DISTRIBUTIONAL PATTERNS IN CONTEMPORARY TERRESTRIAL AND MARINE ANIMALS

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ABSTRACT. The factors controlling the distribution of terrestrial vertebrates and neritic invertebrates are briefly discussed and it is concluded that in both cases the separation of continental fragments by ocean should lead to genetic isolation and hence morphological divergence, while suturing of continents should result in convergence, perhaps accompanied by extinction through competition. Four distributional patterns relevant to plate tectonics are distinguished. *Convergence* and *divergence* refer respectively to the degrees of resemblance of faunas in different regions either increasing or decreasing in the course of time. *Complementarity* in convergence–divergence patterns of contemporary terrestrial and marine animals is the third type, and *disjunct endemism* the fourth. The examples cited have a bearing on the closure of the Proto-Atlantic ocean, of Asia on Europe in the Late Palaeozoic and of Africa on Eurasia in the Tertiary, as well as the Late Mesozoic disintegration of Pangaea.

MOST articles on zoogeography have concerned themselves with restricted groups of living or fossil animals. A few synthesists such as Ekman (1953) and Darlington (1957) have covered a wide range of organisms either on land or in the sea and portrayed general patterns of distribution. It probably requires a non-specialist like myself to have the temerity to compare distributional patterns in terrestrial and marine animals in the quest to understand the underlying geographic controls. Nevertheless, I feel no need to apologize for the sort of exercise presented in this paper, in which an attempt is made to discern patterns that may be of significance to plate tectonics, from a wealth of published and unpublished data. Only by critical argument and discussion on the more general issues can we hope to clarify our thoughts and forge useful investigative tools for future specialist application.

I must here acknowledge my debt to the many authors of the *Atlas of Palaeobiogeography* (Hallam (ed.), 1972b) whose work I quote. In the succeeding text this will be referred to simply as 'Atlas'.

FACTORS CONTROLLING DISTRIBUTION

(a) *Continental vertebrates*

Having written at some length already on this subject (Hallam 1967) I shall deal with it only briefly here.

Climate imposes restraints of various kinds to a variable degree according to the group in question. Notable reductions in diversity towards the poles occur in all classes, with large reptiles the least tolerant to cold. Geographic barriers, notably wide stretches of sea water, are nevertheless more potent means of effecting restrictions on migration. During more equable eras, such as the Mesozoic, when large reptiles occurred over much wider ranges of latitude than today, they must have been overwhelmingly the most important limit to dispersal.

All groups of continental vertebrate are confined to some degree by barriers of sea or ocean, excepting birds, which have a poor fossil record and hence may be disregarded. The so-called primary freshwater fish, that is, those rigorously restricted to fresh water, and including the lungfish, are considered to be among the most useful of all groups in vertebrate zoogeography. Amphibia are also severely restricted by barriers of sea water, though frogs are comparatively mobile and show a greater propensity for island colonization. Among reptiles and mammals, small size and high reproductive rate obviously increase the chances of successful colonization following chance dispersal by, for instance, drifting logs. On the other hand small creatures would be more likely to starve on a long crossing. Therefore even narrow marine straits are highly effective barriers.

Simpson (1940a) has distinguished three means of migration of land animals between areas partly or wholly separated by sea. *Corridors* are land bridges allowing free migration of the fauna in both directions. *Filter bridges* differ from corridors in that climate or some other factor 'filters out' some of the potential migrants (thus the Bering land bridge in the Pleistocene was usable only by cold-tolerant animals). *Sweepstakes routes* allow the chance migration across sea on natural rafts, and is the means by which oceanic islands are colonized. Unlike corridors or filter bridges, which lead to a high degree of homogenization of the faunas of different areas, this type of migration can affect at most only a very small proportion of the continental fauna, and will lead to the development of ecologically unbalanced faunas of low diversity. Islands indeed are often places of 'refuge' for comparatively primitive groups (e.g. the tuatara in New Zealand, lemurs in Madagascar).

It is a safe generalization that the splitting up of a formerly continuous piece of continent will lead to genetic isolation and hence morphological divergence of the land fauna, while the suturing of two continental areas formerly separated by ocean will result in the homogenization of the corresponding faunas by cross migration, perhaps accompanied by extinction through competition of the less well-adapted groups. Parallel evolution and evolutionary convergence may lead to similar morphologies in ecologically related groups, in land areas isolated from each other, but is unlikely to affect whole faunas. Furthermore, close taxonomic study usually reveals such cases for what they are, and hence can eliminate them from consideration. Thus there is no doubt that the Australian marsupials evolved in isolation, despite the many striking superficial similarities to certain placentals.

