal trends except in silts and clays.
G: Greenland; SW: Switzerland; for others see fig. 6.

of more local influence, and might have varied with time and changes in palaeogeography. Amongst the most likely factors are local variations in salinity and trophic resource supply (VALENTINE 1971) and the degree of environmental heterogeneity and stability.

The markedly higher diversities in Scotland in the offshore silt and clay facies add a further aspect to the discussion. This may be explained by the dominance of these two facies types at Staffin in north-western Scotland from Middle Callovian times onwards (Fig. 6). In accordance with the time-stability hypothesis (SLOBODKIN & SANDERS 1969) this biotope, with its high environmental predictability, should be colonised by a fauna of higher diversity than the shelf clays developed over much shorter periods in Dorset and Normandy. However, although very similar faunas were developed in facies 5 (siltstones) in both north-western and north-eastern Scotland, the diversity values are significantly different (Fig. 9). This may again be due to the persistence of this facies at Staffin as well as the more restricted nature of the Moray Firth Basin (Fig. 1).

FAUNAL COMPOSITION

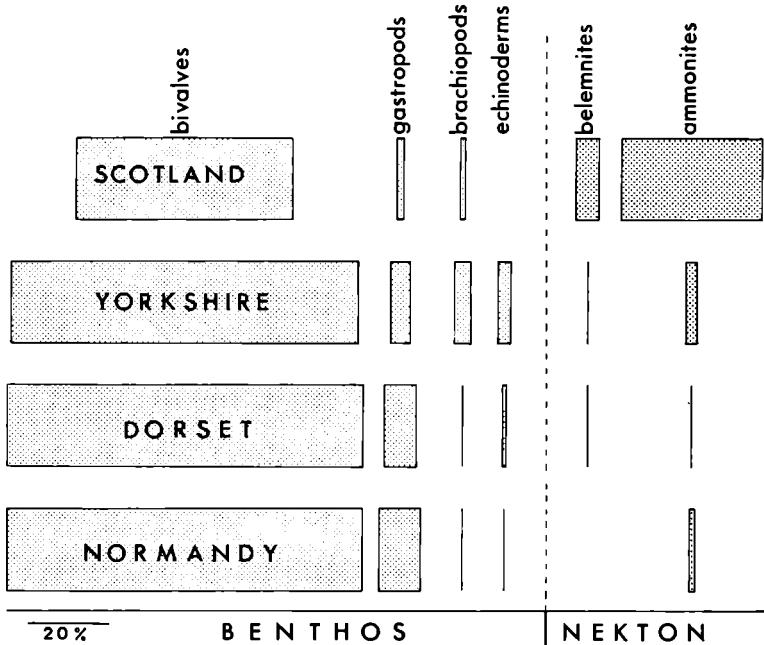


Fig. 10. Composition of the macrofauna and numerical abundance of the main faunal groups in the study area. Note the abundance of cephalopods in Scotland compared to their scarcity further south (from FÜRSCHE & SYKES in press).

In summary, the regional diversity patterns determined contradict a simple model of environmental gradients operating in the Boreal Realm and stress the importance of local factors which influenced faunal distribution, but can only be revealed by detailed analysis. The results from Scotland also indicate that the more offshore stable regions of the Boreal Sea contained diverse faunas which contradicts its interpretations as a low predictability, high stress environment (e. g. HALLAM 1972, 1973).

Regional variation in faunal composition

Fig. 10 illustrates the abundance of faunal groups in the various basins studied. From Normandy to Yorkshire bivalves comprise over 80% of the faunas, and cephalopods are rare elements. In contrast, belemnites and ammonites constitute an important part of the Scottish faunas. This may be explained by the prevalence of shallow water, more marginal sediments in England and Normandy (at least in sections available for study), and also by the proximity of Scotland to the open Boreal Sea. However it should be noted that limited data collected by one of the authors (R.M.S.) from basinal Upper Oxford Clay (Lower Oxfordian) and Ampthill Clay (Upper Oxfordian) of eastern England indicate that cephalopods are again an important faunal element.

