BIOGEOGRAPHIC PATTERNS OF TERRESTRIAL VERTEBRATES IN THE SOUTHWEST PACIFIC

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(Received January 7, 1980)

ABSTRACT


A unified biogeographic history of the Southern Hemisphere biota is beginning to emerge, and vertebrates, invertebrates, and plants are seen to exhibit many similarities in the patterns of their phylogenetic relationships. Terrestrial vertebrate biogeographic patterns are reviewed based on present knowledge of phylogenetic relationships; the major patterns (generalized tracks) and their taxonomic components include: (1) Australia—South America: leptodactyloid-like frogs, possibly hylid frogs; melolaniid and chelid turtles; ratite, galliform, anseriform, and caprimulgiform birds; marsupials, possibly monotremes; (2) New Zealand—South America: leiopelmatid frogs; ratite, sphenisciform, and gruiform birds; (3) New Caledonia—New Zealand: gekkonid and scincid lizards; gruiform birds; (4) New Zealand (+ New Caledonia)—Australia/Southeast Asia: gekkonid and scincid lizards; most birds; vespertilionid bats; (5) Australia—Southeast Asia: ranid, microhylid frogs; agamid, scincid, varanid lizards; pythonine, colubrid, elapid snakes; many non-passeriform and passeriform birds; murid rodents.

In most cases generalized tracks are best interpreted as vicariance of an ancestral biota into two or more descendant biotas. Dispersal across geographic or climatic barriers is less efficacious as an explanation for generalized tracks than is vicariance; post-vicariance dispersal is a hypothesis difficult to test. Centers of origin and pathways of dispersal of component elements of a generalized track prior to vicariance can be investigated using cladistic analysis.

INTRODUCTION

It has become apparent in recent years that the distributional patterns of plants and animals are related in some manner to the complex history of the world’s lands and oceans. In this regard, probably few subjects have received more attention than the history of the southern continents and their biota. Much has been written about this (Keast, 1971, 1973; Raven and Axelrod, 1972; Cracraft, 1974a, 1975a, b; Stevens, 1977), and as this paper will attempt to point out, many interesting problems remain to be investigated. In one sense a study of the Southern Hemisphere biota is of special significance because it is a microcosm, so to speak, of biogeographic analysis in general.
the history and controversy surrounding the method of biogeography has traditionally relied on the biota of the southern continents for many of its examples. One need only list the names of Hooker, Darlington, Simpson, Hennig, Brundin, and Croizat to evoke a feeling for the role the Southern Hemisphere biota has played in the conceptual development of biogeography. I would suggest, and I suspect the papers of this symposium will provide ample evidence, that all the long-standing questions regarding the method of biogeographic analysis are still with us.

The purposes of this paper are two-fold: (1) to use the distribution patterns of Southern Hemisphere vertebrates to illustrate some of the controversies in biogeographic method and to relate this discussion to the question of reconstructing the history of the Southern Hemisphere biota as a whole, and (2) to up-date our knowledge about terrestrial vertebrate distribution patterns in the Southwest Pacific region of the southern continents.

What is the method of biogeography?

There has been much heated discussion over the past few years about the proper method of biogeographic analysis. Basically, two schools of thought have emerged. On the one hand, we have the vicariant biogeographers who seek to explain biogeographic patterns primarily in terms of the vicariance of an ancestral biota into two or more descendant biotas. Dispersal of faunal elements from one region to another is accepted under this model but is not considered to have been important in establishing world biogeographic patterns. On the other hand, more traditionally oriented biogeographers, while clearly recognizing the vicariance of biotas via continental drift or other geological or climatological events, continue to emphasize the role of dispersal in explaining major patterns of distribution.

At first the differences between the two schools might seem to be minor, merely reflecting a greater or lesser emphasis on the role of dispersal, and to some extent this is true. However, I think the differences are fairly fundamental and seem to be philosophical in tone: the vicariance school extols the virtues of the testability of biogeographic hypotheses and focuses its analyses at the level of whole biotas, whereas the more traditionalists do not discuss the question of testability to any significant extent and concern themselves with explaining the distribution patterns of individual components of a biota.

