

CENTERS OF ORIGIN AND RELATED CONCEPTS

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Abstract

Croizat, L., G. Nelson, and D. E. Rosen (*Department of Ichthyology, The American Museum of Natural History, New York, New York 10024*) 1974. *Centers of origin and related concepts*. *Syst. Zool.* 23:265–287.—The concept of center of origin in the Darwinian sense is often accepted and used as if it were a conceptual model necessary and fundamental to historical zoogeographical analysis. But in certain respects it is inconsistent with the principles of common ancestry and vicariance² (e.g., allopatric speciation), and its application to concrete examples of animal distribution generally yields ambiguous results. In the following pages we present a critique of the concept of center of origin, and outline an alternative conceptual model, involving generalized patterns of biotic distribution (generalized tracks). We assume that a given generalized track estimates an ancestral biota that, because of changing geography, has become subdivided into descendant biotas in localized areas. We assume that in such areas, more or less biotically isolated from one another by barriers to dispersal, the descendant biotas differentiate and produce more modern patterns of taxonomic diversity and distribution. We reject the Darwinian concept of center of origin and its corollary, dispersal of species, as a conceptual model of general applicability in historical biogeography. We admit the reality of dispersal and specify how examples of dispersal may be recognized with reference both to sympatry and to generalized tracks, but we suggest that on a global basis the general features of modern biotic distribution have been determined by subdivision of ancestral biotas in response to changing geography. [Biogeography; distribution; evolution.]

GENERALIZED TRACKS

1. Distributions (tracks)

a. The distribution (track) of a species or monophyletic group of organisms may coincide with the distributions (tracks) of other species and groups.

b. Coincident distributions involving monophyletic groups (coincident individual tracks) confirm the reality, and are components, of a general biotic distribution (generalized track).

c. The distribution of most species and of most monophyletic groups coincides with that of some other species or group and may, therefore, occupy part or all of some generalized track.

d. The most generalized tracks include the largest number of, and the most biologically diverse, groups of organisms both fossil and recent, and are, therefore, the most thoroughly confirmed.

2. Distributions (tracks) and biotas

a. All species are components of biotic systems (biotas) that tend to persist through time despite their more or less gradual change in distribution and species composition.

b. Modern biotas are descendants of one or more ancestral biotas that existed in the past.

c. Ancestral biotas subdivided (vicariated) in response to a changing geography, the history of which is, therefore, correlated with their subdivision and differentiation (vicariance).²

d. A generalized track estimates the biotic composition and geographical distribution of an ancestral biota before it subdivided (vicariated) into descendant biotas.

e. The components of one generalized track are geographically and biotically more closely related among themselves than they are to the components of some other generalized track. Therefore, descendant biotas (vicariants) resulting from the subdivision of an ancestral biota are biotically and geographically more closely related

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among themselves than they are to the subdivisions of some other ancestral biota.

3. Distributions (tracks) and dispersal

a. Some coincident distributions may include components of different generalized tracks, where generalized tracks, or one or more of their components, overlap.

b. Overlap of generalized tracks, or any of the components of different generalized tracks, reflects geographical overlap of different biotas due to dispersal.³

c. The occasional species, or group, whose distribution does not occupy part of a generalized track may have been distributed by chance dispersal.

d. Attempts to explain the distribution of individual plant and animal groups, based on their ecology and means of dispersal, may ignore and obscure existing generalized tracks and the ancestral biotas they represent.

If a given type of geographical distribution (individual track) recurs in group after group of organisms, the region delineated by the coincident distributions (generalized track) becomes statistically and, therefore, geographically significant, and invites explanation on a general level. The first step toward such generalization is to determine what major types of coincident distributions (generalized tracks) recur in the world biota, the number of individual tracks composing each, and the variety of organisms incorporated (Croizat, 1964:21). By this means ancestral biotas may be estimated and compared according to their geographical extent, and the number and diversity of their biotic elements. Interpreted as an ancestral biota, a generalized track serves as a constraining reference for interpretation of its individual elements. Thus a group of freshwater fishes (Galaxiidae), widely distributed in the temperate parts of the southern hemisphere, might by itself be interpreted, perhaps even credibly, as an example of transoceanic dispersal from some center of origin (McDowall, 1973a, 1973b). But when galaxiid distribu-

tion is compared with that of other southern hemisphere organisms, many of which have similar distributions but different means of dispersal, e.g., earthworms, freshwater crustaceans and their parasites, molluscs, and birds (Whitley, 1956), in addition to midges (Brundin, 1966) and plants of many different groups (e.g., Croizat, 1952; Good, 1964) a general problem is posed, concerning the original distribution and subsequent history of a pan-austral biota, of which the Galaxiidae might be only a small part (Rosen, 1974). Thus, an ancestral pan-austral biota, including ancestral Galaxiidae, might once have been geographically widespread, and later subdivided into local areas of evolution (Australia, New Zealand, New Caledonia, South America, and Africa) in relation to disruptive geological events.⁴ Given these two alternative models (dispersal of Galaxiidae from a center of origin versus subdivision of a pan-austral biota), how might they be compared and evaluated on the basis of distributional data of organisms? The problem is one of different realities: the reality of long-distance dispersal versus the reality of a pan-austral biota. Can evidence be found that long-distance dispersal of Galaxiidae occurs, e.g., that galaxiids spawned in Australia were, or are, regularly distributed in the ocean from Australia to South America? Or, alternatively, can the pattern of galaxiid distribution be found in other groups for which long-distance dispersal is not known to occur; and if so, is the accumulation of individual tracks large and varied enough, as determined by comparison with worldwide standards, to justify the interpretation of galaxiid distribution as part of a subdivided ancestral biota?⁵ If not—if the distribution of the Galaxiidae were unique, or unparalleled by a significant sample of the world biota, chance dispersal would be indicated (the “sweepstakes” dispersal of Simpson, 1940:152; see item 3c above). Indeed, the only conclusive evidence for chance dispersal may be the demonstration that a given distribution is unique, unparalleled by that of any other living organisms,

and free—for other interpretation as it were—from the constraining reference of a generalized track. Unfortunately, few zoogeographers have ever envisioned, much less attempted explicitly, the necessary first step toward historical interpretation: the determination of the historical biotas as represented by generalized tracks. The bulk of historical zoogeography consists of repeated attempts (e.g., Darlington, 1957, 1965) to explain individual case after case of distribution with reference to the Darwinian concepts of center of origin and dispersal of species according to the means available to each—concepts that seem to us inapplicable on the general level of the historical biotas (as represented by generalized tracks). Centers of origin and means of dispersal only vary from species to species, and do not explain general patterns of biotic distribution (cf. Croizat, 1952, 1958a, 1960, 1964).

The significance of a generalized track may be demonstrated with reference not only to a subdivided continental biota, the parts of which are separated by oceans, as in the case of the austral biota; but also to a subdivided marine biota, the parts of which are separated by land. A simple and dramatic example is the subdivided ampho-American biota, the parts of which are now separated by the Panamanian isthmus. Of this biota Ekman (1953:30) wrote:

“In spite of the fact that the isthmus of Panama nowadays represents an unsurmountable barrier for sea animals, the tropical eastern Pacific and the tropical West Atlantic constitute nevertheless a faunistic unit. This emerges not from a one-sided consideration of the distribution of the species but becomes all the clearer if we consider the genera. This state of affairs . . . may be attributed to historical causes.” “Some species, though only few in number, are found in identical development on both sides of Central America. In other cases Atlantic and Pacific species are to be found more closely related to each other than to other species. This suggests that they must have evolved from a common ancestor.”

Ekman's concept (1953:31) embodies aspects of a generalized track:

“In determining the relationship of the various faunas to one another and the history of their distribution it is important that conclusions should be drawn not from a more or less subjective general impression of faunistic studies but as far as possible from numerical statements about the composition of the fauna which will permit statistical comparisons.”

From assembled data of American warm-water crabs and echinoderms Ekman showed that 2% of the crab species and 18% of their genera, and 0.3% of the echinoderm species and 10% of their genera, occur in the Pacific and Atlantic. He concluded that the species common to both, whether endemic in American waters or more or less circumtropical, seem to be all ancient species that have changed little in their external morphology since the time of formation of the Panamanian isthmus. The shared genera Ekman collectively regarded as a good indication of the close relationship of the Atlantic and Pacific faunas as parts of a common American (ampho-American) thermophile biota. Other conspicuous ampho-American elements include molluscs, crustaceans, and fishes. As cited by Ekman, the numbers of vicariant pairs of species are impressive: 80 pairs of warm-water crabs, 40 pairs of echinoderms, 100+ pairs of fishes, and so on. The conclusion to be drawn from this evidence is that there is a generalized transisthmian track, thoroughly confirmed, which may be part of a larger circumtropical track; that hundreds, and probably thousands (Briggs, 1974), of ancestral species (an ancestral marine biota) once occupied a sea, and later a seaway connecting the Atlantic and Pacific basins; and that the populations of these ancestral species (biota) were subdivided by the gradual subdivision and final interruption of this seaway. There is no evidence of east- or west-bound traffic of dispersing species through the seaway, either before or after its interruption. But there is every indication of wholesale allopatric speciation (vicariance) that began at the time of interruption, and that, as measured by taxonomic differentiation, proceeded at different rates in different groups of organisms

(Rosenblatt, 1963). Like the austral biota, the amphi-American biota was initially recognized on the basis of biogeographical, not geological, data:

“This conclusion of a former direct connection was reached by Günther [1869:398] before the geologists demonstrated an ancient channel across what is now Central America and his views were subsequently fully confirmed by geology, an example of the legitimacy of drawing in certain cases geophysical conclusions from purely zoogeographical premisses” (Ekman, 1953:36).

