

HISTORICAL BIOGEOGRAPHY AND EARTH HISTORY: PERSPECTIVES FOR A FUTURE SYNTHESIS¹

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It has now become almost cliché to speak of the revolution in the earth sciences and its ensuing revitalization of biogeography. Certainly much of the biogeographic literature of the past several years has been produced in response to our rapidly changing knowledge of earth history. While we can applaud the recent advances in biogeography, it is questionable whether we should be overly optimistic about obtaining a synthesis of the geographical history of plants and animals on the one hand and earth history on the other. I say this not because a synthesis is impossible, but because a synthesis will only be produced when the majority of workers reach some general agreement on the theoretical bases for reconstructing the historical biogeography of organisms. The reason for this statement is simple—observations are theory-laden. Indeed, individual theoretical biases—some of which we may not be consciously aware—determine the kinds of data we collect and thus the manner in which we order those data. If biogeographers differ in their theoretical approaches, then it can be expected that the observations are likely to differ as well as the interpretations. That this is a major problem in biogeography today is easily demonstrated by comparing the papers of Darlington, Brundin, and others among zoologists, and Thorne, Smith, Raven, Axelrod, Croizat, or van Steenis among botanists.

I believe most biogeographers would subscribe to the belief that the biotic and geologic worlds have evolved together, and that major distributional patterns of both plants and animals should be similar to each other and relate to major historical changes in geography and climate in a parallel manner. If this is true, then a synthesis would appear possible, and it would seem useful to begin an examination of the factors necessary to affect it. The purpose of this paper is, first, to examine the various theoretical approaches to historical biogeography and attempt to resolve some of the conflicts among them, and second, to outline several biogeographical patterns in which the distributional history of plants and animals seems consistent with earth history. One of the themes of this paper is that a lack of theoretical perspective has prevented us from seeing some of these common patterns. It is not my purpose to provide the synthesis I have been talking about; that would take far more space than is available here. Rather, I wish to discuss ideas that might facilitate zoologists and botanists alike finding some common ground in the analysis of historical biogeography.

THEORETICAL APPROACHES TO HISTORICAL BIOGEOGRAPHY

As noted above, historical biogeography is in a transitional period in which many, if not most, biologists no longer look at the world's continents and oceans

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from a stabilist point of view but rather from that of a mobilist. The theoretical foundations of historical biogeography are also in a state of flux, and several models or methods of analysis have been proposed as being useful for interpreting biogeographic history.

A major controversy exists, on the one hand, between a group of workers who have attempted to outline what they believe is a logically consistent methodology for reconstructing the geographic history of plants and animals and, on the other hand, the critics of that methodology. The theoretical approach developed by the former workers involves the construction of hypotheses about the phylogenetic relationships of the organisms in question and the subsequent inference of their geographic relationships (Hennig, 1966*a, b*; Brundin, 1966, 1972*a*; Nelson, 1969; Cracraft, 1973*a*). The opponents of this theory focus their criticism on the phylogenetic model of these workers and advocate a biogeography which does not have a precise deductive link with phylogenetic hypotheses, *e.g.*, Darlington, 1957, 1965, 1970); this has been termed the common-sense approach to biogeography (Rotramel, 1973). The crux of the controversy between the two schools of thought is whether biogeographic history is deducible from phylogenetic history and (1) if it is, what will be the logical steps in inferring biogeography from phylogeny, and (2) if it is not, how is biogeographic history then to be reconstructed? Both these theoretical approaches show some similarities in that they usually look upon biogeography in terms of centers of origin and dispersal from these centers, a conceptual framework in use since the time of Darwin. A third theoretical approach to biogeography de-emphasizes the concepts of centers of origin and dispersal and attempts to analyse distribution patterns in terms of subdivision (vicariance) of ancestral biotas (Croizat, 1962; see particularly Croizat *et al.*, 1974). A discussion of these three approaches will comprise this section of the paper.

APPROACH NO. 1: THE PHYLOGENETIC SYSTEMATIC THEORY OF BIOGEOGRAPHY

The phylogenetic systematic theory of historical biogeography is simply stated. From an hypothesis of phylogenetic relationships and knowledge of the distributions of the species under consideration, one can infer the distribution of the ancestral (hypothetical, unknown) species of each lineage in the phylogeny. This process completed, one has constructed a biogeographic hypothesis about the centers of origin and direction of dispersal that is most parsimonious for the given phylogenetic hypothesis (see Nelson, 1969, for a detailed discussion of the reasoning involved). Thus, if one considers four taxa (A–D) assumed to be related as in Fig. 1, we first ask what were the distributions of the ancestral species (open circles). Two alternatives are presented in Fig. 1, and it should be apparent that one, Fig. 1A, is more parsimonious than the other. In the former the center of origin is in Asia with subsequent dispersal to North America, whereas in the latter the origin is postulated as being in North America with dispersal to Asia. Parsimony is applied on the basis of the number of dispersals (dotted circles) required by each hypothesis. It is evident that hypotheses about the distributions of ancestral species are not influenced by the taxa A–D being fossil, extant, or a combination of both.

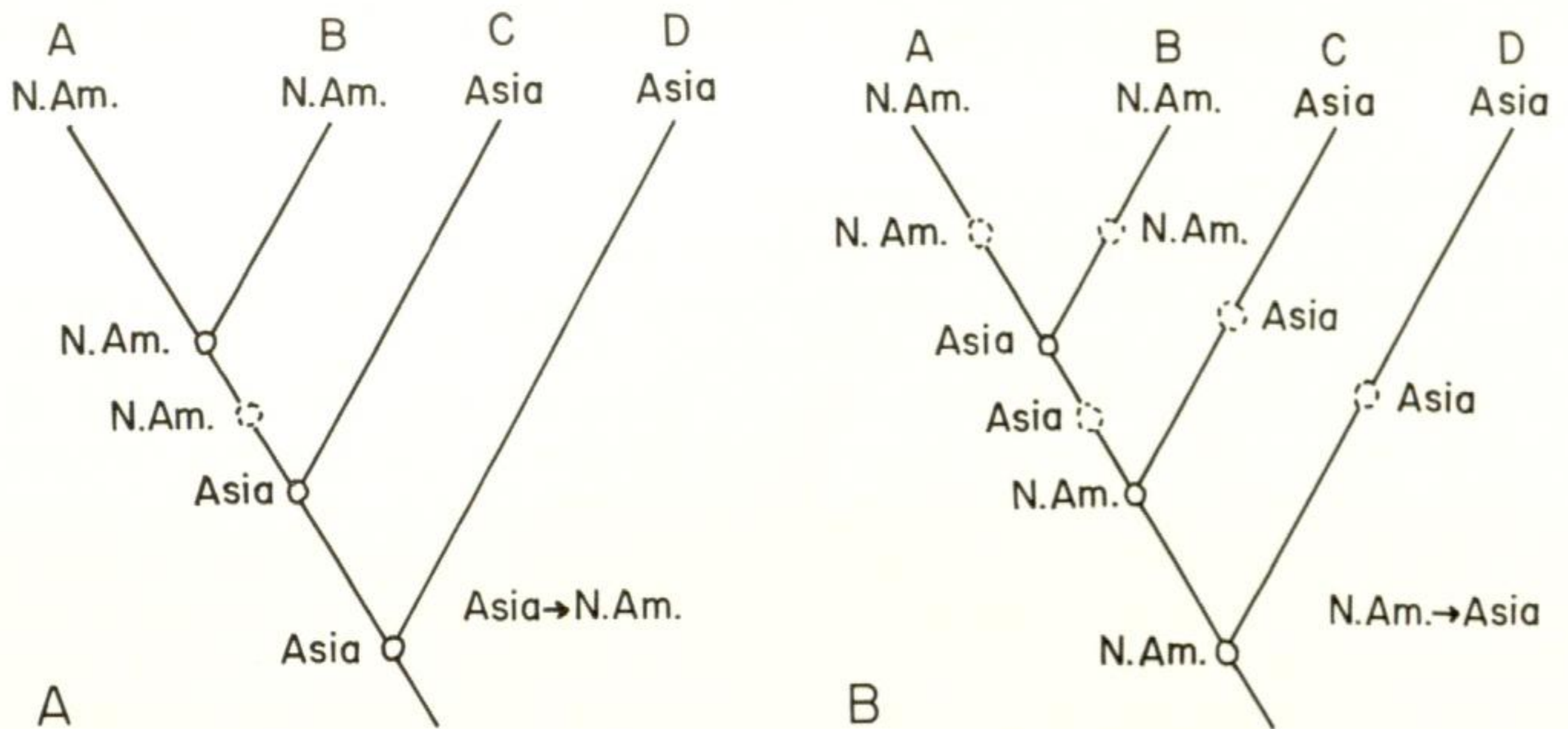


FIGURE 1. Two biogeographic hypotheses about four taxa (A–D) whose relationships and distributions are as shown. Geographic distributions of ancestral species (open circles) are postulated as are dispersal events (dotted circles). In A distributions of ancestral species are determined using the reasoning of Hennig-Brundin; the center of origin is postulated to be Asia with one dispersal to North America. In B an admittedly extreme biogeographic hypothesis is constructed to illustrate the concept of choosing among hypotheses on the basis of parsimony; thus hypothesis A is to be preferred. See text and Nelson (1969).

