

STATISTICAL METHODS FOR THE STUDY OF BIOGEOGRAPHY

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ABSTRACT. Methods for assessing the degree of contiguity of land masses from plant and animal distributions are discussed, and how hypotheses based on them might be tested. Most methods require the distribution patterns of numerous organisms to be combined in some way, and thus they lead to the concept of biotal distances (a form of floral or faunistic dissimilarity between land areas).

Various factors affect biotal distance, such as the mobility of organisms, climatic control, and barriers to migration. Biototal distances may reflect present-day contiguity of land masses, or the contiguity at the time when the taxon under study began its radiative evolution.

Illustrations from conifers and crustacea are given, together with estimates of fit to the present and to earlier epochs, and comments on the potential of such methods for elucidating the geography of earlier periods.

A NUMBER of statistical methods are now available for studies on biological distributions in relation to the geographic relationship between land masses. Some of these utilize statistics derived from biogeographic data that are descriptors of a single locality, such as indices of biological diversity, endemism, or climate. These lend themselves mainly to univariate studies, often leading to conclusions about one parameter (e.g. determining likely palaeolatitudes). Examples of their use are given by Valentine (1967, 1971), Valentine and Moores (1970), Stehli (1968, 1970), and Cook (1969), while Hecht (1969) made a multivariate study from which palaeotemperatures could be deduced.

In this contribution we shall discuss the methods for assessing geographical contiguity from biological distributions, in which dissimilarities between land faunas and floras are used for multivariate studies. Such methods can doubtless be employed also for marine geography, although we confine ourselves here to land masses. We shall, too, consider mainly large-scale, predominantly global, problems. Useful background is contained in Simpson (1952, 1953), Edwards (1955), Darlington (1957, 1965), Ager (1963), Gressitt (1963), and Westoll (1965).

Until recently few trials of statistical treatment of biogeographic distributions had been made, though there have been some attempts to relate faunas and floras to ancient geographies (e.g. Caster 1952, Simpson 1953, Ager 1963, Darlington 1965, Melville 1966). The next step is clearly to employ numerical indices of similarity between biotas, as was done for example by Simpson (1953), Savage (1967), and Williams (1969), and to use these for testing palaeogeographical hypotheses. There is now a considerable literature on the statistics of biotal similarity, and the reader will find useful information in works such as Sokal and Sneath (1963), Greig-Smith (1964), and Williams and Lance (1969). Then one may attempt to reduce the biotal similarities between numerous geographic areas into a simplified scheme that can be related to geography. This involves reducing the multidimensional relationships between the areas to a few dimensions that express the major variation patterns of the animal and plant distributions. For regional studies two dimensions are

required, while for global studies a three-dimensional fitting to a sphere is needed. Examples are given by Sneath (1967*a*) on world distributions of conifers and Holloway and Jardine (1968) on distributions of birds, bats, and butterflies in Australasia. After this the goodness of fit between the biotal distributions (now most conveniently expressed as biotal distances) and the actual geographic positions may be estimated.

The reduction of dimensionality can be done by various forms of factor analysis (e.g. principal component analysis), though Holloway and Jardine prefer non-metric multidimensional scaling (see Kruskal 1964) because it does not assume linearity of regression.

The major factors obtained by reducing the dimensionality can also be subjected to trend surface analysis (Fisher 1968, Gittins 1968). In this way the major patterns of biological variation are treated as if they were altitudes on a map, and broad trends are then looked for. In the papers cited the areas were fairly small, and the main trends were climatic.

Tobler *et al.* (1970), in a study of the flora of the New Zealand region, approach the problem through a form of analysis of variance, and introduce the concept of partitioning the variation into the components attributable to different factors (size of island, position, and immigration rates).

There is considerable overlap between studies such as those mentioned above and the construction of biogeographical provinces by statistical methods (e.g. Hagmeir and Stults 1964, Hagmeir 1966, Kikkawa 1968, Kikkawa and Pearse 1969, Holloway 1969).

There are of course a number of essentials for work of this nature. Organisms must obviously be correctly identified and the localities accurately recorded. The taxonomic units must be comparable throughout the region or time-span. The basis of the taxonomy may well occasion some argument in view of the work of Hennig (1960, 1966) and Brundin (1966) but Darlington (1970) has sharply criticized their methods, while Colless (1967, 1969) argues that Hennig's methods are basically phenetic. It therefore seems likely that phenetic classifications will be adequate in most cases, and they might with advantage be extended (as suggested by Holloway and Jardine 1968) by using numerical taxonomic techniques and then appropriately weighting the contribution to biotic resemblance by some function of the phenetic similarities of the phenons thus produced.

The choice of data is also critical. Darlington (1957) and Westoll (1965) discuss this at some length. Clearly it is whole faunas or floras, covering as many organisms as possible in the chosen taxon, that should be stressed, for otherwise it is usually easy to find examples of single distributions to support almost any hypothesis. Lastly the quantity of data is also important as well as its quality, and this point will be illustrated by the examples shown below.

The underlying logic of using biotal distances to provide testable hypotheses about geographic relations is, in brief: areas of which faunas and floras are extremely similar are likely to be geographically contiguous; while those with very dissimilar biotas are likely to be separated either by a barrier to migration or by considerable distance. There are obviously exceptions, but the point is whether this principle holds sufficiently to allow it to be usefully employed. The general validity of such

a concept is intuitively obvious; indeed it would be difficult to imagine circumstances under which biotal differences were uncorrelated, or negatively correlated, with geographic separation. Numerical support for the principle has been provided by several studies (e.g. Valentine 1966, Sneath 1967*a*, Holloway and Jardine 1968), and indirectly by work on the construction of biotal provinces cited above. Moderate degrees of isolation do not destroy the general concordance (e.g. with the island faunas reported by Heatwole and McKenzie 1967). When numerous areas are available, the constraints on the reduction of dimensionality are likely to be strong enough to prevent indeterminate results even if some of the individual biotal distances are indeterminate or of low significance (e.g. complete dissimilarity of biotas). At present we lack comparative studies with different coefficients of biotal distance, and this is an area requiring investigation.