In the shallow-water facies of England and Normandy faunal composition varies little with facies. However in Scotland the onshore-offshore diversity gradient is also accompanied by marked faunal changes (FÜRSICH & SYKES in press).

Faunal similarities and endemism

The faunas of the various regions have also been compared using SIMPSON's (1947) Similarity Coefficient. Table 1a shows the degree of similarity of the bivalve faunas of the main outcrop areas at generic level. The relatively high degree of similarity agrees with data presented by HALLAM (1972, table 5). However analysis at the species level (table 1b) shows this picture to be misleading. Especially striking is the different composition of the Scottish bivalves faunas, which have little more than half the species in common with the remaining areas. The same pattern is apparent when the complete benthic macroinvertebrate fauna of two widely distributed facies types (fine-grained sandstones and pelletal, oolitic, or shelly limestones) is analysed (table 2). At the species level, the limestone faunas exhibit, from Yorkshire down to Switzerland, a markedly low degree of similarity as do the faunas of the fine-grained sand facies from Greenland to Normandy. The faunal difference within the Wessex Basin (i. e. between Dorset and Normandy) is perhaps the most surprising of these observations.

Table 1. Simpson Similarity Coefficients for bivalves.

a) on the generic level

Normandy	Dorset	Yorkshire	Scotland	
77	77	82	100	Scotland
77	86	100		Yorkshire
88	100			Dorset
100				Normandy

b) on the species level

Normandy	Dorset	Yorkshire	Scotland	
54	56	53	100	Scotland
71	78	100		Yorkshire
78	100			Dorset
100				Normandy

Table 2. Simpson Similarity Coefficients for benthic macroinvertebrates in two types of facies.

l i m e s t o n e s (f a c i e s 1 0)

Switzerland	Normandy	Dorset	Yorkshire	
47	62	45	100	Yorkshire
47	60	100		Dorset
48	100			Normandy
100				Switzerland

f i n e - g r a i n e d s a n d s t o n e s (f a c i e s 6)

Normandy	Dorset	Yorkshire	Scotland	Greenland	Greenland
22	26	11	52	100	Scotland
38	43	53	100		Yorkshire
40	43	100			Dorset
38	100				Normandy
100					

Discussion

Initially one might interpret these results as signifying marked endemism in the faunas of the various basins. Indeed ARKELL (1929—1937) recognized endemic bivalve assemblages such as the '*Corbis*' assemblage of the Malton Oolite of Yorkshire, the *Opis* assemblage of Upware in Cambridgeshire, and the *Astarte* assemblage within the '*Trigonia*' *clavellata* Beds of Dorset (see also BROOKFIELD 1973, table 4). However, hardly any of the faunal elements quoted by ARKELL (and reiterated by BROOKFIELD 1973) are truly endemic — their absence in neighbouring basins is often only a reflection of the facies pattern. For example, the rarity of nuculids in Yorkshire north of the Market Weighton Axis reflects the scarcity of fine-grained argilla-

ceous facies in that region. Moreover several species which seem to have had a restricted distribution in England are found to occur over many other parts of the north-western European shelf (see also ARKELL 1929—1937, p. 379).

However as table 2 illustrates, the facies pattern alone cannot account for the low degree of similarity between faunas. Rather, faunal distribution patterns may have been sculptured by the existence of discrete basins, often separated by physical or physiological barriers. This temporal limitation on the free exchange of faunas prevented the spread of an homogeneous benthic fauna over the Subboreal shelf.

Also, both facies types of table 2 (limestones and fine-grained sandstones) represent mainly shallow-water environments which can be subdivided into numerous subenvironments; with only subtle environmental differences the latter could have supported different faunas, and thus not been strictly comparable. (This is another limitation of the approach used in this paper.)

