CORRESPONDENCE

Origin of the Mesozoic 'Boreal' realm

SIR—Marine faunas from Jurassic and Cretaceous rocks of the northern hemisphere show the presence of two contrasting faunal realms, known as Tethyan and Boreal, or by equivalent names. The differentiation of these realms has been widely regarded as due to difference in climate, and Arkell (1956) assumed this in his discussion of Jurassic faunas. Hallam (1969) has argued against this assumption, and concluded that the most important factor was lowered salinity in a land-locked northern sea. But Sellwood (1972, p. 154) has rejected this suggestion, and returned to the notion that temperature was the most important factor.

It also seems to me that Dr Hallam's suggestion should at any rate be questioned, because of the persistence of the two faunal realms through the Cretaceous period. This applies especially to the Upper Cretaceous, when chalk deposition replaced detrital sedimentation in much of the Boreal region. The picture of a land-locked Jurassic Boreal sea is also based (Hallam, 1969, p. 15) on the absence of a north Atlantic Ocean. This probably existed by the Upper Cretaceous; and Casey (1971, p. 166) believes that it had opened by the Volgian (Upper Jurassic). This change did not lead to disappearance of the Boreal faunas. One might, perhaps, think of the extinction of the Perisphinctaceae in Hauterivian and Barremian times, but this affected Tethyan forms as well as the northern ones

In addition, a feature of the Boreal Chalk is the occurrence of large faunas of Hexactinellida, at various horizons from Cenomanian to Upper Campanian. The largest known fauna, from the German Campanian, contains rather more dictyonine species (104) than are known from the whole world at present. It seems very unlikely that these typically deep-water sponges, which would probably be specially sensitive to physicochemical variations, could exist in such numbers in water of lowered salinity. More probably, their presence is an index of normal salinity in at least the bottom water, and Gripp (1958) has suggested an influx of deep Atlantic water at bottom level. It is possible to envisage a less saline surface layer, maintained by density stratification; but Boreal elements controlled by salinity would then probably be restricted to upper water plankton and nekton, and thus not include benthos such as, *e.g.* the Boreal inoceramids.

It might still be asked, however, whether temperature differences alone were sufficient to account for the differentiation of these faunas. The Cretaceous Boreal region was not boreal in the modern climatic sense. The present boreal region *sensu* Ekman (1953) is cold-temperate, with mean annual surface temperatures ranging from 2–3°C to 12–13°C between its northern and southern limits. By comparison, the palaeotemperatures recorded by Cretaceous belemnites are mainly warm-temperate or subtropical. Other evidence also fits this picture; for instance, reef-corals and crocodiles occur in the Campanian of southern Sweden, and a large reef-coral fauna (30 species; Umbgrove, 1925) is known from the Maastrichtian of Holland. We are therefore not dealing with a contrast between boreal and warm-water faunas in the modern sense, but only with faunal divisions of an overall warm-water region, grading northward from tropical to warm-temperate.

Attempts to make comparisons between modern and Mesozoic faunas can thus picture the Tethyan and 'Boreal' regions as tropical and warm-temperate/subtropical respectively, in so far as analogy is possible. On the east side of the modern Atlantic, the nearest climatic counterpart of the 'Boreal' realm of Mesozoic times is the Mediterranean–Atlantic region, whose Mauretanian–Lusitanian sectors extend between the tropical and cold-temperate (= boreal s.s.) regions. Hallam's figures comparing the diversity of modern Bivalvia at different latitudes (1969, p. 5) are, however, based on forms which range from tropical to just arctic. This suggests that one reason for the difference which he shows between the modern and Mesozoic patterns could be inclusion of both forms of southern origin, and members of a cold-water boreal–arctic fauna which had no Jurassic counterpart.

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Extra-tropical conditions are, however, not simply a matter of poleward lowering of temperatures. If the Earth's rotational axis had the same tilt in Mesozoic times as at present, this caused seasonal fluctuations in both incident radiation and the pattern of alternate light and darkness. These variations will have increased away from the tropics, towards polar zones in which a diurnal alternation of light and dark was replaced by a seasonal alternation. They occurred independently of temperatures; and, unlike climates, the seasonal illumination changes had the same pattern as at present. These factors might be specially important in a period in which genera of tropical origin could migrate to higher latitudes than at present.