Both schools recognize the importance of phylogenetic relationships and thus identify the individual track as a significant biogeographic datum. Thus, a track is a line connecting the distributions of two taxa that are hypothesized to be each other's closest relative (i.e., Hennigian sister-groups). Coincidence of a number of individual tracks forms a generalized track which invites some general explanation. It is at this point of the analysis that the two schools begin to differ. The vicariance biogeographer would postulate the generalized track to represent an ancestral biota that became vicariated into
two descendant biotas and would then search for some geological or climatic event that may have resulted in this vicariance (Croizat et al., 1974). The more traditional biogeographer would, I think, not deny the possibility of a vicariance event but rather than applying that event to each component of the generalized track would attempt to identify those that are likely the result of dispersal postulated to postdate the vicariant event. These two interpretations can be illustrated by the writings of the following workers:

According to the vicariance viewpoint:

"A generalized track which includes the individual tracks of many different monophyletic assemblages may connect adjoining or distant clusters of distributions. These clusters of distributions may be inferred to be fragments of the distribution of a parent biota . . . One feature of the method is that it requires no prior judgments about a former history of dispersal and the geological ages of distributional events are resolved by application of the method"

[Rosen, 1975, pp. 432–433]

Recently McDowall (1978) criticized the vicariance approach from a dispersalist point of view:

"...individual tracks demonstrate only the reality of existing biotic relationships and say nothing about any hypothetical ancestral biota . . . which can be shown to have existed only by the collection of fossils. The inclusion of any extant individual taxon within the ancestral biota is by assumption . . . Instances can be found . . . where parts of the fragmented biotas, which appear to belong to a generalized track (and thus to the hypothesized ancestral biota), are in fact the result of recent dispersal . . . if the biota did exist, how much of the biota persisting on the geographical fragments was derived from the ancestral biota can never be determined".

[McDowall, 1978, p. 90; italics added, see below]

The dispersalist argument, as typified by McDowall (1978), seems founded along two lines of argumentation: first, an empirical one in which "known" dispersal events are said to make a general vicariance explanation untenable, and second, a philosophical one which essentially states that hypotheses are not to be admitted into our analytical system because of our inability to actually know the truth of what is being hypothesized.

Thus, the first argument can be epitomized by McDowall’s (1978, p. 91) own example:

"If the whitefaced heron (Ardea novaehollandiae) coincides with an Australia–New Zealand track, is its dispersal and the age of its distributional event related to the subdivision of an ancestral biota, and resolved by the generalized tracks method? If so, then this bird is in New Zealand and Australia as a result of a geologically caused vicariance event in the Mesozoic! This is demonstrably false. The species dispersed from Australia to New Zealand in the twentieth century. How many more taxa in the Australia–New Zealand track did the same?"

The vicariance biogeographer would respond to this example by noting that the whitefaced heron is taxonomically undifferentiated within the areas of allopatry (Australia–New Zealand) and therefore of no significance as far as defining an individual track within the generalized track (see below). If there were reason to believe the heron of New Zealand is taxonomically
distinct and the sister-group of the Australian form, then a track would be indicated. Whether dispersal might be involved is a separate issue.

The second argument of the dispersalist is a fundamental one, it seems to me, because to accept it would probably require the abandonment of any rational scientific approach to historical biogeography. The argument is that we are not to concern ourselves with knowledge, the truth or falsity of which cannot be known. This attitude is implied in the italicized portions of the quotation cited above, and is much more explicitly stated in other passages (McDowall, 1978):

"that a generalized track estimates an ancestral biota is wholly an assumption, even if a reasonable one, which can not be proved or disproved". [p. 90]

"... common patterns have common causes. While this [working principle of vicariance biogeography] may often be true, to assume its general truth is another matter". [p. 91]

"The assumption [that generalized tracks invite a general explanation] has no demonstrated logical or scientific basis — it is a guess, even if a good one, and should be recognized for what it is. And there is no way that it can logically be questioned or falsified. It is probably correct in some instances, wrong in others, and there is no way of deciding which. If one accepts the assumption as correct, one proceeds on that basis, and that appears to be the end of the matter. There is no basis here for sensible discussion".

[p. 91]

"Is the explanation for this geographically caused vicariance dating back to the Mesozoic? Or is it dispersal? There is no way of knowing". [p. 91]

"If independently derived biogeographic and geological hypotheses are in harmony, support for the hypothesis is evident. But there is no proof that the two events were coincident in time". [p. 92—93]

"How can one test for events that may occur once, a few, or even many times but which leave no trace of having occurred?" [p. 95]