It should be emphasized that this methodology describes a mode of reasoning applied to a phylogeny that *is considered as given*. Of course, the phylogenetic relationships of taxa A–D may not be those portrayed in Fig. 1 (there are 13 additional possibilities), but that is another matter for discussion and is not directly relevant to the *reasoning* used to construct biogeographic hypotheses. If this mode of inference is followed, the center of origin is postulated to be located in the area where the phyletically primitive species are distributed.³ This is simply a consequence of the reasoning—a methodological principle—and does not follow from any intuitive or prior belief that primitive species *must* have remained, at the center of origin of the group as a whole. I will return to this point shortly.

APPROACH NO. 2: CLASSICAL EVOLUTIONARY BIOGEOGRAPHY

This is the approach often associated with the names of Darwin, Matthew, Simpson, Darlington, and Mayr. The principles of this school are rather loosely formulated but might be listed as follows (see especially Darlington, 1957: 31–35):

1. The center of origin of a taxon is that area showing the greatest species and generic diversity. Darlington (1957: 31–32) notes that this criterion is more reliable for dominant, expanding groups than for those that are declining in diversity or area.
2. The degree of differentiation of a group is roughly proportional to the length of time that group has occupied the area in question.

³ By “phyletically primitive” species I refer to those species which have branched off earliest within a lineage; this concept is independent of any considerations of whether these species are primitive or advanced morphologically (see discussion later in text).

3. The area occupied by a group is more or less proportional to the age of the group.

4. Distributions of peripheral groups that are more nearly continuous with the distribution of the "central" populations are probably younger than those peripheral populations with widely separated (relict) distributions.

5. Related, competing, or "associated" taxa tend to arise in the same areas as the taxon under consideration. Darlington (1957: 33) recognizes two corollary principles: (a) "much differentiated forms . . . isolated from the main range of their groups . . . are often not immigrants but relicts persisting where the first groups were once numerous but have become replaced." (b) "if groups arise in certain places because of favorable conditions there, they are likely to begin recession in the same places because of the rise of later families responding to the same conditions."

6. The distributions of primitive forms are not trustworthy for recognizing centers of origin.

7. Fossils provide the best clues for biogeography if the record is "adequate." Simpson (1965: 77) also notes that if the record is "fairly complete, the historical events can be followed with considerable objectivity and little inference."

The above points roughly define the working methods of classical evolutionary biogeography. It must be stressed that few biogeographers advocating this approach would suggest that any one of these methods is infallible; more often, they might say that, taken together, these rules should enable a reconstruction of biogeographic history, but, taken alone, the rules may be misleading. Nor should it be assumed that all evolutionary biogeographers would adhere to each of the above working principles.

Comments on the Conflict between Phylogenetic Systematic Biogeography and Classical Evolutionary Biogeography.—A major critique of the phylogenetic systematic theory outlined earlier was presented by Darlington (1970). Most of Darlington's article was directed toward criticizing a specific model of phylogeny reconstruction advocated by Hennig and Brundin. At this time we need not be concerned with this issue since Brundin (1972a, 1972b) has offered a rebuttal; rather, attention will be directed to the biogeographic aspects of the criticism.

I begin by suggesting that some of the differences between these two schools of thought may not be as deep as first realized. Both, I believe, accept the notion that knowledge of phylogeny is of considerable importance in reconstructing biogeographic history. While it is true that they may be using quite different phylogenetic models—that is, different methods of phylogeny reconstruction (Cracraft, 1974a)—their general picture of how phylogeny relates to dispersal history is sometimes very similar.

The notion that as organisms evolve they disperse over the globe is assumed by both schools. A concept of this dispersal was presented by Darlington (1959: 308, figs. 1–2) and is shown here in Fig. 2. One can draw a phylogeny of a group of organisms (Fig. 2A), and if that phylogeny is transposed to a map so that the organisms occupy their current (or past) distributions (Fig. 2B), then a dispersal history is effectively created. A somewhat more formal way of postulating that history is shown in Fig. 2C. The conclusion which one might draw from these

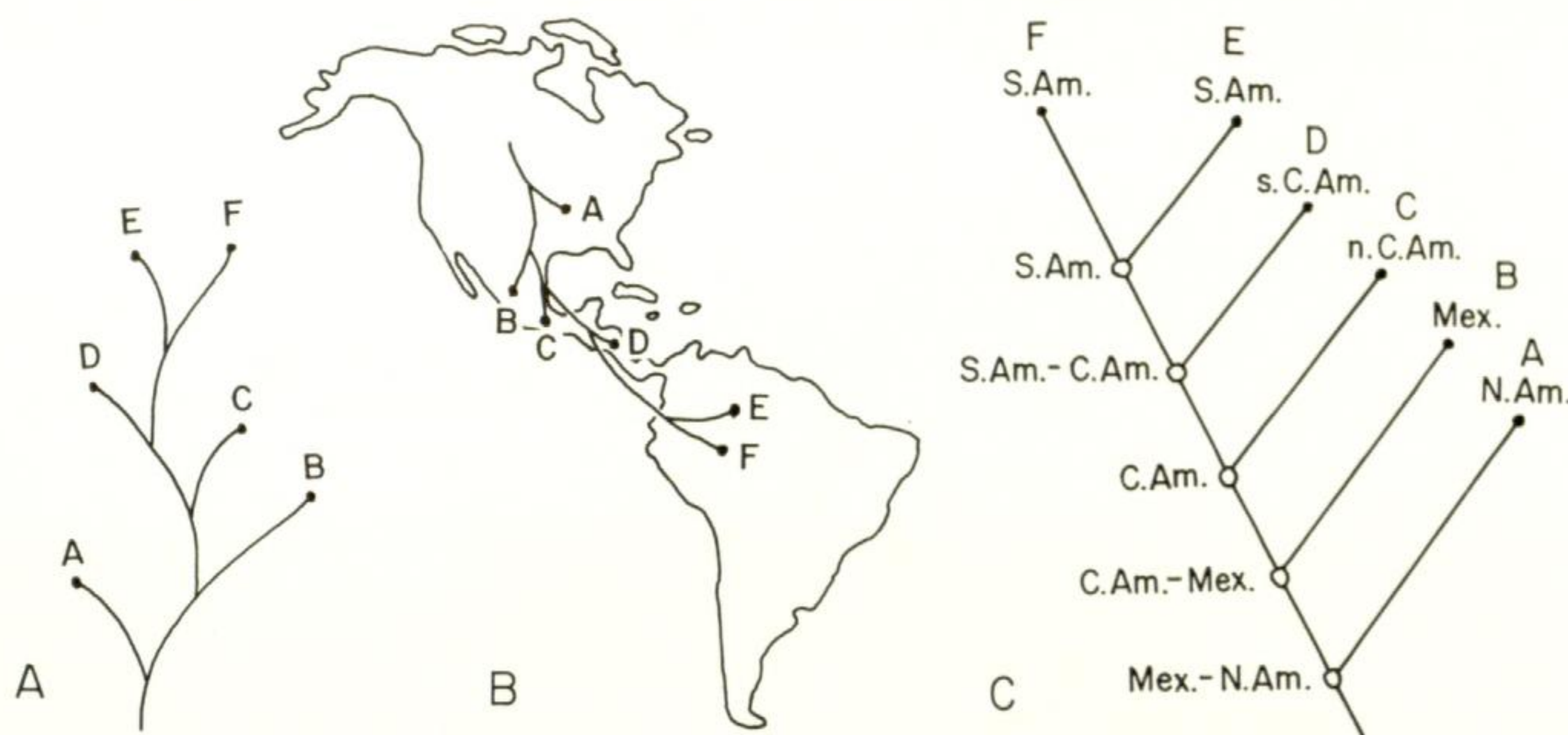


FIGURE 2. The link between phylogeny and dispersal as modified from a discussion of Darlington (1959). In A a phylogeny is presented for six taxa (A-F); this is typical of a phylogenetic scheme accepted by most workers. In B the phylogeny is superimposed on a geographic map; the reader will note the similarities to the example of Darlington (1959:308, fig. 2). It is clear from B that dispersal was from North to South America. In C this biogeographic hypothesis is formalized and the distributions of ancestral species (open circles) are postulated. One group of biogeographers (Darlington) advocates A-B, whereas another (Hennig-Brundin) advocates C; the differences are minimal.

workers' discussions is that if Darlington, Hennig, or perhaps most other biogeographers were presented with an agreed-upon phylogeny, all might arrive at similar concepts of dispersal history. Differences would probably develop depending on the degree to which one or more individuals might want to depart from parsimony in choosing among alternative hypotheses. Indeed, one point which will be developed below is that this departure from parsimony may be a major cause of the misunderstanding among these workers.