Seasonal illumination changes will have influenced 'Boreal' ecology because of their effect on the growth of phytoplankton, and hence also on dependent zooplankton. Even at present British latitudes, the abundance of plankton is markedly seasonal. In a polar zone of seasonal darkness, phytoplankton would probably be abundant in summer, but would be absent in winter except for dormant stages. These fluctuations would affect all other forms close to plankton in the food chain, either as adults or in juvenile stages. One thinks here especially of the young forms of ammonites and belemnites, and perhaps the smaller kinds of adult ammonites; but many kinds of animals which are benthos as adults have planktonic larvae. Further, plankton-dependent forms which entered a polar zone would need to be either migratory or able to store food reserves, to survive from one season to another. One would not expect the latter ability in immigrants of Tethyan origin.

Lowered intensity and penetration of light, and seasonal variations in both, might also themselves have been factors in limiting the northward spread of Tethyan reef-corals, assuming that these were dependent on zooxanthellae. It is true that a large reef-coral fauna lives in southern Japan at present; but its vertical range is restricted (5–40 m depth; Yabe & Sugiyama, 1935) at even this latitude (*c.* 30–35°N).

A polar zone of seasonal darkness would presumably also have an influence on minimum 'Boreal' temperatures. In summer, surface temperatures in a sea which extended within it could be similar to those of adjacent regions; but a dark winter period would be one of cooling. Here at least, the 'Boreal' climate could show considerable seasonal changes, although these would to some extent depend on the pattern of cloud cover. Some authors believe that Jurassic polar temperatures can never have fallen to 0°C; but it might be asked whether the minimum polar winter temperature can have failed to fall at least to near that level. One might also ask whether the alleged equability of the Mesozoic 'Boreal' climate may not be partly illusory. For instance, when reef-corals were present in Scotland or Sweden, one might think of Ekman's figures (1953, p. 3) of 16–18°C as the minimum tolerated by modern subtropical faunas. But in southern Japan, which he treats as subtropical, reef-corals at one of the northernmost localities (Tateyama-wan; Yabe & Sugiyama, 1935, p. 207) can apparently tolerate temperatures which fall below 15°C for five months in a year, to a minimum of 12.1°C.

In this light it seems possible that the Mesozoic 'Boreal' faunas reflect the influence of seasonal conditions at extra-tropical latitudes, as well as simply of lower mean temperatures than those of the Tethyan region, and that seasonal factors may have been the more important. At least for northerly localities, this seems possible even after allowance for later changes in latitude, due to continental drifting. The factors here specially envisaged are seasonal fluctuations in (a) the abundance of plankton, which, as now, will have formed the prime basis of the whole marine food chain, and (b) surface and shallow-water temperatures, of which the minimum temperatures would probably be more important than maximum or mean temperatures. Immigrants of Tethyan origin would at least have no special adaptations to markedly seasonal conditions; and it could be critical to know whether those which reached northerly localities were still able to breed there, or whether their presence was maintained by external recruitment. Reproductive adaptation to northern seasons would probably cause genetic isolation from Tethyan parent stocks, as well as also resulting in new northern forms having temperature-controlled southern limits.

This suggestion should not be read as claiming that either seasons or temperatures can explain the whole basis of Mesozoic zoogeography, which would clearly be incorrect. For instance, in the Upper Cretaceous, the faunal changes seen between south-eastern England and Yorkshire seem related to the influence of contrasting water masses, with Atlanto-West Tethyan and Russo-Germanic distributions. They also occur acrosss the site of the submerged former Anglo-Belgian island, where a topographic rise could form a barrier to the free flow of bottom water. The coincidence of sudden abundances of Hexactinellida and the formation of phosphorites, in the Glauconitic Marl of southern England and the Santonian of Ireland, suggest incursions of deep Atlantic water. Many features of the fauna of the Chalk also probably reflect its special substrate. But Mesozoic 'Boreal' seasons would have a continuous influence on plankton and shallow-water benthos, irrespective of hydrography, geography or sedimentation, or of changes in these factors.

Last, the lack of a Mesozoic 'Antiboreal' fauna could reflect the position of Antarctica. The northern 'Boreal' faunas lived mainly in epicontinental waters. If the present position of Antarctica was occupied then by open ocean, polar seasonal conditions would affect the pelagic fauna only, with no corresponding development of an 'Antiboreal' shelf-fauna. If no land was in or near a polar zone of seasonal darkness, southern temperatures would also have been higher than northern ones.

References

Arkell, W. J. 1956. *Jurassic Geology of the World.* Oliver & Boyd Ltd, Edinburgh and London.

Casey, R. 1971. Facies, faunas and tectonics in late Jurassic–early Cretaceous Britain. *In*: Middlemiss, F. A., Rawson, P. F. & Newall, G. (Eds) *Faunal Provinces in Space and Time*, pp. 153–68. Seal House Press, Liverpool.

Ekman, S. 1953. *Zoogeography of the Sea.* Sidgwick & Jackson Ltd, London.