The important feature of the amphi-American biota for historical biogeography is that it demonstrates how comparable in detail may be the generalized tracks of a continental biota of which the parts are separated by water, and a marine biota of which the parts are separated by land. It demonstrates also how capricious may be proposals to explain, with reference to means of dispersal but without reference to generalized tracks, the presence of closely related forms, identical or not as to species, on each side of a barrier. It demonstrates finally how desirable may be the consideration that a given distribution (track) is potentially a member of a generalized biotic distribution (generalized track), as in the examples discussed below for the avian genus *Columba* (fig. 1) and the decapod genera *Typhlataya* and *Gecarcinus* (fig. 2).

The internal structure of a generalized track may be closely correlated with the historical subdivision of an ancestral biota. Among south temperate fishes now inhabiting the Gondwanian fragments, for example, closer ties are indicated among South America-New Zealand-Australia than any of these with Africa. Examples are the retropinnid osmeroids (smelts) of New Zealand-Australia; the galaxiids, with a single form in Africa and many interrelated forms in South America-New Zealand-Australia; and the petromyzonid (lamprey) *Geotria australis* of South America-New Zealand-Australia, but not Africa (Rosen, 1974). Following the initiative of Brundin (1966), Keast (1973:331; also Edmunds,

1972) analyzed the contemporary southern biota relative to the separation sequence of Africa, South America, Australia, and New Zealand, and observed that

“The ‘southern ends’ of these continents contain a range of temperate, or cold temperate, biotas quite different from those of the sub-tropical or tropical regions to the north” and that there “is good evidence that the former have had long and continuous histories as southern, cool-adapted forms.” Keast (1973:338) concluded that “The contemporary southern temperate biotas of South America and Australia are much more closely related than either is to the African one. Since this pattern is repeated in a wide variety of groups, of widely differing ecological requirements, there can be no doubt that this is a fundamental difference and is not an artifact resulting from secondary extinction in Africa. The biological data, hence, confirm the geological data that Africa separated off earlier from the Gondwana landmass.”

What may be reflected in the history of the pan-austral biota is subdivision caused by large-scale geographical changes, i.e., the fragmentation of ancestral populations, and their subsequent isolation and differentiation, due to continental fracture and displacement. The existence of large-scale changes does not alter the fact that a given ancestral biota is also subject to subdivision through subtler changes, involving climate, elevation, flooding, erosion, glaciation, and other factors that lead to reproductive isolation of localized parts of the biota. Vicariance, therefore, is a more general phenomenon than continental fracture and displacement, even though vicariance may be well exemplified by those geological processes and their subsequent effects on the course of biotic evolution.

To the extent that vicariance underlies organic distribution, sympatry (range overlap) is evidence of subsequent dispersal (note 3). After observing sympatry, one may infer that dispersal has occurred; but the observation alone does not specify whether one member of the sympatric pair dispersed, and if one member dispersed, which one of the pair did; or whether both dispersed. For example, in the salamander genus *Plethodon*, widely distributed in the

United States, there are 28 unit taxa (definable, named populations), divided into two main groups, which are here assumed to be monophyletic (Highton, 1962, 1972; Brodie, 1970; Highton and Henry, 1970). One group includes eight western *Plethodon*; and the other, with two subgroups, 12 small and eight large eastern *Plethodon*. There is no sympatry between western and eastern *Plethodon*, but there is considerable sympatry among the members of each group, and among the members of the two eastern subgroups. Only a few of the 28 unit taxa are not sympatric with any other *Plethodon*. Within the western group, each of a number of cases of sympatry involves the widespread *P. dunni* or *P. vehiculum* as one of a sympatric pair. Possible interpretations include (1) that a widespread form dispersed into the more restricted ranges of the other unit taxa, or into the range of their common ancestor before it vicariated, and (2) that the unit taxa sympatric with *P. dunni* or *P. vehiculum* arose by vicariance from a widespread ancestral species that had already dispersed into the range of the population ancestral to *P. dunni* or *P. vehiculum*. Similar sympatric distributions occur among the 12 eastern small *Plethodon* and eight eastern large *Plethodon*.

We consider that two general factors are responsible for the complexity of the modern world biota: (1) a continuing temporal sequence of vicariance events, and (2) subsequent dispersal modifying earlier vicariant patterns. Without a history of vicariance, the modern world biota would consist of only one or a few species, most if not all of which would be sympatric. Without a history of dispersal, the modern world biota would consist of no or few sympatric species, although it might have become subdivided into numerous allopatric fragments (vicariants). Vicariance, therefore, produces geographical differentiation and multiplication of species, and dispersal produces sympatry and the possibility of interspecific interaction (competitive exclusion, ecological differentiation, extinction). We identify geological change as the general

causal principle of vicariance, but at present we are unable to identify a general causal principle of dispersal; we imagine that the causes of dispersal are as numerous as the species that have dispersed, although perhaps these causes may be grouped into several classes of phenomena, e.g., physiographic, hydrographic, climatological, biological, and such other factors that may on occasion act to open an environment to a species that previously found it closed to dispersal. 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 geographical 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.

CENTERS OF ORIGIN

“Every animal species originated from a few ancestors in a limited area; if a particular species is now found to be widespread, it must of necessity have reached parts of its present range at an earlier period” (Udvardy, 1969:7).

Applied to a species, the concept of center of origin is a “limited area” in which a “few ancestors” of a species may be supposed to have originated, and from which the species may be supposed to have dispersed to achieve its present distribution. Applied to a group of species, the concept is the “limited area” in which a “few ancestors” of the first existing species may be presumed to have originated. The other species of the group may be presumed to have been derived from the first either in the “limited area” of origin, or in some other area to which the first species dispersed.⁶

“The concepts of centers of origin and dispersal are deeply ingrained in biogeographic thought

and supported by so much evidence in the best known cases that other concepts have received little attention. Yet in many specific cases the nagging questions of what the center was or whether there was a center do arise. What is commonly seen in the fossil record seems to suggest that evolution always occurred somewhere else" (Olson, 1971:738).

As early as 1901, Briquet (1901:65–66) stated that the concept of centers of origin ("le principe monotypique") had exerted an unfortunate influence ("a joué un rôle fâcheux") upon phytogeographical research. In his opinion the concept implied numerous assumptions of dubious validity that had to be accepted before a center of origin could be worked out for any given group (cf. Favarger and Küpfer, 1969; Croizat, 1971a). Cain (1943) reviewed the criteria by means of which centers of origin were recognized in phytogeographical studies (Croizat, 1964:595ff). According to Cain at least 13 different criteria had been advanced, not one of which was really reliable. He concluded that

"There seems to be only one conclusion possible, and it carries implications far beyond the scope of the present discussion of criteria of center of origin. The sciences of geobotany (plant geography, plant ecology, plant sociology) and geozoology carry a heavy burden of hypothesis and assumption which has resulted from an over-employment of deductive reasoning. What is most needed in these fields is a complete return to inductive reasoning (Raup, 1942) with assumptions reduced to a minimum and hypotheses based upon demonstrable facts and proposed only when necessary (Hultén, 1937). In many instances the assumptions arising from deductive reasoning have so thoroughly permeated the science of geography and have so long been a part of its warp and woof that students of the field can only with difficulty distinguish fact from fiction" (Cain, 1943:151).

Independently of Cain, Croizat came to the same conclusion and, accordingly, attempted to work out a more inductive approach to historical biogeography (bibliography in Nelson, 1973).

To some extent the conclusions of Briquet and Cain are echoed in the writings of zoologists, e.g., Kinsey (1936:58):

"C. C. Adams some years ago (1902) listed several criteria for the recognition of the center of origin of any taxonomic group; and while only scant argument for and no specific test of the principles was then presented, these criteria have found some approval and have been repeatedly quoted as usable means for finding what I do not believe ever existed."

Nevertheless, criteria for recognition of centers of origin are still listed as routine preliminaries for zoogeographical analysis (e.g., Erwin, 1970:184).