Yet though biotal distance will to some extent reflect geographical distances, there are many factors that interfere, both by making the relationship non-linear (for example, exaggeration of the width of barriers to spread) and by introducing haphazard variation commonly called statistical error or scatter (for example, accidents of sampling). A possible example of an accident of sampling in the work we report below is the record of *Triops australiensis* from near Aurora, Wyoming, U.S.A., which is in the collections of the Australian Museum, Sydney, under No. P.8395. However, one of us (K. G. McK.) considers that the determination of this taxon is likely to be in error. An advantage of basing data on museum collections is that the specimens are available for rechecking in instances such as this when it seems that the taxonomy may be at fault.

Some factors, too, alter the relationships only in certain geographical directions (e.g. latitude versus longitude; biological effects of longitude are still poorly known, see Kiester 1971). Factors that have major effects on the distribution of a given organism include environment (barriers to spread, soil, climate, ocean and wind currents), ecology (ability to compete with other organisms and to colonize new areas, see Elton 1958, MacArthur and Wilson 1967), mobility (survival in water or air, size and weight, ability to fly), and history (source of ancestral populations, past land or sea connections or climates). At first sight the difficulties are formidable; we may hope, however, that using various statistical techniques workers can gradually elucidate the influence of these factors until they can draw conclusions of some reliability.

Among these factors, mobility has always drawn much attention since the days of Wallace (1880). Yet there has been little work on how to estimate it; the most useful publications seem to be by Simpson (1952, 1953), MacArthur and Wilson (1967), and Mitchell (1970). It is of course difficult to get estimates independent of the influence of past geography; the Hawaiian fauna and flora is probably the best case for analysis, and Simpson (1953) calculates the probability of colonization per year for various groups (less than 2×10^{-7} for land mammals, 3×10^{-6} for land birds, about the same for land snails, and about 5×10^{-5} for insects and angiosperms). Animal groups that seem to have low mobility include land mammals, amphibia, freshwater fishes, Dermaptera, freshwater triclads, the ostracode families Darwinulidae and Cytheridae, and termites (Darlington 1957, Popham and Manly 1969, Ball and Fernando 1969, McKenzie and Hussainy 1968, Emerson 1952), and among

plants conifers and *Notofagus* (Florin 1963, Gaskin 1970). Extremely mobile groups include fungi (Ainsworth 1961, notes that about half the genera of fungi are known from more than one continent and this is probably a serious underestimate) and bacteria (except for a few obligate parasites, most genera and probably a majority of species are found in every continent except Antarctica).

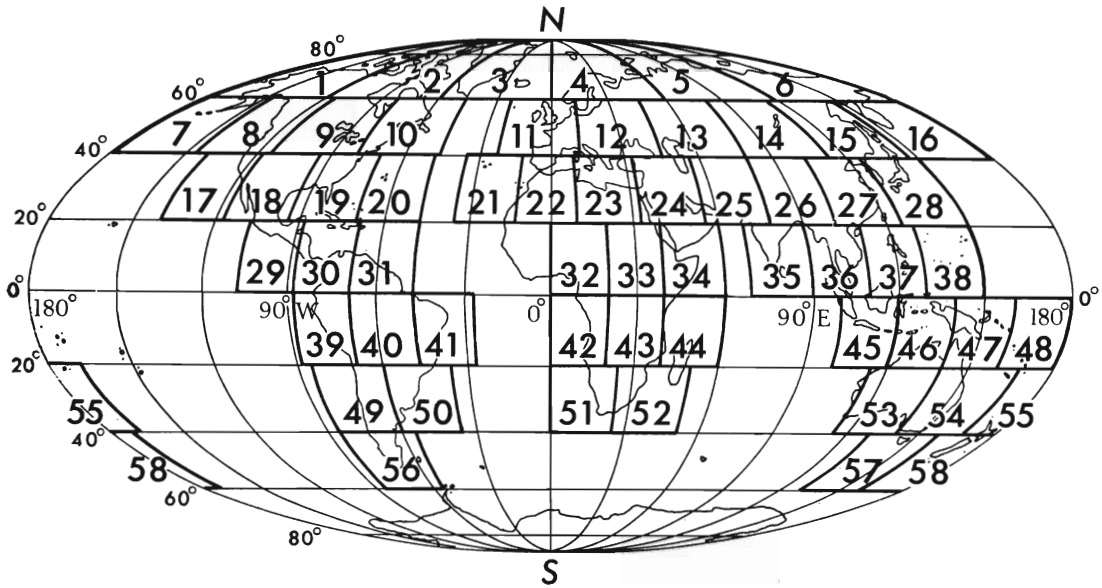
There is, however, some danger in giving too much attention to problems of mobility, for although non-mobile organisms may best reflect evidences of past continental positions, the corollary would be that highly mobile organisms may be better indicators of contemporaneous positions. If one wishes to test hypotheses about early periods, therefore, it may be preferable to study well-sampled fossils of that period of taxa that are known to be readily mobile, than to try to extrapolate from the present using non-mobile organisms. It is clear that there is considerable concordance between geography and distributions of organisms that can move fairly freely on continents and archipelagos (e.g. see Hagmeir 1966, Holloway and Jardine 1968, Kikkawa and Pearse 1969, and for marine organisms Valentine 1966, Stehli and Wells 1971). There are, of course, still considerable effects from factors like climate and ocean currents (see Darlington 1957, Fell 1967).