One might reasonably conclude from these quotations that McDowall (and other dispersalists in sympathy with his views — and there are no doubt many) is interested in only that which we can have certain knowledge of. But surely science cannot proceed in this manner. The significance of generalized tracks is that they are comprised of taxa postulated to be sister-groups, that is, allopatric taxa postulated to have taxonomically differentiated on either side of a barrier. Thus, a generalized track is in some sense analogous to a theory of relationships for two species: just as we hypothesize the two species to have been previously one, likewise the two biotas are postulated to have been one. Knowing whether the biota existed is beside the point, for scientific knowledge would seem not to advance by this method. Rather, we are interested in formulating hypotheses and subjecting them to some rational evaluation but without concern for whether they are true or not. I would suggest that adopting the position that

"There is, to my knowledge, no way of discriminating between forms lying within generalized tracks that have achieved their existing range by geological/vicariance events and those that have achieved the same range by dispersal/vicariance". [McDowall, 1978, p. 101]

denies all possibility of a rational approach to biogeographic analysis and thereby eliminates hope of a growth in our knowledge. Logically, the position
stands as a refutation of any hypothesis simply on the grounds that we cannot in fact assess its truth. So regardless of how reasonable McDowall’s case may sound, I have profound philosophical reasons for rejecting it: we simply have two different epistemological worldviews.

Historical biogeography can be approached from two viewpoints: the analysis of pattern and the analysis of process. Clearly, knowledge of pattern is essential, for without it there would be no way of evaluating hypotheses about process. I believe the primary goal of historical biogeography is to elucidate the distributional pattern of genealogy. Basically, this consists of determining phylogenetic (cladistic) relationships and displaying them on a map: Croizatian individual tracks are a direct manifestation of this procedure. It is then of interest to see whether individual tracks coincide with one another; indeed, it is easily seen that individual tracks are not randomly distributed and that generalized tracks are formed. I view generalized tracks as essentially hypothetical in structure—not only because my philosophical worldview accepts all scientific statements as being theory-laden but also because individual tracks are themselves hypotheses.

The most significant point about generalized tracks is that they pose the major question of historical biogeography: why are biotic distributions nonrandom? It is at this point that the biogeographer considers hypotheses about process to explain the existence of generalized tracks, and there seem to be only two processes: vicariance and dispersal.

McDowall (1978) is correct in noting that we can never know for certain whether individual components of a track exhibit their differentiation as a result of vicariance or following dispersal. But the problem at hand is not the explanation of each individual track or component; the relevant issue is to formulate a hypothesis to explain the generalized track. In most cases vicariance is to be preferred because it is the simplest hypothesis, not because there is any a priori reason to believe its truth, but because its adoption seems to involve the fewest ad hoc assumptions.

A vicariance explanation appears to require only one fundamental assumption: that speciation, for the most part, proceeds allopatrically following isolation by a newly formed barrier. Modern day studies of speciation suggest this is a reasonable working assumption.

On the other hand, to invoke dispersal as a causal explanation for a generalized track necessitates more complex justification. First, one must assume that the non-random pattern of phylogenetic relationships signified by the generalized track is the result of numerous independent dispersal events. As such, this explanation would not seem to be open to any meaningful criticism— in effect, dispersal could be used to explain everything, thereby explaining nothing. Moreover, a dispersal hypothesis generally assumes that taxonomic differentiation postdates a recognized vicariance event. There seem to be only two kinds of data that perhaps could be used to examine that assumption. The first is paleontological support of some kind, but what form might this take? If the hypothesis is that the dispersal postdated the
vicariance event, and if we assume that differentiation took place soon after colonization, then the discovery of a fossil of the descendant species prior to vicariance would falsify this hypothesis. The absence of that fossil taxon in the recipient area prior to vicariance would be consistent with the hypothesis. If we hypothesize dispersal and differentiation prior to vicariance, then the falsifier would consist of showing that the ancestral species or its descendant were not present in the recipient area: paleontological data could not provide such a falsifier because of the ad hoc statement that search for the fossil has been inadequate, or that sediments of the critical age are not present. In general, then, it would seem that paleontology has little or no relevance for examining dispersal hypotheses.

The second kind of data that is used to infer dispersal is the extent of differentiation: usually it is assumed that the degree of differentiation is directly related to the time of isolation. This argument, of course, must be based on an assumption of a uniform rate of evolution across the entire spectrum of taxa contributing to the comparison. Such an assumption would appear to be unwarranted; moreover, it could be invoked only if we knew the precise cladistic relationships of the species involved, if we could quantify (more or less) change, and if we in fact knew the age of the speciation (dispersal) event, which is what we are trying to estimate in the first place. Thus, except for an intuitive feeling on the part of the biogeographer, there is no objective way to predict the time of dispersal from the degree of differentiation.