Despite its disadvantages, the quest for centers of origin continues to be a dominant theme of modern zoogeography. Mayr, for example, sorted the North American bird fauna into its presumed centers of origin (Mayr, 1946b:14–15; also, Cracraft, 1973). Of some 100 families he listed 29 as "unanalyzed" for reasons such as these:

"Most of the families of shore birds also are so widespread as to make it impossible to trace their origin." "Among the strictly terrestrial birds, there are eight families [Mayr listed only seven] that are so widespread or so evenly distributed as to make analysis difficult at the present time." "The evidence indicates that all of these families originated at such an early date (Eocene or Cretaceous) that subsequent shifts in distribution have obliterated most of the clues." Mayr nevertheless guessed that the "Caprimulgidae may well be of New World origin." He added that "The woodpeckers (Picidae) are represented about equally well in the Americas and the Oriental regions. They are rather poorly developed in Eurasia and Africa and are absent from the Australian region and from Madagascar. This pattern of distribution suggests a New World (but very early) origin for the family, although the fact that their nearest relatives, the wrynecks (Jynxidae), are exclusively Old World would seem to indicate the opposite." For the Hirundinidae he stated that "It is uncertain whether the family originated in South America . . . or whether the 'old-American' swallows are descendants of early invaders from Asia."

Mayr's attempt to resolve centers of origin thus caused him to abandon nearly 30% of the North American avian families as "unanalyzed"—and, presumably, unanalyzable beyond the ambiguous conclusions quoted above.

Darlington (1957:236) opened his chapter on bird distribution by stating that

"In some ways, birds are the best-known animals. Almost all existing species of them are probably known, some 8600 full species (Mayr 1946a; Mayr and Amadon 1951), plus thousands of geographical subspecies, and the distributions of many of the species are known in detail. Of all vertebrates, birds are the ones I know best myself. I have watched them almost all my life and have collected them in a small way in northern South America and Australia. I have had the benefit of many conversations about them with the late James L. Peters and with Ludlow Griscom and James C. Greenway, Jr., of the museum staff. And Dr. Josselyn Van Tyne and Professor Ernst Mayr have read stages of the manuscript of this chapter and made useful criticisms of it; Professor Mayr has allowed me to use his carded references on bird geography. I have therefore had unusual opportunities. Nevertheless, I still find the distribution of birds very hard to understand. The present pattern is clear enough, though complex. But the processes that have produced the pattern—the evolution and dispersal of birds—are very difficult to trace and understand."

To us, Darlington's remarks convey the curious idea that, according to his method of analysis, the better the data the more difficult is their interpretation—even to the point of impossibility. In our opinion, a properly devised method of analysis should make short work of statistically optimum data such as those of the birds (cf. Croizat, 1958a, in which bird distribution is analyzed).

Analyzing the geography of *Columba*, Darlington (1957:272–273) stated that

"The one genus of pigeons common to the Old and New Worlds is *Columba* (from which domestic pigeons are derived). This genus is an example of ambiguity of numbers clues. It is nearly cosmopolitan. There are about 32 species of it native in the Old World and about 20 in the New, and the Old World species are more diversified, which suggest an Old World origin. But all 20 New World species occur in South and Central America and the West Indies. One of the Central American species extends into western North America north to southwestern Canada, but the genus is otherwise absent from the main part of North America, above southern Florida. There are about 14 species in temperate Eurasia and associated islands; 11 in the main part of Africa and closely associated islands, but none in Madagascar; 5 in the tropical Oriental Region etc.; and 2 in the Australian Region, but only one of them

reaches Australia proper, and only the eastern part of the continent; and none reaches New Zealand. Thus detailed, the numbers suggest a tropical American origin of *Columba*, dispersal to the Old World through the north (not by the existing western North American species but perhaps by an earlier one), and spread through the Old World from the north. The absence of the genus in Madagascar and the more remote part of Australia is consistent with this history. Alternatively, the genus may have originated in temperate Eurasia and radiated from there and then radiated secondarily in tropical America. Or (and I think this is most likely) it may have had a still more complex history."

In the above account, Darlington seems to hesitate among ambiguous clues, always grasping for an ever-elusive center of origin. His analysis of *Columba* tends to confirm the opinion of Fraipont and Leclercq (1932: 7) that the quest for a center of origin leads to an "effarante paléogéographie où les mers et les continents, les plantes et les animaux dansent, sur une terre épileptique, une ronde sans repos." Indeed, *Colomba* as conceived by Darlington seems to have flittered so restlessly between the Old World and the New that its wanderings through space and time are opaque to analysis.

Mayr and Phelps (1967) attempted to determine the centers of origin of the avifauna of the *cerros* and *mesas* of southeastern Venezuela (their "*Pantepui*") with reference to the Andes, the coastal cordillera of Venezuela, and the Brazilian shield. But it is equally reasonable to begin with the premise that the birds of *Pantepui* and of the cordilleras to the north and west had a common origin in a widespread fauna, that was later subdivided by the events of Tertiary geology into Andean, cordilleran, and pantepuian groups. Mayr and Phelps (1967: 293) considered this possibility (their "plateau theory"), but dismissed it for the reasons that *Pantepui*

"is geologically vastly more ancient than its bird fauna" and that "The irregular distribution within *Pantepui*, the different degrees of differentiation from the nearest relatives, and the various degrees of differentiation within *Pantepui* all contradict the assumption that the present fauna of *Pantepui* is the remnant of an old, formerly uniform plateau fauna."

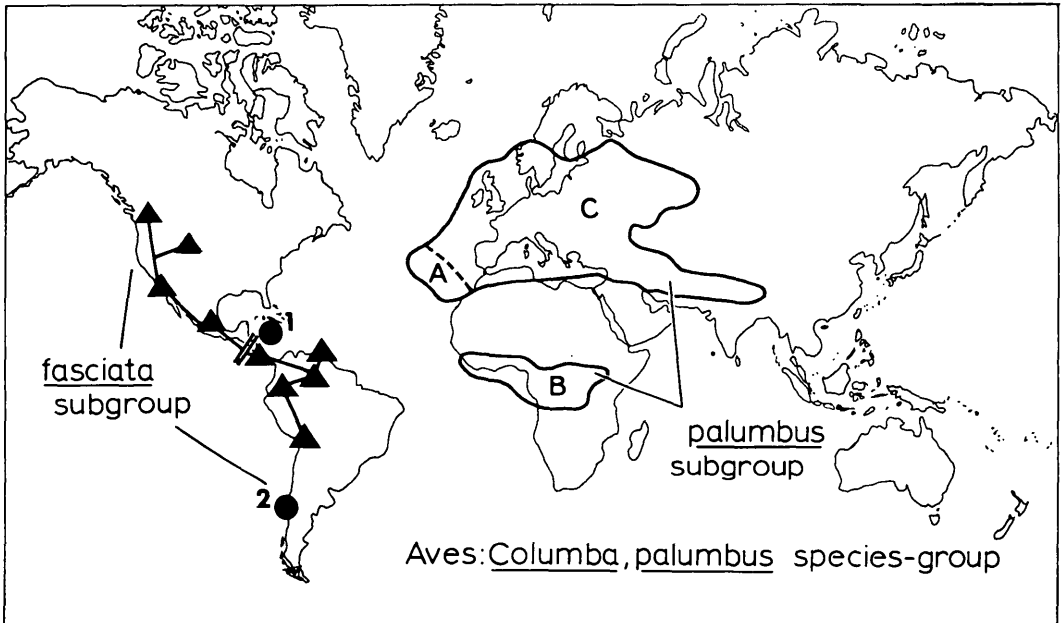


FIG. 1.—Distribution of *Columba* (Aves: Columbidae), species-group *palumbus* (partly after Johnston, 1962). The species-group includes two sub-groups: *palumbus* and *fasciata*. The distribution of the *palumbus* sub-group, in Eurasia and Africa, is circumscribed: A, Atlantic sector (Canary Islands, Madera, Azores) in which occur *C. palumbus maderensis*, *C. p. azorica*, *C. trocaz*, *C. bollii*, *C. junoniae*; B, range of *C. uncinata* (a classic west African taxon); C, range of *C. palumbus* outside the Atlantic sector. The distribution of the complex *C. fasciata*/*C. albilinea* (the former to the northwest of the double bar, Panama/Costa Rica, the latter to the southeast) is indicated by full triangles connected by a line (track); *C. caribaea* (Jamaica) by circle 1; and *C. araucana* (Chile and Argentina) by circle 2. The New World species form the *fasciata* sub-group.

Instead they (1967:297; cf. Haffer, 1970) favored the view that “the subtropical fauna of Pantepui is derived from that of other subtropical regions by ‘island hopping’” (their “distance dispersal theory”; cf. Deignan, 1963:264: “so overwhelming is the evidence of sedentation in birds, especially in the tropics, that the whole hypothesis of dispersal of birds by island hopping must be suspect”). Mayr and Phelps (1967: 286) noted that the age of Pantepui has been variously estimated as Proterozoic to Eocene, but omitted any discussion of the age of the bird fauna. They stated, however, that

“it is evident that there is a completely even gradation from endemic genera to species that have not even begun to develop endemic subspecies. Fewer than one-third (29 species) of the characteristic upper zonal element of Pan-

tepuí (96 species) are endemic species. These facts are conclusive evidence for the continuity and long duration of the colonization of Pantepuí” (1967:291).