EXAMPLES

We present below some examples based on world-wide distributions of conifers and certain freshwater crustacea. The example on conifers employed the distribution of 58 genera of conifers and taxads mapped by Florin (1963), and has been reported earlier (Sneath 1967a); it is briefly discussed for comparison with the new analyses. The crustacean data were obtained by one of us (K. G. McK.) from records of Notostraca and Conchostraca from museums all over the world. The numbers of collections of these organisms that had been acceptably identified as to species were recorded against the geographical areas used for the earlier study, and termed, for convenience, the quadrats (the reference numbers are shown in text-fig. 1). The number of collections is, of course, only an imperfect reflection of abundance, and in the present context we felt it was better to use only presence or absence in a quadrat, yielding the coefficient ϕ . However, we did one analysis using the actual number of collections (yielding the coefficient r , see below) for comparison. We have used symbols somewhat different from those in the earlier study, in order to accommodate the tectonic plates now believed to be involved in continental movements.

The Notostraca provided data on 61 species (31 of the genus *Triops* and 30 of the genus *Lepidurus*); they were available for 39 quadrats. The Conchostraca records were of 151 species of 17 genera, and 44 of the quadrats could be scored. We followed the techniques used in the study on conifers, of which a summary is given below.

The required reduction in dimensionality of biotal distances necessitates fitting the distances to the surface of a sphere by allowing, in effect, the points representing the quadrats to slide about until their configuration fits the biotal distances (as arcs) as well as possible. To achieve this three vectors or coordinates were extracted by principal components analysis from the matrix of four-point correlation coefficients (ϕ) between pairs of quadrats. The points in 3-space were then projected

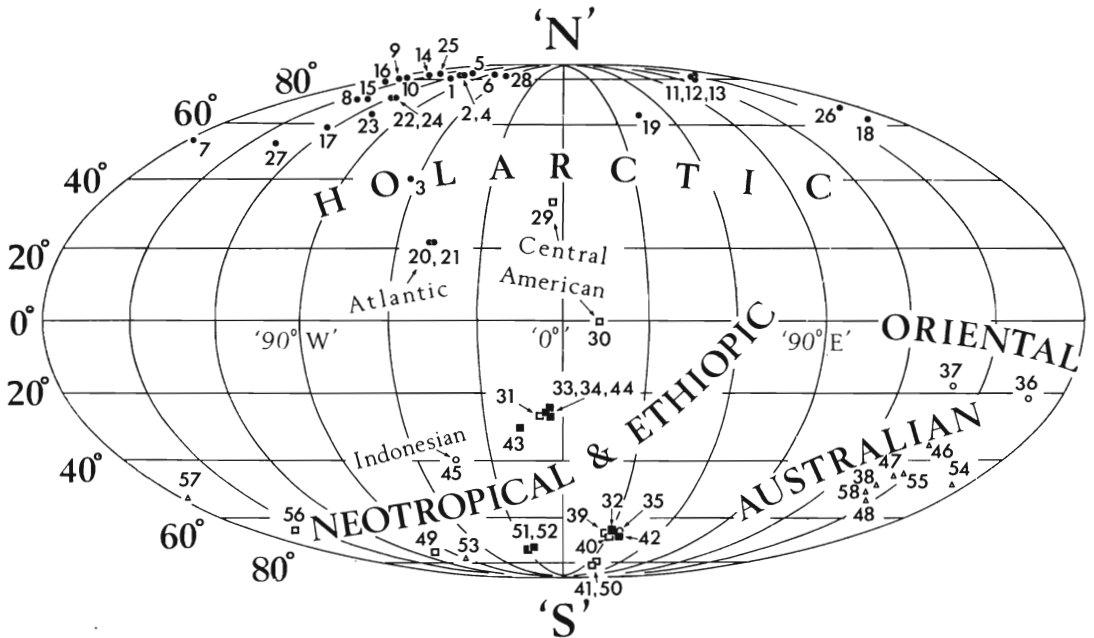


TEXT-FIG. 1. The 58 land areas used in the analyses (Mollweide's projection). From Sneath (1967a), reproduced by permission from *Nature*.

from their centroid on to a sphere as follows: first the coordinate means were subtracted from each coordinate to yield the new coordinates x , y , and z ; $\sin(\text{latitude}) = y/\sqrt{(x^2 + y^2 + z^2)}$ and $\tan(\text{longitude}) = z/x$. A point very close to the centroid will have an indeterminate position (small changes in biotal composition due to sampling errors will, for example, alter the projection a good deal), but this is unavoidable, for such a point is biotically unlike all others and cannot have a unique position on a sphere. In the studies reported here none of the points were extremely close to the centroid. The variances of the vectors were not first made equal (this would have had only a minor effect on the results).

Such a projection will show the points (representing quadrats) in their correct relative positions. But it will not show what axis 'corresponds' to geographical north and south. A partial answer can be given by rotating the projection to give the best fit between the points derived from the biotal distances and the centres of the quadrats on the globe, using a three-dimensional fitting method (Sneath 1967b). These fitted projections are shown in text-figs. 2-6.

The confidence limits to be placed on the position of a point in these figures are not easy to estimate, but a rough guide can be obtained by taking the standard error of ϕ as about $1/\sqrt{(n-3)}$ where n is the number of taxa, and treating the result as a cosine, to give the standard error as an arc. The shift of origin before projection on to a sphere may increase this somewhat. Although the standard error may seem unrealistic if all available taxa were used, it does give some idea of the reliability of the results by showing the sort of variation expected if one studied samples of size n from comparable taxa. The index of misfit between the spherical biotal pattern and the geographical positions of the quadrats is symbolized as d_h^2 , and its standard