The marked faunal dissimilarity between Yorkshire and Scotland might be accounted for by the presence of persistent shallows or even a land barrier in the area of ZIEGLER's (1975) 'Mid North Sea High'. Similarly the marked faunal differences within the Wessex Basin may be explicable only in terms of subtle environmental changes not discernable from normal facies analysis.

The high degree of similarity at the generic level and the lack of true endemic species can be explained by the absence of permanent barriers and the low evolutionary rates of bivalves which prevented speciation during short-time separation (see also p. 156).

Distribution patterns of selected faunal elements

B r a c h i o p o d s are very rare throughout the study area except for some localities in Yorkshire, e. g. Filey Brigg, where *Thurmanella acuticosta* CHILDS and one species of '*Terebratula*' form low diversity nests in a nearshore high energy environment.

C r i n o i d s occur only as allochthonous faunal elements (in form of ossicles) in lag deposits in the Glashvin Silt Member at Staffin (north-western Scotland) and as paraautochthonous stems (*Millericrinus*) associated with the brachiopod nests at Filey Brigg. **E c h i n o i d s**, especially *Nucleolites scutatus* LAMARCK, are a common element of many benthic associations of England and Normandy, although their numbers vary erratically. They are almost completely absent from Scotland and Greenland.

The distribution pattern of Oxfordian coral genera and their decrease in diversity northwards has been commented upon frequently (e. g. ARKELL 1935, ZIEGLER 1964, HALLAM 1969). In the study area, corals are found in the form of low diversity patch reefs (less than 13 species) only in Yorkshire, Oxfordshire, Cambridgeshire, Dorset, and Normandy). The age

of the colonial coral *Enallocoenia* from the Charcot Bugt Sandstone of Milne Land, East Greenland, formerly thought to be mid Oxfordian (HÅKANSSON et al. 1971, BEAUVAIS 1977) has now been established as Bathonian (per. comm. T. BIRKELUND and J. H. CALLOMON).

Bryozoans are generally rare and are only found encrusting mollusc shells in England and Normandy).

Discussion

The notable rarity or absence of such stenohaline groups as corals, brachiopods, crinoids, and bryozoans has been taken by some authors (e.g. HALLAM 1969) to indicate a lowered salinity or at least salinity fluctuations in the Boreal Realm. However, the virtual absence of these groups together with echinoids from the Oxfordian of Scotland and Greenland is in marked contrast to the abundance of ammonites and belemnites in these two areas (Fig. 10). This precludes salinity as the dominant factor regulating faunal distribution and, having already argued against a temperature gradient as a dominant factor controlling faunal distribution, we must examine further alternatives.

All groups discussed in this chapter show a maximum abundance and diversity on the northern margin of the Tethyan Ocean from where they migrated northwards. This migration was probably severely hampered as the relatively uniform and mainly carbonate environments gave way to a mixed clastic/carbonate regime in northern France and England. This area of complex geography (Fig. 1) and rapidly changing facies pattern most likely represented a region of high environmental heterogeneity and fluctuations (e.g. varying input of clastic material, fluctuating resources, local variations in salinity, shifting barriers and local current systems etc.). Migration over this area of low environmental stability may have proved difficult and prevented the establishment of diverse benthic faunas. Competition of the usually more eurytopic bivalves might have added to the colonisation failure of most other groups, especially brachiopods. The distribution of brachiopods and crinoids clearly seems to be related to the degree of environmental stability and predictability: They form an integral part of submediterranean carbonate communities (Fig. 11) but like *Thurmanella acuticosta* adopted an opportunistic strategy when found in the mixed carbonate/clastic areas. It is worth noting that this species occurs quite isolated in Yorkshire: a second species is known from the Paris Basin (CHILDS 1969) emphasising the importance of basin configuration and partially effective barriers for brachiopod distribution and speciation.

