

Methods of palaeobiogeographic analysis

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SUMMARY

Some of the problems and difficulties facing palaeobiogeographers are noted and several testable models outlined. There follows a review, beginning with the Quaternary and ending with the Palaeozoic, of analyses involving planktonic, benthic and terrestrial animals and plants. These demonstrate how the type of analysis, and the precision and confidence level of interpretation, varies considerably with the age of the fossils in question.

RESUMEN

Se señalan algunos de los problemas y dificultades con que se enfrentan los paleobiogeógrafos, poniéndose de manifiesto numerosos modelos experimentales. Sigue una revisión, empezando por el Cuaternario y acabando con el Paleozoico, de análisis que implican animales planctónicos, bentónicos y terrestres, y plantas. Así se demuestra cómo el tipo de análisis, y la precisión y nivel confidencial de interpretación, varía considerablemente con la edad de los fósiles en cuestión.

RESUM

S'assenyalen alguns dels problemes i dificultats amb que s'enfronten els paleobiogeògrafs i es posen de manifest nombrosos models experimentals. Segueix una revisió, començant pel Quaternari i acabant pel Paleozoic, d'anàlisi que impliquen animals planctònics, bentònics i terrestres, i plantes. Així es demostra com el tipus d'anàlisi, i la precisió i nivell confidencial d'interpretació, varia considerablement amb l'edat dels fòssils en qüestió.

INTRODUCTION

The expansion of palaeobiogeographic studies in the last decade has been spectacular, due primarily to the stimulus provided by the widespread acceptance of plate tectonics. As with all rapidly growing fields, however, there has been a tendency in some of the research to follow current fashions somewhat uncritically, and difficulties have arisen for a variety of reasons. This might have happened because of inadequate or unsatisfactory definition of terms, a failure to consider enough factors, or an inability to find sufficient evidence to support a given interpretation convincingly. There has also been dispute about the most useful and meaningful methods of quantifying data, and undertaking measures of «biotic distance», and about the respective importance to be attributed to data from different groups of fossil organisms, if the results appear to be in conflict.

This by no means exhausts the list of problems, and it should be obvious to everyone that good palaeobiogeographic

analysis is heavily dependent on sound modern taxonomy, which is not always available. Nevertheless there is no reason to be unduly daunted because considerable progress has been made, but there is abundant scope and need for more discussion on methods of analysis.

I am not concerned here either with choice of statistical techniques (Hughes, 1973; Sneath and Mckenzie, 1973) or with a precise definition of terms like «faunal province» (Middlemiss and Rawson, 1971). Instead, in conformity with the primary aim of this symposium, attention will be concentrated on conceptual matters.

On a gross scale the distribution of organisms is controlled primarily by climate, by the relative position of continents and oceans and by eustatic changes of sea level (Hallam 1981). For the Quaternary only the first and third factors have varied with time but for more remote periods changing continental positions assume major importance.

As a consequence of the acceptance of plate tectonics a new school of biogeographers has emerged who enthusiastically support the phenomenon of *vicariance* (Croizat *et al.*, 1974; Rosen, 1978; Nelson and Rosen, 1981). In earlier times the disjunct distribution of such organisms as the «southern beech» *Nothofagus* and the flightless ratite birds was interpreted in terms solely of organic dispersal from centres of origin and subsequent survival of local relict populations, characteristically in true or ecological islands. The alternative vicariance model postulates that the continents have dispersed rather than the organisms. It would be difficult to find a palaeontologist today who would deny the reality of continental drift but few would be inclined to be as dismissive of the organism migration alternative as the most zealous advocates of vicariance. Fossil evidence points strongly, for instance, to the notion that the ancestors of both elephants and Man dispersed from African centres of origin.

As in any branch of science there is a vital need to generate testable models. By taking into account what is known about the dispersal potential of living invertebrate larvae in the ocean I have proposed the distinction of two patterns of changing faunal distributions with time, related to plate movements (Hallam, 1973, 1974). The term *convergence* refers to the degree of resemblance of faunas increasing from an earlier to a later time, as two continents approach each other, while *divergence* refers to the reverse phenomenon. It is methodologically desirable to use as many fossil groups as

possible. The more groups show a common pattern of change, the greater confidence we can have in our interpretation. Table 1 lists a number of examples of convergence and divergence phenomena.