Classical evolutionary biogeographers have raised a number of issues which purportedly directly invalidate the methodology of phylogenetic systematic biogeography or which are thought to provide a more reliable basis for reconstructing biogeographic history.

The Problem of Primitive Groups.—The notion that centers of origin can be identified by location of "primitive" groups has been greatly misunderstood by many biogeographers. In fairness, it should be said that advocates of the phylogenetic systematic theory have themselves not fully appreciated the problems involved and have contributed to this misunderstanding. One cause of the confusion is definitional, that is, what is meant by a "primitive" group. Darlington (1970: 10-11), for example, argued against Brundin's (1966: 56) statement that "... within the total distribution area of a group the species possessing the most primitive characters are found within the earliest, those with the most derivative characters within the latest occupied part of the area." Brundin here and elsewhere (1972a: 73-74) uses primitive in the sense of "morphologically primitive" instead of "phyletically primitive" and there may not be a precise relationship between the two (Fig. 3). To my knowledge Brundin has not used "primitive" in

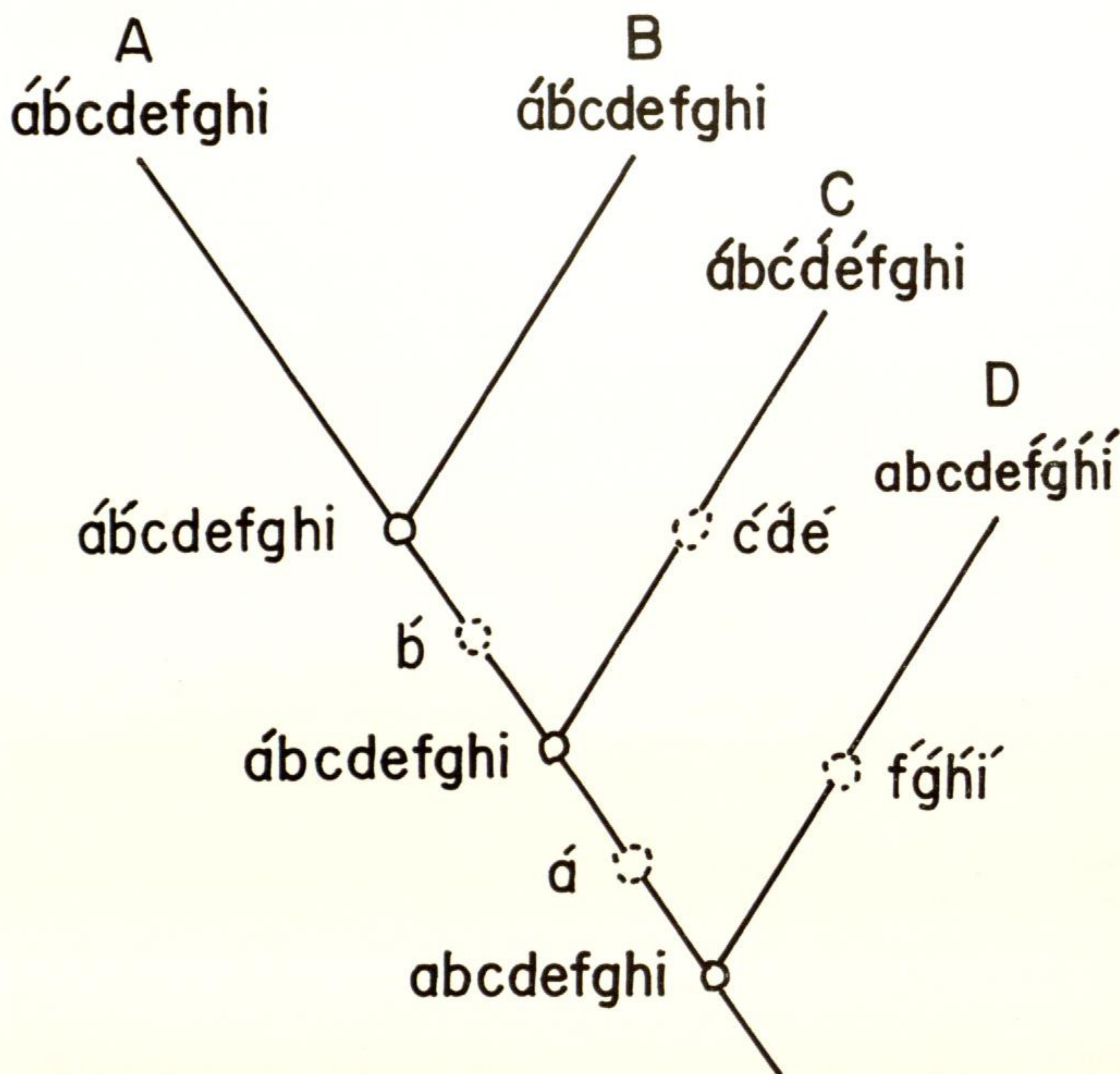


FIGURE 3. Diagram to show that phyletically more primitive groups (C,D) can possess a greater proportion of advanced character-states (letters with prime marks) than do phyletically more advanced taxa (A,B), which can have a greater proportion of primitive character-states (letters without prime marks). See text.

the phyletic sense (*contra* Nelson, 1972), although other phylogenetic systematists have made clear that centers of origin will reflect the distribution of genealogically primitive groups (Nelson, 1969, 1972; Cracraft, 1973*a*, 1973*b*, 1974*b*). Even this latter concept of primitive is sometimes ambiguous in that precise comparative statements are probably not possible in all cases. However, most workers have a general idea of what this means, and it is outside the content of this paper to pursue the idea in greater detail. Because hypotheses about the distributions of ancestral species are based on given concepts of phylogenetic relationships, the location of the center of origin will necessarily reflect the distribution of the phyletically primitive species. Unfortunately, we have very poor knowledge of relationships for most groups of organisms, and thus we seldom can make the precise biogeographic inferences that are possible when a particular phylogeny is well documented. Even though taxa that branched off earliest need not exhibit

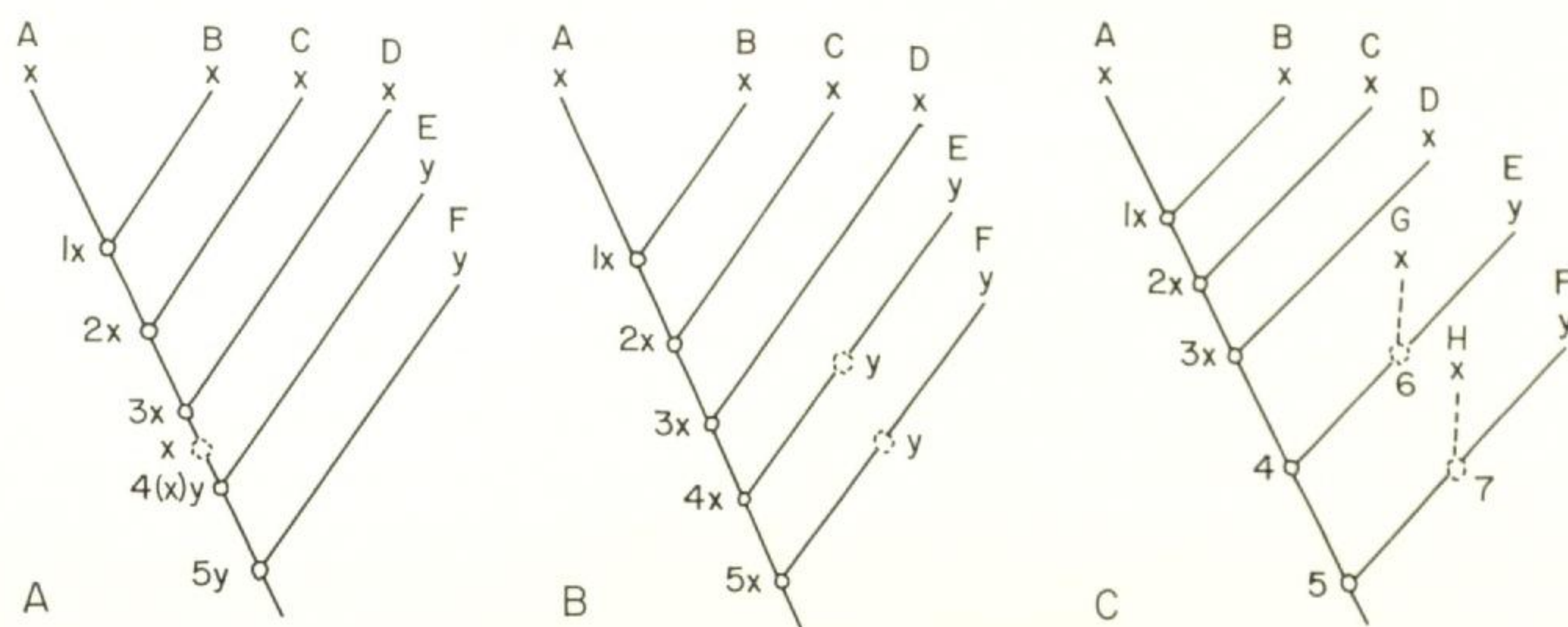


FIGURE 4. Three hypotheses for six taxa (A-F) found in two areas (x,y). In A hypotheses about the location of ancestral species (open circles, 1-5) are constructed using the reasoning of Hennig and Brundin; the center of origin of the group as a whole is postulated to be in y with one dispersal (dotted circle) to x. In B the hypothesis of Darlington is examined in that the center of origin is identified as the area (x) where advanced, dominant, highly diverse groups (assumed here to be taxa A-D) are found; it is thus necessary to postulate the independent dispersal of E and F to y. Hypothesis A is more parsimonious than B. In C the necessary conditions to fulfill the Darlington hypothesis (B) are examined; the presence of additional taxa (G,H) distributed in area x lend support to B. See text for additional details.

the greatest proportion of primitive characters (Fig. 3), it may be that they are, more often than not, more primitive morphologically than later groups. I believe this is the intuitive conclusion of most systematists and that it can be shown to be true for a number of groups.

