CONCLUDING REMARKS ON SYMPOSIUM

by P. H. A. SNEATH

ABSTRACT. This comment made at the end of the symposium underlines the nature of the biogeographic and palaeontologic problems to be faced in taking advantage of the new palaeomagnetic data concerning past positions of continents.

THE sub-title of this symposium is 'Methods of assessing relationships between past and present biologic distributions and the positions of Continents', a theme which has been effectively illustrated by many of the papers given. A unique feature of the conference, and one which has vitally contributed to its success, has been the set of continental reconstructions by Smith, Briden, and Drewry, which were made available in advance to other authors. This has allowed the biologists to relate their own data to a uniform set of palaeogeographical hypotheses, thus permitting a coherent critique of the present geophysical evidence, as well as more specific suggestions for improvements in these reconstructions of past geography.

It is evident from the contributions and discussion that the firmness of the present geophysical evidence rapidly decreases as one goes back in time: for the Tertiary, data on sea-floor spreading and palaeomagnetism are both available for cross-checking; the evidence is much poorer for periods before the Cretaceous; while in the Palaeozoic the data is perhaps even more uncertain and fragmentary than the patchy data on biogeographical provinces.

One point that has apparently received little study is whether rates of movement of tectonic plates have been constant over long periods of time. This could be of some significance, because it might help in deciding whether longitudinal movements are likely to have occurred during those periods when only palaeolatitudes can at present be estimated. There appears to be no strong evidence that the present mean rate of formation and destruction of crust (about $2\frac{1}{2}$ km^2 per year) has changed much during the Cainozoic. Yet certain periods (e.g. Late Ordovician, Late Cretaceous) may have been times of greater movement, while the symposium maps give the impression that there was very little movement during much of the Mesozoic. Both theoretical arguments (e.g. steady output of energy) and empirical findings (e.g. comparisons for well-documented epochs) could be used here.

Turning next to the methodology of using biologic distributions, there are first some general points that emerge from the papers presented. It is clear that many of the methods have considerable promise (shown, for example, by the concordance between biology and geography of the Atlantic region in the Palaeozoic). We are now moving out of the early descriptive phase into an analytic and increasingly numerical phase. This brings with it several problems: the need to avoid selecting only those data that support a preconceived theory while ignoring the rest; the need to discover causal connections between distributions and general factors that influence them, and to separate the effects of these factors; and the need to develop

[Special Papers in Palaeontology No. 12, pp. 331–334]

criteria for the significance of the conclusions. These have rough parallels (though by no means negligible ones) in statistics. The first is covered by sampling theory, the second by correlations and analysis of variance, and the third by statistical significance tests. It is here, perhaps, that the contributions have not been as strong as one might like, but we may hope that they will catalyse new work on these aspects. We may also hope that an increasing numerical emphasis will bring new power and conviction to the work of the future.

From the technical aspect it may be that non-parametric statistics (and their analogues in other situations, e.g. multidimensional scaling) may be best until more is known about the underlying statistical distributions. Similarly, although in theory the biogeographic distributions of different organisms might receive different emphasis according to their significance for palaeogeography, it will be difficult to arrive at satisfactory schemes of weighting that reflect this appropriately.

One class of biological methods employs indices that are in principle applicable to single localities, such as diversity or deduced latitude. Endemism is also a partial reflection of biotal position in so far as high indices imply geographic or ecologic isolation. These methods may prove to be more powerful than has commonly been thought. An example is provided by Vine in this symposium in his study of the diversity gradient hypothesis of Stehli, which is based on the observation that the greatest diversity of present-day organisms is in the tropics (with some exceptions, e.g. penguins, see Stehli 1968). Such methods would be especially powerful if theoretical and empirical rules can be discovered, similar to the relation between diversity and area enunciated by Preston (1962).

Diversity as a function of latitude clearly must vary with the taxonomic rank of the groups considered: for all taxa of high rank, e.g. classes, the greatest diversity is doubtless in the tropics; but the proportion of genera showing this behaviour is well below 100%, because many genera are restricted to high latitudes. The shape of the curve of diversity pattern against taxonomic rank would be of considerable interest. It might allow the latitude to be estimated with some reliability from a single locality, instead of requiring almost a global distribution of samples. The work of Valentine (1967, and this symposium) has a similar aim, for it implies that we may be able to recognize from the biotal pattern at a single locality whether this locality was on a continental shelf, an island arc, and so on.