I have termed a third biogeographic pattern *complementarity*. Complementarity in the distributional changes of contiguous marine and terrestrial animals is recognisable when one group exhibits convergence and the other divergence. This happens, for instance, when a land connection is created between two hitherto isolated areas of continent, so allowing convergence of the terrestrial faunas to take place, whilst severing of a once continuous land mass gives rise to divergence as a result of genetic isolation. Just the converse is true for the faunas of the seas that envelop land masses. Thus the study of changing distributions of terrestrial and marine faunas in conjunction can provide a valuable means of cross checking palaeogeographic inferences. Examples of complementarity will be mentioned below.

Whilst the importance of climate and plate movements in controlling organic distributions is widely acknowledged by palaeobiogeographers, pre-Quaternary sea-level changes have been largely neglected, yet there is a growing body of modern research indicating more or less profound palaeogeographic changes through time which are directly attributable to eustasy (Vail *et al.*, 1977; Evans 1979). Continental areas with their terrestrial faunas can be just as effectively isolated by the spread of epicontinental seas as by the creation of new oceanic straits by sea-floor spreading, though the former phenomenon is much more readily reversible, by a subsequent marine regression.

As regards marine faunas, the most obvious testable model involves relating the incidence of endemism amongst neritic groups to the relative height of sea level. At times of high sea

level there should be comparatively free communication between shelf seas whereas at times of low sea level increased physical restrictions should promote greater genetic isolation and hence morphological divergence. Thus there should be an inverse correlation between degree of endemism in given groups of organisms, and relative height of sea level. The latter can be approximately determined by plotting the areal distribution of marine sediments on the continents and making best estimates of palaeogeography for successive time periods.

The methods of palaeobiogeographic analysis, and confidence levels of interpretation, vary considerably with the age of the fossils being investigated. It is therefore useful to survey a number of examples extending back through time, starting with the period about which we know the most.

QUATERNARY

Those who study the biogeography of the Quaternary have the inestimable advantage of dealing with species that for the most part survive today. Therefore for many species their environmental tolerances are known precisely. Since climate has been the most significant fluctuating variable it is natural that the attention of biogeographers has been concentrated on the correlation of species migrations with climatic changes.

For many years pollen samples have been analysed and the data presented as spectral diagrams, with a view to understanding more about changing air temperatures, and we have become very familiar with, for instance, the inference of climatic deterioration in Europe from a sequence in a given peat deposit ranging from a mixed oak forest via a coniferous forest to a tundra spectrum (West, 1979).

Plate tectonic event	Convergence	Divergence
Closure of Proto-Atlantic (Ordovician, Silurian)	Trilobites, graptolites, corals, brachiopods, conodonts, anaspids and thelodonts of the two continents flanking the Proto-Atlantic	
Closure of Urals Seaway	Post-Permian continental vertebrates of Eurasia	
Opening of Atlantic (Cretaceous, Tertiary)		Cretaceous bivalves and benthonic foraminifera of Caribbean and Mediterranean. Upper Cretaceous ammonites of U.S.A. and W. Europe-N. Africa. Post Lower Eocene mammals of North America and Europe. Tertiary mammals of Africa and South America
Opening of Indian Ocean (Cretaceous)		Bivalves of East African and Indian shelves
Closure of Tethys (Late Cretaceous) (Mid Tertiary)	?Ammonites of Eurasia and Africa-Arabia. Mammals of Eurasia and Africa	Molluscs, foraminifera etc. of Indian Ocean and Mediterranean-Atlantic

Table 1. Correlation of plate tectonic events and changes in faunal distributional patterns. References cited in Hallam (1974).

This method is now being supplemented and cross checked by analysis of beetle elytra, which have a high preservation potential and hence are abundant fossils in terrestrial and fresh water deposits. The beetle species exhibit remarkable evolutionary stability and their response to pronounced climatic change, like that of most Quaternary species, has been to migrate rather than suffer extinction. Thus certain species common in British deposits are found today only in parts of Asia (Coope, 1979).

As regards changing temperatures of oceanic surface waters, planktonic foraminifera have proved the most useful. Thus in subpolar waters changes in the coiling ratio and percentage abundance of the cold-tolerant *Glabigerina pachyderma* are an excellent first-order indicator of oceanic sensitivity to climate through the last few hundred thousand years (Ruddiman *et al.*, 1977). The method is quantitative but simple. More sophisticated is the method of transfer function analysis developed by Imbrie and coworkers (Imbrie and Kipp, 1971; Imbrie *et al.*, 1973). Factor analysis has enabled five statistically independent and ecologically significant assemblages to be separated, namely tropical, subtropical, subpolar, polar and gyre margin. All but the last of these are related to surface water temperature. An ecological response model has been developed and a linear equation deduced that allows estimates to be made of surface temperature from information on the relative abundance of the assemblages. Impressive results using this method have been obtained by a team of scientists working for the CLIMAP project (1976), whose goal was to obtain a world map of surface water temperatures 18000 years before the present, at the time of the last glacial maximum.