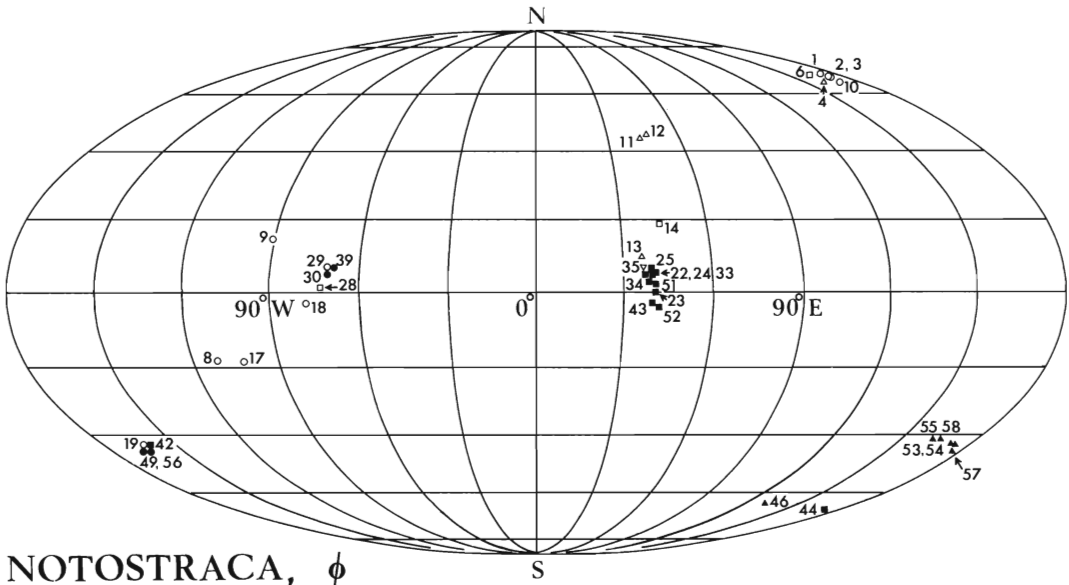


TEXT-FIG. 2. Conifer genera. The positions of the points representing the 58 quadrats, numbered as in text-fig. 1, after fitting to the present-day positions of the centres of the quadrats. The conventional biogeographical provinces are shown as: ● Holarctic; ○ Oriental; ■ Ethiopic; □ Neotropical; △ Australian. From Sneath (1967a), reproduced by permission from *Nature*.

The first three principal component vectors account for 29.27, 23.67, and 7.65% of the biotal variation respectively. The index of misfit, d_h^2 , to the present-day positions of the quadrats is 0.792 with standard error 0.148. The per cent of the variation in the first three biotal vectors accounted for by these present geographical positions is 60.4. The standard error of a point in this figure is estimated to be about 7.7°.

error is about $d_h^2 / \sqrt{\frac{1}{2}(h-1)}$ where h is the number of quadrats. The expected value of d_h^2 for a random arrangement of points is 2.0, and one can regard $\frac{1}{2}(2-d_h^2)$ as the proportion of the variance of the three vectors 'explained' by geography. The proportion of the total variation is rather lower, since the three vectors themselves account for only part of the biotal variation. These statistics are given in the legends of text-figs. 2-6.

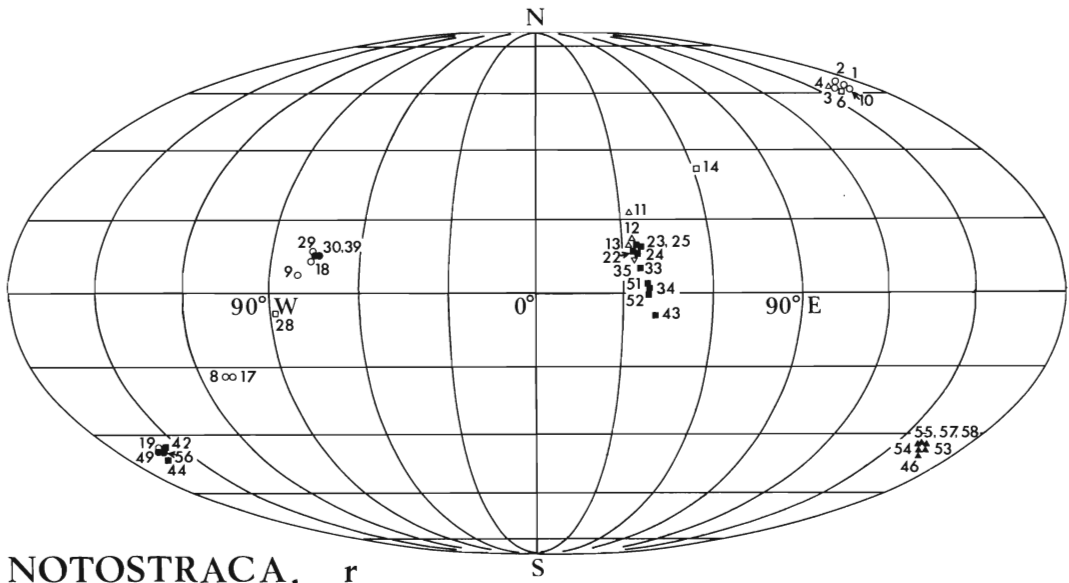
Conifers. It is seen from text-fig. 2 that quadrats from the same continents are generally grouped together. Also, the positions bear some resemblance to the presumed positions of the continents in the Late Palaeozoic, especially for the southern continents. These southern positions could well reflect Gondwanaland before it broke up in the Late Triassic; the points for South America, southern Africa, and southern India are grouped fairly closely, while those for Australia are relatively isolated, in keeping with the relevant geophysical evidence (text-fig. 7). The closeness of the points representing the Holarctic reflects the close similarity in conifer floras of this region, and there is nothing to suggest the pattern of the northern Palaeozoic floras discussed by Just (1952). A few quadrats, which possess very few conifers, have an uncertain position, notably 20 and 21 which both possess only *Juniperus*.