(b) *Neritic benthonic invertebrates*

As with continental animals, the distribution of the neritic benthos is controlled primarily by climate and geography. At the present day there is a strong correlation between faunal diversity and latitude, the most varied faunas occupying the tropics (Fischer 1960). The climatic barriers tend to be gradational, unlike the geographic barriers, which are of two types, land and deep ocean. It is obvious that a continental area separating two oceans will act as a barrier to intermigration of the marine organisms. What is not so readily apparent is that wide stretches of deep ocean may be almost as effective in preserving genetic isolation (Ekman 1953). This is because the length of life of the planktonic larvae, the means by which the benthonic organisms disperse, is normally too short to survive the slow drift across an ocean as wide as

the Atlantic (Thorson 1961). Thorson investigated data on the larvae of about 200 invertebrate species and found that only 5 per cent remain in the plankton for more than three months. Even this is too short a time to allow transcontinental colonization except by the occasional 'transport miracle'.

More recently, the analysis of plankton tows and current systems in the Atlantic has clearly demonstrated that a number of gastropod and other invertebrate species with amphi-Atlantic distributions have larvae capable of crossing the ocean in low latitudes in either direction (Scheltema 1968, 1971a, 1971b). Newell (1971) has pointed out that a number of reef coral species have pan-tropical distributions, implying transoceanic migration of larvae. It appears that Thorson, by largely confining his attention to cold-water species, underestimated the proportion of shelf benthos with teleplanic larvae, that is long-lived larvae found in surface waters right across the ocean.

Lagaaij and Cook (in Atlas) note that many Recent bryozoan species have very wide distributions but short larval life. In this case transoceanic transport might be by adult rafting on seaweed and driftwood, a mechanism of migration that can also be invoked for byssally attached pteriomorph bivalves (Hallam 1967). However, it is now known that shallow seamounts and guyots may possess a wide variety of benthos, and there are strong hints that at least some short-lived larvae of shelf taxa can be dispersed across wide sectors of ocean by this means (Thiel 1970).

Although Thorson's principal conclusions must be amended, it remains true that oceanic barriers are effective in restricting the migration of a large proportion if not the majority of the shelf benthos. It is quite possible that teleplanic larvae are a highly sophisticated late development in evolution, and can be disregarded, say, further back than the Tertiary. On the other hand the fact that teleplanic larvae are commoner in warmer water could be significant for more equable periods in the past. Since capacity for transoceanic migration is likely to be proportional to the length of time the larvae can survive in the plankton, the wider the deep ocean barrier the more different should be the faunas of the two opposing shelves. This is quite clearly true in that, for instance, the faunas on the east and west sides of the Pacific have even less in common than those on the two sides of the Atlantic (Ekman 1953). Therefore, making due allowance for the effects of temperature and the factors discussed above, and assuming a normal pattern of currents and counter-currents, degrees of similarity of neritic benthos should under favourable circumstances give information on the amount of separation by deep ocean.

PATTERNS OF DISTRIBUTION

Such are the complexities of the subject that it would be futile to seek any absolute measure of similarity between given faunas. Considerable progress can be made, however, if attention is concentrated on changing degrees of resemblance through time. This dynamic approach has several advantages. Animals of quite different biology, including migration potential, can be grouped together (this can be especially important in dealing with fossils for which life habits are poorly understood). The specific factors controlling the migration of particular organisms need not be precisely known. The work of different taxonomists, whether 'lumpers' or 'splitters',

can be used so long as it is self-consistent. Finally, introduction of the time factor is of especial significance in what is primarily a geological quest.

If the data lend themselves to quantitative treatment which will not give a spurious air of precision, the use of Simpson's (1947) similarity coefficient can be recommended as being easy to understand and quick to calculate. If N_1 represents the smaller fauna, N_2 the larger, and C the number of taxa in common, then the degree of resemblance can be expressed as $100C/N_1$, which gives a percentage. So far this coefficient has only been applied by a small number of vertebrate palaeontologists.

It will be convenient to distinguish four interrelated patterns of distribution.

(a) *Convergence*

This term refers to the degree of resemblance of faunas in different regions increasing from an earlier to a later period. Several examples will be cited:

1. Throughout the Tertiary a highly distinctive mammalian fauna inhabited South America, the strong endemism signifying isolation of the subcontinent by ocean during that time. At about the close of the Pliocene or start of the Pleistocene a drastic change took place, with the introduction of many groups hitherto confined to North America, such as mastodonts, tapirs, camels, and dogs, and the simultaneous extinction of much of the indigenous fauna, such as borhyaenids, notoungulates, and liptoterns, presumably as a result of the new competition. It has been estimated that before the two subcontinents were united by a land bridge there were about 29 known families of mammals in South America and about 27 different ones in North America. After the union the Pleistocene faunas show 22 families in common (Simpson 1940*a*, *b*).

2. The Lower Tertiary mammalian fauna of Africa has a strong endemic element, suggesting a substantial degree of isolation at that time. In about the early Miocene, similarities with Eurasia increased appreciably, the invasion of Eurasian groups leading to reduction and extinction of some of the African endemics, while proboscoids, which had originated in Africa, migrated freely into Eurasia (Kurtén, in Atlas; Savage 1967).