In the case of corals the zone of late Cimmerian rifting may also have played a part in geographically limiting this group. Differential uplift gave rise to widespread clastic detritus, whilst bentonites have now been found in the Tobar Ceann Siltstone Member and Glashvin Silt Member in Scotland, in the Coral Rag of Oxfordshire (pers. comm. O. E. ALI) and the Malton

Faunal composition

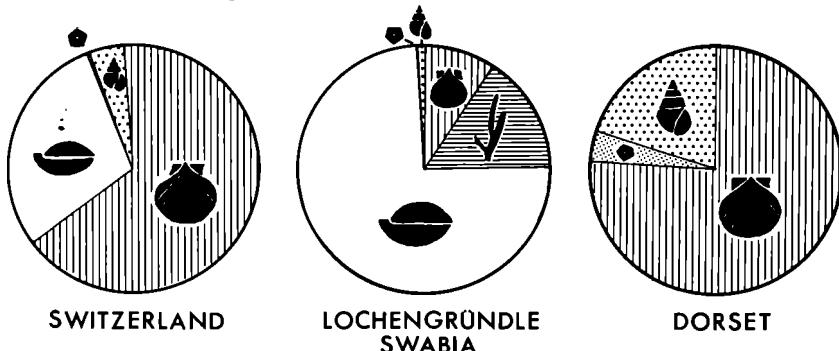


Fig. 11. Composition of macrobenthos in pelletal, oolitic, or shelly limestones (facies 10) of Switzerland and Dorset, and in sponge reefs from the Swabian Alb. Whilst in Switzerland and Swabia (Submediterranean Province) brachiopods form an integral part of benthic communities they are rare within the Subboreal Province (e. g. Dorset).

Vertical ruling: bivalves; horizontal ruling: bryozoans; spaced stippling: gastropods; dense stippling: echinoderms; white: brachiopods.

Oolite of Yorkshire (pers. comm. D. S. SIDDIQUI). Thus changes in environmental stability would seem to overshadow any latitudinal temperature gradient and explain the rapid diversity decrease of corals. Similarly the absence of edinoids in Scotland does not necessarily attest to adverse conditions for this group in that region, but might be better explained by colonisation failure from the south due to adverse conditions en route.

Currents are one further possible agent responsible for the distribution pattern of many Oxfordian benthic invertebrates. They have been already invoked by ZIEGLER (1964) and IMLAY (1965) as contributing to the differentiation of the Tethyan and Boreal Realms, whilst more recently GORDON (1974) and AGER (1975) have attempted to portray the palaeocurrent system during various stages of the Jurassic. It is interesting to note that in AGER's reconstruction the main current system for the area under discussion was southward. If correct, this would be a potent factor limiting northward migration of planktic larvae of those benthic invertebrates radiating from the Tethyan margins.

Ammonite versus bivalves diversity gradients and composition

One final point arising from the quantitative data awaits discussion: the pronounced southward increase in diversity and change in composition shown by the ammonites (Figs. 2, 3). This is in marked contrast to the irregular

diversity pattern and change in faunal composition exhibited by the bivalves. It is generally accepted that the center of ammonite radiation was the Tethyan Realm. Forms which migrated northward established the distinct boreal fauna by speciation in a geographically isolated area. As in the case of other faunal groups already discussed, northward migration might have proved difficult due to extensive areas of environmental instability. Once a group of ammonites reached the more uniform area of the Boreal Sea speciation and propagation could easily have taken place. It may be argued that this was the principal cause of the sharp decline in ammonite diversity. Fluctuations in salinity may have been important, but only in the partly very shallow subboreal region not in the offshore areas of the Boreal Sea.

The lack of a distinct boreal bivalve fauna in contrast to the ammonite fauna seems to be a function of the evolutionary rates of the two groups: in the case of the rapidly evolving ammonites periodic isolation was sufficient to give rise to successive endemic boreal faunas (POŻARYSKA & BROCH-WICZ-LEWINŃSKI 1975) whilst for the slowly evolving bivalves (HALLAM 1976) these periods of geographic isolation did not lead to speciation.

