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GUEST EDITORIAL

From generalized tracks to ocean basins—how useful is Panbiogeography?

PROLOGUE

In 1993, in a brief review of different methods of analyzing patterns of distribution (Cox & Moore, 1993), I commented upon the methodology of panbiogeography. These comments were later criticized by Grehan (1994). In writing a reply to Grehan, I found that it was necessary to construct a wider analysis and review of panbiogeography, so that my original comments, as well as Grehan's criticisms, can be seen in the context of Croizat's original views as well as in that of the more recent elaboration of his theory by Grehan and others.

INTRODUCTION

There is probably no other field of biological enquiry that is as bewildering as that of biogeography. Evidence there is, in abundance, but it consists of an immense diversity of patterns; from essentially world-wide, to taxa found in only one isolated locality; from wholly contiguous, to taxa found today in several continents separated by hundreds or thousands of miles of open ocean. The biogeography of islands adds another layer of complexity, in the need to make sense of their varying patterns of diversity and of the ways in which their biota has been affected by the area or location of the island.

By both instinct and training, scientists are drawn to attempt to reduce apparently meaningless patterns to an ordered series that can be seen as the result of the interaction of a restricted set of characteristics of the world of nature. In the case of the comparison of island biotas, this impulse resulted in McArthur & Wilson's *Theory of Island Biogeography* (1967) which, though initially welcomed, now seems to lack the wide applicability that its authors had suggested. In the larger sphere of biogeography in general, Croizat's theory of Panbiogeography (Croizat, 1952, 1958, 1964) can be interpreted as a similar, but perhaps more successful, attempt at generalization.

Some scientific theories are proposed simply as a reaction to unexplained facts. The *Theory of Island Biogeography* is a good example of this, for no-one had previously attempted to provide any similar synthetic explanation. Other theories are, in addition, a reaction to a previous theory that the author finds unacceptable or inadequate. Croizat's Panbiogeography is an excellent example of this, for it is a formidable expression of his (justified) belief that Darwin's theory of local evolution followed by dispersal over the pattern of geography seen today (except where it had been modified by comparatively minor changes in sea-level or climate) was inadequate to explain many of the facts of world biogeography. If Darwin's theory was correct, then the only way in which one could explain the apparently irrational, disjunct patterns of distribution seen in many living organisms, as well as of some fossils (such as the Permo-Carboniferous *Glossopteris* flora) was by the invocation of chance dispersal on a massive scale. Croizat saw this as a convenient way of escape, which allowed biogeographers to suggest an apparent 'explanation' that was in fact merely an unargued statement of belief, and which provided no basis that could be tested. Its widespread use, then, relieved them of any need to provide any other, more rigorous and integrative pattern of explanations for the problems they faced.

Two factors may have combined to hinder the evaluation of Croizat's ideas. Firstly, the extreme forcefulness of his rejection of dispersal as the mechanism of *all* spread from location to location led him to the extreme (and unnecessary) rejection of dispersal as a possible mechanism under any circumstances. Secondly, his ideas are expressed in a terminology different from that used in other theories of biogeography. I shall, in this paper, attempt to 'translate' the theory of Panbiogeography, as expressed by Croizat and elaborated by his supporters, into terms that are similar to those used in other theories, and then to assess the extent to which they are acceptable and useful, while answering Grehan's (1994) criticism of the views expressed in my brief review of Panbiogeography (Cox & Moore, 1993).

CROIZAT'S THEORY OF PANBIOGEOGRAPHY

In his methodology, Croizat followed van Steenis (1934–35) in first mapping the locations in which an individual taxon is found, and then linking these locations by a series of lines that he called 'tracks' or 'graphs of geographic distribution'. He found that, in many cases, the tracks of many taxa, belonging to a wide variety of organisms, could be combined to form a 'standard' or 'generalized' track. This concordance of pattern convinced him that these generalized tracks were a reflection of an underlying reality. However, these tracks did not conform to what might have been expected if the distribution of the organisms reflected the prevailing assumptions that each had evolved in a limited area, and had dispersed from there over the modern pattern of geography. This was either because the taxon is found in scattered locations (for example, around the margins of the Pacific or Atlantic, or also on several Pacific islands), or because it is absent from areas that were thought to have been on its dispersal route. Croizat felt that it would be surprising if any single taxon had managed by chance to cross the intervening gaps, and incredible that a considerable variety, with different ecologies and methods of distribution, should have been able to do so. This led him to reject both the concept of origin in a limited area, and that of dispersal.

Croizat's methodology does not, therefore, include any use of the concept of 'dispersal' in the commonly-accepted sense of extension of range across a barrier—what Pielou (1979) refers to as 'jump dispersal'. He fleetingly recognizes that it may take place, as where he rhetorically poses the question of the origin of the biota of Krakatoa after the 1883 eruption. But he then avoids answering the question by asserting that there are many examples of vicariism, and that 'immobilism—as the cause of vicariism—enjoys preeminence above mobilism' (Croizat, 1964 p. 216), and 'evolution has vicariant form-making for its fundamental law' (Croizat, 1964, p. 625).

In place of the concepts of local origin and dispersal, Croizat suggested that any widespread but disjunct distribution was merely the relict of a formerly continuous distribution. So, for example, the bird genus *Sasia* 'is today in Borneo and Nepal because generalized picumnine birds in pre-*Sasia* level of evolution were once distributed to include within their range Borneo and Nepal' (Croizat, 1964, p. 208). (This quotation also illustrates his belief that evolution could take place in parallel, independent fashion from more generalized ancestors.) Croizat suggested that these patterns were also often of great antiquity. Thus, after discussing the disjunction of *Oenothera* and of many other animals and plants that are found in localities scattered along the western margin of both North and South America, 'The ancestral populations of all these plants and animals were 'on the spot' long before the rise of the Rocky Mountains and the Andes' (Croizat, 1964, p. 546). Having dismissed dispersal (in the conventional sense) as the possible cause of any disjunction, Croizat was then logically free to accept the date of any disjunction that is due to geographical or geological events as indicating the date by which any taxa separated by that event were already in existence. So, for example, having accepted a mid-Jurassic date for the appearance of the Mozambique Channel, he concluded that the Euphorbiaceae, which are found in Madagascar as well as in Africa, had already differentiated by that date (Croizat, 1964, p. 360). Similarly, the ancestors of the Proteaceae, Compositae etc. were already in Australia between the Permian and the Triassic (Croizat, 1964, pp. 173–4), and the explanation of disjunct distributions involving North America and the Old World required the origin of the angiosperms in the Triassic/Jurassic, and the origin of genera such as *Jasminum* and *Menodora* in the Early Cretaceous (Croizat, 1964, p. 25).

Even if it had taken place in the very distant past, however, the extensive areas occupied by some taxa required explanation. Croizat (e.g. 1964, p. 211) explained this as the result of alternating periods of 'mobilism' and 'immobilism'. If the environment of a species living in one area became favourable, the species would be able to spread to neighbouring areas using its ordinary powers of survival, such as flight, setting up breeding territories, etc. (Croizat was here excluding the exceptional or '*extra-ordinary*' methods that had been invoked by earlier biogeographers to explain the crossing of barriers between areas of distribution.) This would represent a period of mobilism, during which the active movement precluded the spatial isolation that is necessary for local differentiation into new taxa. This would be followed by a period of immobilism, during which the stability of range provided an opportunity for evolutionary change. Croizat referred to this as 'form-making', which he defined Croizat (1964, p. 6) as 'the process responsible over space in time for the appearance of a certain taxonomic group at a certain point of the map.' He expressed the whole process as 'dispersal = form-making + translation in space'. Croizat did not, however, believe that there was a rigid distinction between the periods of mobilism and of immobilism: 'At no time will dispersal be so fixed as to exclude slight migration, or so unfixed as to exclude a measure of form-making' (Croizat, 1964, p. 711).