TERTIARY

Though there are apparently some Pliocene exceptions, it is generally true that no Tertiary species are extant, so that ecological comparisons must be drawn at the level of genus or family. Furthermore, climatic inferences are likely to be less precise than for the Quaternary, because of the increased probability of changes in ecological tolerance over a time period measured in tens of millions of years.

It has been well established for many years, from study of terrestrial plants and neritic invertebrates, that global climatic deterioration took place from the Palaeogene to the Neogene, and modern work has considerably amplified this story. As regards terrestrial plants it is possible to obtain very informative results from the analysis of fossil leaves. An excellent correlation exists between the type of leaf margin and climate, with the percentage of species with entire-marginal leaves, i.e. lacking lobes and teeth, increasing systematically with temperature. In areas of high mean annual temperature and precipitation the leaves tend to be entiremargined, evergreen, large and with a leather-like (coriaceous), texture, a high proportion of «drip tips» and tendency towards palmate venation. Wolfe (1978) shows how these criteria can be applied to a study of climatic change in the northern hemisphere through the Tertiary.

While the technique of Imbrie and Kipp (1971) cannot be applied to fossils older than Quaternary, a somewhat similar method has been used by Haq *et al.* (1977) on calcareous nannoplankton and planktonic foraminifera to learn more about the Palaeogene temperature history of Atlantic surface waters. High, mid- and low-latitude assemblages were recognised using factor analysis and the migrations of these

assemblages interpreted as recording climatic change.

As in the Quaternary (Imbrie *et al.*, 1973) an important check on planktonic foram results can be undertaken by palaeotemperature analysis using oxygen isotopes. The isotopic results confirm the findings of Wolfe (1978) that there was a sharp decline in global temperatures in the late Eocene to early Oligocene (Hallam, 1981).

Tertiary biogeography involves much more, of course, than study of changing climates. Thus two of the most significant events can be described in terms of the principle of complementarity mentioned above. The creation of the Central American land bridge in the late Pliocene resulted in convergence of North and South American terrestrial faunas and divergence of Caribbean and East Pacific marine faunas. Similarly, Tethyan marine faunas split up into Indian Ocean and Atlantic — Mediterranean components following the end Oligocene-early Miocene establishment of a land corridor from Africa to Eurasia in the Middle East region, which allowed cross migration (and hence convergence) of the terrestrial faunas of those continents. Final destruction of Tethys was due to a major fall of sea level in the late Oligocene, long after late Cretaceous collision of Africa with the Eurasian landmass. Through most of the Palaeogene a Tethyan epicontinental seaway isolated the African terrestrial fauna, as best recorded by mammal distributions (Hallam, 1981).

Mammal distributions also throw light on other important plate tectonic events. Thus divergence of the European and North American faunas after the mid Eocene is a consequence of sea floor spreading in the Norwegian — Greenland Sea, isolating the New World from the Old, while the strong similarities of mid Eocene mammals of India and Mongolia indicate that India had collided with the Eurasian continent by that time (Hallam, 1981).

MESOZOIC

In the equable world of the Mesozoic climatic factors were much less important in controlling organic distributions than in the Cenozoic, and both plate movements and sea level changes become correspondingly more important. It cannot in consequence be uncritically assumed that the well known Tethyan — Boreal provinciality exhibited by Jurassic and Cretaceous ammonites and belemnites necessarily relates to climatic differences. Nor can we assume that the ecological tolerance of Mesozoic genera surviving today has persisted unchanged. Thus, amongst the Bivalvia, *Pholadomya* is at present an inhabitant of the deep sea while *Astarte* and *Thracia* are now restricted to cold waters, whereas the general evidence of facies associations indicates clearly that back in the Jurassic they flourished in a warm, shallow neritic environment. Consequently the Mesozoic biogeographer is more dependent for his interpretations than his Cenozoic counterpart on a variety of evidence from a wide range of organisms and palaeogeographic inferences based on facies analysis. His methods are correspondingly more eclectic.