Conclusions and palaeobiogeographic model

- a) Faunal diversity is clearly influenced by the type of facies.
- b) The overall diversity of the benthic macroinvertebrate fauna decreases northwards from the Subboreal to the Boreal Province. This is due to the more uniform environment of the Boreal Sea which resulted in low habitat diversity.
- c) In contrast to the strong latitudinal diversity gradients exhibited by ammonites and corals, no regular diversity gradient is displayed by the remaining benthos.
- d) Variations in diversity of benthic faunas within the Subboreal Province seem to reflect a region of environmental instability and heterogeneity, mainly a result of a complex physiogeography and rapidly changing facies patterns.
- e) In the study area, the benthic faunas of the various basins exhibit a low degree of similarity at species level. This seems to reflect a series of interconnected but strongly differentiated basins in which physical and physiological barriers were frequently operative.
- f) The rarity or absence of many major fossil groups in Greenland and Scotland is primarily not the result of a temperature or salinity gradient, but may be explained in terms of limited migration from dispersal centres on the margins of the Tethyan Ocean.

Fig. 12. Model of Oxfordian palaeobiogeography. Explanation in the text. Bent arrows: migration routes; straight arrows: prevalent ocean currents; stippling: temporary physical or physiological barriers. (From FÜRSCHE & SYKES in press).