It is important to note here that Croizat uses the word 'dispersal' as referring to a pattern of distribution, and *not* in the sense, that he had rejected, as referring to a process of extension of range across a barrier. His formulation might be 'translated' as 'the pattern of distribution of a taxon is the result of natural extension of range, that did not involve the crossing of barriers, followed by independent evolutionary change within populations that have become, to a greater or lesser extent, separated from one another'. Croizat's tracks do not, therefore, imply any concept of movement: 'A track is expressed by a line on the map along which forms of closely related affinities are found. A channel of this kind should of course not be understood as tantamount to a line of flight or the like . . . . a track stands for a chain of centers of form-making and distribution, each center arisen by fragmentation of the range formerly held by ancestors at a lower level of evolution than their descendants' (Croizat, 1961, p. 1615).

Having, then, replaced Darwinian dispersal with a concept that he found more convincing, Croizat still had to explain those patterns of distribution in which the different areas occupied by the taxon are widely separated by environments in which they could not ever have existed—as in the case of the ocean that surrounds terrestrial taxa found in such Pacific island groups as the Hawaiian or Galapagos archipelagos. Because biogeography is, obviously, the result of observations in both biology (systematics) and geography, and because modern geography is clearly inappropriate as the canvas upon which to present the results of modern systematics, Croizat believed that systematics was the only reliable basis for his theories. If the systematics was correct, the patterns must then be the result of alterations in geography, and he accordingly suggested that land had once extended much further westwards from the Americas. He thus writes of a 'land limit' (I would not identify it as a fast, immovable shore, of course) which departing from Revilla Gigedo interests next Galapagos, eventually to reach Peru. This 'land limit' can further be extended to the islands off Chile . . . . and also without difficulties to Hawaii. . . . . to this limit (and possibly beyond) ran the rims of geosynclinal 'foreland insular galaxies and the like which life could use to further its movements.' (Croizat, 1958, p. 799). Similarly, 'The western longitudinal half of the New World, which is now a thin 'Andean' or 'Cordilleran' strip, was in epochs bygone a considerable bulge of land into the Eastern Pacific' (Croizat, 1964, p. 90). He viewed both North and South America as composite continents, formed by fusion of land that had originated in the Pacific with land that had originated in the Atlantic (Fig. 1).

Croizat seems to have been intent on minimizing the extent to which dispersal (in the conventional, non-Croizatian sense) had to be invoked in order to explain patterns of distribution. So, even though he stated that the rise of the Himalayan Mountains had caused discontinuities in the distributions of races and species of plants and birds there (Croizat, 1964, p. 63), he did not assume that the gaps between the locations of some taxa around the Pacific were the result of extinction after the taxa had dispersed to these locations. Instead, he suggested that the biota had arrived in each of these locations as part of the biota of an island that had become fused to the mainland, by what he called 'horstian dispersal'. 'In *horstian* dispersal involving the insular festoons off a mainland . . . the islands in the festoon interplay in distribution *both among themselves and with the mainland* in the criss-crossing manner . . . In the case where the nascent Andes 'sucked in' pre-Andean cores, the Andes also received life from said cores in the *horstian* manner.' (Croizat, 1958, p. 492, footnote; his italics) Similarly, 'Onagraceous plants later to become modern *Oenothera, Fuchsia*, etc., were dwelling *both* north and south of the equator ages before the present geography began to take shape. We can still form pretty concrete and critical ideas of where these ancestors mainly stood . . . whether strewn in origin along an axis Baja California/Peru, of which the Galapagos and Revilla Gigedo are surviving mites, or clustering in ages long past around cores of land that still survive here and there embedded and inlaid into the geography of our times from Mexico to Argentina' (Croizat, 1964, p. 547). Croizat also suggested that the biota of the Cape region of South Africa, and that of Madagascar, had arrived there in 'horstian' fashion (Croizat, 1964, p. 278).

Croizat did, therefore, see past geological events as having had possible effects upon the biogeographical patterns of today. In 1993 (Cox & Moore, 1993, p. 242) I commented that '. . . . even after plate tectonics became widely accepted, Croizat for a long time refused to accept that theory, preferring other geological mechanisms'. Grehan (1994) feels that this is misleading. He states that Croizat did not object to the theory of plate tectonics, that he compared tectonics and tracks, that he discussed the spatial relationships between mid-oceanic ridge systems and the distribution of organisms, that he produced a plate tectonic model for the Americas, and that he only rejected 'Wegener's Theory' in so far as it conflicted with the patterns of Pacific dispersal. However, these comments confuse plate tectonics both with tectonics in general, and with Wegener's

FIG. 1. "Croizat's (1961) plate tectonics model for the formation of the Americas by fusion of different geological and biological systems out of what are now (a) the Pacific and (b) Atlantic basins. This origin is sometimes reflected in organisms with (a′) western and (b′) eastern main massings having trans-Pacific or Atlantic baselines respectively (redrawn after Croizat, 1961)." Figure and caption from Grehan (1991), p. 351.

theory of continental drift, which came long before plate tectonics. 'Tectonics', in the geological sense, is merely a general word relating to movements of parts of the Earth's surface, either vertically or horizontally, whereas 'plate tectonics' refers to the precise theory of division of the Earth's surface into separate areas, or plates, that move as a whole relative to one another. So neither the fact that Croizat compared 'tectonic lines' in the West Indies with the distribution of *Columba*, nor his acceptance (or otherwise) of Wegener's theory is relevant to my comments on his attitude to plate tectonics.

Similarly, what Grehan presents as Croizat's 'plate tectonic model for the formation of the Americas' (Fig. 1) is nothing of the kind. It instead illustrates Croizat's view that the margins of the Americas had either received areas of land, with their biota, by 'horstian dispersal' from the neighbouring ocean basins, or had themselves once extended further out into those basins. As will be argued below, neither of these concepts is supported by our modern, detailed knowledge of plate tectonics, and the fact that the much later concept of terranes parallels horstian dispersal is irrelevant to Croizat's attitude to plate tectonics.

Croizat thus believed that the apparent movement of organisms across the map was in fact merely the result of the movement of segments of the Earth's surface. These had originated at the periphery of one continent and, bearing their biota, had traversed the ocean before becoming attached to the margin of another continent bordering that same ocean. Those of his 'tracks' that linked the resulting areas of distribution of the taxa involved therefore crossed the ocean basins (even if over a geography different from that of today) rather than crossing the pattern of land-masses seen today (Fig. 2). Where two tracks intersected, Croizat therefore believed that the location, which he named a 'node' or 'gate', marked a biogeographical and geological boundary. Because they had received units of land, with their living cargoes, from more than one direction, and across different oceans, Croizat viewed today's continents as biogeographically (as well as geologically) composite.