NOTOSTRACA, ϕ

TEXT-FIG. 3. Notostraca species, ϕ coefficient. The position representing 39 quadrats are shown, fitted to the present-day globe as in text-fig. 2. The quadrats are symbolized as follows: \circ N. America; \triangle Europe; \square Asia; ∇ India; \blacksquare southern Africa; \bullet South America; \blacktriangle Australia; and the symbols are as near as possible consistent with the tectonic plates.

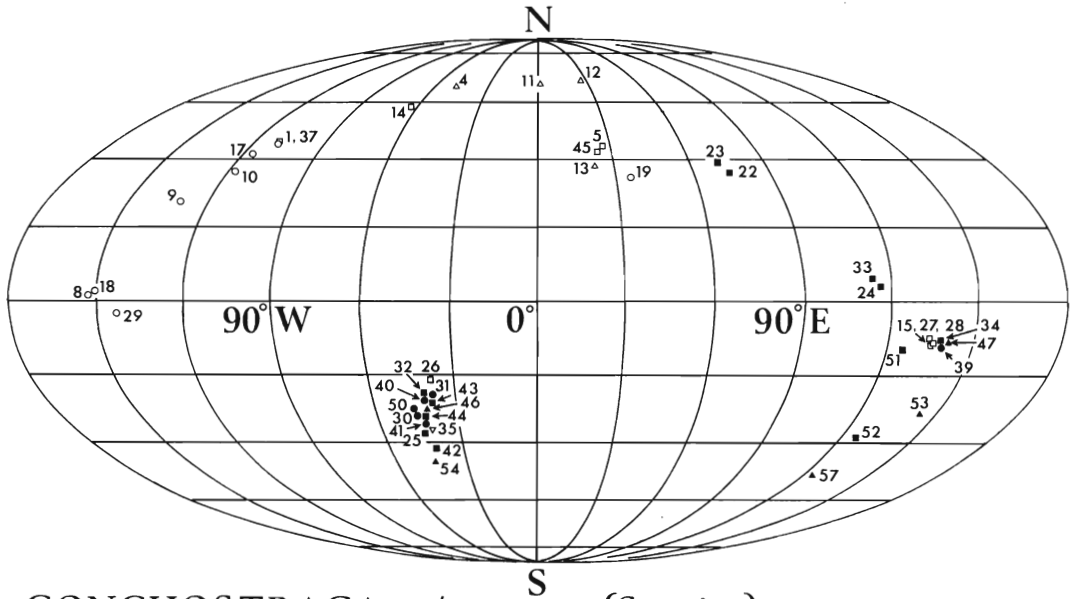
The first three component vectors account for 11.25, 10.21, and 8.15% of the biotal variation respectively. For present-day positions of the quadrats the misfit, d_h^2 , is 0.613 with standard error 0.141. The per cent of the variation in the first three biotal vectors accounted for by present geography is 69.33. The standard error of a point in this figure is estimated to be about 7.5°.



NOTOSTRACA, r

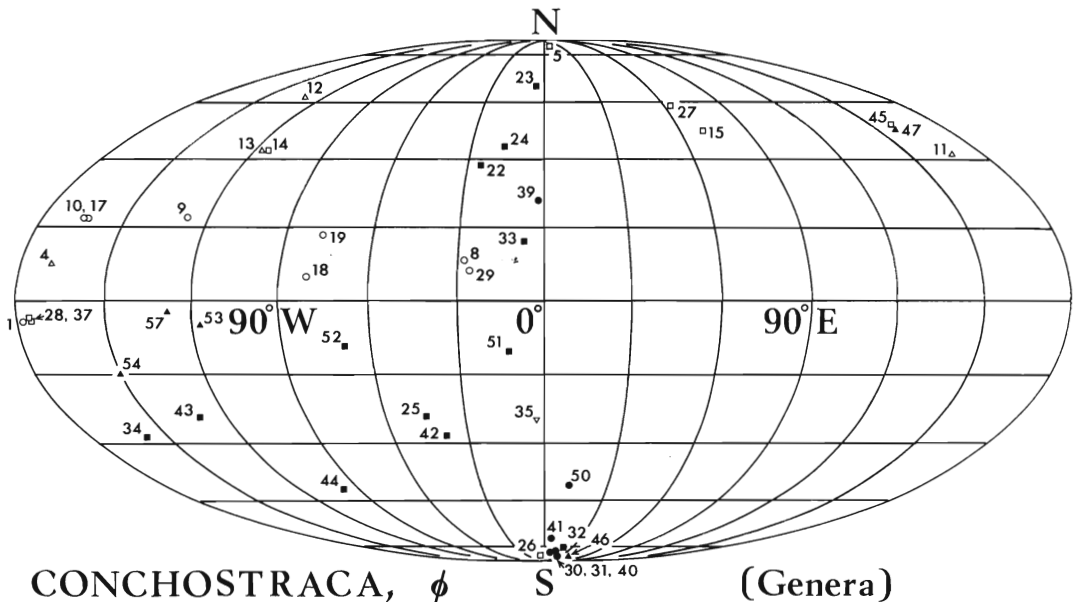
TEXT-FIG. 4. Notostraca species, r coefficient. The positions representing 39 quadrats, conventions as in text-fig. 3.

The corresponding percentages of the vectors are 12.26, 11.59, and 10.49% respectively; d_h^2 is 0.611 with standard error 0.140, with present geography accounting for 69.47% of the three vectors. The standard error of a point is again about 7.5°.