Mayr and Phelps did not consider the possibility that these “facts” might simply reflect different evolutionary rates, rather than “chance colonization” (1967:298) by means of “long-distance flights” (1967:301).

The quest for a center of origin often leads to equivocal conclusions and conflicting opinion. For another example (fig. 1), the lone pigeon that occurs in southwestern Canada is *Columba fasciata*. This species is distributed from British Columbia to Trinidad and Argentina, and was once divided into two species: *C. albilinea* (South and Central America to Panama/Costa Rica); and *C. fasciata* (North America). According to Johnston (1962), it belongs to

the *palumbus* species-group, which is itself divided into two sub-groups: a *palumbus* subgroup and a *fasciata* subgroup.⁸ In the *palumbus* subgroup are included five species endemic to western Eurasia/north-western Africa, Equatorial Africa, and particularly, the Atlantic islands (Madeira, Canaries, and Azores). The *fasciata* subgroup includes three species, all American. The attempt to determine the center of origin and subsequent dispersal of this group leads to a basic disagreement between those zoogeographers who would accept transatlantic relationships at their face value, and those who accept the Matthewian thesis that transatlantic relationships are impossible except via the Bering landbridge or through the agencies of remote chance. But how could one or another school of zoogeographers begin to evaluate the truth of the matter without first understanding the nature of the preconceptions that produce their disagreement? Moreover, neither school might consider the hypothesis that the ancestors of the *palumbus* group were already widely distributed—from which hypothesis it follows that the subsequent history of the species group involved neither a center of origin nor transoceanic (or transbering) dispersal.

The relation between centers of origin and the distribution of “primitive” and “advanced” taxa may, likewise, lead to conflict (Lutz, 1916). As an example, we refer to certain cetoniid Coleoptera (Wiebes, 1968: fig. 4; Croizat, 1971a:394, 397, fig. 2B): *Goliathus russus*, endemic to the Congo (Zaire) Basin, differs more sharply from the adjacent *G. fornasini* (Kenya, Tanzania [Usambara], Mozambique, etc.), *G. aureosparsus* (Nigeria), and *G. higginsii* (Ivory Coast) than these three species differ among themselves (Wiebes, 1968:30, mentioned “more examples of this phenomenon in other groups of African Cetoniidae,” and Croizat noted numerous other cases in plants and animals, and discussed some as examples of “wing dispersal”). Some zoogeographers would assume that one species or group, e.g., the species (*G. russus*) in

the center of the assemblage, is relatively more primitive (or “plesiomorphous”) than the remaining three, and that it should be assumed to indicate, or to occupy, the center of origin of the group as a whole; these zoogeographers assume that relatively primitive species are generally less apt to disperse than their relatively advanced (or “apomorphic”) relatives (Hennig, 1966:232; Brundin, 1972). Other zoogeographers would assume that one species or group, e.g., the centrally located species, is advanced and that it indicates, or occupies, the center of origin of the group as a whole; these zoogeographers assume that relatively advanced species are generally less apt to disperse than their primitive relatives (Darlington, 1957:554–555, 1970). Other zoogeographers would assume that one species or group, especially if it were fossilized and demonstrably older than its relatives (the “right fossils in the right places” of Darlington, 1957:35) is actually ancestral to the other members of the group, and therefore reveals directly the center of origin (e.g., Simpson, 1940).⁹ Still other zoogeographers might approach the problem with different sets of apriorisms. The conflict of opinion resulting from different apriorisms raises the question of the applicability of the concept, and even the existence, of a center of origin as envisioned in these discordant approaches. We would point out that, if a center of origin is imaginary, all of its corollaries are equally imaginary; and by an opportune choice of examples, anyone can “prove” whatever he wishes to “prove” about it.

CHARLES DARWIN

The question naturally arises, who first thought of the idea of center of origin? The idea seems to be very old, for Spanish clerics thought about the center of origin of the Indians they encountered in the New World shortly after 1492 A.D. (Croizat, 1960:1367–1372). The idea was one of the basic assumptions of Darwin’s zoogeography:

"We are thus brought to the question which has been largely discussed by naturalists [e.g., Swainson, 1835], namely, whether species have been created at one or more points of the earth's surface. Undoubtedly there are very many cases of extreme difficulty, in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points, where now found. Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle" (1859:352); "Hence it seems to me, as it has to many other naturalists, that the view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted, is the most probable" (1859:353); and "Whenever it is fully admitted, as I believe it will some day be, that each species has proceeded from a single birthplace, and when in the course of time we know something definite about the means of distribution, we shall be enabled to speculate with security on the former extension of the land. But I do not believe that it will ever be proved that within the recent period continents which are now quite separate, have been continuously, or almost continuously, united with each other, and with the many existing oceanic islands" (1859:357-358).¹⁰

It is apparent that Darwin was concerned with the origin of species, but he produced no factual evidence for his belief that species originate in centers from which they disperse, either actively or passively according to the means available to them, to points far and near in time and space. Darwin simply affirmed that his belief "captivates the mind," and that he who rejects it is guilty of invoking a miracle against the true cause of evolution.¹¹ Indeed, so overwhelmingly important to Darwin were means of dispersal that he believed knowledge of them would permit resolution of paleogeographic problems (but whatever the resolution, Darwin believed that continents and oceanic islands will never be found to have been in connection). In short, the zoogeography of Darwin is based on the preconditions of (a) centers of origin, (b) dispersal of spe-

cies according to available means, and (c) permanent continental outlines. To these, Wallace (1876) and, especially, Matthew (1915) added the thesis that dispersal proceeded from Holarctica to the rest of the earth,¹² and laid the foundations of the zoogeography of writers such as Simpson, Mayr, Darlington,¹³ Schmidt, Hershkovitz, B. Patterson, MacArthur, and numerous others of the modern era (e.g., Sauer, 1969; Tobler et al., 1970).

Darwin's treatment of geographical distribution in the *Origin of Species* is less interesting than in the *Voyage of the Beagle*, at any rate in our opinion (cf. Ghiselin, 1969). There is no need to repeat here what has been detailed in many pages elsewhere (Croizat, 1964:592-706), but we would point out that Darwin in the *Voyage* was already aware of the general phenomenon of vicariance; with respect to three species of Galapagos "mocking birds" he stated that

"I examined many specimens in the different islands, and in each the respective kind was *alone* present. These birds agree in general plumage, structure, and habits; so that the different species replace each other in the economy of the different islands" (1839:475). He added that "it never occurred to me, that the productions of islands only a few miles apart, and placed under the same physical conditions, would be dissimilar" (1839:474). In a later edition he added, with reference to the Geospizinae, that "Seeing this gradation and diversity of structure in one small, intimately-related group of birds, one might really fancy that, from an original paucity of birds in this archipelago, one species had been taken and modified for different ends" (1846:148)

—a statement made without appeal to a center of origin and dispersal.¹⁴ As for his interpretation of the biogeography of the Galapagos, it was incisive:

"It would be impossible for any one accustomed to the birds of Chile and La Plata to be placed on these islands, and not to feel convinced that he was, as far as the organic world was concerned, on American ground" (1839:474). In a later edition he expanded on this theme: "I have said that the Galapagos Archipelago might be called a satellite attached to America, but it should rather be called a group of satellites,

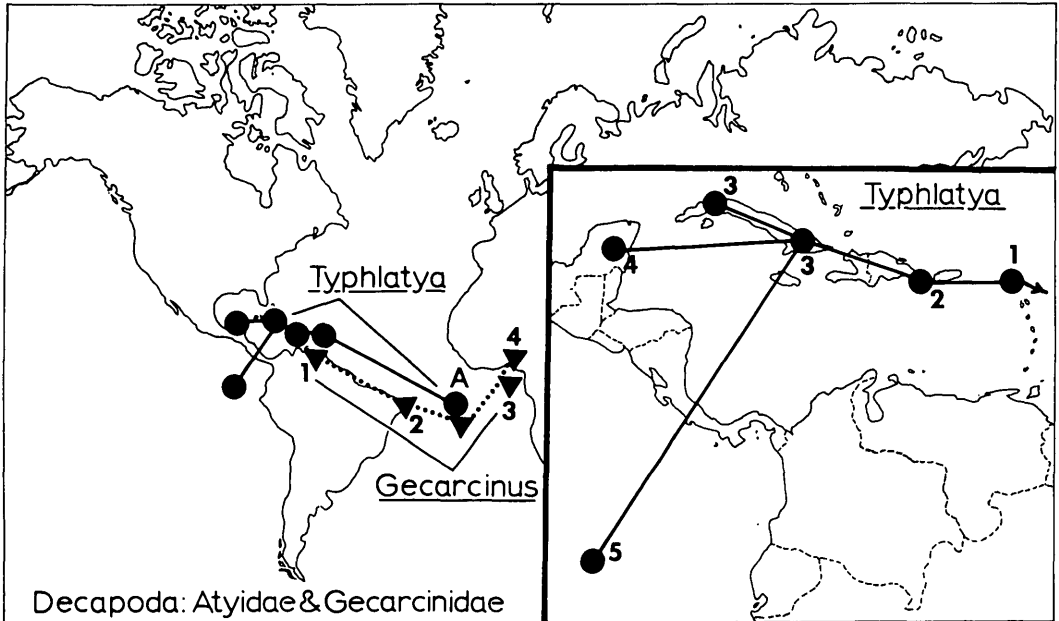


FIG. 2.—Distribution of *Typhlatya* (Decapoda: Atyidae) and *Gecarcinus lagostoma* (Decapoda: Gecarcinidae) (partly after Chace and Hobbs, 1969; Chace and Manning, 1972).