Palaeobiogeographic model

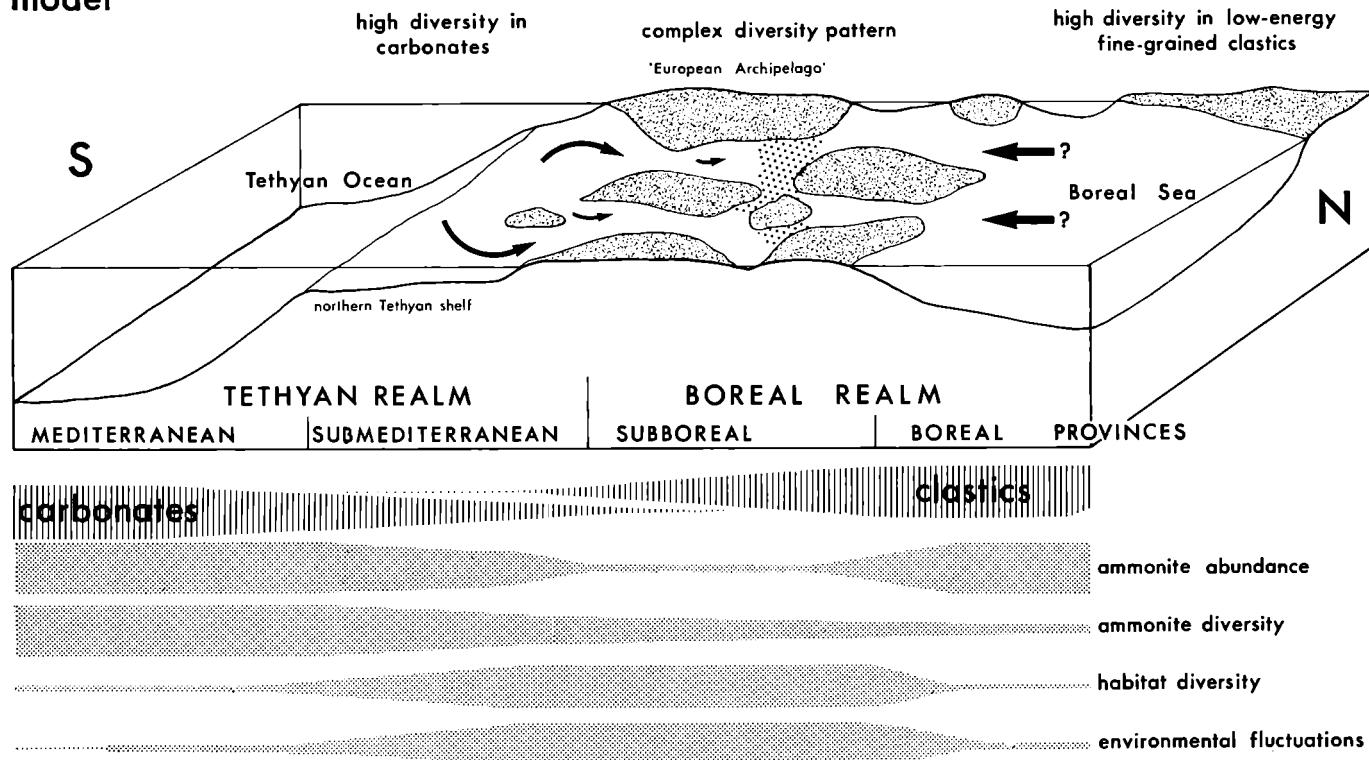


Fig. 12 (Legend see p. 156)

g) The available evidence suggests that it was within the Subboreal Province that environmental stability was lowest, and that stability and predictability increased again in the Boreal Province.

h) The presence of a distinct Boreal ammonite fauna, but a uniform bivalve fauna from Boreal to Subboreal provinces may be accounted for by their differing evolutionary rates: temporary isolation of rapidly evolving ammonites produced endemic groups in time intervals too short to produce similar changes in the slowly evolving bivalve stocks.

The foregoing conclusions may be incorporated into a tentative palaeobiogeographic model for the Boreal Realm (Fig. 12): Between the Tethyan Ocean (Mediterranean Province) and the shallower Boreal Sea (Boreal Province) existed an extensive shallow shelf (Submediterranean and Subboreal Province) on which clastic influx from the north interfingered with the carbonates that predominated in the south to create a complex facies pattern. The presence of several islands ('The European Archipelago' (AGER 1975, p. 25)) broke up the northern part (Subboreal Province) into a series of basins and produced a complex geography. The resultant intricate facies pattern produced high habitat diversity, whereas the shallow nature of most basins rendered them susceptible to high environmental fluctuations. Several faunal groups such as ammonites and brachiopods, had a limited tolerance of these high stress conditions and occurred only sporadically in the Subboreal Province. However the bivalves seem to have been better adapted to this environment and dominate the benthic faunas. Intermittently effective barriers (dotted areas in Fig. 12), physical or physiological in nature, made migration (bent arrows) from the Tethyan Ocean difficult for many faunal groups (see also POŻARYSKA & BROCHWITCZ-LEWIŃSKI 1975), whilst a predominantly southerly directed current system (straight arrows) might have enhanced this effect. No simple factors such as regional temperature or salinity gradients can explain the existence of the Boreal Realm during Oxfordian time. Local salinity and temperature variation probably contributed towards general environmental fluctuations, especially in the Subboreal rather than the Boreal Province. Whilst all existing models regard the Boreal Province as the region with the highest environmental fluctuations, we suggest that the offshore parts of the Boreal Sea represented areas of relatively high environmental stability and predictability: At Staffin, the *Dacromya* community of SYKES (1975a) persisted unchanged for six subzones!

Acknowledgements

We would like to thank Dr. W. J. KENNEDY, Oxford, for critical reading of the manuscript.

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Bei der Tübinger Schriftleitung eingegangen am 13. Mai 1977.

A n s c h r i f t d e r V e r f a s s e r :

- Dr. FRANZ THEODOR FÜRSICH, Institut für Paläontologie und Hist. Geologie, Richard-Wagner-Str. 10/II, 8000 München 2, W-Germany.
- Dr. RICHARD M. SYKES, c/o Sarawak Shell Berhad, Lutong, State of Sarawak.