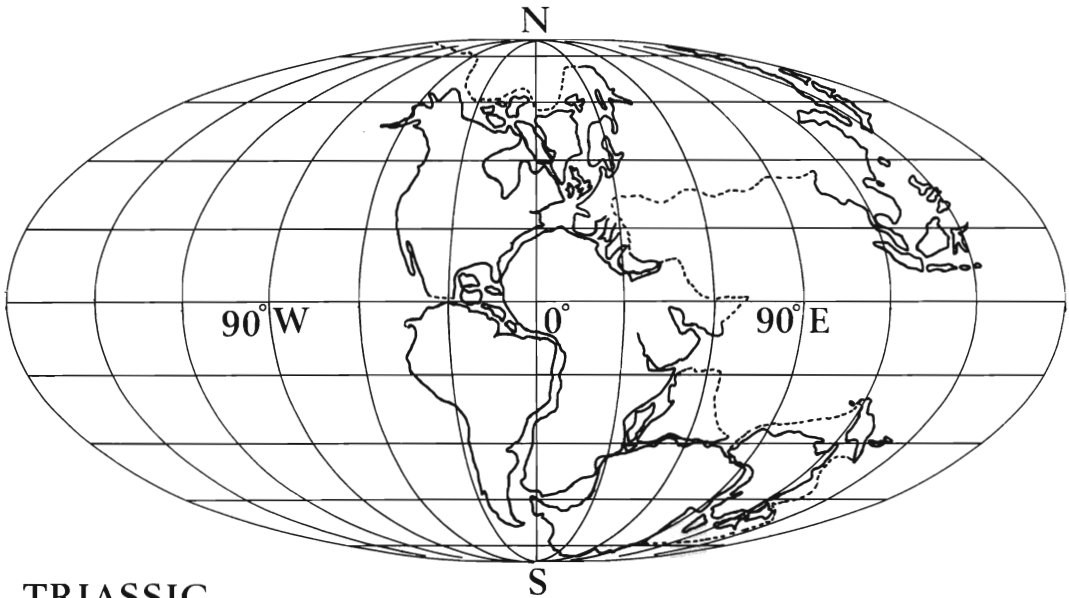
CONCHOSTRACA, ϕ (Species)

TEXT-FIG. 5. Conchostraca species. The positions representing 44 quadrats, conventions as in text-fig. 3. The corresponding percentages of the vectors are 10.35, 8.51, and 5.96% respectively; d_h^2 is 1.122 with standard error 0.242, so that present geography accounts for 43.91% of the three vectors. The standard error of a point is estimated to be about 4.7°.



CONCHOSTRACA, ϕ (Genera)

TEXT-FIG. 6. Conchostraca genera. The positions representing 44 quadrats, conventions as in text-fig. 3. The corresponding percentages of the vectors are 24.73, 16.22, and 12.91% respectively; d_h^2 is 1.280 with standard error 0.276, and present geography accounts for 36.04% of the three vectors. The standard error of a point is estimated to be about 15.5°.



TRIASSIC

TEXT-FIG. 7. Positions of land masses in the Triassic as reconstructed by Smith *et al.* (1972) (this symposium, p. 18, text-fig. 9).

Similarly, southern India (35) is placed with western Africa and central South America (32, 39, 40, 42) because they all have only the genus *Podocarpus*. The significance of these positions depends on how significant it is that these quadrats do not possess any of the other genera. One sees here an example of the drawbacks of an insufficient quantity of data. The per cent of variation accounted for by the three vectors is fairly high, 60-59, and the misfit to present geography is not excessive.

Notostraca. The distribution pattern (text-fig. 3) is not greatly dissimilar to that for the conifers. There is again a cluster of points representing largely Arctic quadrats, and presumably this reflects mainly climatic factors. Apart from the Arctic quadrats there is a Nearctic group of points, with some Central and South American quadrats intermingled, and also a Palearctic-Indian-African cluster. The Australian quadrats are fairly distinct, and display a weak affinity to Madagascar. These southern clusters may perhaps be thought of as palimpsests of a former Gondwana geography. The four points 19, 42, 49, and 56 represent scattered African and American localities, but they each possess only one species (*Triops dominguensis*, *T. macrophthalmus*, *T. frenzeli*, and *Lepidurus patagonicus* respectively) not found elsewhere, and this gives small negative correlations between them; their position must be taken as very indeterminate. Quadrats 29 and 39 (Central and South America) each possess only one species (in this case *Triops longicaudata* in both), and quadrat 55 has only *Lepidurus viridis*; the positions of these must also be regarded as very uncertain in a statistical sense. On the other hand, the known notostracan fauna of some quadrats (in this instance including all references in the literature) is very limited. Thus, in quadrat 55, no other notostracans apart from *Lepidurus viridis* are known and only

two notostracan species are generally accepted as present in Australia (Longhurst 1955, Williams 1968), although several species and subspecies have been described from there. Further, there are very few records of any kind from South America. For example, one of us (K. G. McK.) collected no notostracans in Chile and Argentina during a recent field trip; and a search of the literature indicates that only two species, *Lepidurus patagonicus* Berg 1900 and *Lepidurus hatcheri* Ortmann 1911, have ever been recorded for quadrat 56.

The distribution pattern of Notostraca differs from that of the conifers in that the points representing the southern continents are somewhat less close together. In this the distribution is more like that of the present-day continents, and indeed the misfit d_h^2 is rather lower, 0.613, than that for the conifers (0.792). However, the first three vectors account for only 29.61 per cent of the biotal variation, so in this respect the analysis is less satisfactory. Further, it has already been noted that the positions of some southern quadrats are statistically uncertain.

The correction coefficient r gives results broadly similar to ϕ (text-fig. 4). The main differences are moderate changes in the position of European quadrats (11, 12) and one Australian quadrat (46). The quadrat containing northern Madagascar also has a markedly different position. The reason for these changes is not obvious, but may depend on heavy collecting in certain localities, which would give unusually large numbers of records, and this in turn would affect the values of r . This is likely to be true for quadrats 11 and 12 at least.