Main map.—The track for *Typhlatya* (see below for inset) is the solid line interconnecting circles. The track for *Gecarcinus lagostoma* is the dotted line interconnecting triangles. A, Ascension Island; 1, Trinidad; 2, Fernando de Noronha; 3, islands of the Gulf of Guinea; 4, Cameroon (cf. Croizat, 1968b: figs. 13–16, 22).

Inset.—The American stations of *Typhlatya*: 1, Barbuda (*T. monae*); 2, Mona (*T. monae*); 3, Cuba (Oriente, Pinar del Rio; *T. garciai*); 4, Yucatan (*T. pearsei*); 5, Galapagos (*T. galapagensis*); arrow to right of station 1 represents part of track between Barbuda and Ascension Island (A) as shown in main map.

physically similar, organically distinct, yet intimately related to each other, and all related in a marked, though much lesser degree, to the great American continent" (1846:172).

Darwin viewed the Galapagos, at least metaphorically, as a fragment of the Americas, isolated from that continental land-mass long enough to evolve its own biota, but not long enough to have lost its American ties. Whatever Darwin might have speculated about centers of origin and dispersal does not detract from this basic view of a marine outpost of continental America that, for all we know of biotic distribution, carried with it from the mainland the ancestors of its actual biota of today.¹⁵

With reference to a fragment of rock collected on Ascension Island, Darwin remarked that it contained remains of "sili-

ceous-shielded, fresh-water infusoria, and no less than twenty-five different kinds of the siliceous tissue of plants, chiefly of grasses." He stated that

"we may feel sure that at some former epoch the climate and productions of Ascension were very different from what they now are. Where on the face of the earth can we find a spot on which close investigation will not discover signs of that endless cycle of change to which this earth has been, is, and will be subjected?" (1846:297).

The spirit of this passage ill agrees with the preconceptions of the *Origin*, many of which persist to the present day (center of origin, dispersal according to available means, and permanent continental outlines). But the fragment of rock and its contents agree well with recent data from Ascension

(Chace and Manning, 1972): the discovery of two endemic shrimps, one of which belongs to the genus *Typhlatya*, known also from Caribbean islands (Barbuda, Mona, and Cuba), Mexico (Yucatan), and—incredibly by the modern map (fig. 2)—Galapagos.¹⁶ Similar distributions are shown by other groups, and sometimes even by single species (fig. 2).

On the Beagle's return to England, Darwin possessed at least the rudiments of the principles of modern systematics and biogeography. He understood vicariance clearly enough to visualize the Galapagos as a cluster of lesser areas of evolution.

Darwin was also certain that an obvious nexus bound the history of the earth with that of its inhabitants: plants and animals, past and present. He had evidence in his hands that "oceanic islands" such as Ascension had a very different biological and geological past.¹⁷

Upon his return to England, Darwin unfortunately, and perhaps tragically for biology, began building theories of "geographical distribution" based on concepts of species and their centers of origin and dispersal. In so doing Darwin avoided the general problem of vicariance (biological differentiation in time and space), as represented particularly by the material he himself collected during the voyage of the Beagle.

The majority of naturalists today accept concepts such as center of origin as fool-proof fundamentals of biogeography without having much understanding of their history and real meaning, and without any awareness of the conflict in Darwin's own views (vicariance versus center of origin and dispersal).¹⁸

Having failed to dissect these concepts (center of origin, vicariance) to their core, contemporary zoogeographers founder in a self-created morass of chance hops; great capacities for, or mysterious means of, dispersal; rare accidents of over-sea transportation; small probabilities that with time become certainties; and other pseudo-explanations. Where such conceptual imprec-

ision leads is exemplified by the statement that

"the close relationship between the Old and New World members of the Pantropical element, whose ranges are now widely discontinuous, proves that . . . a faunal exchange must have taken place, and this places the zoogeographer in a real quandary. The customary solution for the problem is to ignore it" (Mayr, 1946b:36).¹⁹

But ignoring fundamental problems because they conflict with the principles of the geographical distribution of a Darwin or a Matthew is a form of bias repugnant to the spirit of science.

Nevertheless, Darwin did write that

"it is obvious, that the several species of the same genus, though inhabiting the most distant quarters of the world, must originally have proceeded from the same source, as they have descended from the same progenitor" (1859: 351).

The principle of common ancestry implies vicariance, applicable to species and biota alike, meaning specifically that an ancestral species (or biota) with characters (or species) $a + b + c + d + \dots + n$ subdivides into an assemblage of species (or descendant biotas), each distinct by a different combination of characters (or species), e.g., $a + b + c' \dots$, $d + e + f \dots$, $a' + c + f \dots$. This process of subdivision (vicariance) is geographical, involving particular geographical areas for species and biotas alike, such that the resulting species (or descendant biotas) vicariate, i.e., replace each other geographically without any of them migrating from one area to another. Vicariant patterns are generally shown by the various species within a genus, the subspecies within a species, and the varieties within a subspecies; and generally by higher taxa as well (e.g., Hoffstetter, 1973). But because the geographical subdivision of species into subspecies has occurred more recently within a given lineage than the formation of groups of species (e.g., genera) in that lineage, vicariance is generally more precise today for taxa of lower rank (notes 2 and 3).

The principles of common ancestry and vicariance do not require that species must ever have migrated from a center of origin in the Darwinian sense. But suppose we do interpret the above text by Darwin to refer to species originating in centers, spreading therefrom by means of dispersal often of the mysterious and unknowable kind. In an avian genus of some 10–20 species and subspecies, we might consequently imagine that one of the species or subspecies originated at some center, corresponding to a point on the map, and then dispersed to other centers corresponding to other points on the map, there to give rise to the other species and subspecies, which then dispersed to achieve their present respective geographical distributions. Such interpretation, which requires a center of origin and dispersal therefrom, is inconsistent with the principles of common ancestry and vicariance—the basis for the practice and philosophy of modern systematics since the days of Wagner (1889), Kleinschmidt (1926, 1930), and Rensch (1929; cf. Croizat, 1964: 177–216).

The discordance between these principles (common ancestry and vicariance) and the “geographical distribution” of Darwin (1859) and Matthew (1915), and those who took their cues from them, is stark and seemingly impossible to reconcile. It may be fortunate for biology that geophysics has finally managed to show how brittle are the foundations of the aprioristic “geographical distribution” of Darwin, Matthew, and others—at least with respect to belief in stable geography. But the biogeographical solution—as opposed to the geophysical—was outlined by Cain in 1943 and its principles as we see them today are (Croizat, 1973): to do away with aprioristic “theory” and the authority that supports such “theory”; to formulate explicit methods of statistical analysis (based on the concept of generalized tracks) that yield unambiguous and repeatable results; to reject affirmations lacking a demonstrably objective basis (centers of origin); to admit that ideas and beliefs have a history; and, in the

search for that history, to be candid with students so that they may not wander in a world of make-believe and pretense—however reputable and orthodox that world might seem. In reality, science does have an orthodoxy of its own, demanding repeatable results and independent confirmation. No one well informed of the zoogeography of our times can have an illusion about its manifest disreputability.

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NOTES

^a The terms *vicar*, *vicariad*, or *vicariant*; *vicarious* or *vicariant species*; and *vicariance*, *vicarism*, or *vicariation* have acquired a variety of meanings in biology (Cain, 1944:265–273; Schilder, 1956:90–92; Udvardy, 1969:192–194; Hennig, 1966; Lemée, 1967; Neill, 1969). On the one hand, they may designate ecologically similar but geographically separated species, for example of different land masses, as in a comparison between a marsupial and a placental; or they may designate ecologically different species living in the same area: in either case the two species involved may, or may not, be closely related. On the other hand, they may designate what Jordan (1908:75) termed *geminata species*—closely related species, usually very similar, that occupy adjacent (allopatric) areas separated by a barrier. This usage, apparently the original and most common one (Wagner, 1868:9, 1889:56; Hesse, 1924; Marcus, 1933; Geptner, 1936; Hesse et al., 1937; Cain, 1944; Ekman, 1953; Dansereau, 1957; Polunin, 1960; Good, 1964; Schmithüsen, 1968; Schmidt, 1969; Valentine, 1972), is similar to our own, and implies a common ancestry for the geminate pair. We view all of the components (species and species clusters) of a monophyletic group as primarily (originally) allopatric. The separate components of the group are therefore, *vicariants*, and the historical process giving rise to them, *vicariance*, as embodied in the following premises and conclusions:

a. Allopatric species (*vicariants*) arise after barriers separate parts of a formerly continuous population, and thereby prevent gene exchange between them.

b. The existence of races or subspecies of a species that are separated by barriers (*vicariance*) means that a population has subdivided, or is subdividing, not that dispersal has occurred, or is occurring, across the barriers.

c. The earliest stages (races and subspecies) of differentiation (*vicariance*), separated by complete or incipient barriers to gene exchange, are entirely allopatric.

d. Sympatry between species of a monophyletic group implies dispersal of one or more species into the range(s) of the other(s) (note 3).

e. Allopatric speciation (*vicariance*) predominates over other forms of population differentiation; allopatry is the rule and sympatry the exception in present-day distributions of the species of a given monophyletic group.

f. *Vicariance* is, therefore, of primary importance in historical biogeography, and dispersal is a secondary phenomenon of biotic distribution.