Croizat believed that his painstaking, extensive cataloguing and assembly of biogeographic data made the resulting system of generalized tracks an extremely robust analytical tool. Where the pattern of distribution of a taxon did not conform to this, he therefore felt it quite reasonable to examine this anomaly, in order to find out whether a re-interpretation of the original data could remove the biogeographic misfit. So, for example, on finding that the biogeography of *Ficus* did not conform to his system, he spent a considerable amount of time (and 72 pages of text in Croizat, 1968) in analysing the systematics of the group—though he was unable to produce a new classification

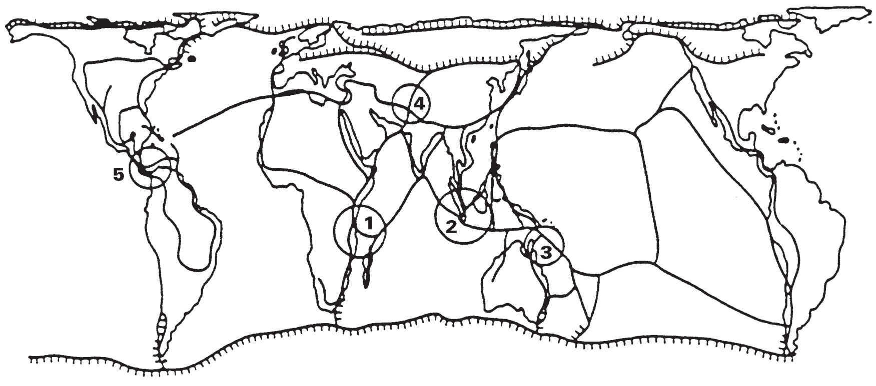

FIG. 2. The main features of global biogeography summarized by Croizat. The lines represent major standard tracks of the globe. The hatched lines highlight northern 'boreal' and southern 'austral' tracks. The major biogeographic nodes involved with intercontinental tracks are numbered 1–5. Note how the Americas are represented twice to emphasize the different Pacific and Atlantic connections. Figure and caption from Grehan (1991), p. 342.

that better conformed to its biogeography. For the same reasons, he undertook an extensive review of the biogeography and systematics of the carnivorous plants and their allies (Croizat, 1961).

Croizat similarly believed that his data on the biogeography of living organisms was so extensive and mutually reinforcing that there was little point in seeking additional data from the distributions of fossils. 'Fossil life cannot genuinely contradict living life' (Croizat, 1964, p. 715) and, because the latter provides so much more information, it provides a better standard. 'Living dispersal much sooner explains fossil dispersal than the other way around' (Croizat, 1964, p. 170).

In my brief 1993 review, I stated that Croizat ' ... paid little attention to the implications of the fossil record'. Grehan (1994) suggests that this is incorrect, and comments that Croizat (1964) provides at least 21 separate entries on fossils and fossilization. However, it is ingenuous to suggest that the twenty-one entries are an indication of Croizat's detailed use of fossils in his methodology. Though Croizat occasionally mentions the fossil occurrence of a group, as in an example of *Acer* that Grehan mentions and figures, nowhere does he make a detailed integration between the fossil record of a group, and therefore its palaeodistribution, and the distribution of the same group today. Most of these entries refer to general statements, such as pointing out the supposed coincidence of the end of the Permo-Carboniferous glaciation and the appearance of the first fossils of mammals, birds and angiosperms, or to an observation that the extinct mammal faunas of the Siwaliks are a perfect biogeographical match for those of southern South America, because in both the extinction was due to orogeny. Furthermore, many of the entries are repetitive, Croizat making the same point several times. For example, four of them (Croizat, 1964, p. 212, 439, 682, 723) refer to the observation that the age of the earliest known fossil is not necessarily the same as the time of origin of the group in question.

Grehan also provides a quotation in which Croizat states that both the coconut and the sedge have the same track because both are found in Europe *(Nipa* as a fossil in the Eocene London Clay, and *Carex* living in the Iberian Peninsula), as well as in the Far East. In fact, this is the *only* example in Croizat's (1964) book of a comparison between the occurrence of a fossil and that of a modern form—and even this is between two different, unrelated genera. Croizat's general approach to fossils was that the fossil record was very limited, and that we do not really understand the morphology and evolution of living organisms, so that fossils are of even less value in establishing the significance of biogeographic patterns (Croizat 1964, pp. 353, 365). He also states that fossils cannot 'contradict' living forms (Croizat, 1964, pp. 450, 715), but that we *can* use the morphology of living forms to contradict that of fossils (Croizat, 1964, p. 307). In fact, nearly all of his comments on the fossil record seem to be implicit justifications of his lack of use of that information.

Croizat also felt that climatic changes, and especially the comparatively recent changes due to the Ice Ages, had been too glibly and frequently used in order to explain details of current biogeography. And, since he did not believe that active extension of range had been a significant factor in determining the current patterns of biogeography, he was firm in his rejection of any suggestion that such recent climatic changes had been an agent for these. So 'climate and ecology do effectively limit the distribution of living forms to ranges of favourable survival, but do not explain why and how these forms got there' (Croizat, 1964, p. 34). He did not believe that recent climatic changes could have caused the endemicity of small areas in the Cape Floral Region, and states that even '*very recent climatic change* may profoundly affect distribution—by reducing formerly widespread populations. But it was not a *recent* climatic change that was responsible for the vegetation surviving there today; this was the by-product of *very long* geological time' (Croizat, 1964, p. 281–2, his italics). Croizat similarly did not use ancient climatic changes as a possible explanation of disjunct patterns of distribution.

PANBIOGEOGRAPHY AFTER CROIZAT

Croizat published his ideas in the 1950s and 1960s. The leading biogeographers of those days, such as Simpson, Darlington and Mayr, had developed their theories during the first half of the century, and had accepted the evolutionary views of Darwin/Wallace and the stability of modern geography and geology, which also seemed to have successfully weathered Wegener's heresies. It was, then, perhaps natural that the reaction of these biogeographers to Croizat's theories, which similarly used biogeographical data as a basis for radical modification to geography and geology, was to seek reasons (or excuses) to reject or ignore them.

Unfortunately, it was all too easy to find such reasons or excuses. Croizat not only rejected the facile use of dispersal as an explanation of all and every example of trans-barrier distribution—he rejected dispersal in any shape or form. Faced with the problem of finding another explanation of the extensive areas of distribution found in many taxa, he merely assumed that the whole area had been occupied by the taxon *ab initio*—which seemed to remove the whole concept of spread from any scientific enquiry (just as 'dispersal' had previously removed it). Geologists could see no evidence for Croizat's suggestion that the Americas had once extended far westwards into the Pacific, or for his concept of 'horstian' dispersal.

It was not until the 1970s that Croizat's suggestion that the gaps between the existing locations of taxa might have appeared *within* an original continuous pattern became one of the concepts that led to the vicariance theory of biogeography (Croizat, Nelson & Rosen, 1974—but see also Croizat [1982], in which he states that the 1974 joint paper misrepresented his views). This has since become generally accepted as an alternative to the view that a new species might arise subsequent to dispersal over an existing barrier. Biogeographers such as Rosen (1975) also realized the potential of Croizat's generalized track as a tool for unravelling the biogeographical complexity and history of a biota, and made it into an even more effective tool with the use of area cladograms (Rosen, 1985). The generalized track technique has also been used in analysing the distribution of South American crayfishes (Morrone & Lopretto, 1994). Both the vicariance biogeographers and most of those who employ Croizat's generalized tracks technique explicitly accept that classic Darwinian dispersal may also take place (see Platnick, 1976; Rosen, 1978; Page & Lydeard, 1994).