3. Between the Late Palaeocene and Late Eocene, the mammalian faunas of Asia and Europe increased in similarity (Kurtén, in Atlas). The Asian–North American similarities had remained strong throughout this time. One may infer, in conjunction with geological evidence, that whereas the Bering land bridge operated at least intermittently, a north–south epicontinental seaway had in the earlier time prevented east–west migration across Eurasia to a considerable degree.

4. The Devonian Heterostraci of eastern Asia and the Asiatic U.S.S.R. exhibit strong endemism and are placed in a separate Tungussian Realm (Halstead and Turner, in Atlas). No Carboniferous tetrapods are known, moreover, from this region (Panchen, in Atlas). On the other hand, Triassic tetrapods are found in Asia and are not significantly distinct from those in other parts of the world (C. B. Cox, in Atlas). This faunal convergence is consistent with the views of Hamilton (1970), who argues that the Asian and European continents were separated by ocean until the end of the Palaeozoic, the subsequent line of suturing being marked by the Urals. The evidence of the previously cited case indicates, however, that the barrier could instead have been a relatively narrow epicontinental seaway. Persistent and

marked contrasts between the pre-Permian neritic invertebrate faunas of Europe and eastern Asia would support the notion of separation by a wide ocean.

5. The bivalve faunas on the two sides of the North Pacific show a higher degree of resemblance in the Late Cretaceous than the Early Cretaceous (Hallam 1967, Kauffman, in Atlas). This is consistent with North America moving westwards towards Asia in the course of the period, hence reducing the amount of oceanic separation.

6. Through the course of the Ordovician and Silurian, both marine invertebrates (trilobites, graptolites, corals, brachiopods, conodonts) and land vertebrates (anaspids and thelodonts) of two highly contrasted faunal provinces in the North Atlantic region tend to lose their regional distinctiveness, so that by the Late Silurian or Early Devonian only one faunal region is discernible (various authors in Atlas). The nature of this convergence accords well with the notion of the 'Proto-Atlantic ocean' closing from north-west to south-east in the course of the Caledonian Orogeny (Wilson 1966, Dewey 1969). The sharp nature of the faunal contrast in the Early Ordovician, with very few taxa in common, could signify either a wide oceanic separation or a narrower separation running parallel to a climatic belt, with a strong temperature contrast from one faunal province to the other.

(b) *Divergence*

This is in simple contrast to the previous case.

1. With the creation of the Panama isthmus in the Pliocene, divergence commenced among the benthonic invertebrates of the Central American region and so-called 'geminate' species were produced on the Atlantic and Pacific sides of the isthmus as a consequence of the newly imposed genetic isolation (Ekman 1953). An excellently documented example of this change, for the genus *Argopecten*, is given by Waller (1969).

2. In the Lower Tertiary, invertebrate faunas exhibited a high degree of similarity throughout the length of the Tethys. At a time which can be dated as Late Oligocene or Early Miocene, this general unity was abruptly disturbed. Indian Ocean benthonic foraminifera and molluscs differ strikingly from those of the Mediterranean countries (Adams 1967, Hallam 1967). At the same time Atlantic and Mediterranean foraminiferal faunas diverged (Berggren and Phillips 1969). Interpretation of these facts will be deferred until the next section.

3. Whereas the Lower Cretaceous bivalves and larger benthonic foraminifera of the Caribbean and Mediterranean regions exhibit very few differences, at least at the generic level, the succeeding Upper Cretaceous faunas are more divergent, with endemism in both areas giving rise to new genera of local distribution (Kauffman, Dilley, in Atlas). This divergence conforms with what one might expect as the Atlantic widened progressively during the Cretaceous (Hallam 1971a). A shelf sea connection still existed in the North Atlantic but the faunas in question (e.g. rudists, alveoline, and orbitoid foraminifera) were without much doubt stenothermal and confined to the tropics or subtropics.

4. During the Cretaceous the bivalves of the East African and Indian regions diverged as endemism developed in the two areas. This is thought to relate to the creation of an oceanic barrier in the course of continental drift (Kauffman, in Atlas).

5. The rather uniform distribution of Mesozoic reptiles does not lend itself to a division into faunal provinces (Charig 1971). In notable contrast, the Lower Tertiary mammalian faunas of South America, Africa, Australasia, and the northern continents were strikingly divergent, an effect which is readily explicable by the Late Mesozoic break-up of the supercontinent Pangaea (Kurtén 1967).

6. After the Early Eocene, divergence of mammalian faunas took place between North America and Europe (McKenna 1971). This is consistent with the evidence of magnetic anomalies suggesting that ocean-floor spreading towards the Arctic severed the 'De Geer' land link in the north at about this time.