³ The general phenomenon of sympatry, including all cases of overlap (or coincidence) of distribution of unit taxa (definable, named populations) is itself evidence of dispersal. Sympatry is more prevalent among the members of more distantly related and, therefore, relatively older taxa, e.g., between a fish species and a crustacean species. We assume that most sympatry of this sort, between distantly related species, was caused by dispersal in the remote past, before the formation of the most recent ancestral biotas, as estimated by the generalized tracks displayed by the modern world biota. But sympatry (range overlap of reproductively isolated populations) is the same phenomenon at all taxonomic levels. For example, in the Middle American fish genus *Xiphophorus* there are 18 unit taxa grouped in two sections. Of nine examples of sympatry, five occur between members of different sections, and the other four examples occur between members of one section, in which the sympatric pairs are separated phylogenetically by two or more genealogical bifurcations. In the platyfish section of the genus, the distribution of unit taxa is completely allopatric (Rosen, 1960:fig. 4), a picture typical for groups displaying unaltered vicariance. In this connection, Sokal and Crovello (1970:148) point out that the criterion of reproductive isolation for the recognition of "biological species," for which the occurrence of sympatry is an ingredient, may be questioned on the grounds that the "well circumscribed biological species is *not* the rule but the exception." Indeed, acceptance of an allopatric speciation model is consistent with little or no sympatry at the lowest taxonomic levels. But regardless of the extent of broad sympatry (evidence of significant dispersal), we consider that vicariance underlies and antedates nearly all cases of sympatric distributions. Current practice in biogeography, how-

ever, involves an initial assumption of dispersal from a center of origin. But is it not reasonable that, before the causes and means of dispersal may be investigated in any specific case, evidence should first be found that dispersal has occurred?

⁴ An ancestral pan-austral flora was recognized long ago by Hooker (1853:xxi; 1860:325–326): "I was led to speculate on the possibility of the plants of the Southern Ocean being the remains of a flora that had once spread over a larger and more continuous tract of land than now exists"; "the many bonds of affinity between the three southern floras, the Antarctic [which according to Hooker occurs in "Fuegia, the Falkands, and Lord Auckland's and Campbell's group, reappearing in the alps of New Zealand, Tasmania and Australia"], Australian, and South African, indicate that these may all have been members of one great vegetation, which may once have covered as large a southern area as the European now does a northern. It is true that at some anterior time these two floras [southern and northern] may have had a common origin, but the period of their divergence antedates the creation of the principal existing generic forms of each." The recognition of a corresponding pan-austral fauna came later (Huxley, 1868; Hutton, 1873), but its existence was soon denied by Wallace (1876:159, probably following Darwin, see below): "The north and south division truly represents the fact, that the great northern continents are the seat and birth-place of all the higher forms of life, while the southern continents have derived the greater part, if not the whole, of their vertebrate fauna from the north; but it implies the erroneous conclusion, that the chief southern lands—Australia and South America—are more closely related to each other than to the northern continent. The fact, however, is that the fauna of each has been derived, independently, and perhaps at very different times, from the north, with which they therefore have a true genetic relation." The Darwin-Wallace influence was such that many later botanists rejected even Hooker's well founded notion of an ancestral pan-austral flora in favor of dispersal from northern centers of origin: "all the great assemblages of plants which we call floras seem to admit of being traced back at some time in their history to the northern hemisphere"; "The extraordinary congestion in species of the peninsulas of the Old World points to the long-continued action of a migration southwards. Each [peninsula] is in fact a *cul-de-sac* into which they [species] have poured and from which there is no escape"; "The theory of southward migration is the key to the interpretation of the geographical distribution of plants" (Thiselton-Dyer, 1878:441; 1909:311, 316). The view that the pan-austral biota is a mere artifact of independent dispersal from the northern hemisphere (e.g., Wallace and Thiselton-Dyer, 1885) was later termed the "monoboreal relic hypothesis" (Schröter, 1913:921) and

had much appeal earlier in this century (Matthew, 1915). The history of this period is well covered by Du Rietz (1940; also Wittman, 1934, 1935). Other authors viewed the pan-austral biota as an artifact due to chance dispersal over southern water gaps, a practice maintained for some years, especially by zoologists (e.g., Darlington, 1957, 1965; cf. Axelrod, 1952). Both views of the pan-austral biota as an artifact were historically based on a priori acceptance of stable geography: "Writers on geographical distribution now occupied themselves, to use Darwin's words, 'in sinking imaginary continents in a quite reckless manner' and in constructing land bridges in every convenient direction. They were brought back to the stern reality of fact when Dana in his *Manual of Geology* [1863:732, also 1847:92] first made the unexpected statement: 'The continents and oceans had their general outline or form defined in earliest times.' From this view Darwin, supported as he was from his own reflections, never deviated. Writing to Hooker in 1856 he said, 'you cannot imagine how earnestly I wish I could swallow continental extension, but I cannot.'" "Half a century has elapsed since Dana laid down his memorable principle [stable geography]. Time has strengthened and in no way diminished its force. But though adopted by Darwin and Wallace it is still ignored by those who prefer facile speculation to the sober contemplation of established facts" (Thiselton-Dyer, 1912:237, 239). Cf. Darlington (1957:22): "A synthesis of this sort—putting Wallace and Darwin together, so to speak, and adding geology and other things in reasonable proportions—ought to be the purpose of modern zoogeographers. Of some it is"; Raup (1942:328): "the effect of Darwinism upon the floristic view of plant geography was not so great as upon other views. The reasoning remained inductive in large measure, with conclusions growing slowly out of masses of fact which were sorted laboriously into patterns of coincidence and suspected actual relationship"; and Turrill (1953:226): "The modern tendency has been mainly against his [Darwin's] views in this respect, at least among botanists." Recent commentary about the history of the pan-austral biota may be found in Pantin et al. (1960), Gressitt (1963), Brundin (1966, 1970, 1972), Corro (1967, 1971), Valentine (1972), and Keast (1973).

⁸ Assuming that galaxiids are Gondwanian, i.e., that their present distribution represents geographical isolation of fragments of one or two widespread species by fracture of the Gondwana landmass, one may be tempted to ask where the ancestral galaxiid species originated. Did it originate in some center, corresponding to a point on the map, and from there disperse across Gondwana? This question should be considered in relation to (1) the fact that the galaxiids have a sister group, the salmonids of Laurasia and (2) the pos-

sibility that the Gondwanian galaxiids and the Laurasian salmonids may be vicariants that formed in response to the initial fracture of Pangaea into Laurasia and Gondwana. If so, then the ancestral species common to both groups may already have been widespread over Pangaea, and the question of dispersal of the ancestral galaxiid species becomes unnecessary and, perhaps, irrelevant. We do not deny that, at some point or other, dispersal might have played a role in the formation of the ancient Pangaeian distributions, of which we now have only the vicariant remnants; or that some dispersal, as indicated by sympatry between modern galaxiid species, has occurred since. But we see no need to assume that more dispersal occurred than is indicated by the evidence.