These methods rely on congruence—if the pattern of tracks or cladograms is identical for a number of taxa, but differs in a particular detail for another taxon, then it is reasonable to suppose that the aberrant pattern suggests a different history. It is now normally assumed that the majority pattern is the result of vicariance, and that the aberrant pattern may therefore be the result of dispersal—though, as Page & Lydeard (1994) point out, the situation could be reversed, the congruent pattern being the result of a geography that facilitated dispersal and provided little opportunity for vicariance. The explanation of congruent biogeographic patterns in island groups as being the result of vicariance can also be strengthened where these can be parallelled by patterns of change based on geological evidence. The use of these methods led to the appearance of a balanced approach to the problems of island biogeography, e.g. Page & Lydeard (1994) on the West Indies; Michaux (1994) and Boer & Duffels (1996) on the East Indies. These papers integrate distributional, phylogenetic and plate tectonic information to reveal interesting congruences, some of which also support Croizat's suggestions that such 'nodes' as Sulawesi may be composite in both their geology and their biota.

The generalized track and area cladogram approach has also been used by Craw (1988) in a study of the biogeographic relationships between New Zealand and the Chatham Islands. However, he then extends this analysis by the use of a series of concepts which involve new definitions of Croizat's 'track', 'baseline' and 'main massing', and the use of new terms: 'polarity' or 'orientation', and 'ocean baseline'. This technique has been developed by Craw and Grehan in a series of papers since 1978, and is the unique feature of their approach. They and their supporters are almost the only workers who describe their approach as 'Panbiogeography', and it is important to distinguish these new features from Croizat's original methods. Perhaps because of the mid-oceanic position of New Zealand and the surrounding areas, the New Zealand panbiogeographers pay particular attention to the relationship between the biogeographic patterns and the oceans, as will be seen.

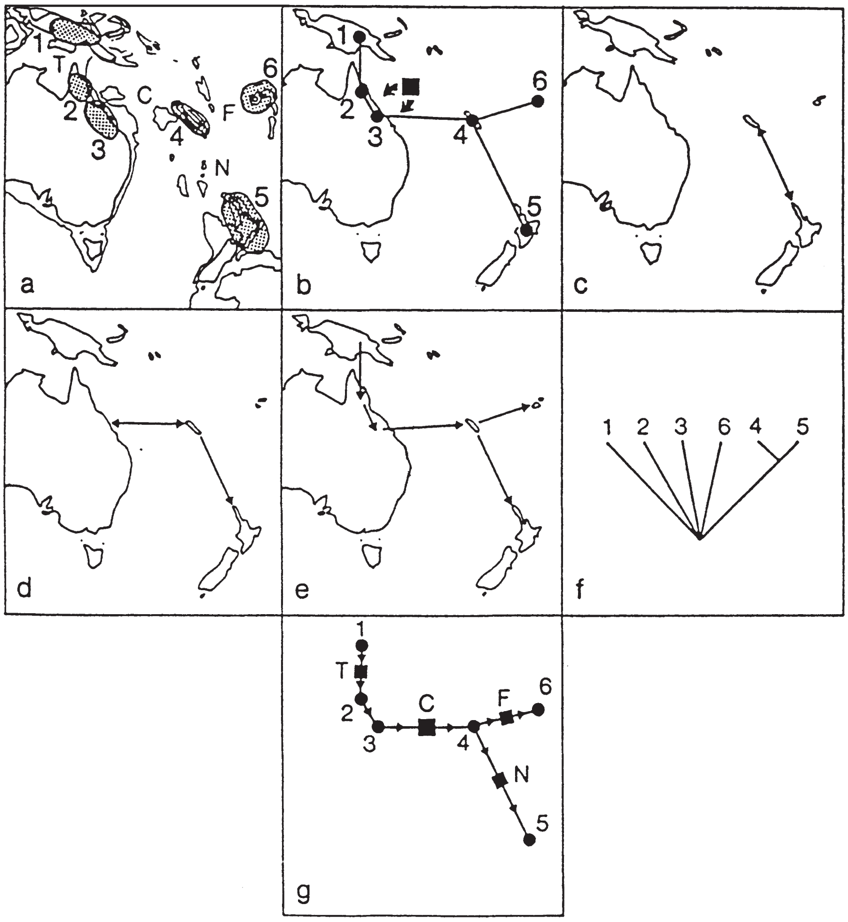

FIG. 3. Track construction, orientation and baseline identification: (a) Taxa 1 to 6 .....are geographically distributed in various parts of Australasia. (b) The track for taxa 1 to 6 with the main baseline (Coral Sea) identified. (c) The initial step in orienting the track by linking the sister taxa in areas 4 and 5. (d) The second link is formed between areas 3 and 4 which then serves to orient the link 4 to 5. (e) The links 1 to 2 and 3 are formed with area 6 being linked to the nearest neighbour in area 4. (f) The fully unresolved phylogeny of taxa 1 to 6. (g) The fully oriented track for taxa 1 to 6 with baselines identified. Figure and caption from Craw & Page (1988), p. 168.

Craw & Page (1988, p. 166) define a track as a 'minimal spanning graph or tree, i.e. an acyclic graph that connects all the localities occupied by a taxon such that the sum of the lengths of the links connecting each locality is the smallest possible'. The 'defining characteristics' of a track are discovered through the orientation of that track. 'Tracks are oriented (i.e. given direction with respect to a sea or ocean basin) by an ordering of collection localities for nearest geographic neighbours within a taxon.' (Craw, 1983, p. 433). The term 'polarity' is also used in the same sense as 'orientation'. However, for the New Zealand panbiogeographers (as for Croizat), a track does not represent a pathway of travel, but is a graphic representation of 'phylogenetic relationships displayed against a geographical baseline. It delineates the area occupied by the ancestral form prior to the evolution of the present form' (Craw, 1979, p. 105). A standard or generalized track therefore represents the pattern of distribution of an ancestral biota (Craw, 1983).

This 'ordering of collection localities' can also involve the concept of a 'main massing', which is a centre of numerical, genetic or morphological diversity (Craw, 1982, 1985)—though Page (1990, p. 289) comments that the concept is 'horribly vague'. The density and geographical closeness of the taxa in a main massing are considered to provide an indication of the origin of the orientation of the track. Page (1987) gives a theoretical example of this technique (Fig. 3). He states that, if the taxa in New Caledonia and New Zealand are sister taxa, a line is drawn between these two groups of islands. The polarity (or orientation) of that line is established by extending it to the next nearest area occupied by the taxon, in Queensland. The fact that New Caledonia is closer to Queensland