(c) *Complementarity in patterns of convergence and divergence*

The creation of a land connection between the hitherto isolated areas of continent should lead to a convergence of the continental faunas, while severing of a once-continuous land mass will give rise to divergence as a result of genetic isolation. Just the converse is true, of course, for the faunas of the seas which envelop the land masses. In other words, contiguous continental and marine faunas should react to the geographic changes in a complementary manner in terms of convergence and divergence. This method of approach provides a means of cross-checking the interpretations. The following examples should serve to illustrate its value.

1. As already mentioned, the rise of the Panama isthmus at the close of the Tertiary had the joint result of convergence of the continental and divergence of the marine faunas (text-fig. 1). While this particular geographic change need not necessarily
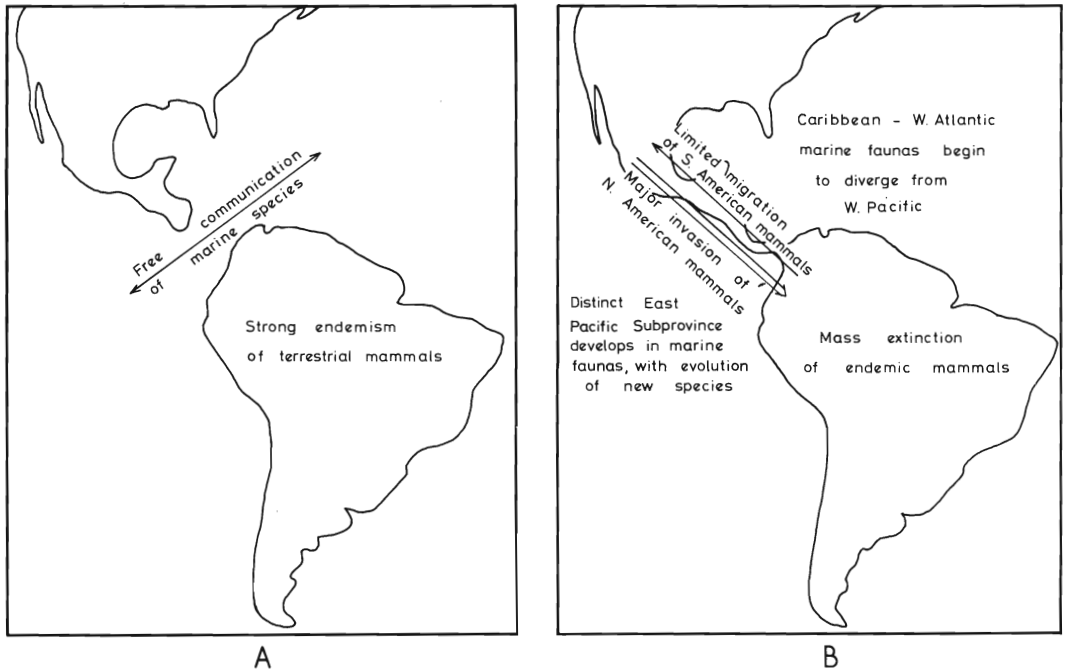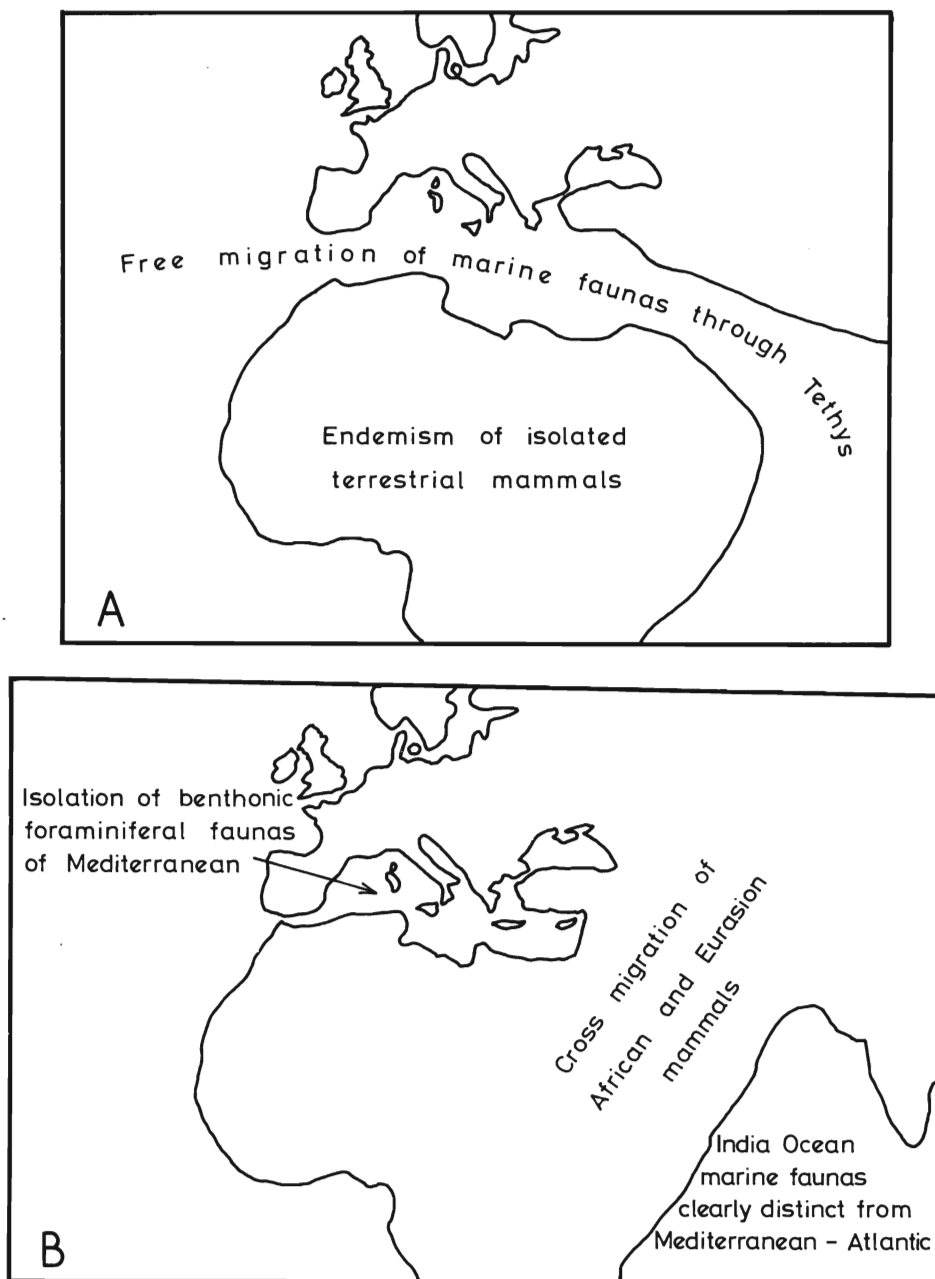