Conchostraca. The results from the Conchostraca are more puzzling and a little disappointing. When all the 151 species were analysed the results (text-fig. 5) showed relatively poor resemblance to the present-day positions of quadrats, with a good deal of intermingling of points from different continents, and high misfit (1.122). Some clusters of points are recognizable, it is true: thus most of the North American ones are fairly close, though with an oriental intruder. But the Australian and Ethiopian clusters are fragmented into two groupings. In one of these, a loose cluster of three Australian quadrats is associated with a loose cluster of four Ethiopian quadrats and with three poorly determinate Palaeartic points; in the other, two Australian quadrats cluster with four Ethiopian points, five Neotropic points, and with the three quadrats which include the Indian plate, i.e. 25, 26, and 35. On the other hand, the Neotropic quadrats cluster well. The loose association of northern quadrats is rather like that of the conifer plot although it does not fit as well. A hint at an earlier geography is perhaps provided by the cluster of Neotropic, Indian, and some Australian and Ethiopian points, since it is these plates which formed Gondwanaland.

The corresponding analysis using the 17 genera (occurrence of any species of the genus in a quadrat was scored as presence of the genus) was unsatisfactory since only the Neotropic quadrats cluster at all well (text-fig. 6), but it shows features that may offer a partial explanation. It can be seen that in text-fig. 5 there are six points at the same position in the east (15, 27, 28, 34, 39, 47). These are quadrats which each possess one species and furthermore each is a species unique to that locality. In the generic analysis, each of these quadrats is scored (as is obvious) for the corresponding single genus, but the genus is not now unique only to that quadrat; it is

also found elsewhere in the world. Therefore different correlations appear, and the points have different positions. If all the quadrats had possessed many species of many genera, this effect would be minimal, and the analyses based on species and genera would be very similar. It therefore seems as if the quantity of data in the Conchostraca records is too small to obtain useful results.

This conclusion is supported by the low recovery of variance by the first three vectors in the species study (24.82 per cent), though it is not very low in the genus study (53.86 per cent). In the latter, however, the number of genera, 17, is very small, and consequently the error estimates are large. If the species had been more widely distributed then there would probably have been fewer quadrats whose positions were largely determined by presence or absence of just one or two species, and one would have expected a clearer species analysis.

The biotal distributions in text-figs. 2-6 are notably bunched. Evidently the width of barriers is exaggerated. It is possible that some statistical transformation would ameliorate this effect. There is of course no distinction between sea barriers and land barriers in such diagrams. It may be noted that mountain ranges are not apparent as barriers, but there are suggestions that deserts are faintly represented.

It is possible, at least in principle, to compare biotal distributions with positions of land masses in earlier geological periods. An attempt was made earlier (Sneath 1967*a*) to fit the conifer data to the reconstruction of Irving (1967) for the Permian. This gave slightly better fit (d_h^2 0.692, with standard error of 0.157) than the fit to the present day, but the improvement was not statistically significant. The crustacean data does not look promising in this regard. It may be noted that the fitting method gives best fit to chords, not to arcs, though this is partly compensated for by recentring to the centroid of the land masses (this may be far from the centre of the sphere when all the continents are joined).

DISCUSSION

The data reported upon above clearly have considerable limitations. Yet it is through such attempts that biogeographers may begin to learn how to handle problems of this kind. Evidently quite large quantities of good data are required, and improvements in statistical methods may also be needed. Discussion will for the present centre about how far the biotal distributions reflect past history. Darlington (1957) considers that mammals and perhaps freshwater fish may reflect some aspects of Cretaceous geography, but that possibly no group of living animals can tell us anything about earlier periods. The most important factor here is evidently mobility. Replacement of ancient forms by new colonizers will obscure the old patterns (cf. Valentine 1971). An example of this in the Conchostraca data is the distributions of living members of the family Limnadopsidae which are exclusively Australian (genus *Limnadopsis*) whereas the distributions of fossil taxa assigned to the family are wholly ex-Australian (Tasch in Moore (ed.) 1969). A similar situation is exemplified by the living and fossil distributions of cyprinotine Ostracoda (McKenzie 1971). It is probably the high mobility of butterflies that explains the absence of any relics of continental drift in the Indian butterfly fauna (Holloway 1969). It may well be differences in mobility that contribute most to the differences between conifer

patterns and those from the two groups of crustacea. Probably, all three originated in the Palaeozoic. Conifers appear to have arisen in the Carboniferous (Florin 1963), modern-looking Notostraca are represented in the Permian and Triassic, and the available evidence suggests that conchostracans transferred from an original marine habitat of life in continental aquatic environments during the Carboniferous (Tasch in Moore (ed.) 1969). But it may be that conifers are less mobile. Certainly, Notostraca and Conchostraca are known to possess desiccation-resistant eggs which have a high potential mobility, e.g. via dust storms or in mud caked to the feathers and feet of birds.

A conclusion one may draw from studies of Simpson (1952) and MacArthur and Wilson (1967) is that the amount of pattern remaining from an earlier period is likely to decay at an exponential rate, and thus the remaining pattern at a given time will vary approximately inversely as the logarithm of mobility (expressed for example as invasion rate). Thus, although we may only be able to estimate the power of magnitude of mobility, it is the power of magnitude that is important. The low mobility of mammals and conifers may allow us to see something of the Late Mesozoic. There may be no organism so immobile as to show anything of earlier periods. Organisms with much greater mobility would then allow only a glimpse of the most recent continental movements, and it is perhaps significant that the latest of these, the opening of the North Atlantic and the drifting of Australia to Malaysia, may be faintly indicated by the examples, in that the northern transatlantic distance seems small, and the Australasian distance large, in all three examples.