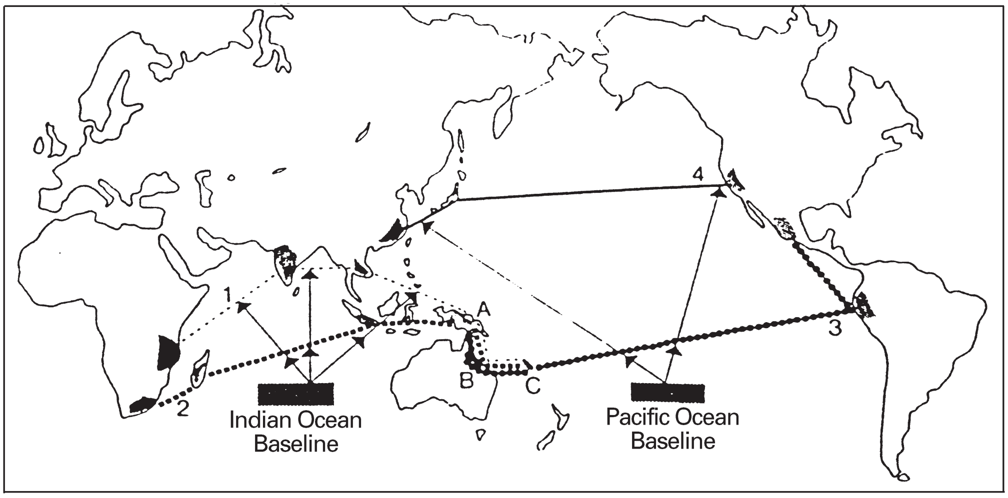

FIG. 4. Mapping of generalized tracks onto a baseline and the concept of a node. Tracks 1 (dashed line) and 2 (squared line) cross or circumscribe the Indian Ocean and can be mapped onto the same baseline. Similarly tracks 3 (beaded line) and 4 (thick straight line) can be mapped onto a Pacific Ocean baseline. Tracks 1, 2 and 3 intersect in areas A, B and C which are recognized as a node. Figure and caption from Craw (1988), p. 416.

than to New Zealand establishes the polarity as running from Queensland to New Caledonia and thence to New Zealand. In similar fashion, the line can be extended back to New Guinea, which is then regarded as the origin of the track as far as these taxa are concerned. If Fiji were to be added, it would be linked to the track via New Caledonia, because it is closest to that island, and would take its polarity from there.

Like Croizat, the New Zealand panbiogeographers aggregate a number of individual tracks into a generalized or standard track because they are ‘compatible/congruent according to some previously specified criteria (e.g. shared baseline, compatible distributions, or congruent area cladograms)’ (Craw, 1989, p. 493). Presumably because the generalized tracks are assumed to be the result of some geological or geographical features or processes that caused the disjunct pattern of distribution, each is assigned to one of a more limited number of ‘baselines’. A baseline may be recognized as resulting from the linkage of two areas of main massing within a taxon; this then acts as an origin of polarity for any other related tracks (Fig. 3).

Geography, phylogeny and geology may be all be used in allocating a track to a particular baseline and, perhaps because of the mid-oceanic position of New Zealand and the surrounding areas, these panbiogeographers concentrate on the interpretation of tracks that cross seas or oceans, and allocate each track to an ‘ocean baseline’ (Craw & Page 1988; Craw, 1988).

‘Relative geographic proximity of a distribution to an ocean basin is the most general feature determining a particular ocean baseline, but in some cases choice of ocean basin may not be readily apparent where, for example, the organism or group is widespread relative to an ocean. In these situations the analysis may include information on relative phylogenetic affinities, either within the group or the relationship to other taxa’ (Grehan, 1988, p. 579). This method results in the identification of a small number of such baselines (the Atlantic, Indian, Southern and Pacific Ocean baselines) across each of the major ocean basins (Fig. 4). ‘The natural biogeographic regions for terrestrial and freshwater organisms are not present-day land areas but the world’s major ocean basins’ (Craw & Page, 1988, p. 180). It is hypothesized that the relationship of these baselines to the ocean basins reflects a relationship to an underlying tectonic process: ‘Panbiogeographers attempt to integrate track geometry with the geometry of the major tectonic features on the earth’s surface (e.g. mid-oceanic ridges, rift lines and transform faults) .... The initial idea of a track baseline as an ocean or sea basin is transformed so that the baseline for a track is where that crosses a major tectonic feature’ (Craw & Page 1988, p. 171). In the case of the Atlantic, Indian and Southern Oceans, this is identified as possibly the widening of these oceans from spreading ridges (cf. Grehan, 1991, Figs. 5 and 17). In the case of the Pacific Ocean, it is instead suggested (e.g. Grehan, 1994) that it may be associated with the movement across the Pacific Ocean of accreted terranes, at least some of which may be fragments of a hypothetical Pacifica continent.

Croizat believed that the intersection of two or more different sets of tracks implied that the point of intersection (his ‘node’ or ‘gate’) is biotically composite, and that this is because it is geologically composite. The New Zealand panbiogeographers point out that many of his nodes, such as the Altai region of Western Tibet, the Tenassarim region at the northern end of the Malay Peninsula, as well as western Borneo and the Celebes, are areas that are now in, or close to, regions that modern plate tectonic theory regards as points of convergence or collision of different plates (Craw & Weston, 1984). They similarly point out that Croizat's 'horstian' theory, that various biotic locations around the periphery of the Pacific were the result of the accretion of formerly separate Pacific islands, is now parallelled by the modern theory of moving terranes that became absorbed in the periphery of the continents surrounding the ocean basins (Craw & Weston, 1984).

DISPERSAL AND CENTRES OF ORIGIN

As noted in the Introduction, the fact that Darwin accepted the prevailing view of stabilist geography inevitably forced him to explain disjunct patterns of distribution as having resulted from chance dispersal across the intervening barriers. This was therefore also accepted by all those who later continued to accept stabilist geography, such as Matthew, Simpson, Mayr and Darlington. However, following acceptance of plate tectonics and of the vicariance approach that stemmed from Croizat's work, it is now difficult to find any biogeographer who, confronted with an unexpected pattern of distribution, would still assume dispersal rather than attempt first to consider the possibilities of a vicariant explanation.

It is, therefore, puzzling that the panbiogeographers present themselves as still struggling against a pervasive Darwinian school of biogeographers who reject their ideas because the panbiogeographers reject dispersal—though they do not give references to these supposedly recent rejections. Grehan (1994, p. 461) refers to 'dichotomies of ecology *v* history, and dispersal *v* vicariance. The imposition of binary oppositions requires the selection of one alternative as if this choice represents the real, natural world. Panbiogeography represents a research programme that is working to deconstruct the strict demarcation between these artificial dichotomies.' In fact, most biogeographers today would accept the reality of both sides of the above two equations, and merely seek in any instance to establish which was the more likely to have taken place.

Though Craw (1989) has stated that panbiogeographers, too, accept dispersal in the Darwinian sense, he also states that it is 'clearly a secondary phenomenon that follows if speciation is allopatric, for before any species can disperse it must have become a species through a process of speciation. If speciation is allopatric then vicariism (whether geographic or ecologic) is prior or primary to dispersal.' (Craw, 1989, p. 531). But it is equally possible that the transformation into a new species only took place *after* dispersal across the pre-existing barrier, and as a consequence of its adaptation to the new conditions experienced after that dispersal. Panbiogeographers still seem to be extremely reluctant to accept the equal possibility of vicariance and of dispersal, and to approach the analysis of biogeographical patterns with an open mind.

In minimalizing any discussion of dispersal, panbiogeographers are also able to avoid any discussion of centres of origin, and they refer to this disparagingly as a 'Darwinian concept'. But, if evolution takes place, it is unlikely that any new taxon will appear at the same time over the whole of the range of its ancestor, by parallel and simultaneous change. Instead, it will appear in one area, to the environment of which it is particularly adapted, and spread from there as and when further evolutionary, environmental or plate-tectonic change permits. Having identified the location of the earliest known occurrence of a taxon, a historical biogeographer will therefore attempt to establish what other areas of the world's surface were in communication with that, and then to accept that the taxon might have evolved anywhere within that area. So, for example, the earliest known marsupials are found in both North and South America in the Late Cretaceous. However, since South America at that time was still in communication with Antarctica and Australia, marsupials may have evolved anywhere in the four continents, and spread from there to the rest of that great area. Only further discovery can resolve the problem further, but that does not detract from the usefulness of the technique in seeking to establish the boundaries of the "centre of origin" of the taxon in both time and space. In acknowledging that this provisional explanation may need to be modified in the light of further discovery, the technique is no different from most other scientific methods of analysis and hypothesis.