Darlington (1957: 552-556), in contrast to advocates of the phylogenetic systematic approach, believes that primitive taxa are usually not located at the center of origin of a group but rather in more peripheral areas (see also Briggs, 1966, 1974; Horton, 1973). The resolution of the conflict lies in the way one presents a logically convincing argument that primitive groups are in peripheral areas in any specific instance. To my knowledge no classical evolutionary biogeographer presented these arguments, apparently because of a failure to realize, as Brundin (1972a: 74) notes, that "a careful establishment of strict monophyly and sister-group relationships is a necessary prerequisite for a realistic interpretation of a distribution pattern." Let us consider a distribution pattern of a monophyletic group (Fig. 4) in which four taxa (A-D) are located in area x and two other taxa (E-F), which are also the most primitive phyletically, in area y. Given the phylogeny depicted in Fig. 4, what biogeographic hypotheses can be constructed and which one is most parsimonious? In Fig. 4A the distribution of ancestral species (open circles) is determined using the reasoning advocated earlier. Perhaps the most parsimonious hypothesis is that species 4, which is ancestral to taxon E and its sister-group, A + B + C + D, was distributed in area xy, but because taxon F is distributed in area y, we might conclude that ancestral species 4 was probably also in y. If true, then sometime prior to the splitting of ancestral species 3 we would postulate dispersal (dotted circle) to area x. In Darlington's conception of this distribution pattern (Fig. 4B), where area x is considered the center of origin and primitive species are located peripherally in

area y, it would be necessary to postulate two independent dispersals to area y by the ancestors of E and F. The hypothesis of Fig. 4B is less parsimonious than that of Fig. 4A because it requires a greater number of dispersals to account for the distribution pattern. *This is not to argue the truth of either hypothesis, only their parsimony.*

But what conditions are necessary in order to satisfy the hypothesis of Darlington that primitive groups are distributed peripherally? Clearly we need additional taxa, fossil or Recent, related to taxa E and/or F and distributed in area x (I have omitted the possibility of other taxa, also in area x, that originated prior to ancestral species 4 or prior to species 5; in any case the reasoning is still similar). If we only had taxon G related to E as shown in Fig. 4C, then it would probably be most parsimonious to postulate that ancestral species 4 and 6 were distributed in xy (a clear choice between x and y cannot be made). If we only had taxon H related to F, then again it would be most parsimonious to postulate ancestral species 4, 5, and 7 to be in xy, but intuitively we would greatly suspect multiple invasions of area y. If both taxa G and H were known, an hypothesis of multiple invasions would probably be most parsimonious. In any case, the critics of the phylogenetic systematic theory of biogeography have not presented arguments of this kind, and therefore their claims for the peripheral distribution of primitive groups appear unsupported. There may be isolated examples of peripherally located primitive taxa, but I am unaware of any evidence, rigorously analyzed, that would suggest this to be a wide-spread phenomenon of animal distribution patterns.

The Problem of Fossils.—Phylogenetic systematists advocate a theory of historical biogeography that treats fossils much like Recent organisms; fossils are assumed to provide us with a point in space and time just as Recent organisms and are not assumed to possess any inherently special significance for constructing phylogenetic hypotheses (see Schaeffer *et al.*, 1972). Classical evolutionary biogeographers, on the contrary, often find fossils of special importance, thus Darlington's (1957: 35) remark that the "best clues [for biogeography], of course, are fossils—the right fossils in the right places. . . ." He goes on to note that fossils need to be interpreted carefully, but his biogeography relies heavily upon them nevertheless, and one is never given a clear exposition as to how they are to be interpreted.

It should be evident from the preceding discussions that the rules of inference used in phylogenetic systematic biogeography are applicable to either Recent or fossil taxa or both simultaneously. Indeed, it is not at all evident why fossils should be subject to a separate process of phylogenetic or biogeographic reasoning. If they can be, this has not yet been formalized. Set within a framework of a phylogenetic hypothesis, fossils can be extremely important for biogeographers, but considered outside this framework, the well known problems of recovery in space and time could easily result in erroneous interpretations.

APPROACH NO. 3: THE VICARIANCE MODEL

The two approaches to biogeography discussed above generally are concerned with recognizing centers of origin and pathways of dispersal; the geographical

history of the world's biota is considered interpretable within this framework. Yet another approach has been proposed which does not attempt to recognize centers of origin or dispersal pathways. The basic premises of this latter biogeographic model are (see Croizat, 1962; Croizat *et al.*, 1974):

1. The distribution of a group can be represented by one or more lines (tracks) connecting the ranges of all members of that group (subspecies of a species, species of a genus, etc.).
2. Many overlapping individual tracks between two areas form a generalized track which represents the distribution of an ancestral biota that has subsequently subdivided (vicariated) into the two descendant biotas.
3. Biotic distribution is to be looked upon as the result of subdivision (vicariance) of ancestral biotas rather than as origin in one region and dispersal to another.
4. Evidence for dispersal is seen in the sympatry of individual or generalized tracks.

The above four points briefly outline the approach advocated by Croizat (1952, 1958, 1962; see also Nelson, 1973, for a review of Croizat's work; DuRietz, 1940, applied the vicariance model to explain bipolar plant distributions). In his voluminous writings Croizat has never elucidated this model in a concise manner, but the main ideas of the vicariance of biotas can be found in *Space, Time, Form: The Biological Synthesis* (Croizat, 1962: 186–189, 209–210). The most detailed explication of the model, and the basis for much of the following comments, can be found in the paper by Croizat *et al.* (1974). Their position is best summarized by the following (Croizat *et al.*, 1974: 269):

"We conclude, therefore, that historical biogeography, *i.e.*, the study of the history of the world biota, is to be understood first in terms of the general patterns of vicariance displayed by the world biota. Sympatry (dispersal) means, after all, that a population has broken away from the original geographic constraints responsible for vicariance, and that the original vicariant pattern has, to some extent, become obscured as a result. Operationally, we consider that biogeographical investigation begins with the determination of general patterns of vicariance, and the determination of the geological changes that caused them."

Significance of the Vicariance Model.—Many of the principles embodied in the vicariance model have the potential for improving the study of biogeography. The model de-emphasizes the excessive reliance upon centers of origin and dispersal routes that has characterized biogeography since the time of Darwin (see, for example, Darlington, 1957; Ross, 1974: 209–244). Detailed discussions of chance dispersal that have little relevance for the discovery of important generalizations permeate the biogeographic literature. Most of this is rightly rejected by the vicariance model. Numerous studies, especially recent ones that attempt reinterpretations of "stabilist" biogeographic patterns in terms of the newer data on continental drift, have been based on prior conceptions about world geography and not on the patterns exhibited by the organisms themselves. This was one of the problems that forced Darlington (1957) to postulate numerous Holarctic dispersals and widespread extinctions to explain vertebrate distribution in the Southern Hemisphere. The vicariance model places primary emphasis on con-

structing hypotheses using biological data and not preconceptions about geological history and it is to Croizat's credit that he was one of the earliest biogeographers to insist that plant and animal distributions are not compatible with stable continents. Thus, the concept of generalized tracks focuses attention on the search for climatic and/or geographic factors that might have been responsible for the vicariance of ancestral biotas.

The vicariance model is applicable to the study of whole biotas instead of isolated groups, and in so doing forces upon the biogeographer a higher level of generality than is seen in most biogeographic analyses. The model stresses that biotas evolve as wholes and that significant changes in climate and/or geography must affect entire biotas. This viewpoint is too often ignored in traditional considerations of regional biogeography.