⁹ The concept of "limited area" of origin is, of course, relative. Early Darwinians tended to assume that species originate from one or, at most, one pair of organisms, and that species generally have, consequently, a very small center of origin: "A new species recently come into existence would naturally, at least on any theory of evolution, have a limited range because it would have come into being at one locality and not have had time to extend its range"; "We must imagine each species setting out from its centre of origin and gradually extending itself by actual or passive migration right and left and in every possible direction from this focus" (Beddard, 1895:12–13; also Bartholomew et al., 1911:3). On this matter Darwin himself was equivocal: "It is also obvious that the individuals of the same species, though now inhabiting distant and isolated regions, must have proceeded from one spot, where their parents were first produced" (1859:351–352). "With those organic beings which never intercross . . . , all the individuals of each variety will have descended from a single parent. But in the majority of cases, namely, with all organisms which habitually unite for each birth . . . , the individuals of the species will have been kept nearly uniform by intercrossing; so that many individuals will have gone on simultaneously changing, and the whole amount of modification will not have been due, at each stage, to descent from a single parent" (1859:355–356). Despite the modern view (e.g., Fisher, 1930; Haldane, 1932; Dobzhansky, 1937; Waddington, 1939; Huxley, 1940, 1942) that, for sexually reproducing organisms at least, the unit of evolution is a population rather than an individual or pair, the early Darwinian view is still sometimes maintained: "If a species is strictly monophyletic, then all of its individuals are the descendants of one and the same ancestral plant and their total range, however extensive and peculiar it may be, must have grown by the processes of dissemination from the tiny area occupied by this ancestor" (Good, 1964:34). But even in the context of population biology, the process of "speciation" has often been viewed as necessarily beginning with a small population of

restricted distribution: "Never, since the days of the hypothesis of special creation, has it been maintained that a species originally arose over the whole of the area upon which it now occurs." "It is clear . . . that the large areas now occupied by many species must almost always, if not always, be due to spreading [dispersal] from others [areas] originally much smaller" (Willis, 1922:10-11; cf. Croizat, 1958b); "Of vital importance . . . is the determination of that initial territory whence . . . a species began its dispersal whereby it reached the present boundaries of its area." "There are no grounds for presuming that a new species will not extend its area beyond the limits of the region of its origin. It will, without any doubt, begin to spread in all directions open to it, and the region of its origin will constitute the center of the area being formed" (Wulff, 1943:27); "when a new species evolves, it is almost invariably from a peripheral isolate [population]" (Mayr, 1963:513; also Takhtajan, 1969:27). For biogeography, the consequences of these views, embracing the concepts of center of origin and dispersal on an a priori basis, have been far-reaching, even though post-Darwinian authors often considered a center of origin to be relatively large, e.g., the "Holarctic centers" of Matthew (1915:172) and the "Old World tropics" of Darlington (1957:570-577; 1959b).

However large the size might have been imagined, the concepts were the same: "This I believe to be the type of pattern that would be shown by almost any form of life that had run its entire course from origin to extinction. A form appears in some center or 'cradle,' not an exact spot that could be marked with a monument but, say, a single biotic district or province. Thence it tends to spread steadily in all directions until it encounters insuperable barriers. After a time it begins to contract." "An excellent descriptive analogy is provided by the expansion and contraction of ice caps" (Simpson, 1940:144); "successive 'dominant forms of life' . . . rise and spread over the world, each dominant group competing with, destroying, and replacing older groups, then differentiating in different places until overwhelmed by the rise and spread of the next dominant group." "We know now that this process of evolution, spread, and replacement of successive dominant groups is the main process (infinitely more complex in detail than my description of it) that makes the main patterns in animal distribution" (Darlington, 1959a:311; also 1957:552-556, 1959b:488; cf. Darwin, 1859:325-326 and e.g., Newbigin, 1948:9; Beaufort, 1951:2; Takhtajan, 1969:137; Banarescu, 1970:246; Laubenfels, 1970:21); "It is a basic tenet of zoogeography that an animal group arises in and spreads from a single area, its center of origin. For larger, more inclusive groups, as the more primitive members move out from the center of origin, successively more advanced forms evolve

in the center. As they in turn spread, they tend to eliminate the more primitive forms by competition. A large group that has been in existence for a long time typically shows a pattern of distribution in which the primitive species are located at the periphery of the range, in areas that the more advanced members have not yet reached or have reached only recently" (Goin and Goin, 1973:113). In contrast to these authors, we would separate the concept of vicariance from any and all a priori considerations of presumed population size and distributional extent of species at the time of their origin. We view vicariance as a phenomenon that may be displayed by populations of any size and geographical extent.

⁷ Peters (1948:86) placed the wrynecks in a subfamily (Jynginae) of Picidae, but such placement would not make Mayr's interpretation any easier. However understood taxonomically, Picidae are a biogeographically interesting family, for the genus *Picumus* is represented by about 25 species in South America (Schauensee, 1964:187) and one species in southeast Asia and Malaysia (Peters 1948:88-97)—totally isolated from its congeners.

⁸ Johnston's taxonomy clarifies the transatlantic nature of the relationship between these two subgroups (Goodwin, 1959, is less clear on this point). The relationship seems transatlantic (fig. 1) also because (1) *Columba* in America may be secondarily distributed north of Mexico (Cracraft, 1973:509); were the genus distributed transpacifically, one might expect it to be better represented in the United States and Canada, as are generally the groups of plants and animals with transpacific distributions (Croizat, 1968a:236ff, figs. 29-30); (2) the considerable differentiation in the Atlantic sector, and the predominantly western distribution of *C. unicincta*, are common adjuncts of transatlantic relationships (Croizat, 1952, 1958a, 1960, 1964).

⁹ "Here the paleontologist comes to the rescue. His discoveries are the historical documents of animal distribution" (Simpson, 1940:137-138; cf., e.g., Furon, 1958:41: "Il ne peut pas y avoir d'histoire biogéographique certaine sans paléontologie"); "It is extremely difficult, if not impossible, to reconstruct former distributions and colonization routes, if there is no fossil evidence (Mayr, 1952:255); "In a really good fossil record the earliest, most primitive fossils of a group will be at the place of origin, and later and more derivative fossils will clearly show directions of movement" (Darlington, 1959a:314; 1959b:495). Exaggeration of the significance of paleontological data has been common, one might say even traditional, in biology since the time of Darwin; statements in the literature abound to the effect that "Verification of the actual history of a group . . . depends ultimately upon finding fossilized remains of its members" (Stahl, 1974:1). In contrast, we view the role of paleontology in historical biogeography as the same as its role in phylogenetic sys-

tematics, i.e., as an additional source of information for historical analysis (Schaeffer, Hecht, and Eldredge, 1972). Thus, paleontological data, if they reveal examples of sympatry or overlap of generalized tracks, might justify an inference of dispersal. In our opinion such an inference is neither more or less reasonable, justifiable, significant, certain, verified, or easily performed for paleontological than for neontological data.

¹⁰ When writing about permanence of continents both Darwin and Matthew (1915:172) appealed to qualifying phrases such as "within the recent period" and "in later geological epochs" (cf. Croizat, 1971b). Modern writers have generally argued for continental stability only during the late Mesozoic and Cenozoic (e.g., Mayr, 1952; Hubbs, 1958), in the belief that the mammalian fossil record, as interpreted mainly by Simpson, was conclusive evidence in favor of stability (cf. McKenna, 1973). But for biogeography, as opposed to geophysics (for which Kasbeer, 1972), the important issue is not that the continents were, or were not, recently connected; for biogeography the issue is that the continents were, or were not, connected recently enough so that their subsequent separation significantly contributed to the vicariance displayed by the modern world biota. Traditionally, many persons considered the issue to involve only a choice between different means of dispersal (overland or oversea, respectively): "On a more theoretical level there has been a long-running . . . argument in southern biogeography. Many persons, like Hooker, have thought that dispersal must have occurred across land connections in the far south. Others, like Darwin, have postulated dispersal across far-southern water gaps" (Darlington, 1965:5). But the issue as we view it (see note 2 above) involves a choice between two basic explanatory principles (vicariance versus dispersal) on the basis of their relative generality: are the general patterns (generalized tracks) of modern biotic distribution due to vicariance (in response to a changing geography) or to dispersal (over a more or less stable geography)?

¹¹ "As Darwin's main problem was the origin of species, nature's way of making species by gradual changes from others previously existing, he had to dispose of the view, held universally, of the independent creation of each species and at the same time to insist upon a single centre of creation for each species; and in order to emphasize his main point, the theory of descent, he had to disallow convergent, or as they were then called, analogous forms. To appreciate the difficulty of his position we have to take the standpoint of fifty years ago, when the immutability of the species was an axiom and each was supposed to have been created within or over the geographical area which it now occupies. If he once admitted that a species could arise from many individuals instead of from one pair, there was no way of shutting the door against

the possibility that these individuals may have been so numerous that they occupied a very large district, even so large that it had become as discontinuous as the distribution of many a species actually is. Such a concession would at once be taken as an admission of multiple, independent, origin instead of descent in Darwin's sense" (Gadow, 1909:322; cf. Gadow, 1913:61).

¹² To a paleontologist specializing in mammalian faunas, the abundance and diversity of Eurasian and North American Tertiary fossils may suggest that life originated in Holarctica, radiating from there to the rest of the earth. But what happens when the field of mammalogy is left behind? Schmidt (1946:152) was forced to admit that "There is a general agreement of the South American, Australian, and African faunas in certain primitive elements, among which may be mentioned lung fishes; leptodactylid frogs; pleurodiran turtles; the more primitive groups of snakes and lizards; and the marsupials (absent from Africa). The list might be greatly extended among invertebrate groups." Schmidt nevertheless disposed of this conflict with the Holarctic theory by asserting simply that "These primitive faunas are probably the accumulated remnants of repeated dispersals in the late Paleozoic and early Mesozoic, i.e., from the 'Holarctic' fauna of those early ages."