The question of bipolarity in the distributions may also be raised. It certainly appears as if all three distributions are bipolar in that they all show a separation into northern and southern associations, with the exception of the study based on Conchostraca genera which, as we have seen, was generally unsatisfactory. Such bipolarities may possibly be interpreted as indicating the Gondwana and Laurasia of an earlier geography. In the Notostraca plots, the bipolar pattern is broken down somewhat by the incorporation of several Palaeartic quadrats into the Ethiopian cluster. It is known that at the generic level in Notostraca, *Lepidurus* occurs throughout the Palaeartic and Nearctic but also in the southern Neotropic and in southern Australasia and New Zealand; *Triops*, however, never occurs beyond 60° N. (Longhurst 1955), although it is widespread in both the Palaeartic and Nearctic provinces, and also occurs in the southern Neotropic region, northern Australia (Williams 1968), and throughout Africa. Since *Lepidurus*-like fossils are known from South Africa, the absence of *Lepidurus* there today together with the restricted southern distributions of this genus in southern South America, southern Australia, Tasmania, and New Zealand suggest that *Triops* may have moved into regions formerly occupied by *Lepidurus*. This suggestion may account for the clustering of some Palaeartic and Ethiopian points and the northerly orientation of this cluster as a whole, which is a feature of figs. 3 and 4, and which obscures the otherwise bipolar pattern of the Notostraca plots.

Nevertheless, even if we cannot see very far back into history by such means, this does not detract from the interest of these methods for studying fossil distributions in relation to their contemporaneous geography. As better fossil records are accumulated this will become increasingly practicable and as noted earlier it might be well to choose organisms believed to be highly mobile for studies of this kind.

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DISCUSSION

N. Jardine (King's College, Cambridge). METHODS FOR RELATING THE EVOLUTION AND DISPERSAL OF ORGANISMS TO PAST CONTINENTAL ARRANGEMENTS.

The purpose of this contribution is to make two points about the methods which can be used to relate the evolution and dispersal of organisms to past continental arrangements.

The first point concerns the relative extents to which geophysical evidence can help biologists to interpret present and past distributions of organisms, and to which evidence for the present and past distributions of organisms can help geophysicists to reconstruct past continental arrangements and past climates. This is a matter of assessment of the hardness of evidence. The dated reconstructions of continental arrangements since the Late Cretaceous based on sea-floor spreading data constitute hard evidence. The earlier reconstructions based on palaeomagnetic data are less reliable. But it is probable that geophysical data will play a much larger role than information about the past distributions of organisms in the eventual reconstruction of more reliable maps for this earlier period. The same may be true in the reconstruction of past climates. The world's winds and ocean currents are jointly determined by the arrangement and surface topography of land-masses and the bottom bathymetry of the oceans. Reliable reconstructions of past climates may eventually be obtained using geophysical data. However, information about the past distributions of organisms may help to clarify problems which prove unsusceptible to geophysical methods. For example, the plate-tectonics of the Scotia Arc and of the Caribbean is so complex that it may be impossible to date precisely the periods of marine isolation of South America from Antarctica and from North America. Studies of past distributions of marine organisms may resolve this question.

On the other hand I believe that hard evidence for past continental arrangements (and hopefully past climates) based on geophysical data will revolutionize biologists' interpretations of the dispersal and evolution of organisms.

The second point concerns the ways in which biologists can use such evidence. I suggest that two quite different approaches are needed: one for land organisms for which oceans are a complete or almost complete barrier to dispersal, and marine organisms for which land is a barrier to dispersal; the other for more mobile organisms. For immobile land organisms one can regard moving land-masses as agents of dispersal, and one can assume that isolation of land-masses provides opportunities for adaptive differentiation in the absence of competitors which evolve elsewhere. For such organisms it is reasonable to attempt to *deduce* aspects of dispersal and evolution from comparison of their present and past distributions with past continental arrangements. This is what Cox (1972) and Jardine and McKenzie (1972) have attempted for the marsupials. The diverse hypotheses which have been proposed to explain the present distribution of marsupials were reviewed by Clemens (1971). Cox's and Jardine and McKenzie's reconstructions of marsupial dispersal in the light of plate tectonic evidence agree in concluding that marsupials must have reached Australia from South America via Antarctica. They differ in their speculations about the reasons

for the absence of placentals from Australia. This difference cannot, apparently, be resolved by the available evidence. It may eventually be resolved by further records of fossil mammals, by discoveries about the climatic history of Antarctica, or by further study of the plate tectonics of the Scotia Arc.

When dealing with more highly mobile organisms one cannot use deductive methods. For example, it is reasonable to deduce that the evolutionary divergence of Australian marsupials from other marsupials must have occurred before the separation of Australia from Antarctica. But no such deduction can be made for groups of Australian flowering plants, because long-distance dispersal of flowering plants is established by their occurrence on such remote oceanic islands as the Hawaiian islands which have been isolated by large tracts of ocean since their volcanic origin. It is, of course, plausible to use continental rearrangements to explain recurrent patterns of disjunct distribution of mobile organisms, but it is difficult to see how such explanations can be more than tentative. An alternative approach is the use of statistical methods of the kinds described by Sneath (1967), Sneath and McKenzie (1972), Holloway and Jardine (1968), and Jardine (1972), which seek some reflection of the present and past disposition of areas by analysis of the distributions of large numbers of organisms. But these methods yield results which are very difficult to interpret, because it is difficult to disentangle the effects of climatic discontinuities and geographical isolation on the faunal and floral differences of areas. Sneath and McKenzie (1972) suggested that the power of such statistical methods should be tested on the present-day distributions of organisms before they are applied to incomplete information about past distributions. Many of the methods are highly sensitive to missing information. Similarly much further investigation of the dispersal capacities of present-day organisms under known climatic conditions is needed.

In conclusion I suggest that if biologists are to combine geophysical and biological evidence to clarify the principles of dispersal and adaptation of organisms they should seek the hardest available evidence. At present the hard geophysical evidence is the reconstructions of continental arrangements since the Late Cretaceous. Hard biological evidence is more difficult to come by. In the present state of knowledge it appears that it is (relatively) immobile organisms with (relatively) good fossil records which can most profitably be investigated.

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