TEXT-FIG. 1. Changes in patterns of terrestrial and marine faunal distribution following creation of central American land bridge. A = Tertiary, B = Late Pliocene–Pleistocene.

have anything to do with plate motions, its significance as an illustrative example is clearly evident.

2. The Late Oligocene or Early Miocene divergence of invertebrate faunas along the length of the Tethys agrees closely in time with the evidence of significant cross migrations of mammals between Africa and Eurasia (text-fig. 2). These changes are likely to mark the time of definitive disruption of the Tethys as the sea withdrew from the Near and Middle East. In terms of plate tectonics, this must be a consequence of the impingement of Africa–Arabia on Eurasia, and it is significant that in the Miocene there was considerable mountain uplift, sometimes allied with tectonic compression more or less along north–south lines, both in the Betic zone of Spain and in the ranges of Turkey and Iran. This interpretation accords well with the analysis of Smith (1971), who deduces that Africa–Arabia began northward movement towards Eurasia from Late Eocene times onwards. The late Upper Cretaceous thrusting of deep-sea deposits and ophiolites on to the continental margin in parts of the Middle and Near East suggests compressive activity at an earlier stage, but these movements cannot have closed the Tethyan seaway definitively.

Limited points of terrestrial contact across parts of the Tethys might well have existed in the Early Tertiary, however, though the marine faunal data suggest that they could not have persisted for long. This is indeed suggested by the fact that Africa appears to have been less completely isolated in the Lower Tertiary than either Australia or South America. On the other hand intercontinental connections were not especially effective for mammal migrations even in the Lower Miocene, perhaps because of ecological and shallow sea barriers (Savage 1967). Though the detailed picture is complicated there seems no reason to question the general validity of what is proposed above.

3. In another instance the facts from continental and marine faunas are less clearly in accord. While Kauffman (in Atlas) argues that the divergence of Indian from East African bivalves in the Cretaceous signifies that the drifting away of the former subcontinent from other parts of Gondwanaland had commenced early in the period, remains of several Late Cretaceous dinosaur genera of huge dimensions and evidently low dispersal potential are known both from India and other parts of the world, implying free land communication. Thus *Titanosaurus* is recorded from India, South America, Africa, and Europe, *Laplatosaurus* from India, Madagascar, and South America, and *Antarctosaurus* from India and South America (Charig, in Atlas). Assuming the identifications are correct, the facts may be reconciled by postulating that morphological divergence following genetic isolation in the Early Cretaceous had not had time to proceed beyond the species level, because of a slow rate of evolution. Unfortunately Lower Cretaceous dinosaur remains are very rare and even in the Upper Cretaceous richly fossiliferous deposits are found in only a few parts of the world. The records for contemporary bivalves are obviously much fuller, but the factors controlling their distribution less well understood. An early-to-middle Cretaceous disruption of this part of Gondwanaland would be consistent with the evidence of magmatism (K. G. Cox 1970) and palaeomagnetism (Briden 1967, McElhinny and Luck 1970). Dietz and Holden's (1970) claim that India became isolated by ocean as early as the Late Triassic is quite unacceptable on faunal grounds.