Some of the New Zealand panbiogeographers, however, use the term 'centre of origin' in a quite different sense. Thus Grehan (1994, p. 452) states that 'some kind of 'centre of origin' concept is required to resolve the contradictions created by Darwin's birthplace concept of origin'. To him, it is the ocean baselines that now represent centres of origin, presumably because to him they represent the foci of many generalized tracks or patterns of distribution.

AN EVALUATION OF PANBIOGEOGRAPHY

Such New Zealand workers as Craw and Grehan claim that Croizat's concept of 'horstian dispersal' has been validated by the recognition of accreted terranes embedded in the Pacific margin of the Americas, and that further support has been given by the hypothesis that some of the terranes might originally have been part of a now-lost 'Pacifica' continent. They also claim that, by adding the concept of ocean baselines, they have provided a valuable additional analytical tool, which provides a preferable alternative to the system of biogeographic regions. These claims can be considered in turn.

Horstian dispersal and accreted terranes

Croizat's original concept of horstian dispersal, that land had once extended westward from North America to the Hawaiian Islands, is untenable in the face of the evidence from the sea-floor that these islands today are merely the most recent expression of a 'hot-spot'. The eroded remains of other, older islands are still identifiable as submerged sea-mounts, up to 85 my old, extending to the edge of the Kurile trench, having been carried by the motion of the Pacific plate, initially northwards and later westnorthwestwards. The Marquesas, Line Islands, Tuamotus, Cook-Austral Islands, Samoan Islands and the Marshall-Gilbert-Ellis chains of the Central Pacific are similar expressions of underlying volcanic sources which cause the appearance of a line of islands as the Pacific plate passes northwestwards above it; the islands at the northwest end of each chain are therefore the oldest, and those at the southeast end are the youngest (Kearey & Vine, 1990). The island chains that lie to the north and west of these islands (such as the Aleutians, Kuriles, Izu-Bonins, Marianas, New Britain, Solomons, Tonga and Kermadecs) are all island arcs, which have formed where Pacific plate lithosphere is disappearing into ocean trenches. They are therefore the result of westward or northwestward movement of the plate, and could not have been the agents of eastward dispersal of biota across the Pacific.

There seems therefore to be no alternative to the view, long accepted by most biologists, that the restricted taxonomic diversity of the biota of all these Pacific islands is due to overseas dispersal, and not to impoverishment of a once-richer biota following its separation from North America. The fact that their floras become steadily less and less diverse as one moves eastwards or northwards is consistent with the view that most of them have originated in the continents to the west. Trans-oceanic dispersal is also supported by the nature of the biota, which contains a high proportion of organisms that can easily arrive by air (e.g. the spores of ferns; the light seeds of herbs rather than the heavy seeds of trees; insects or birds rather than flightless animals). Overseas dispersal of this kind is not merely theoretical for, since Croizat's day, it has been well documented in studies of the colonization of the island of Rakata, which was created by the eruption of Mt Krakatau in 1883 (Thornton, 1996).

The New Zealand panbiogeographers also suggest that recognition of accreted terranes in the western parts of the Americas provides a mechanism that supports Croizat's belief that the trans-Pacific patterns of distribution can be explained without recourse to the dispersal of organisms. This concept originated from Chamberlain & Lambert's (1985) suggestion that most of the cordillera of western North America, from western Alaska as far south as San Francisco, was originally a separate microcontinent, that they called Cordilleria, itself an amalgam of over thirty microplates and terranes. They suggested that Cordilleria lay on the Kula plate and was transported eastwards on that plate, its initial collision with the North American craton having taken place about 95 my ago; it was then moved *c.*1500 km northwards along the western edge of the craton as the Kula plate moved northwards. Nur & Ben-Avraham (1977, 1978) suggested that areas such as this, now embedded in the circum-Pacific continents, had originated as parts of a single continent, which they called Pacifica and which lay adjacent to Australia/New Zealand/Antarctica within Gondwana. They suggested that Pacifica had broken up, perhaps in the mid-Permian, the fragments then being carried on the Kula, Farallon and Phoenix plates, which lie respectively to the north, north-east, and east to south-east of the Pacific plate, to collide with Asia and the Americas from the late Jurassic to the late Cretaceous. Finally, Kamp (1980) suggested that Pacifica plus eastern New Zealand had separated from the rest of Gondwana in the Carboniferous, and that Pacifica had split from eastern New Zealand in the Late Triassic.

The basic problem for any biogeographer wishing to use these ideas to explain the disjunctions in the circum-Pacific biota lies in the time-scale involved. The problem can be approached from two directions: the geological and the systematic.

Studies of the linear magnetic anomalies resulting from magnetic reversals and recorded by the process of seafloor spreading, have made it comparatively easy to interpret the plate tectonic history of the central and eastern Pacific. If organisms have been carried passively eastwards and westwards to the opposite margins of the Pacific Ocean following the break-up of a single original homeland continent, the resulting fragments of land must have been carried on the plates that border the continents around the edge of the Pacific. The Farallon plate, which borders the Americas, is separated from the Phoenix plate, which borders Australia, by the enormous Pacific plate. It would, then, be the appearance of this latter plate, between the Phoenix and Farallon plates, that initiated this break-up and dispersal. However, the Pacific plate appeared about 185 million years ago (Hilde, Uyeda & Kroenke, 1977)—long before the origin of the angiosperm groups whose disjunct pattern of distribution provided the starting-point to this discussion. Lovis (1989) points out that, in any case, most of the accreted terranes are essentially marine and could not have rafted a terrestrial biota from place to place.

If one instead starts with the systematic evidence, the recent paper by Crane, Friis & Pedersen (1995) provides much useful evidence. After reviewing the important recent advances in our knowledge of the early history of the angiosperms, they conclude (Crane *et al.*, 1995 p. 31) 'Current studies of the fossil record show an orderly sequence of appearance of angiosperm remains beginning with putative magnoliid pollen in the Valanginian, and triaperturate pollen of eudicots around the Barremian-Aptian boundary (or slightly earlier). By the early Cenomanian there are diverse magnoliids, a variety of hamamelids and a few rosiids, which show clearly that several angiosperm families had already differentiated. By the Campanian, Maastrichtian and Palaeocene, many extant families in all subclasses had already differentiated.' It follows that, in order to have been able to carry a diversity of angiosperms to scattered locations around the Pacific rim of the Americas, the break-up of Pacifica would have had to commence between the Cenomanian and the Campanian—i.e. between 95 and 65 my ago. That date is long after the appearance of the Pacific plate, whose expansion is supposed have separated the American and the Asian-Australian representatives of the disjunct angiosperm families, and after the first geological evidence of the docking of fragments at the end of their lengthy journey across the Pacific. Crane, Friis & Pedersen also rule out any appeal to a hypothetical earlier dating for angiosperm evolution that might make such a trans-Pacific journey more plausible, for they state (Crane *et al.*, 1995, p. 31, immediately following the above quotation) 'Claims of pre-Cretaceous angiosperms need to confront this orderly sequence, and although the literature on angiosperm origins is replete with putative pre-Cretaceous angiosperms, most have been shown to be stratigraphically misplaced, unrelated to angiosperms, lacking in diagnostic characters, or too poorly preserved for reliable determination. .... In our view, the absence of distinctive triaperturate pollen grains in numerous, rich, Triassic and Jurassic palynofloras from both hemispheres precludes the long cryptic period of evolution implied by some estimates of rates of evolution, at least for eudicots.'