The gross geographic relationships of continents and oceans are thought to be well understood because the ocean floor records a spreading history dating back into the Jurassic. Plate movements did not become significant for biogeography until Cretaceous times, when the main episode of dispersal of Pangaea components began. One striking consequence is the divergence («vicariance») of terrestrial faunas on the continents as they split up and moved apart. Thus whereas early

Mesozoic reptiles are cosmopolitan in distribution late Mesozoic and Cenozoic reptiles and mammals differ significantly between continents (Kurten, 1967). Not all the regional differences are attributable to continental breakup, however. Thus the division of northern hemisphere late Cretaceous dinosaur faunas into «Euramerican» and «Asiamerican» provinces is a consequence of the creation of the North American mid continent epeiric seaway following a major eustatic rise of sea level (Cox, 1974).

Sea-level changes apparently also controlled to a large extent the incidence of endemism among neritic invertebrates, or at least bivalves. However, whereas Hallam (1977) deduced for the Jurassic an inverse correlation between relative height of sea level and bivalve endemism (i.e. high sea level — low endemism) the reverse effect was claimed for Cretaceous bivalves by Kauffman (1973). Here is a readily quantifiable subject well worthy of further investigation in a wide variety of fossil groups.

PALAEOZOIC

The Palaeozoic biogeographer faces a more severe problem than his Cenozoic and Mesozoic colleagues insofar as there is much less certainty about relative continental positions, and there are wide disparities between various proposed palaeogeographic reconstructions. Thus Ziegler *et al.* (1977) take into account a variety of geological, biogeographic and palaeomagnetic evidence suggesting considerable movement of continental sectors during the course of the era. In stark contrast, Gray and Boucot (1979), in an editorial article in a symposium devoted primarily to Palaeozoic biogeography, argue for a stable Pangaea on the basis of sedimentary facies and biogeographic data.

This raises the crucial question of how to weight biogeographic against geological and palaeomagnetic data, and suggests that more rigorous methods of analysis must be adopted in an attempt to resolve controversy on the geographic location of continents and oceans.

Consider for instance the analysis of Whittington and Hughes (1972) on Ordovician trilobite provinces. They used a method of non metric multidimensional scaling to distinguish four provinces in the early Ordovician, which merged into only two by the end of the period. While their analysis nicely confirms the Iapetus story (see below) there are awkward points about their implied early Ordovician palaeogeography, which suggests among other things that Australia and South America were closely associated and quite distinct from other areas of the world (Asaphopsis Province).

This does not necessarily mean, however, that these two continents were physically connected, and isolated by ocean from other continents, because Fortey (1975) has shown that representatives of three of the four provinces distinguished occur together in Spitsbergen. He has also demonstrated the importance of facies control, something not considered in Whittington and Hughes' world wide survey, and argued that only the inferred shallowest-water trilobite community exhibits high endemism, and is therefore best suited to studies of provinciality. The lesson should be clear — biogeographic studies should take into account facies differences, and relatively cosmopolitan fossil groups distinguished from those exhibiting high endemism.

Another area of actual or potential controversy concerns the role of climate. Thus Cocks and Mckerrow (1973) invoke a strengthening climatic zonation to account for an increase in

brachiopod endemism from the Silurian to the early Devonian. In contrast, Johnson and Boucot (1973) argue that the reduction of brachiopod endemism from the early to the late Devonian was the result of increasingly free communication as seaways became less restricted. Since this is presumably a consequence of eustatic rise of sea level (House, 1974) comparison suggests itself with changing Jurassic bivalve distributions (Hallam, 1977). Clearly the role of sea-level change should be taken into account before conclusions are drawn about climate. Ziegler *et al.* (1977) nevertheless consider, on the basis of their literature review, that Palaeozoic floral and faunal provinces reflect a persistent climatic zonation of the earth.

To conclude on a more positive note, the greatest success story to date in Palaeozoic biogeography has been the convincing demonstration of convergence of faunas on the two sides of the closing Iapetus Ocean through the course of the Ordovician and Silurian (Table 1 and Ziegler *et al.* [1977]). Mckerrow and Cocks (1976) have attempted to establish the relative rates of migration of different groups across the ocean, and inferred that pelagic forms (graptolites) crossed first, followed by groups with pelagic larval stages (trilobites, brachiopods). Groups lacking such a stage (ostracods) were not able to cross until the ocean had closed at one point, while faunas limited to fresh or brackish water, such as many Devonian fish, did not cross until there were non-marine connections between the continents on either side of the closing ocean.

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