TEXT-FIG. 2. Changes in patterns of terrestrial and marine faunal distribution as a result of the partial closure of the Tethys between Africa and Eurasia. A = Late Mesozoic–Early Tertiary, B = Late Oligocene–Early Miocene. (The Early Tertiary palaeogeography differed from the Mesozoic with the two continents closer together, perhaps joining up locally, but free marine communication persisted from east to west and Africa was still substantially isolated by sea.)

(d) *Disjunct endemism*

This term is introduced here to describe a type of regionally restricted distribution of a group of fossil organisms in which two or more component parts are separated by a major physical barrier and hence not readily explicable in terms of present-day geography. In the case of continental or shelf organisms such a barrier could be a zone of deep ocean (text-fig. 3). A classic example is provided by the Early Permian
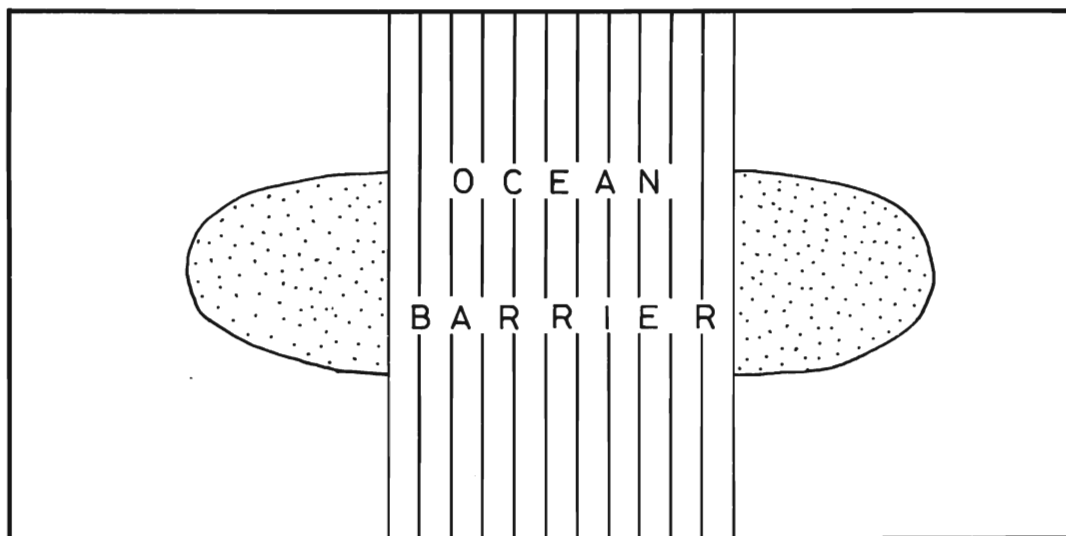

TEXT-FIG. 3. Portrayal in very simplified diagrammatic form of disjunct endemism. Vertical lines = ocean, unornamented = continent, stippled = area of distribution of formerly endemic group.

reptile *Mesosaurus* (text-fig. 4). At quite an early stage in the continental drift controversy the question posed was: Why was an aquatic organism capable of migrating across the South Atlantic not distributed more widely than in Brazil and South Africa?

Some further good examples may be cited among Late Jurassic dinosaurs (Charig, in Atlas). Thus (text-fig. 4) three genera occurring in the United States have also been found only in Portugal (*Atlantosaurus*), Tanzania (*Barosaurus*), and Tanzania, Algeria, and Portugal (*Brachiosaurus*). Indeed, the distribution of the latter two genera, and a number of others, points clearly to at least an intermittent land connection between East Africa and North America persisting until quite late in the Mesozoic.