In summary, then, vicariance explanations of generalized tracks are more economical than those of dispersal. This is not to deny the presence of dispersal components within a generalized track, only that it is difficult to make a scientific evaluation of them. I can think of two ways in which a vicariance explanation could be falsified or challenged. The first is to refute the sister-group relationships of the individual tracks and thereby eliminate the necessity of a speciation (vicariance) event. The second is to appeal to geology and argue that there is no evidence for a vicariance event, or even better, that there is strong evidence against one. For example, I have previously invoked the latter "falsifier" in a discussion of the Australian—Southeast Asia and South America—Central America tracks (Cracraft, 1975a); both tracks—and their structures—are not strictly comparable to typical vicariance tracks—seem explicable in terms of dispersal.

In an attempt to formulate a more rigorous approach to vicariance biogeography, Platnick and Nelson (1978) and Rosen (1978) have extended previous work to detail a method to help solve the problem I have been addressing: how do we distinguish between the two causal processes, vicariance and dispersal. Basically, they show that the primary datum of biogeography is the three-taxon statement, that is, a statement about the interrelationships of three taxa, each endemic to a different area:

"Analysis of three-taxon statements involves converting a hypothesis about the interrelationships of taxa (a cladogram indicating relative recency of common ancestry) to one concerning the interrelationships of areas (a cladogram indicating relative recency of
common ancestral biotas). The generality of the area hypothesis may be tested by comparison with other groups endemic to the relevant areas. If the area hypothesis is corroborated as general, a statement of the relative recency of interconnection among areas is obtained, and evidence from historical geology may allow us to specify the nature of those interconnections and thereby the cause of those distributions that conform to the general pattern”.  

Clearly, if numerous phylogenetic patterns conform to a given area-cladogram, then a vicariance explanation will be strongly indicated; dispersal, after all, would not be expected to yield consistent patterns across diverse taxonomic groups. As these authors note, dispersal can be made consistent with any area-cladogram, and thereby loses its utility as a scientific hypothesis: how can it be criticized?

If the vicariance approach is open to criticism, it is that the model de-emphasizes testable, pre-vicariance dispersal hypotheses for individual groups within generalized tracks and therefore may underestimate the role dispersal has played in establishing those tracks (in this context I am not referring to the role of dispersal advocated by dispersalist biogeographers such as Darlington and McDowall; see below). Moreover, the area-cladogram concept of some vicariance biogeographers (Platnick and Nelson, 1978; Rosen, 1978), although indispensable for the analysis of general biogeographic pattern, may be misleading if area-cladograms are used to infer the biogeographic histories of individual groups distributed in these areas (see Brundin, in press, for an extended discussion of this problem).

As pointed out by Platnick and Nelson (1978) traditional dispersalists invoke dispersal across an isolating barrier whereas the vicariance model readily accepts dispersal prior to the initiation of the vicariance event. Confusion will persist in the minds of many unless this point is understood. The discussions of the previous pages were directed against invoking across-barrier dispersal as an explanation of generalized tracks. These arguments do not stand as a rejection of dispersal prior to vicariance; this aspect of dispersal, although clearly recognized by vicariance biogeographers, has not been appreciated sufficiently. Brundin (in press) notes that some recent papers in vicariance biogeography ignore the detailed analysis of this pre-vicariance dispersal, choosing not to concern themselves with centers of origin and pathways of dispersal upon the pre-vicariance landscape (see the Discussion for some examples among the vertebrates).

Moreover, cases of supposed vicariance, when subjected to critical phylogenetic analysis, can sometimes be interpreted as dispersal. For example, the distributions of Andean species have been explained as the vicariance of widespread ancestral species following uplift of the mountain ranges. Phylogenetic analysis of the chironomid midges, however, indicates that, at least in this group, their biogeography is best interpreted as involving northward dispersal of southern cool-temperate forms. The relationships of the Andean chironomids are to taxa to the south, not to tropical counterparts in the adjacent lowlands. This does not mean, of course, that vicariance has not been
involved, only that phylogenetic patterns suggest peripheral dispersal, apparently across some geographic barriers.

Traditional dispersalist biogeographers cannot take comfort from this discussion. Virtually to the person they have ignored the importance of phylogenetic (cladistic) relationships in evaluating biogeographic hypotheses. If hypotheses about dispersal are to be testable, they must be expressed not only in terms of phylogenetic pattern but also in terms of generalized tracks.