¹³ Darlington (1957:22), although crediting Matthew for having done "much to counteract the more irresponsible historical zoogeographers," credits Darwin and to some extent Wallace, rather than Matthew (Darlington, 1959a:313, 315; also 1959b:488-489, 1965:57-59; cf. Simpson, 1965:53; Romer, 1973:345), with being "extraordinarily, almost incredibly, right about a hundred years ahead of his time," because Darwin made passing reference to "the more dominant forms, generated in the larger areas and more efficient workshops of the north," and to "The living waters . . . [that] have flowed with greater force from the north so as to have freely inundated the south" (cf. Darwin, 1859:380, 382). According to Darlington, "Darwin was not guessing about these things. He presented evidence and reached correct conclusions. No one could have reached correct conclusions just by guessing. That he saw and understood *all* these things ["the fundamental concepts of evolutionary zoogeography"], which together are the whole heart of the subject, makes him pre-eminent in evolutionary zoogeography." Cf. Thiselton-Dyer (1909:308, 316): "If an observer were placed above a point in St. George's Channel from which one half of the globe was visible he would see the greatest possible quantity of land spread out in a sort of stellate figure. The maritime supremacy of the English race has perhaps flowed from the central position of its home. That such a disposition would facilitate a centrifugal migration of land organisms is at any rate obvious, and fluctuating conditions of climate operating

from the pole would supply an effective means of propulsion." "If, as is so often the case, the theory [of southward migration] now seems to be *à priori* inevitable, the historian of science will not omit to record that the first germ sprang from the brain of Darwin." "He was in more or less intimate touch with everyone who was working at it." "It is hardly an exaggeration to say that from the quiet of his study at Down he was founding and directing a wide-world school."

¹⁴ Nevertheless, in the same edition Darwin stated that "The archipelago is a little world within itself, or, rather, a satellite attached to America, whence it has derived a few stray colonists, and has received the general character of its indigenous productions" (1846:145).

¹⁵ Holden and Dietz (1972) place the historical beginnings of the Galapagos at about 40 million years ago. They suggest that the present-day Galapagos are simply the most recent (late Pliocene) islands of a volcanic chain with easterly components that subsided as new, more westerly islands emerged. They state (1972:269) that "The Galapagos Islands contain many endemic birds and bizarre animals which have required millions of years for their evolution in isolation. By our model, the modern Galapagos Islands may have inherited faunas from a whole series of ancestral 'Galapagos islands' which existed over a span of 40 m. y. Presumably the animals would have little difficulty negotiating the short span of water to a new volcanic island as an older extinct volcanic island drifted eastward and subsided beneath the sea (a subsiding 'stepping stone'), adding itself to the end of the Cocos and Carnegie ridges. To date, no guyots have been reported from either the Carnegie or Cocos chains, but this still is not conclusive evidence that these ridges were not subareal at some time in their history."

Holden and Dietz (1972; also Malfait and Dinkleman, 1972) discuss the history of the submarine Carnegie ridge that extends between the Galapagos and western South America. They point out that the history of the Galapagos is directly related to the history of the Panamanian isthmus, which is connected to the Galapagos by the undersea Cocos ridge. The region including these features they term the "Galapagos Gore." The gore encloses these two ridges, which bifurcate at the Galapagos and extend eastward. Together, the ridges form the sides of an isocles triangle, with the Galapagos at the apex and the Panama fracture zone at the base. It is apparent, therefore, that the Panamanian isthmus formed over a considerable period of earth history, and was closely related to dynamic changes in land and water configurations of the entire region bounded by Central America, northwestern South America, and the Galapagos Islands. The formation of the isthmus was characterized by Nemeth and Libke (1972:19): "Uplift and downwarping throughout

the Oligocene and Miocene resulted in the first uninterrupted connection of Central and South America, completed during the Pliocene." This geophysical history and the zoogeographic suggestions of Holden and Dietz, who view the Galapagos as part of a Cocos-Carnegie ridge system that is subsiding in its eastern part, contrasts with the Darwinian view of the Galapagos as true "oceanic islands" without proximity, or any possible historical connections, to the mainland (cf. Croizat, 1958a:746-859, particularly figs. 105 and 110).

A review of the subject of "oceanic islands" is beyond the scope of this paper. But we would point out that the concept of "oceanic island"—an island that arose out of the ocean, far from any continent as judged by modern geography, and that must have been populated by means of chance dispersal—was developed by Darwin (1859:388-406) and, as an overpowering apriorism, has since influenced numerous biogeographers from Wallace (1881) and Guppy (1906) to Carlquist (1965) and MacArthur and Wilson (1967). We note, however, that Jeannel (1942:131) denied that in the Atlantic there were "oceanic islands" in the Darwinian sense (also note 16). Skottsberg (e.g., 1956), who did much to counter an aprioristic approach to Pacific island biogeography (see particularly Du Rietz, 1940:237-240), commented on the spirit of those times: "Guppy relied on fruit-eating doves as carriers of seeds from island to island in bygone times. As they are sedentary today he concluded that they had changed their habits: that once they had been great travellers" (Skottsberg, 1960:455); "When confronted with a peculiar insular flora like that found on many islands in the Pacific, our first thought invariably is: Where did it come from? and how did it get there? In our eagerness to answer these questions and our impatient desire to explain everything, we have tried to form theories before enough is known not only of the geology and physical geography of the Pacific, but even of the plants themselves, their taxonomy and geographical distribution. I am afraid that this is attacking the problem at the wrong end. It even may be worth while to ask why we always assume that everything there is in the Pacific must have come from some distant place. Nobody asks where the Chinese, or Malayan, or Brazilian floras came from. We are quite satisfied to believe that they have developed right where they are, that their early history goes back so far that it is useless, for the present at least, to ask any but general questions as to their origin" (Skottsberg, 1928:914); "How we are to get away from the controversy arising from the fact that some of the present strongholds of this [austral] flora are to be found on supposedly very young volcanic islands, I do not know. When the biologists ask for a little more land of greater age which has disappeared and become succeeded by volcanic

chains, the geologists refuse them assistance. All evidence is contrary to the assumption that the present Pacific flora, with the exception of already widespread species of the seashore, is travelling from one island to another" (Skottsberg, 1928:917; see also note 16).

¹⁶ The explanation of this Ascension-Caribbean bond given by Wilson (see below) agrees, from the geophysical side, with conclusions about how "new" islands and mountains manage to retain in their biota very "old" elements (Croizat, 1964: 247ff, 258, fig. 50): "An alternative explanation of the origin of the Ascension shrimps was proposed by J. Tuzo Wilson (in litt.): 'another possibility which I think much more likely and intriguing from your point of view is that Ascension is only the latest in a series of islands whose remains form scattered seamounts and ridges from Ascension Island to the Cameroons in one direction (the Guinea Rise) and in the other direction to the northeast corner of Brazil. The idea that I proposed in the *Scientific American* [Wilson, 1963] was that there had been a continuously active centre from the time that Recife separated from the Cameroons and that these two chevron-shaped ridges formed as a result of continuous volcanic action at the center now represented by Ascension Island. If that is so, it is just conceivable that forms of life might have survived on Ascension from the time when the Atlantic was very narrow and the forerunners of Ascension were in contact with Brazil and the Cameroons'" (Chace and Manning, 1972:6).

¹⁷ Even though Darwin harbored questionable notions about "barriers to dispersal," as, for example when he stated that the Andes "have existed as a great barrier, since a period so remote that whole races of animals must subsequently have perished from the face of the earth" (1839:399), he could still have worked quite constructively from his own notes and observations. In a later edition this passage was modified to read "these mountains have existed as a great barrier since the present races of animals have appeared" (1846: 78). But by modern estimates the Andes are a relatively recent Tertiary feature. When they arose, the genera and species of passeriform birds, for example, were already modern enough to be assignable to extant families and genera (Howard, 1950). The Andes may accordingly have risen under the roots and feet of the immediate ancestors of the species and subspecies still living there today (Croizat, 1971a:383, fig. 1).

¹⁸ The contrast between Darwin the keen observer and Darwin the casual theoretician has spawned an equivocal literature, in which Simpson (1949:268), for example, extols Darwin as "one of history's towering geniuses" and Himmelfarb (1959:viii), for example, views him as "limited intellectually and insensitive culturally" (cf. Croizat, 1964:592-706; Vorzimmer, 1970; Ghiselin,

1973; Hull, 1973). Accordingly, it is difficult to judge the history and present status of "Darwinism," and few naturalists seem willing to accept the chore.

¹⁹ Cf. Darlington (1957:606-607): "I have tried to keep my mind open on this subject and have made a new beginning by trying once more (as I have done before) to see if I can find any real signs of drift in the present distribution of animals. I can find none." "Although I have made this trial as fairly as I could, I think the results were to be expected"; and (1959a:313): "I think all this can fairly be summarized by saying that Darwin considered the evidence he had and decided that *as far back as he could see* the main pattern of land had been the same as now, although many details had changed. Fifty-six years later Matthew, with much more evidence, reached the same conclusion, but saw farther back and in much more detail than Darwin could. And now, with still more evidence, we can see still farther back and in still more detail than Matthew could, but the conclusion is still the same. As far back as we can see, the distribution of animals and other evidence suggest a main pattern of land like the present one, in spite of all the details that have changed."

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