Interesting examples of disjunct endemism can also be cited from Jurassic invertebrates. For instance, the highly distinctive pectinid genus *Weyla* is widely distributed in abundance in the Lower Jurassic of the western part of the Americas from Oregon to Chile and also occurs commonly in Madagascar and East Africa (Hallam 1971*b* and text-fig. 5). Apart from spasmodic occurrences in Pakistan and Morocco it has been found nowhere else. Its absence from the intensively researched European deposits certainly cannot be ascribed to collection failure or misidentification.
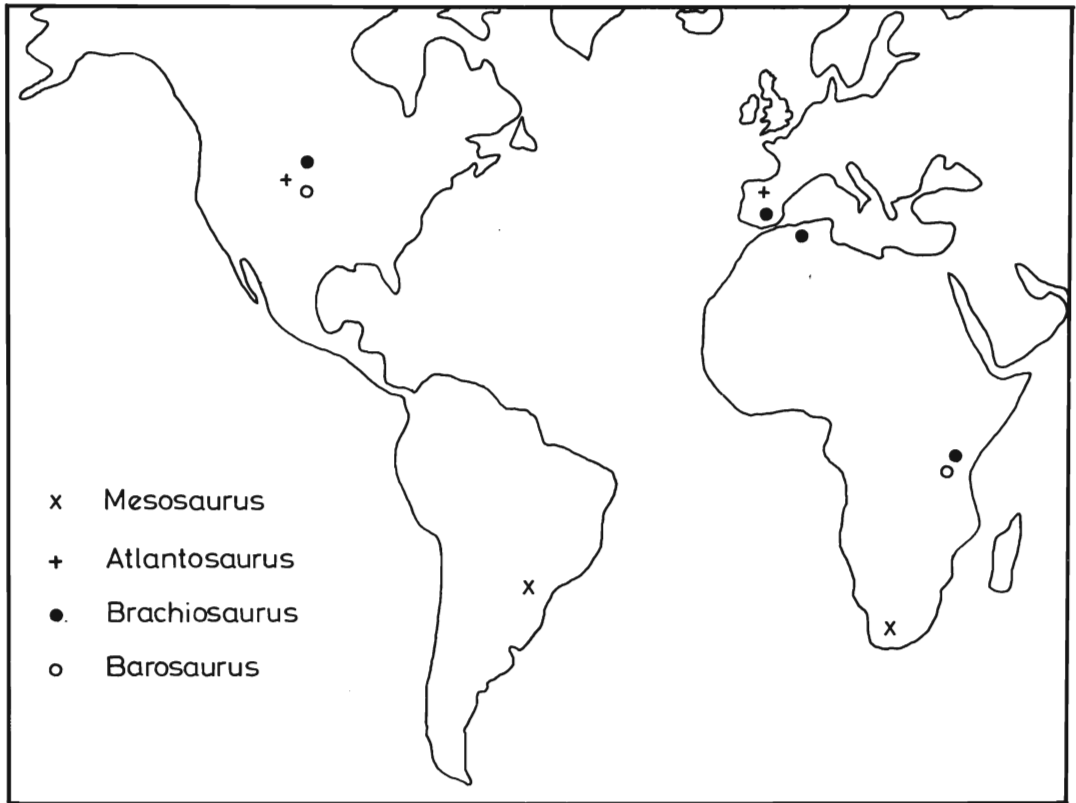
TEXT-FIG. 4. Disjunct endemism in some terrestrial reptiles of the Permian and Jurassic.

How is one to account for such a curious distribution? Since *Weyla* can hardly have migrated from the eastern Pacific to East Africa via either Europe, New Zealand, or Indonesia without leaving behind a fossil record in those regions, it must presumably have utilized a narrow seaway directly from Patagonia via the margin of South Africa, despite the fact that no marine deposits of the right age have yet been found south of Tanzania or Madagascar. Presumably such deposits underlie the sea-bed offshore, an inference that receives some encouragement from the recent discovery of (the first) marine Upper Jurassic sediments in Cape Province (Dingle and Klinger 1971). One may further infer that the seaway was probably shallow and epicontinental, having preceded the drifting apart of the Antarctic–Australian component of Gondwanaland. The occurrence in Australia of Jurassic dinosaur genera known elsewhere, of marsupials, and of the living lungfish *Neoceratodus* is otherwise inexplicable. Intermittent land connections are easily established by modest regressions of an epicontinental seaway, and definitive isolation by ocean of Australia–Antarctica can hardly have taken place long before the Mid Cretaceous (cf. C. B. Cox 1970). The presence of such a seaway for the Upper Jurassic is also suggested by the fact that Tithonian ammonites in western South America have stronger affinities with East Africa than with the Indonesian–Australasian region (Enay, in Atlas).
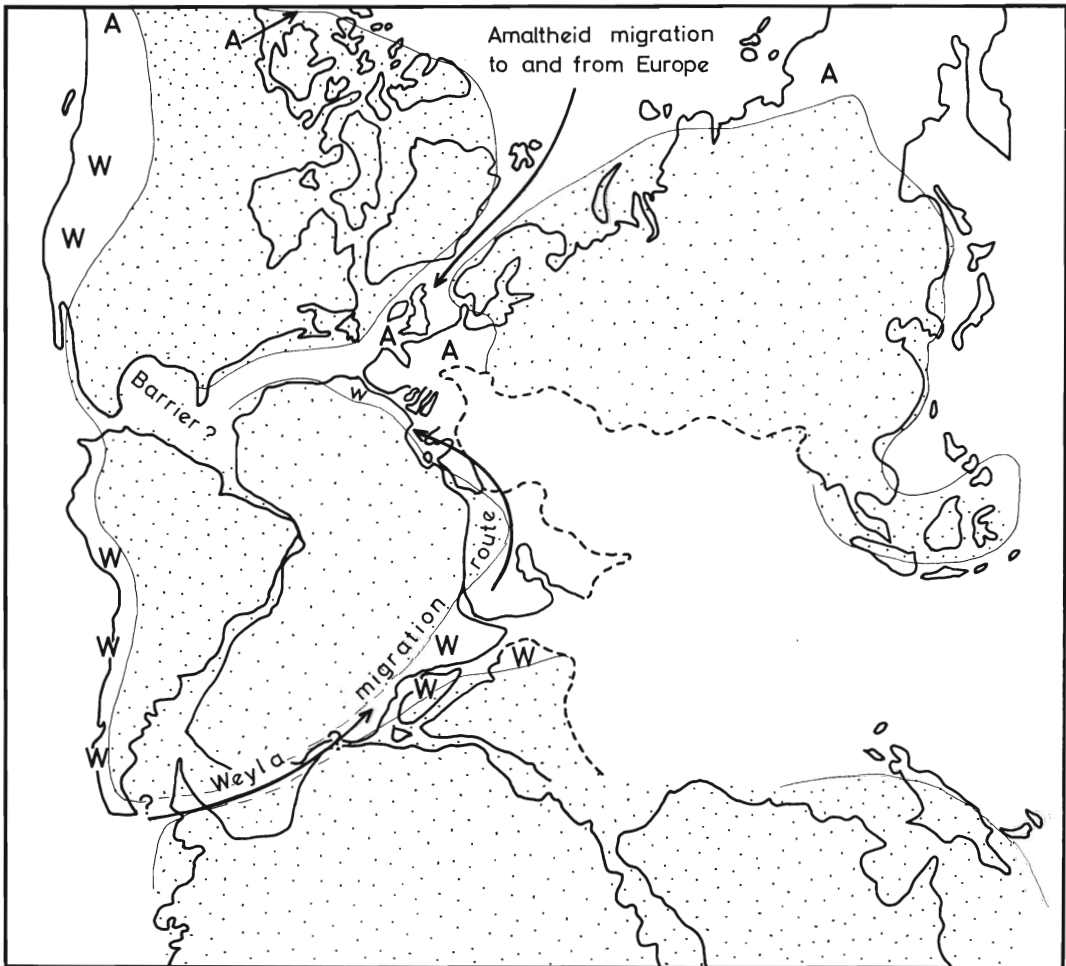
TEXT-FIG. 5. Distribution of Lower Jurassic *Weyla* and amaltheids, with postulated migration routes. Stippled areas signify presumed land.