SOME BIOGEOGRAPHIC PATTERNS OF TERRESTRIAL VERTEBRATES IN THE SOUTHWEST PACIFIC

In this section I want to review and outline some major biogeographic patterns of terrestrial vertebrates in the Southwest Pacific region (Fig.1). One hesitates to call these patterns generalized tracks because other biotic elements will not be discussed. Nevertheless, all these patterns seem to have some generality in that plants and other animals exhibit notable coincidence in their distributions with those of the vertebrates.

Without doubt the central problem of any analysis of vertebrate biogeography is our lack of understanding of phylogenetic relationships. This is

![Diagram of some generalized tracks occupied by terrestrial vertebrates in the Southwest Pacific.](image-url)
underscored by the fact that as these relationships have become better known over the past five years or so, the biogeographic patterns have become strikingly clarified. Hence, it is certain we have much to look forward to in the ensuing years.

This deficiency in our knowledge of relationships presents us with a critical problem: for only a few groups is it possible to construct three-taxon statements or four-taxon statements in the manner suggested by Platnick and Nelson (1978) and Rosen (1978). In many cases a general statement of relationships can be made, but at this time these statements cannot be formulated as precise phylogenetic hypotheses. Moreover, the geological picture of the Southwest Pacific is quite complex, therefore a clear-cut areal cladogram does not emerge from present data. For example, the times of separation between New Zealand and New Caledonia (the vicariance event here was probably marine transgressions), New Zealand and New Caledonia from Australia, New Zealand from West Antarctica, and West Antarctica from South America are probably all Late Cretaceous in age. Certain biological data presented below suggest that the break between New Zealand and New Caledonia postdated those between New Zealand and South America (via West Antarctica) and between New Zealand and Australia. Unfortunately, not enough is known about relationships to construct moderately corroborated hypotheses based on the vertebrate taxa alone.

Consequently, in this paper I will simply convey what the current phylogenetic data indicate about biogeography and from these make some areal cladogram hypotheses that can be tested by future data. In this discussion I am making no prior assumptions about the age of any taxon. As mentioned above, I find no firm basis on which to state that a particular sister-group relationship involving a group of species, genera, or families is of some more or less specified age. I simply cannot tell, and prefer to let the geographical patterns of genealogy speak for themselves. I will, however, attempt to hypothesize the age of some branch points based on the presumed age of a vicariance event.

*Australia—South America track*

There is fairly strong evidence now for a generalized track running from Australia across East Antarctica to South America, and vertebrates contribute significantly to it (Table I). In addition to ceratodontid and osteoglossid fishes, many terrestrial vertebrates are involved.

Amphibians exhibit some very suggestive transantarctic patterns, but statements about phylogenetic relationships are hopelessly imprecise at this time. The cyclorane and myobatrachine frogs of Australia, which may or may not be closely related, are generally considered to be allied to leptodactyloid frogs, particularly those of South America (Lynch, 1971; Heyer, 1975). The Australasian hyloid-like frogs of the genus *Litoria* are said to be distinct from Asiatic hylids (Tyler, 1971), and this opens the possibility for a link with South American forms.
TABLE I

Vertebrate components of generalized track between South America and Australia

<table>
<thead>
<tr>
<th>South America</th>
<th>Australia</th>
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<tbody>
<tr>
<td><strong>Amphibians</strong></td>
<td></td>
</tr>
<tr>
<td>Leptodactyloids</td>
<td>Myobatrachidae</td>
</tr>
<tr>
<td>Hylidae</td>
<td><em>Litoria</em> hylids</td>
</tr>
<tr>
<td><strong>Reptiles</strong></td>
<td></td>
</tr>
<tr>
<td>Meiolaniidae</td>
<td>Meiolaniidae</td>
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<tr>
<td><em>Hydromedusa</em> chelids</td>
<td><em>Chelodina</em> chelids</td>
</tr>
<tr>
<td>Other chelid genera</td>
<td><em>Pseudemydura</em> chelids</td>
</tr>
<tr>
<td></td>
<td><em>Emydura—Elcya</em> chelids</td>
</tr>
<tr>
<td><strong>Birds</strong></td>
<td></td>
</tr>
<tr>
<td>Rheidae (+ Struthionidae)</td>
<td><em>Casuariidae + Dromiceidae</em></td>
</tr>
<tr>
<td>Suholder Galli</td>
<td><em>Megapodiidae</em></td>
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<tr>
<td>Other anatids (+ anhimids)</td>
<td><em>Anseranatidae</em></td>
</tr>
<tr>
<td>Nyctibiidae + Caprimulgidae</td>
<td><em>Aeogothelidae + Podargidae</em></td>
</tr>
<tr>
<td><strong>Mammals</strong></td>
<td></td>
</tr>
<tr>
<td>Prototheria (?)</td>
<td>Prototheria (Monotremata)</td>
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<tr>
<td>Metatheria</td>
<td>Metatheria</td>
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</tbody>
</table>

Within reptiles several groups of turtles are components of this track. The fossil meiolanids are distributed in Australia and South America, but to my knowledge there has been no critical analysis of their relationships. The relationships of the chelid turtles, on the other hand, have been studied extensively by Gaffney (1977). His results indicate a complex pattern of transantarctic relationships (Fig.2). At least two individual transantarctic tracks are suggested, but given the pattern of relationships it would appear some dispersal has occurred.