Finally, and perhaps most importantly, the model has significant explanatory powers with regard to the distribution of the world's flora and fauna. One of the best examples is the biota of the southern continents which, for the most part, can be interpreted satisfactorily in terms of an ancestral biota that was present at one time on the Gondwanaland supercontinent and is now fragmented (vicariated) due to continental breakup and drift (see following section). It is probably not necessary to interpret most of this biota in terms of centers of origin and dispersal and to do so involves the acceptance of unnecessary (nonparsimonious) assumptions. It is probable that by applying the vicariance model to the world's biota we will greatly increase our understanding of historical biogeography.

Criticisms of the Vicariance Model.—The vicariance model has been applied by relatively few workers (see Croizat *et al.* 1974, for a review), and no one other than Croizat (1952, 1958, 1962) has used it to interpret a large segment of the world's biota. The following comments are designed to focus attention on what seem to be the major problems with the model as it is currently stated and with the ways certain biogeographic data can be interpreted using the model.

The precise relationship between phylogeny and biogeography has not been fully discussed by advocates of the vicariance model. Whereas Croizat (1952: 526) does appear to acknowledge a close connection between phylogeny and biogeography, he has not defined this connection in any precise manner and occasionally suggests that biogeography is not "subordinate" or "subservient" to "taxonomy" (Croizat, 1952: 546, 1970: 317). Most of Croizat's systematic data come from studies having a strong bias toward evolutionary systematics and most of these workers were interested in questions of classification and not phylogeny (I base this conclusion on an examination of Croizat's extensive ornithological examples and those from other vertebrates with which I am familiar). Hence, I cannot agree with Nelson (1973: 315) that Croizat's biogeography is very similar to the biogeography of phylogenetic systematists, at least certainly not in the theoretical foundations of each system (*e.g.*, Nelson, 1973: 316). I believe, on the other hand, that the two approaches can be made more or less compatible as Croizat *et al.* (1974) have attempted to do (see comments below).

Croizat's basic datum is the "track" which he considers to be "factual," although he recognizes this interpretation can be questioned (Croizat, 1962: 7–8). My interpretation is that "tracks" are highly theoretical constructs in that some concept

(typically, of relationships) forms the basis of interposing a track between two areas. More attention should be paid to exactly how tracks are to be drawn. If tracks are to represent connections between "sister-groups," then indeed Croizatian biogeography may have something in common with that of the phylogenetic systematists. However, to my knowledge Croizat himself has never specified that tracks are to have this rather precise meaning, and it is reasonably clear from his examples that tracks frequently do not represent sister-group relationships. Indeed, this is not unexpected, because of his reliance on the work of evolutionary systematists whose concept of relationship is not equivalent to that of phylogenetic systematists.⁴

A major problem facing biogeographic analysis is the manner in which dispersal is to be treated as part of a biogeographic hypothesis. I agree with Croizat *et al.* (1974) that when analyzing the history of biotas we must first attempt to understand the general patterns of vicariance, and then, following this, consider whether it is necessary to invoke dispersal to explain the composition of the biota. Nevertheless, an important issue is deciding under what circumstances we can claim that vicariance has explained a particular biogeographic pattern. The vicariance model assumes that a generalized track between two areas is *prima facie* evidence for an ancestral biota that has subdivided (Croizat *et al.*, 1974). In my opinion vicariance of an ancestral biota should only be claimed when one can also identify the event causing vicariance; without this, vicariance as an explanation for historical change is incomplete. This requirement appears consonant with Croizat's panbiogeographic method—that is, the physical and biotic environments evolve together and biogeography is directed toward understanding that unity (Croizat, 1962). In most cases a generalized track probably represents a subdivided ancestral biota, but the generality of this assumption needs to be established more firmly. Thus, we should discover what percentage of generalized tracks can be explained by vicariance and what percentage cannot. We might expect that the largest, most thoroughly documented, generalized tracks will be correlated with easily recognized vicariant events. But is a generalized track in itself sufficient evidence for hypothesizing an ancestral biota that has been subdivided? Perhaps not. It is questionable whether vicariance should be invoked if there is substantial geological evidence against a vicariant event. The most likely examples of this situation involve the biotas of oceanic islands. Either we assume that an as yet unknown vicariant event was responsible for the generalized track to the mainland, despite current geological thinking against such an event, or we accept current geology and invoke dispersal. The importance of geological evidence in constructing biogeographic hypotheses using the vicariance model seems clear. Thus, one cannot use the generalized track connecting the land biotas

⁴ This is not a criticism of panbiogeography *per se*, because clearly Croizat has had to use the available literature. However, it does seem relevant to the arguments of those who wish to draw an unduly close parallel between the biogeography of Croizat and that of phylogenetic systematists. If one is dealing with a large number of tracks between two areas, *e.g.*, Africa and South America, then knowledge of a precise sister-group relationship of each link may not be necessary. We still would be compelled to explain this disjunct distribution. On the other hand, where there are few links, as in New Zealand and South American vertebrates, knowledge that these similarities are sister-group relationships strengthens the argument for vicariance.

of South and Central America as evidence against watergaps preventing dispersal between the two areas (Croizat, 1958, personal communication), while at the same time using the generalized track between the marine biotas of the Caribbean and Pacific as evidence for a vicariant event (closure of the Panamanian landbridge) that subdivided the ancestral marine biota (Croizat *et al.*, 1974).

A final problem needing further discussion is the extent to which biogeographers will seek to explain the vicariance of all taxa of a particular generalized track as the result of the same climatic and/or geographic event. As an example, one could make a strong argument against interpreting all sister-group relationships between South America and Africa as the result of the vicariance of an ancestral biota when the two continents separated about 90 million years ago. Despite the problems of judgment involved in many cases, biogeographers can take information from the fossil record and from a knowledge of relationships and use this to compare probable times of branching with various climatic and/or geologic events. In this way it may be possible to avoid interpretations such as those of Croizat (1970) in which the history of certain avian species and subspecies is thought of as the result of vicariance in the Mesozoic.

DISTRIBUTIONAL PATTERNS: EXAMINATION OF BIOGEOGRAPHIC MODELS

It will be the purpose of this section to suggest that a number of intercontinental distribution patterns for both plants and animals are best explained by the vicariance of ancestral biotas at the time of continental breakup whereas other patterns can be explained best by the dispersal of one biota into another. Thus, we will be examining the power of the previously discussed biogeographic models to explain generalized distribution patterns among continents. I will attempt to show that most of these patterns are relatively consistent with our present knowledge of intercontinental paleogeography and that the extent to which a particular biogeographic model can explain the biologic data is also dependent to a large extent upon the presumed paleogeography.

Throughout this discussion I only propose to treat what appear to be major biogeographic patterns among the larger continents; many smaller, secondary patterns will be ignored. I will first define these patterns for vertebrates (see review in Cracraft, 1974*b*, 1975) and then attempt to generalize them for plants, and where possible, for invertebrates, trying to point out the concordance or discordance of these biologic data. Naturally, because of the paucity of phylogenetic information for many groups of organisms, the generality of the patterns can only be tentatively postulated in some cases.

PRINCIPAL VICARIANT PATTERNS

South America-Africa.—The vertebrate faunal links between close relatives are stronger between South America and Africa than for any two other southern continents (Cracraft, 1974*b*, 1975). Nearly all of these trans-Atlantic associations involve taxa that are predominately tropical. They include at least seven groups of fresh-water fishes, five of amphibians, four of reptiles, two of birds, but no mammals (Table 1). The list of Table 1 comprises those taxa that were most probably representative of or derived from the ancestral biota present on the

TABLE 1. Vertebrate links (sister-groups) between South America and Africa. See Cracraft (1973*b*, 1974*b*, 1975) for details.

South America		Africa
	Fresh-water fishes	
Lepidosirenidae		Lepidosirenidae
Osteoglossidae		Osteoglossidae
Characidae		Characidae
Siluriformes		Siluriformes
Nandidae		Nandidae
Cichlidae		Cichlidae
Cyprinodontidae		Cyprinodontidae
	Amphibians	
Pipidae		Pipidae
Leptodactylidae		Leptodactylidae
Buфонidae		Buфонidae
Microhylidae		Microhylidae
Caeciliidae		Caeciliidae
	Reptiles	
Iguanidae		Agamidae
Gekkonidae		Gekkonidae
Teiidae		Lacertidae
Boinae		Pythoninae
	Birds	
Rheinae		Struthioninae
Other suboscines		Eurylaimidae, Pittidae, Philepittidae

combined continent prior to final breakup in the early Late Cretaceous. If one included the fairly substantial number of taxa that probably dispersed across the Cretaceous-Tertiary watergap, the list for birds would be increased rather markedly and that for mammals would be expanded to include caviomorph rodents and monkeys.

It is to be expected that the links between South America and Africa are strongest in the presumably older groups of vertebrates and that they involve the tropical element of these faunas. The area of Brazil-Gabon was the site of final separation, and presumably this region has been tropical throughout the last 200 million years.