It remains a puzzle why *Weyla* was not able to migrate freely across the Central Atlantic region. It could hardly have been inhibited by the adverse climate of Europe, because its latitudinal range in the Americas is immense. As opening of the Central part of the Atlantic might not have started before the Toarcian (Hallam 1971a) the lack of a free marine connection between Central America and Europe during most of the Lower Jurassic can be tentatively postulated. Such a connection must have been established soon afterwards, because a number of Middle and Upper Jurassic ammonite genera exhibit disjunct endemism between Europe and Central America (Hallam 1971b).

Text-fig. 5 also shows the distribution of amaltheid ammonites, which flourished during the Late Pliensbachian in the Boreal Realm (Hallam 1971b). One may infer from this distribution that a seaway between Greenland and Scandinavia was open during this time, because palaeogeographic data from the continents precludes

migration between western Europe and the Arctic either to the west of Greenland or east of Scandinavia, and migration via the Tethys can be excluded because it was occupied by a totally different ammonite fauna marking another faunal realm.

CONCLUSIONS

·Especially where the faunal data lend themselves to methods of cross checking, palaeozoogeography can make a useful contribution to plate tectonics by helping to establish upper and lower time limits to the disruption or suturing of lithospheric plates. The criticism can be made that faunal data are often imprecise or impossible to interpret unambiguously. This is certainly true in many instances, but the general level of accord of the results cited in this paper and those derived from other fields of Earth Science is surprisingly good and ought to suggest a reasonably high degree of confidence in the type of interpretation adopted. It is necessary, however, to guard against attempting to explain all cases of regional endemism in terms of plate tectonics, or, for that matter, climate. There is indeed a suggestion that at least some cases of endemism of marine organisms in, for instance, the Jurassic might be most readily explicable in terms of contrasts in environmental stability between open ocean and shallow epicontinental seas (Hallam 1972a). Clearly one must take fully into account evidence from non-palaeontological sources in accounting for particular faunal distributions, while avoiding circular argument.

While palaeozoogeography undoubtedly has a useful role to play for some time yet in the working out of past continental relationships, we must look forward to the time when, at least for the last 200 million years or so, a comprehensive series of deep-sea drillings, backed up by further geophysical surveys, will have allowed the establishment of a precise time scale for plate movements over the whole world. This will allow emphasis to be concentrated on the intriguing biological questions, such as the rates of evolution for particular organisms following isolation, the relative ease of migration and colonization in different geographic circumstances, and the relationship of extinction patterns to changing positions of continent and ocean.

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