Birds provide some of the best documented components of the Australia—South American track. The ratites and galliforms have been discussed elsewhere (Cracraft, 1973, 1974b). Another transantarctic relationship is probably provided by the Anseriformes. The South American Anhimidae are the sister-group of the waterfowl family Anatidae. Within the anatids the peculiar Australian magpie goose (*Anseranas semipalmata*) is thought by most workers to be the sister-group of the other waterfowl. A number of the higher taxa of anatids exhibit disjunct distributions around the Southern Hemisphere, so a more detailed analysis of these relationships will be necessary before we can correlate specific branch points with certain vicariance events. Nevertheless, these relationships are suggestive of a transantarctic distribution pattern. Within the caprimulgiforms the Australian—New Zealand groups Aegothelidae and Podargidae appear to be the sister-group of the Caprimulgidae + Nyctibiidae (Fig.3; Cracraft, in prep.). The latter family is South American in distribution as is the monotypic Steatornithidae, the sister-group of the above four families. A transantarctic track is indicated.
Fig. 2. A cladistic hypothesis for the genera of chelid turtles (after Gaffney, 1977). Distributions of common ancestral species are hypothesized (but see also text). At least two transantarctic dispersal events are suggested.

Fig. 3. A cladistic hypothesis of the avian order Caprimulgiformes (Cracraft, in prep.). The relationships within the Aegothelidae follow the evidence of Rich and McEvey (1977). Distributions of common ancestral species are hypothesized.

The distribution of the Monotremata is certainly relict, their closest known relatives apparently being the Laurasian multituberculates. One can only hypothesize that their biogeographic affinities are Gondwanian. It is now
generally agreed that the presence of marsupials in Australia can be attributed to an ancestral distribution across East Antarctica to South America (Tedford, 1974; Lillegraven, 1974), although it should be noted that we lack a precise hypothesis of relationships that would support this interpretation.

**New Zealand—South America track**

Few vertebrate groups of New Zealand seem to have relationships to taxa in South America, although the taxa that do speak strongly for an ancestral biota along this track. The leiopelmatid frogs are primitive in structure and no systematic studies have yet made a strong case for a particular phylogenetic hypothesis. There are, however, two genera (*Vieraella, Notobatrachus*) from the Jurassic of South America that are apparently similar to *Leiopelma* (Estes and Reig, 1973), thus indicating some support for a New Zealand—South American track.

Birds provide all the other vertebrate components of this track. The moas and kiwis are related to ratites and have connections through South America rather than Australia (Cracraft, 1974b). The penguins of New Zealand appear closer to the extinct taxa of Seymour Island than they do to Australian taxa. The extinct genus *Aptornis* of New Zealand seems closely related to *Rhynochetus* of New Caledonia (Olson, 1977, p. 373; S. L. Olson and R. Zusi, in prep.; also see below), and they in turn are related to the monotypic *Euryptygidae* of South America (Cracraft, in prep.), thus indicating membership in this track (Fig.4).

![Fig.4. A cladistic hypothesis for some taxa of the avian order Gruiformes. *Rhynochetus* and *Aptornis* appear related (Olson, 1977; Olson and Zusi, in prep.) and they, in turn, are related to *Euryptyga* and other gruiforms in South America (Cracraft, in prep.). Distributions of common ancestral species are hypothesized. There are several lineages of gruiforms within South America, thus suggesting dispersal of the ancestor of *Rhynochetus* and *Aptornis* across West Antarctica prior to vicariance (see text).](image-url)
New Zealand—New Caledonia track