What is the nature of the pattern in other organisms? The rather marked similarities in the floras of South America and Africa have been discussed by Axelrod (1970), Raven & Axelrod (1974), Thorne (1972, 1973), and Smith (1973). However, the interpretations placed on these similarities differ among these authors, Axelrod and Raven favoring an explanation greatly dependent upon the Mesozoic continuity of the floras, Thorne and Smith preferring long-distance dispersal after continental breakup. Thus, Thorne (1973: 45) believes that the botanical evidence “argues against continental drift as a significant factor in explaining the distribution of seed plants between Africa and South America. If

continental displacement has occurred, the separation of Africa and South America must have attained its present state, or largely so, before the development of the present seed-plant floras of the world, certainly previous to Tertiary and Late Cretaceous time and possibly even previous to Jurassic time."

Data presented by many botanists, some of whom are cited above, strongly indicates that distribution patterns of plants between South America and Africa and among the other southern continents (see below) are basically similar to those of vertebrates and consequently are consistent with the hypothesis of a fragmented Mesozoic biota. Most importantly, I want to suggest that the point of controversy should not be whether continental drift is or is not the explanation for the similarities of the two floras but rather which biogeographic model—vicariant or dispersal—best explains the distributional data.

The similarities of the African and South American floras are impressive. About 276 families are present in the combined flora and 186 are shared; both continents have between 40 and 50 families not shared with the other (Thorne, 1972, 1973). The number of links between these two continents might be further increased if possible sister-group relationships among families could be identified. As far as I am aware, this aspect of plant phylogenetics has played little role in the debates about Southern Hemisphere biogeography or in botany in general (see below, PHYLOGENETIC ANALYSIS OF *NOTHOFAGUS* BIOGEOGRAPHY). Thus, how many of the 40 to 50 South American families not found in Africa have their closest relative on the latter continent? The same could be asked for the African taxa not found in South America. Can we ascribe the isolation of sister-groups on the two continents to divergence following continental breakup as we surely can among a number of vertebrate taxa (Cracraft, 1974b, 1975)? The argument that long-distance dispersal may occur in some or many taxa hardly invalidates the real issue which is the pervasive pattern of phylogenetic relationships among the floral elements of South America and Africa. It is probably futile to speculate on the number of long-distance dispersal events needed to account for the 186 or more links because (1) dispersal is best postulated in taxa that are not part of a well-defined generalized distribution pattern (see Croizat *et al.*, 1974), and (2) there is, in this case, a well documented vicariant event in the early Late Cretaceous separation of the two continents. *I am not arguing against the possibility of long-distance dispersal for any particular taxon, only against its relevance for explaining a major biogeographic pattern when a vicariant event is known.* If parsimony is to be the criterion for choosing among alternative biogeographic hypotheses, as it is in other sciences, then I believe we have to prefer the vicariant hypothesis in this case.

In order to strengthen the above interpretation and to lay groundwork for later discussions, I want to examine several of the arguments proposed by Thorne (1972, 1973) and Smith (1973) against the vicariant pattern of South American and African floras. The major arguments are:

(a) *About 48 African families and 42 South American families have failed to establish trans-Atlantic distributions; these numbers are considered too great if there was once a common flora.* These differences can hardly negate the trans-Atlantic patterns. As noted above, some of these endemics may have

sister-groups on the other continent and thus are themselves links. Some are undoubtedly related to plants in other areas, *e.g.*, to North America or Eurasia, or they may be the result of evolutionary origin and divergence subsequent to continental separation.

(b) *Only 12 families are restricted to South America and Africa.* This is not an important objection in light of the fact that the flora shared between Africa and South America is predominantly tropical and part of a circum-tropical flora of Pangaea. Hence, it is reasonable to expect many of the families to be shared with other tropical regions (see below).

(c) *There is a very strong amphi-Pacific distribution pattern among plants and this is inconsistent with trans-Atlantic vicariance.* The links between Africa and South America must still be explained. The amphi-Pacific similarities very probably reflect the Mesozoic circum-tropical distribution pattern prior to continental separation.

(d) *The Hawaiian Islands received their flora by long-distance dispersal so why not Africa and South America.* These are not comparable situations. In the former we have no evidence for a vicariant event between Hawaii and another land mass, in the trans-Atlantic example we do. It is simply a matter of applying the most economical hypothesis in each case.

The trans-Atlantic relationships of invertebrates are still poorly known. Keast (1972) has reviewed some of the links among Oligochaeta, onychophorans, pseudoscorpions, and many insect groups. It is impossible to tell right now how strong invertebrate links are until much more systematic work is completed.

In summary, distributional data for plants and vertebrates strongly point to the existence of a common ancestral biota on a joined South American-African continent (see especially Raven & Axelrod, 1974: 603–604). This ancestral biota was composed primarily of tropical elements. The similarities between Africa and South America are explained most parsimoniously by vicariance of this ancestral biota.

South America-Australia.—The probable sister-group relationships between South American and Australian vertebrates are shown in Table 2 (Cracraft, 1974*b*, 1975). The links between the two areas are fairly substantial, but they are not as strong as those for South America and Africa. A further important point is that a well-defined tropical component of this fauna is not readily apparent as it was for the South American-African biota. On the other hand, the biota is also not strongly cool-temperate in aspect. Many authors have commented on the similarities of the floras of South America and Australasia, but the plant links between these two areas are in need of more detailed analysis (see DuRietz, 1940, for an admirable review of the earlier literature). It seems probable that these similarities are of two types: (1) basically tropical taxa that are either pantropical or undoubtedly were in the past but are now extinct in Africa and/or southern Asia—in any case, Australian representatives of these groups have predominantly southern Asian affinities, and (2) those taxa, probably temperate or cool-temperate, having links across East Antarctica. A number of botanists, including both those workers supporting and those denying the importance of continental drift for plant distribution, have used (rather loosely sometimes) the

TABLE 2. Vertebrate links (sister-groups) between South America and Australia. See Cracraft (1973*b*, 1974*b*, 1975) for details.

South America		Australia
	Fresh-water fishes	
Ceratodontidae		Ceratodontidae
Osteoglossidae		Osteoglossidae
	Amphibians	
Hylidae		Hylidae
Leptodactylidae		Leptodactylidae
	Reptiles	
Meiolanidae		Meiolanidae
Chelyidae		Chelyidae
	Birds	
Struthionidae		Casuariidae
Suborder Galli		Megapodiidae
	Mammals	
Metatheria		Metatheria

concept of an Australasian or Indo-Australasian flora without clearly distinguishing these two components, or possibly others.

Botanists have commented that the links of Australia and South America via East Antarctica are primarily of temperate or cool-temperate taxa (Good, 1964; Burbidge, 1960; Raven & Axelrod, 1972, 1974; Raven, 1972; Thorne, 1972). It is also evident that in terms of numbers, far fewer taxa link Australia and South America than link the tropical floras of the southern continents. Thus, the botanical evidence suggests probable temperate relationships of Australian taxa to South America and tropical links to the warm areas of the Old World. As Raven & Axelrod (1974) have suggested, these tropical patterns may have been initiated via Southeast Asia as the Australian plate moved northward in the Cenozoic or possibly via Africa-India-East Antarctica in the Cretaceous prior to major continental disruption.

The above patterns for plants are quite consistent with those for vertebrates. The links of both are less strong between South America and Australia than between the other continents, especially between Australia and the tropical regions of southeastern Asia (see below). Many invertebrates show these same distribution patterns, and some of them have been reviewed by Keast (1972). Diverse groups such as earthworms, spiders, fresh-water molluscs, fresh-water crayfishes, and many insects show relationships between South American and Australian taxa. Within the chironomid midges, for example, there are at least nine links among genera of the Podonominae and Aphroteniinae (Brundin, 1966).

The biological and geological evidence, therefore, seems very consistent with the existence of a Cretaceous-early Tertiary biota common to Australia, East Antarctica, and South America. Apparently this biota was predominantly

TABLE 3. Vertebrate links (sister-groups) between South America and New Zealand. See Cracraft (1974*b*, 1975) for details.

South America		New Zealand
	Amphibians	
Leiopelmatidae		Leiopelmatidae
	Birds	
All other ratites (infraorder Struthionos)		Dinornithidae, Apterygidae (infraorder Apteryges)
Spheniscidae		Spheniscidae

temperate, and its present disjunct nature is explainable in terms of vicariance of the ancestral biota.

South America-New Zealand.—The vertebrate patterns between South America and New Zealand are indeed weak, but the relationships of certain taxa are clearly trans-Antarctic and not trans-Tasman (Table 3). It is of interest that those vertebrate links that do exist between South America and New Zealand are clearly of the oldest taxa in the fauna; none of the presumably younger elements are represented.

The close floristic relationships of New Zealand and southern South America have been well documented (Godley, 1960; Couper, 1960; Raven & Axelrod, 1972; Good, 1964). Almost all of these links are within cool-temperate taxa. Invertebrates also exhibit relationships between these two continents (Keast, 1972). The best documented examples are within chironomid midges where Brundin (1966) has discovered at least six or seven links between these two areas.