Like Croizat, Grehan invokes theoretical early extensions of fossil histories, and suggests that, though the earliest recognized angiosperm fossils appeared in the Cretaceous, the group might have originated 'anytime earlier' (Grehan, 1994, p. 460). He uses this to justify the suggestion that there may be a 'common historical relationship' between the patterns of distribution of the fossil bivalve *Monotis* and the living flowering plant *Coriaria*. Grehan gives this as an example of the fact that 'integrated spatial analysis of fossil and living distributions represents a major contribution of panbiogeography to the science of evolutionary biology.' However, I can see no usefulness in such an 'integration' between the patterns of distribution of a Triassic marine mollusc and a living terrestrial flowering plant, while Grehan's *ad hoc* appeal to an unsubstantiated evolutionary event is as unacceptable as the reliance on unsubstantiated dispersal that panbiogeographers so anathematize. Furthermore, Grehan's statement (1994, p. 459) that 'Fossils are often treated as a separate reality in biogeography, and nearly, if not always, in paleontology' is simply untrue, and shows little knowledge of a considerable literature.

I conclude that neither plate tectonics nor the palaeontological record provides any support for the suggestion that the circum-Pacific disjunct distributions are the result of the carriage of organisms across the Pacific on large or small areas of land. These same arguments apply to the panbiogeographers' claim that North and South America are really geologically and biologically composite land masses, having received major biotic elements from both the Pacific and the Atlantic ocean basins (Craw & Page, 1988; Grehan, 1991), and both Cooper (1989) and Lovis (1989) have come to similar conclusions in the narrower context of the origins of the New Zealand biota.

Panbiogeographers claim that it is an independent discipline, the results of which are not privileged over the results arising from geology, ecology and systematics, there instead being a 'process of reciprocal illumination' (Craw, 1988; Grehan, 1994). I would agree with this, and comment that the 'reciprocal illuminations' provided by both geology and systematics strongly suggest that the concept of a Pacific baseline is an illusion arising from an inadequate technique of analysis. It is now time that panbiogeographers ceased merely to complain that other biogeographers do not take their work into account, and instead started to answer the criticisms that have been levelled at their work by showing in what ways these criticisms are wrong. It would also be enlightening if they could show how their methods could explain the biogeography of the Hawaiian Islands, the biota of which is readily interpreted by more conventional methods as resulting from dispersal to and within the Islands plus, at a more detailed level, vicariance.

Ocean baselines

If, as suggested above, the face of the oceans has *not* been traversed by islands or mini-continents carrying a living cargo that is later deposited on the margins of the surrounding continents, there seems little point in trying to combine the generalized tracks to form ocean baselines. Furthermore, the method by which panbiogeographers have allocated taxa to these baselines is quite variable and highly questionable, as can be seen in Craw's (1985) treatment of the biogeography of the primitive frogs, the ratite birds and the southern beech *Nothofagus*, all of which are represented in New Zealand.

The closest living relative of the New Zealand frog *Leiopelma* is *Ascaphus*, which is found in North America. Basing his interpretation on the supposed tectonic history of these two areas, Craw links the two genera directly across the Pacific: 'The distribution of *Ascaphus* in western North America lies largely off the North American craton on the allocthonous (*sic*) cordilleran terranes postulated to have emerged from the Pacific. Other areas such as Mexico and Patagonia where leiopelmatid-ascaphid relatives occur (or occurred) are also not regarded as structural parts of North or South America, but apparently originated in the Pacific' (Craw, 1985, p. 3). It is thus assumed that the present location of taxa represent their original place of origin, and that there has been no extension of their range. If this is a general rule, it is surprising that these taxa are surrounded in their new geographical location by other animal and plant taxa that do not seem to have had any difficulty in extending their range from the 'North American craton' to these intrusive areas. The lack of extension of the range of these frogs is also surprising in view of the fact that they have been in existence for a long time: the earliest ascaphid, *Viaraella*, is from the early Jurassic, and the later Jurassic genus *Notobatrachus* already shows indications of being specialized in the direction of *Leiopelma* (Estes & Reig, 1973), indicating that the divergence between the two living genera had already taken place by then, over 140 my ago. Both these fossil genera are found in Argentina, and a more conventional interpretation of the biogeography of the modern genera would be to see both as relicts of a once-extensive distribution that originated in Gondwana, the ancestors of *Leiopelma* having reached New Zealand before the break-up of East Gondwana.

In the case of the ratites, Craw (1985) bases his decision on phyletic history, stating that closest relatives of the Australian and New Zealand ratites are the ostriches, which he believes originated in Africa. The group is therefore allocated to an Indian Ocean baseline, because this represents the minimum distance between Australia and Africa.

The third taxon, *Nothofagus*, is allocated to the Pacific Ocean baseline, largely because that baseline is considered to join 'main massings' of *Nothofagus* in southwestern South America and in New Guinea. (No regard is paid to the fossil record, which shows that *Nothofagus* was present in Antarctica, and which would therefore suggest a Southern Ocean baseline.) These views are reiterated and supported by Grehan (1988), who states that the allocation to a Pacific Ocean baseline is 'confirmed' by the relationship of *Nothofagus* to *Fagus* of the Northern Hemisphere. (It is therefore surprising that Grehan (1990) states 'it is not crucial to panbiogeographic method whether or not, example, *Nothofagus* is or is not in the Fagaceae'.)

So, in these three examples, the fossil record is used in two cases, but not in the third, and a wholly different criterion (main massing) is used in one example only. The whole methodology is so erratic and variable that it is confusing and unreliable.

Finally, the panbiogeographers claim that the system of standard tracks allocated to ocean baselines provides a more relevant system for biogeographical analysis than the system of biogeographic regions, which largely correspond to the present-day continents. 'Portions of continents, larger islands and island groups are related to one another by standard tracks that span ocean and sea basins. These standard tracks overlap in these land areas indicating that these areas are composite biogeographically rather than being unit regions, sub-regions or areas of endemism. These regions and areas of endemism of de Candollean phytogeography and Wallacean zoogeography are not parts of the real natural world. They are biogeographic and geological boundaries where fragments of two or more ancestral biological and geological worlds meet and combine in space/