Four groups of vertebrates show apparent patterns of phylogenetic relationships between New Zealand and New Caledonia. The geckos of New Caledonia are probably related to those of New Zealand rather than to taxa in Australia—New Guinea (Kluge, 1967; A. P. Russell, pers. comm., 1978), although a proper cladistic analysis has not yet been presented. The scincid lizards of New Zealand appear to have their close relatives distributed, not in Australia, but in New Caledonia and other islands to the north (Hardy, 1977). As noted above, the bird Rhynochetos jubatus of New Caledonia is related to the extinct New Zealand genus Aptornis (two species). The species of Aptornis were flightless and Rhynochetos also, and their sister-species in South America, Eurypyga helias, is virtually so. We would infer, therefore, that the common ancestors of these species had greatly reduced capacity for flight. A parallel example may be found among the rails (Rallidae). The endemic flightless Gallirallus australis of New Zealand apparently has its nearest relationship with the genus Tricholimnas which includes flightless species distributed on Lord Howe Island and New Caledonia (Falla et al., 1966, p. 106). If these relationships are correct, then the inference can be made that the common ancestor was also flightless.1 These latter two examples also lead to the inference that these various avian species, or some as yet unknown ancestors, may have responded to Late Cretaceous vicariance events, thus suggesting that some bird species may be much older than previously thought.

Australia—New Zealand (+ New Caledonia) track

There are strong relationships between Australia and New Guinea, on the one hand, and New Zealand and/or New Caledonia, on the other. To be sure these areas have species in common that are interpretable in terms of dispersal. But these areas also have endemics, and for the reasons given earlier, it is not possible to specify the ages of this differentiation.

The New Zealand—New Caledonian assemblage of geckos appears related to forms in Australia (see discussion in Cracraft, 1974a, p. 233). The syste-

1The systematics of these species of rails is not well known. The species of Tricholimnas sylvestris of Lord Howe Island and T. lafresnayanus of New Caledonia, may not be related. The perplexing situation regarding species interrelationships is exemplified by the latest opinions on the subject (Olson, 1973, p. 398): "there is nothing to indicate a relationship between sylvestris and lafresnayensis. Clearly they have been derived independently and each is more closely related to some volant ancestor than to the other. Whether this ancestor was the same for both species cannot now be discerned." That these species (and G. australis) were all independently derived from a flying ancestor is not yet supported by a well-argued phylogenetic hypothesis; parsimony requires that if we have a hypothesis in which two flightless species are hypothesized to be each other's closest relative, then we should infer that their common ancestor was flightless.
matics of New Zealand and New Caledonian skinks suggest connections to
taxa in Australia—New Guinea and Southeast Asia (Hardy, 1977).

New Zealand has a well-developed endemic avifauna, but the relationships
of the majority of the genera and species are poorly known. Because most
are representative of families present in Australasia, it is reasonable to assume
they are components of an Australia—New Zealand track. However, I can see
no basis for assuming, as most biogeographers have, that this endemic avifauna
is the result of many repeated dispersals across the ocean. Once relationships
are better known, additional evidence for biogeographic connections to Lord
Howe Island and New Caledonia may become apparent.

Of the bats, the one species of vespertilionid, *Chalinolobus tuberculatus*,
is clearly related to congenic species in Australia. The monotypic bat
family Mystacinidae is the sister-group of the Molossidae (Smith, 1976), a
very widely distributed group. Until relationships within the molossids are
better understood, the biogeographic connections of the Mystacinidae cannot
be ascertained.

**Australia—Southeast Asia track**

There can be little doubt that the relationships of a large number of the
vertebrate taxa of Australia define biogeographic connections to Southeast
Asia. Components of this track appear to include ranid and microhylid frogs,
agamid, scincid, varanid, pythonine, colubrid, and elapid reptiles, probably
all oscine passeriform birds, many non-passeriforms, and murid rodents.

Few areas of the world are as complex geologically, and from this one
might reasonably conclude that vicariance patterns are likewise complex. Dis-
persal may not have been as important as previously thought, because bioge-
ographic patterns may have been established by repeated mergings of biotas
(islands — microcontinents — have frequently collided), followed by vicari-
ance. Furthermore, there is the intriguing possibility that if some earth ex-
pansion has taken place, then the Tethys Sea may have been nonexistent in
this area and Australia and Southeast Asia may have been in close proximity
(Stevens, 1977). If so, then there may have been an ancestral biota common
to Australia and Southeast Asia that was vicariated.

**DISCUSSION**

The study of historical biogeography has been characterized here as the
analysis of genealogical pattern mapped on the globe. Upon reflection it
becomes apparent that studies of isolated groups do not, in themselves,
constitute the primary manifestation of a general pattern; rather, it is the
congruence in distribution from one group to another that creates a signifi-
cant biogeographic pattern requiring a general causal explanation. This point
has been emphasized by many previous workers.