The evidence, then, is consistent with the presence of an austral biota common to New Zealand, West Antarctica, and southern South America that was fragmented by continental breakup.

North America-Eurasia.—The similarities of the North American and Eurasian vertebrate fauna are well known, and it will not be my purpose here to recapitulate all these similarities (see Darlington, 1957). Elsewhere I categorized the Recent vertebrate families with respect to primary Gondwanaland or Laurasian Faunal Elements (Cracraft, 1974*b*). The latter element included 16 families of freshwater fishes, 13 of amphibians, and 17 of reptiles. Additionally, many families of birds including the bulk of the passerines (Mayr, 1946; Cracraft, 1973*a*) and placental mammals (McKenna, 1969; Simpson, 1947) can be classified as Laurasian in origin.

Similarly, the floral similarities between North America and Eurasia have long been recognized, and summaries can be found in Thorne (1972), Leopold & MacGinitie (1972), Wolfe (1972), and Wolfe & Leopold (1967).

All of these biotic relationships are best interpreted in terms of divergence following vicariance of more widespread ancestral faunas and floras. Obviously some of the vicariant events occurred at different times. An important one was the opening of the North Atlantic in the Eocene, and present evidence indicates that there have been repeated closures and openings of the Bering Straits during

the Tertiary. Thus, in most cases it is not necessary to invoke dispersal as an explanation for the general biotic similarities of North America and Eurasia.

Tropical Old World.—A final major ancestral biota that was fragmented is that of the Old World tropics. In an earlier paper (Cracraft, 1973*b*) the role of dispersal in accounting for similarities throughout this area was overemphasized, although dispersal from one region to another has undoubtedly occurred in some groups. Thus, many of the Recent disjunct patterns between tropical Africa and tropical Asia are best interpreted as vicariance of a once widespread biota. The situation is complicated in that there have been repeated vicariant events within the fauna by rising and lowering seas and in the Tertiary by orogenic and climatic changes brought about by the collision of India. However, at various times the ancestral biota has included a large number of vertebrate taxa: cypriniform, siluriform, perciform, channiform, and osteoglossiform fishes; caeciliid, bufonid, ranid, and microhylid amphibians; agamid, gekkonid, lacertid, scincid, boid, elapid, and viperid reptiles; and many taxa of birds and mammals (Cracraft, 1973*a*, 1973*b*, 1974*b*).

The similarities in the tropical flora of Africa and southern Asia have been amply documented by Axelrod (1970, 1972), Thorne (1972), and others. The distribution patterns exhibited by both plants and animals across the Old World tropics require a unifying explanation. The most reasonable hypothesis is that of a common biota that has become vicariated; most of the Recent patterns can be explained by disruption and retreat of tropical elements toward Africa and southeastern Asia as much of southern Asia became drier in the Neogene (Axelrod, 1974).

PATTERNS OF DISPERSAL AND MERGING FAUNAS

I now want to discuss two examples of intercontinental biotas in which the links (tracks) are best explained by dispersal of one biota into another rather than by vicariance.

South America-North America.—The geological evidence points very strongly to rather substantial separation of South and North America during the late Jurassic and Cretaceous (see review of evidence in Cracraft, 1974*b*; Raven & Axelrod, 1974). Then, in the Tertiary, southern Central America was gradually built up, increasing the proximity of the two areas until final connection in the Plio-Pleistocene.

Without arguing the details about precisely when a specific group may or may not have dispersed from one area to the other, evidence based on phylogenetic and speciation patterns, levels of differentiation, and diversity gradients strongly suggests that there has been significant interchange of the biotas of North and South America, primarily during the Tertiary although some probably occurred earlier. Among vertebrates, those taxa of the Gondwanaland Faunal Element that dispersed northward included cichlid, characid, and siluriform fishes; microhylid, hyloid, bufonid, and leptodactylid amphibians; iguanid and teiid reptiles; suboscine birds; and marsupial mammals. Those North American (Laurasian) taxa dispersing southward into South America probably included ranid frogs, salamanders, possibly scincid and colubrid reptiles, passerine birds, and placental mammals.

Evidence of a merging of biotas is also seen in plants (Thorne, 1972; Raven & Axelrod, 1974). South America seems to have contributed tropical elements to North America, whereas the latter contributed mainly temperate elements to South America.

Some of the similarities of the North and South American biota may be the result of vicariance of the Pangaeian biota (*e.g.*, among primitive fishes and frogs). If true, these links must represent only the most ancient taxa. Present information indicates that the similarities were initiated long after the breakup of Pangaea.

Australia-Southeast Asia.—The close relationship between many Australian taxa and groups in southern Asia suggests that a common explanation should be sought for this well-defined pattern. In this case, the main pattern is not explicable by vicariance of an ancestral biota (except on a localized scale; see below) but rather by the merging of two faunal elements.

Many Australian vertebrates are more closely related to taxa in Asia than to those in South America. These include ranid, possibly microhylid frogs; agamid, scincid, varanid, pythonine, colubrid, and elapid reptiles; essentially all the oscine passerine birds and many nonpasseriforms as well; and murid rodents. Likewise, a diverse assemblage of plants show distribution patterns similar to those of vertebrates (Axelrod, 1970, 1972; Thorne, 1972; Raven & Axelrod, 1972).

The links between Australia-New Guinea and the Asian continental block are best interpreted as dispersal of one fauna into another at the time the two plates were approaching or after collision. On the other hand, the similarities one sees within any one plate, for example, among the islands of the Asian continental shelf, can be explained by vicariance of a widespread biota present when sea levels were much lower. The same explanation readily applies to the vicariant pattern one sees in the plants and animals of Australia and New Guinea.

PHYLOGENETIC ANALYSIS OF *NOTHOFAGUS* BIOGEOGRAPHY

The southern beeches, *Nothofagus*, are a well known and often cited example of a biogeographically important plant genus. Despite a number of discussions (Godley, 1960; Darlington, 1965; Brundin, 1966; Melville, 1966; Keast, 1972; Moore, 1972; van Steenis, 1972), the biogeography of *Nothofagus* is not known in any detail, most authors merely pointing out that the different "species-groups" are each widely distributed on southern continents. It is known that the dispersal capabilities of *Nothofagus* are greatly restricted (Preest, 1963), thus most authors have concluded that continuous land connections were probably necessary to produce its distributional pattern. Darlington (1965), on the other hand, argued for multiple, independent derivation of *Nothofagus* from the Northern Hemisphere.

In all these writings little mention has been made of the role that phylogenetic relationships might play in deciphering *Nothofagus* biogeography. To my knowledge only Brundin (1966) has discussed this subject with any insight. He noted that because phylogenetic relationships are essentially unknown, it is not possible to reconstruct the exact nature of the distributional patterns within the genus. Brundin's comments on *Nothofagus* have wide applicability for plant