Turning to the other large class of methods, where similarities in faunas and floras are used to reconstruct geographic distances, it seems clear that regional studies are commonly effective in giving acceptable reconstructions of geography. In contrast, global studies are much more difficult, and make heavier demands on the quality and quantity of data. Although it is evident that many factors interfere with simple interpretations, there are plenty of indications that past historical events are reflected in present-day distributions. Though this may be so, historical explanations are apt to be given for any findings that are not immediately explicable by other causes (not a very safe procedure). It is thus of particular significance that contributors to the symposium have made considerable efforts to relate biogeographic findings to the geophysical evidence about the past.

One of the major problems of the biogeographer is to assess the mobility of the organisms he studies. In this, as in many fields, G. G. Simpson has been a pioneer

(Simpson 1952, 1953). Measuring mobility is extremely complex: it cannot be adequately represented by a simple index such as the number of immigrants per year, or the mean dispersal distance. The number of potential colonists, the area occupied by each, the available area for colonization, all these, and other factors, must be taken into account (e.g. see Leston 1957, for an interesting suggestion on this). MacArthur and Wilson (1967) note the great importance of stepping-stones (such as small islands in oceanic dispersal). If the mean dispersal distance is much less than the size of the gaps then almost every colonist must pass along the successive stepping-stones. Different effective dispersal distances can thus allow ready passage of some organisms but not of others. They note that such observations as the large Asian component in the insects and plants of New Guinea but the low Asian component of vertebrates can be explained on these lines. Furthermore, there is some evidence that very small and transient islands are adequate to allow passage of migrants. We face a difficulty here: our conclusions may depend heavily on how readily we are prepared to assume the existence of stepping-stones that have now vanished, and yet we may first need to know about these stepping-stones in order to estimate dispersal distances. Possibly the comparison of organisms with different mobilities may allow these factors to be disentangled.

There is still an acute shortage of biogeographic data of the quality and quantity needed. Much must exist in the literature, though its accuracy will be variable. There must be a wealth of detail on microfossils that awaits study. The proper exploitation of this data will doubtless require up-to-date electronic data processing (e.g. see Cutbill 1971). Also, as Crowson (1970) points out, the rapid ecological changes being brought about by man are destroying information that is critical to biogeographers, so there is an urgent need to gather it while we can; for only a small minority of organisms are the distributions reliably known.

In developing the strategy of new studies I believe considerable attention should first be given to testing out methods with data which we may hope to interpret fairly easily. We should first try to understand factors influencing present-day distributions before we become too eager to apply our methods wholesale to distributions of past epochs. If so, palaeontologists should collaborate closely with neontologists in this phase, by studying extant organisms, both mobile and non-mobile. We are very much at the mercy of our prior assumptions: indeed the use of biogeography to support geological hypotheses has had a long and chequered history; what seemed secure has often been overturned by the studies of the succeeding generation. Thus Alfred Russel Wallace (1880) in his book *Island Life* took the permanence of the present continents and oceans as an unshakeable premiss, and on this built a good deal of evidence in favour of a supposed sunken continent of Lemuria in the Indian Ocean, a concept now in oblivion. Yet there are areas where the biologist can hope to make a unique contribution. He can help the geophysicist in studies on the Palaeozoic, where geophysical data is still so uncertain. He may assist with the problem of estimating longitude, because there are definite biological effects associated with longitude (both on land and sea) although they are not yet well understood (e.g. Kiester 1971, Stehli and Wells 1971, Valentine 1971). It seems likely, for example, that if one performed an ordination using biotal distributions of a series of localities along a line of latitude that one would recover the order and rough spacing of the localities. Biological studies may have a part to play, too, in relation to palaeoclimates, especially since climatic reconstructions for much of the Tertiary may well soon be available.

Most of the contributors have been concerned with validating geographical hypotheses by using biological evidence—as was the main purpose of the symposium. But it will be at least as important in the future (as pointed out by Dr. N. Jardine and illustrated by Dr. W. T. Stearn in the discussion) to use these arguments in the opposite way: to explain biological observations on palaeogeographic evidence, and this may have far-reaching effects on evolutionary theory. Progress may well be slow, but the two disciplines will have much to offer each other, piecing together fragmentary information in a way familiar to geologists, to yield a fabric that is tough enough to stand the strain of new discoveries.

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