Gripp, K. 1958. Rezente und fossile Flachmeer-Absätze petrologisch betrachtet und gedeutet. *Geol. Rdsch.* **47,** 83–99

Hallam, A. 1969. Faunal realms and facies in the Jurassic. *Palaeontology*, **12,** 1–18.

Sellwood, B. J. 1972. Regional environmental changes across a Lower Jurassic stage-boundary in Britain. *Palaeontology*, **15,** 125–57.

Umbgrove, J. H. F. 1925. De Anthozoa uit het maastrischsche Tufkritj. *Leid. geol. Meded.* **1,** xi, 83–126.

Yabe, H. & Sugiyama, T. Geological and geographical distribution of reef-corals in Japan. *J. Paleont.* **9,** 183–217.

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SIR,—Mr Reid's letter offers some interesting speculations on the origin of the Tethyan and Boreal faunal realms in the Mesozoic. In so far as he comments upon a paper of mine on this subject published in 1969 I feel that a few further remarks here would be in order.

I think that to argue, as Reid does, that the two realms persisted into the Upper Cretaceous is somewhat misleading. The picture for the ammonites and belemnites, at least, is altogether more complicated. However, I would not wish to challenge his contention that a straightforward salinity-control mechanism is unlikely. I have in fact for some time abandoned the view that slightly-lowered salinity was a major cause of differentiation and persistence of the Jurassic Boreal Realm, and now support the view that the ecologically more sophisticated notion of environmental stability or predictability is much more likely to have been the principal controlling factor, as I discuss at some length in a recent article (Hallam, 1972).

As regards Reid's suggestion that a simple lowering of temperature away from the tropics was in itself unlikely to have been the most significant environmental control for the Mesozoic faunas, as has been widely assumed, I can only agree wholeheartedly. I am strongly in accord with his view that increased seasonal effects towards the poles, as in illumination and plankton productivity, are likely to have been far more potent in the comparatively equable Mesozoic climate. Attention ought perhaps to be drawn here to the somewhat similar views expressed by Valentine (1971), who argues for the importance of trophic resource stability as the prime factor controlling latitudinal faunal distributions even at the present day. Certainly it seems that the old simplistic notions of temperature control, which have hitherto dominated discussion of the topic of Mesozoic faunal provinces, must be abandoned in the light of modern ecological knowledge.

References

Hallam, A. 1972. Diversity and density characteristics of Pliensbachian–Toarcian molluscan and brachiopod faunas of the North Atlantic margins. *Lethaia* **5**, 389–412.

Valentine, J. W. 1971. Plate tectonics and shallow marine diversity and endemism, an actualistic model. *System. Zool.* **20**, 253-64.

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On some highest Llandovery red beds and graptolite assemblages in Britain and Eire

SIR,—Graptolite assemblages strongly indicative of the *crenulata* Zone have recently been collected by the writer and others from two localities associated with highest Llandovery marine red beds. These are at Doon Rock, Kilbride Peninsular, Co. Mayo, Eire, and Hebblethwaite Hall Gill (SD 69109313), Howgill Fells, Northern England. On Swindale Beck in the Cross Fell inlier, Burgess, Rickards & Strachan (1970) established for the first time the age of the Llandovery red mudstones as belonging to the *crenulata* Zone, although elsewhere it had been shown that this formation is underlain by a *greistoniensis* assemblage and overlain by a *centrifugus* Zone assemblage (Rickards, 1967, 1970).

The Hebblethwaite Hall Gill locality has been recently exposed following the removal by gales of a large tree rooted on the red beds outcrop. Three cm of dark gree graptolitic mudstone (*sensu* Rickards, 1964) are exposed in the core of the anticliny depicted by Rickards (1967, pl. 12) and are positioned approximately in the middle of the 12 m of red beds exposed on this section. The following fauna was obtained with some difficulty: *Monoclimacis* sp., *Monograptus ?marri* (Perner), *M. priodon* (Bronn) common, *M.* sp. nov. (Hutt species), *M. spiralis* (Geinitz), *M. tullbergi* Bouček, *M.* ex gr. *nodifer* Törnquist *sensu stricto*, *Petalograptus* sp. and retiolitid fragments (specimen nos. Sedgwick Museum A81980–81999). The red beds on this section are underlain by graptolitic mudstones yielding a *greistoniensis* assemblage and are overlain by slightly coarser mudstones with a rich *centrifugus* Zone (Wenlock) fauna. Some elements of this undoubted high Llandovery red beds fauna are not very diagnostic zonally, but the abundance of *M. priodon* in this position, and the general nature of the assemblage strongly suggests a *crenulata* Zone age, and indicates that the red beds are of the same