The question thus arises as to the existence of a common pattern in the
distributions of the vertebrates and how those distributions might relate, in their congruences, to other groups of organisms. One way this problem can be investigated is to resolve the phylogenetic data presented earlier into area-cladograms to reveal the commonality of pattern (Platnick and Nelson, 1978; Rosen, 1978). The areas of concern here are New Zealand, New Caledonia, Australia, and South America, consequently other areas of distribution (say, Africa and Madagascar within the ratite birds) can be ignored for the present (see Rosen, 1978, for details of the procedure).

It is evident that several common patterns emerge from the phylogenetic hypotheses presented in this paper and in the literature. First, some vertebrate taxa, including galliform, probably anseriform, and caprimulgiform birds, and chelid turtles have congruent distributions in which South American and Australian sister-taxa have their sister-taxon in South America. This pattern is also paralleled by chironomid midges (Brundin, 1966, in press) and other invertebrates and by the plant genus Nothofagus (Cracraft, 1975a). This congruence in cladistic pattern might be explained by vicariance biogeography as follows: a widespread Southern Hemisphere biota (composed of an ancestral species for each descendant group) was first subdivided so that one descendant was confined to a part of South America and the other, in this case, to another portion of South America, East Antarctica, and Australia. This second descendant was subsequently subjected to vicariance, possibly as a result of the Early Cenozoic northward drift of Australia or the disruption of connections between South America and East Antarctica. Whereas it seems parsimonious to accept this hypothesis regarding the relative sequence of vicariance events, phylogenetic analyses suggest the biogeographic histories of the component groups involve a complex pattern of dispersal and vicariance. For example, the postulated phylogenetic relationships of chelid turtles (Gaffney, 1977) suggest origin of the group in Australia (this conclusion may have to be modified upon analysis of the sister-group of the chelids), dispersal to South America where a number of lineages were evolved, and then secondary dispersal back to Australia by the common ancestor of Chelodina and Hydromedusa (Fig.2). The relationships of chelids would not seem to be consistent with the primitive cosmopolitanism often advocated by vicariance biogeography. Similarly, the cladistics of various avian taxa indicate complex dispersal prior to vicariance, but the data suggest origin of the groups in South America with dispersal to Australia. If galliforms and anseriforms are sister-groups, then a South American origin with subsequent dispersal of both lineages to Australia seems apparent.

A second area-cladogram involves sister-taxa in New Zealand (and perhaps New Caledonia) and South America with their sister-taxon being distributed in South America (rather than in Australia). Examples of this pattern are observed in gruiform birds (Fig.4), possibly leiopelmatid frogs, chironomid midges, and Nothofagus. Vicariance events are interpretable as the northward drift of the New Zealand continental block in the Late Cretaceous sometime after an unknown vicariance event in South America. As with previous
examples, a complex dispersal history can be postulated to underlie the vicariance pattern. With the gruiform birds there are several lineages present in South America prior to the New Zealand distribution (Fig. 4), and these suggest a South American origin and dispersal to New Zealand—New Caledonia prior to vicariance.

The phylogenetic relationships of vertebrates suggest, as Brundin (1966, in press) has postulated for chironomid midges, that each group of an ancestral biota has had a complicated dispersal history prior to vicariance and that these histories are frequently not congruent with one another. Rosen (1978, p. 174) distinguishes between progenerative (the vicariance) and epigenenerative (post-vicariance) aspects of distribution patterns. Of importance for historical biogeography, then, is the dispersal history of the elements of a biota prior to vicariance, and if I read him correctly, it is this aspect of biogeographic analysis which Brundin believes is de-emphasized by some vicariance biogeographers. Reliance solely on area-cladograms will not provide a satisfactory explanation for the biogeographic history of component elements of a biota, but area-cladograms are necessary to draw attention to the commonality in vicariance pattern. Biogeographic history involves repeated cycles of progenerative (vicariance) and epigenenerative (dispersal) events, and not all elements of a biota respond to these events in similar ways (although, as scientists, we must believe there are common patterns). The analysis of biogeographic history, to be complete, should take into account the patterns of vicariance and dispersal, and both seem to be susceptible to study through cladistic analysis.

ACKNOWLEDGEMENTS

I especially want to thank Dr. Peter Ballance for extending an invitation to participate in the symposium leading to this paper. I also am grateful to the University of Auckland, Waikato University, the University of Canterbury, and the American Museum of Natural History (through the F. M. Chapman Memorial Fund) for travel assistance. Ms Penny Pounder kindly drew the figures. This research was also supported by NSF grant DEB76-09661.

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