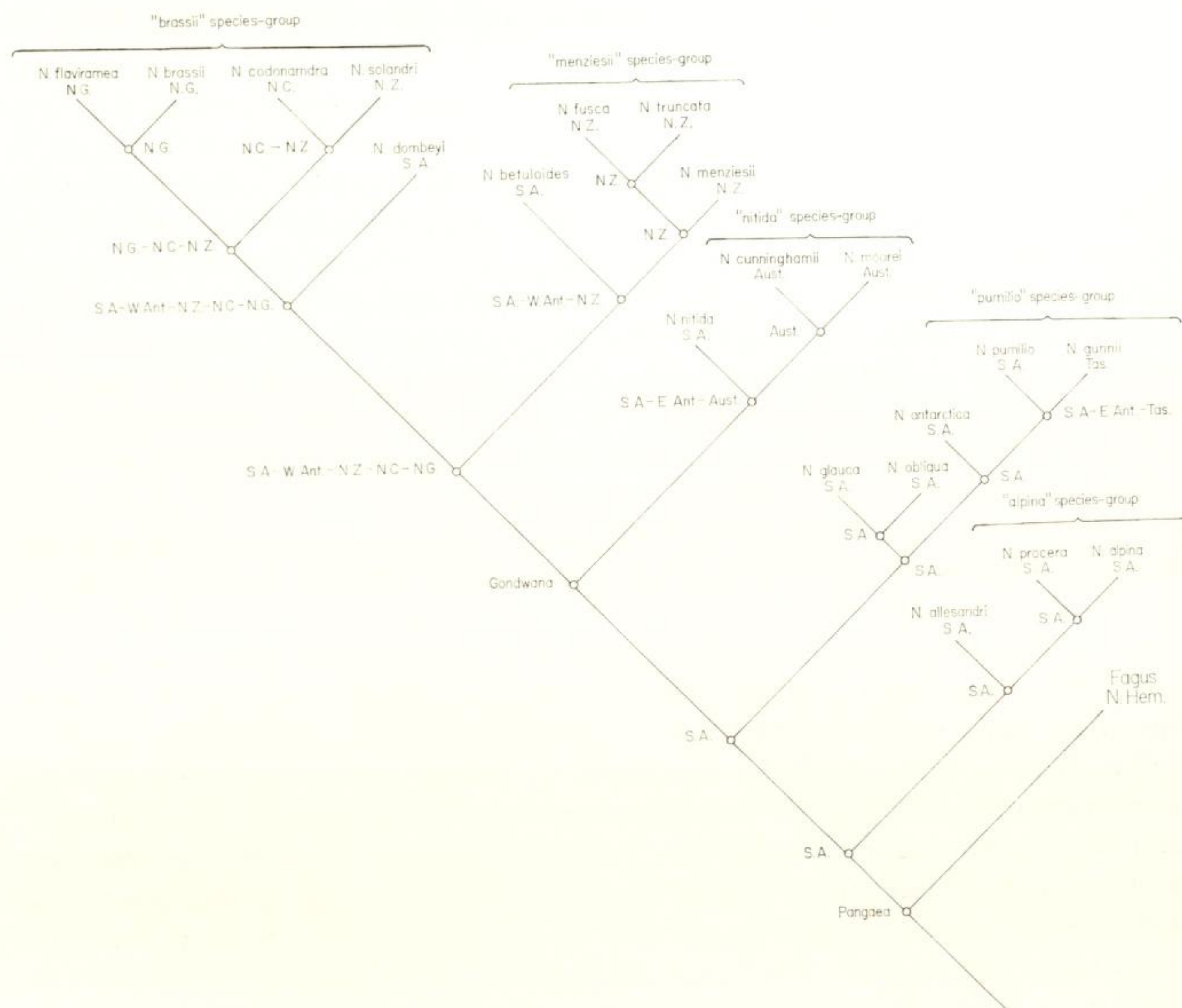


FIGURE 5. A phylogeny of the species of *Nothofagus* (based on Melville, 1973) and a biogeography deduced from it (see text for details). Geographical distributions of hypothetical ancestral species (open circles) are hypothesized. Note that "species-group" names are used for descriptive purposes only and do not refer to traditional groupings based on pollen morphology.

biogeography, for the vast majority of workers in this field have not appreciated the importance of a phylogenetic systematic approach to biogeography.

Recently, Melville (1973) proposed a phylogeny of *Nothofagus* species. His treatment of the biogeographic implications of these relationships was brief. In the discussion that follows I want to use his phylogeny as a basis for reconstructing the biogeographic history of *Nothofagus*. This is considered important because (1) it will be the first attempt at a detailed reconstruction of *Nothofagus* based on a given phylogeny, and (2) it serves as a demonstration of the importance and applicability of phylogenetic systematics to plant biogeography. I emphasize that I am using Melville's phylogeny to illustrate a theoretical point. I am fully aware that fossil data have not been interpolated into the phylogeny. In the case of *Nothofagus* the fossil record must be viewed with a grain of scepticism: it is based almost entirely on pollen morphology, which may not provide sufficient phylogenetic information to allow meaningful biogeographic deductions (see below).

The following biogeographic interpretations are deduced from the phylogeny shown in Fig. 5. It is not my purpose to debate the validity of the phylogeny (Melville provided little supporting evidence), but rather to use it as an example of the reasoning that has been applied extensively to animal distribution (Hennig, 1966a; Brundin, 1966; Nelson, 1969; Cracraft, 1973a). In Fig. 5 I have postulated the geographical distribution of the hypothetical ancestors (open circles) of the different lineages.

The biogeography of *Nothofagus* is organized around four separate trans-Antarctic relationships. The first (“*brassii*” species-group⁵) involves *N. dombeyi* of South America and its sister-group of four species in New Guinea, New Caledonia, and New Zealand; the second (“*menziesii*” species-group) is between *N. betuloides* of South America and its sister-group of three species in New Zealand; the third (“*nitida*” species-group) is *N. nitida* of South America and its sister-group of two species in Australia; and the fourth (“*pumilio*” species-group) is *N. pumilio* of South America and its sister-species, *N. gunnii*, of Tasmania. Two of these links involve relationships across East Antarctica and two across West Antarctica.

One can visualize that the common ancestor of the “*brassii*” species-group was distributed throughout a land mass comprising South America, West Antarctica, New Zealand, New Caledonia, and New Guinea. Separation of the New Zealand continental block away from West Antarctica and South America vicariated the ancestral species into *N. dombeyi* and its sister-group. Later, vicariance isolated the ancestor of *N. flaviramea* and *N. brassii* in New Guinea and the ancestor of *N. codonandra* and *N. solandri* on a land mass including New Zealand and New Caledonia. A subsequent vicariant event, possibly subsidence of the intervening continental crust, isolated *N. codonandra* in New Caledonia and *N. solandri* in New Zealand. All of the above vicariant events, their geography and sequence, are reasonably consistent with what we know of the geology of the region (Raven & Axelrod, 1972).

The common ancestor of the “*menziesii*” species-group was likewise distributed over South America, West Antarctica, and New Zealand prior to continental breakup. When continental separation finally occurred, *N. betuloides* was isolated in South America and the ancestor of *N. fusca*, *N. truncata*, and *N. menziesii* was isolated in New Zealand. Regional geographic isolation within New Zealand can account for the speciation of the three species there.

The ancestor of the “*nitida*” species-group was apparently distributed in South America, East Antarctica, and Australia. Continental fragmentation can be postulated to have isolated *N. nitida* in South America and *N. cunninghamii* and *N. moorei* in Australia.

Within the “*pumilio*” species-group the ancestor of *N. pumilio* and *N. gunnii* is postulated as being distributed in South America, East Antarctica, and Tasmania. Continental fragmentation thus isolated *N. pumilio* in South America and *N. gunnii* in Tasmania. Because of the distribution of *N. antarctica*, *N. glauca*, and

⁵ Species-group names are applied here merely for convenience of discussion and no taxonomic significance is necessarily implied.

N. obliqua in South America, the ancestor of the entire "*pumilio*" species-group was probably South American.

Finally, the "*alpina*" species-group probably has had its entire history in South America. Localized geographic isolation can account for speciation there.

Several important points can be made about the biogeography just postulated. It must be emphasized, however, that the above biogeographic hypothesis is based only on the phylogeny of Fig. 5 and has been presented more as an example of reasoning that might be used in biogeography rather than as a distributional history of *Nothofagus* itself. First, given the hypothesis of Fig. 5, the genus *Nothofagus* provides four trans-Antarctic links, not just one. It may be supposed that a phylogenetic analysis of other plant genera (and families) might also provide evidence of multiple links.

Second, using the hypothesis, it is not necessary to advocate wholesale long-distance dispersal to account for the distribution of the genus around the southern end of the world. Some dispersal may have occurred at various stages in the phylogeny. For example, one might deduce from the phyletic data that the early history of the genus was primarily South American and that subsequent to the origin of the "*pumilio*" species-group there was dispersal to other areas of Gondwanaland. Likewise, the "*menziesii*" and "*brassii*" species-groups probably attained an independent distribution across West Antarctica. Since it is unlikely that a vicariant event occurred across the entire area of South America, West Antarctica, and New Zealand, some dispersal is suggested. Nevertheless, it must be stressed that within the phylogeny of the genus as a whole, dispersal need not be accepted as the prime cause for the Recent distribution pattern.

Third, if the distributional history of *Nothofagus* outlined here is close to reality then it is remarkably consistent with the patterns of vertebrates and invertebrates. This also suggests a common biogeographic history for Southern Hemisphere biota. Patterns for *Nothofagus* show a track from South America across West Antarctica to New Zealand and across East Antarctica to Australia or Tasmania. There are no sister-group relationships between species in Australia and those in New Zealand. Interestingly, there are no close relationships of species in Australia and New Guinea, the latter area showing relationships to New Caledonia and New Zealand. This latter distribution is consistent with past geology, since these areas may have been more or less contiguous before opening of the northern part of the Tasman Sea. Other plant groups show tracks from New Guinea through New Caledonia to New Zealand (Croizat, 1952; Burbidge, 1960).

It is obvious from his phylogeny that Melville (1973) does not consider the traditional "species-groups" which are based on pollen morphology (the *menziesii*, *brassii*, and *fusca* species-groups of most authors; not those of Fig. 5) to be natural groups. Indeed, I am unaware of any evidence that strongly suggests that the three different pollen types characterize monophyletic taxa. Such evidence could only come from a detailed analysis in which ancestral-derived polarities in pollen morphologies could be hypothesized. In this way supposed monophyletic taxa will not be erected on the basis of shared primitive character-states but rather on shared advanced character-states (Hennig, 1966b; Brundin, 1966). This uncertainty about relationships within *Nothofagus* casts great doubts on the systematic

allocation of fossil pollen and any biogeographic interpretations one might draw from them. Biologists have blithely assumed that pollen morphology defines related species-groups, but that may very well not be the case within some, but not necessarily all, species-groups. Relationships within *Nothofagus* are in need of restudy before the biogeographic conclusions of previous authors can be accepted or rejected.

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