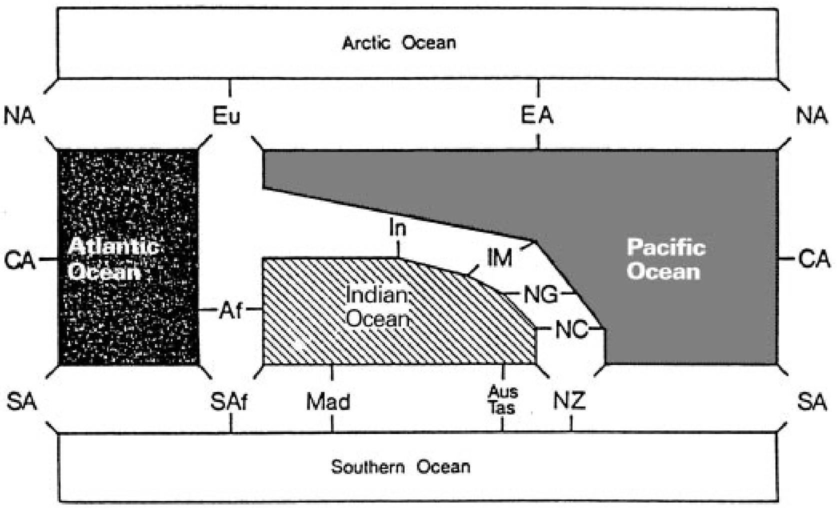

FIG. 5. A new world system of biotic regions based on panbiogeographic analyses. Abbreviations: Af, Africa; Aus/Tas, Australia/Tasmania; CA, Central America; EA, East Asia; EU, Europe; In, India; IM, Indo-Malaya; Mad, Madagascar; NA, North America; NC, New Caledonia; NG, New Guinea; NZ, NeW Zealand; SA, South America; SAf, South Africa. Figure and caption from Craw & Page (1988), p. 181.

time. The natural biogeographic regions for terrestrial and freshwater organisms are not present-day land areas but the world's major ocean basins' (Craw & Page, 1988, p. 180). 'This is illustrated by the novel panbiogeographic system of world biotic regions where the elements (the organisms) and the regions (the environments) are synthesized into one. Here the organism/environment dichotomy is collapsed into a dynamic process metaphysics where geographic distribution [of plants and animals]—is by far not a pack of chance records, but the coherent byproduct of a constant interplay of space, time, form the world over' (Craw & Page, 1988, pp. 183–4) (Fig. 5).

As explained above, there is no evidence to support the assertion that the ocean basins have been the pathways for the long-range dispersal of organisms as passengers on fragments of land. But, even if there had been some truth in the panbiogeographers' belief, the number of organisms involved in these supposed movements across the ocean basins would have been trivial in comparison with the number that have evolved and diversified upon the main continents, or have dispersed from continent to continent when tectonic movements provided new land pathways between North and South America or between Europe, Asia and Africa. It is this, mainly stable, biota that has been used to characterize the classic biogeographic regions, and is far more practical to use this wide-ranging and diverse data as the basis for biogeography, rather than the occasional, hypothetical event.

The validity of the claim that the panbiogeographic regions provide a valuable additional tool for biogeographic analysis can be examined in the context of Craw's (1988) illustration of their use in analysing the biota of New Zealand, and particularly in contrasting them with Fleming's (1979) system of 'biogeographic elements'. (Though Craw (1989) has also used his generalized track technique to analyse the distribution of taxa *within* the New Zealand biota, this analysis does not depend upon the generalized ocean baselines that have been criticized above.)

Apart from very widespread taxa (his 'Cosmopolitan' and 'Holarctic' elements), and those that had no close relatives elsewhere (his 'Endemic' element), Fleming recognized four different elements. Two of these show links with other southern, cool-latitude biotas, and were distinguished as either having arrived in New Zealand before it became separate from other land-masses (his 'Paleoaustral' element) or after that separation (his 'Neoaustral' element). The other two elements show links with subtropical or tropical biotas, further north, and were distinguished as 'Malayo-Pacific' or 'Australian' elements.

Fleming's biogeographic elements are very broad, and he did not attempt to analyse them in terms of past plate tectonic palaeogeography. More serious was the fact that most of his 'elements' include marine organisms (molluscs, echinoderms, fishes) and flying organisms (insects, birds, bats) as well as terrestrial organisms. However, the methods of dispersal of marine organisms, the routes available for their dispersal and their consequent biogeographic patterns, are quite different from those of terrestrial organisms. Similarly, organisms that fly or have wind-dispersed spores or seeds can cross sea-barriers much more readily than can organisms that are confined to terrestrial life and dispersal. Fleming's placing together of members of all these categories is therefore not helpful to biogeographers who are concerned with the origins of the terrestrial components of the biota of New Zealand. For them, there are several important questions. Where did a given taxon come from, and what does its fossil history, or the biogeography of its relatives, tell us of its possible time of arrival in New Zealand? Do other organisms show a similar pattern, suggesting association into a single generalized track? Does its pattern raise any problems that involve either a dispersalist or a vicariant relationship to an ecological barrier and, if so, does this reflect similar patterns in other taxa?

Few biogeographers today, therefore, would accept Fleming's system, and Craw (1988) would have proved very little had he shown that his system of panbiogeographic ocean basin regions is superior to that of Fleming. But in fact it is not, for Craw's Southern Ocean and Pacific Ocean regions each contain examples from six of Fleming's elements, and his Indian Ocean region contains examples from two of Fleming's elements. As a result, Craw's system is inferior to that of Fleming, for it provides no information whatsoever on the time, or the probable geographic origin, of any of the taxa concerned.

The panbiogeographic system of Craw and his supporters merely allocates all taxa to a limited number of baselines corresponding to the ocean basins, with no further comparison of the contents of each ocean-basin group, such as the dates of their origin or dispersal, or of correlation with the dates of tectonic activity in the basins. This may be contrasted with, for example, the results of more traditional biogeographic analysis of the history of the South American mammal fauna. Here, the times of origin and diversification of the different groups, the dates of appearance of new groups in the continent (rodents and primates in the Oligocene, many other groups in the Pliocene-Pleistocene) and their possible source areas, the timing of orogenies and their subsequent effects, via climatic change, on the competitive interaction of the mammal groups, are all integrated into a convincing explanation (e.g. Marshall & Sempere, 1993). It would be interesting to know how panbiogeographers would interpret these phenomena.

Craw is nevertheless convinced of the superiority of the panbiogeographic method, and explains this in the following terms: 'The philosophical basis for the differences between the two biogeographic classifications is the differing conceptions of space underlying each. The elements classification is based on an absolute concept of space and a rigid division between organisms and their environments. The elements classification postulates a separate universe of organisms (the elements) which are moving through absolute geological time into a separate three-dimensional environmental space (the New Zealand subregion). In contrast the panbiogeographic classification is based upon a relational concept of space. Here the rigid organism/environment dichotomy collapses and the regions and elements are synthesized into one.' (Craw, 1988, p. 427-430). I find little scientific substance in these semi-metaphysical 'explanations'.

CONCLUSION

I conclude that Croizat's original formulation of Panbiogeography was valuable in providing the insight and stimulus that eventually led to vicariance cladistics and the technique of constructing generalized tracks, and that there also appears to be an interesting congruence between some of his nodes and the biogeographical patterns of some island groups. However, the more recent modifications to his theory, involving the use of a limited number of 'ocean baselines', do not result in the identification of novel, valuable groupings of biogeographical phenomena that provide new insights into underlying regularities of nature, nor do the ocean basins themselves provide a system preferable to the Wallacean biogeographical regions.

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BIOSKETCH

Before his retirement in 1996, Barry Cox was Professor of Biology at King's College, London. Starting his research career in vertebrate palaeontology, Professor Cox became interested in the relationship between the patterns of distribution of Mesozoic and Early Cenozoic land vertebrates and the patterns of land that resulted from plate tectonics and epicontinental seas. He is currently, with Peter Moore, writing the sixth edition of their book *Biogeography—an ecological and evolutionary approach* (Blackwell Science). He has written many papers on Permo-Triassic mammal-like reptiles, on Mesozoic biogeography and on the principles of historical biography.