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# VICARIANT PATTERNS AND HISTORICAL EXPLANATION IN BIOGEOGRAPHY

DONN E. ROSEN

## *Abstract*

Rosen, D. E. (*Department of Ichthyology, American Museum of Natural History, New York, New York 10024*) 1978. *Vicariant patterns and historical explanation in biogeography*. *Syst. Zool.* 27:159–188.—Geographic coincidence of animal and plant distributions to form recognizable patterns suggests that the separate components of the patterns are historically connected with each other and with geographic history. To seek evidence of these historical connections, cladograms of geographic areas, representing sequences of disruptive geologic, climatic, or geographic events, may be compared with biological cladograms, representing sequences of allopatric speciation events in relation to those geographic areas. Such comparisons, when they meet the minimum requirements of being among dichotomized three-taxon cladograms, can resolve similar or dissimilar historical factors; two-taxon statements do not distinguish between groups with different histories. Congruence of biological and geological area-cladograms at a high confidence level (such as congruence of a five-taxon cladogram or four three-taxon cladograms with a geological cladogram, where the confidence level can be shown in cladistic theory to be 99%) means that specified events of paleogeography can be adopted as an explanation of the biological patterns. In such a cause and effect relationship, where the earth and its life are assumed to have evolved together, paleogeography is taken by logical necessity to be the independent variable and biological history, the dependent variable. Drawing a mathematical simile, the biological cladogram  $y$  (dependent variable), is a function of the geological cladogram  $x$  (independent variable), as in a simple regression of effect  $y$  on cause  $x$  where we are given no free choice as to which is the independent variable. Such a view implies that any specified sequence in earth history must coincide with some discoverable biological patterns; it does not imply a necessary converse that each biological pattern must coincide with some discoverable paleogeographic pattern, because some biological distributions might have resulted from stochastic processes (chance dispersal). Determining that all discoverable biological patterns conflict with a given corroborated or observed sequence of geologic, climatic, or geographic change (i.e., that  $y$  is not a function of  $x$ ), in theory, therefore should falsify vicariance biogeography. Because dispersal biogeography presupposes stochastic processes, and any failure to meet the expectation of a postulated dispersal is explained by an additional dispersal, dispersal biogeography is immune to falsification. Without resort to paleontology or earth history, whether a given historical relationship implied by congruence of biological area-cladograms is the result of dispersal or vicariance can also be thought of in terms which minimize the number of necessary assumptions: did the sedentary organisms disperse with the vagile ones or did the vagile organisms vicariate with the sedentary ones? Cladistic congruence of a group of sedentary organisms with a group of vagile ones rejects dispersal for both. Hence, distributions of sedentary organisms have the potential to falsify dispersal theories as applied to vagile organisms, but distributions of vagile organisms cannot falsify vicariance theories as applied to sedentary ones. The problems that arise in various kinds of historical explanation are exemplified by several specific distributions of fishes and other organisms in North and Middle America and in the larger context of Pangaeian history, and are discussed in relation to current species concepts. [Vicariance; species concepts; biocladistics; biohistory; geocladistics; geohistory; Neotropics; Gondwanaland.]

The patterns of spatial distribution attained by life on earth and the means by which these distributions were achieved are two essential concerns of biogeography. The first of these concerns refers to the manner in which the patterns of distribution are displayed on the world's geography. Such patterns may be analyzed

in various ways, such as noting the numbers of species or groups per region and comparing them numerically or ecologically, or by noting the phylogenetic relationships of the components of one region with the components of another. Phylogenetic comparison of the components of various regions implies a search

for historical connections between biotas in time and space—the pursuit which I identify as historical biogeography. The second concern of biogeography, how distributions were achieved, is a question of mechanisms or processes. When viewed from the perspectives of historical biogeography, the patterns have suggested to some persons that there are two processes that have molded biotas into their present configurations: large-scale dispersal to produce widespread ancestral biotas and later allopatric speciation events which have fragmented the ancestral biotas into their present highly subdivided states.

When patterns are viewed from the standpoints of their numerical species composition or ecological spectra, however, attention tends to be focused on the behavior of smaller biotic aggregations, usually at the population level, and on measuring small-scale changes in population structure over relatively short spans of time. Models of population structure and behavior, such as those of MacArthur and Wilson (1967), specify geographic dimensions that are believed to be in constant biological flux resulting in part from the emigration, immigration, and extinction of the individual species components. Ecological biogeography has tended, therefore, to make its practitioners view modern biotas mainly in terms of Quaternary history, to place emphasis on the study of organisms of high vagility, and to think of the distant past mainly in terms of what can be learned from paleoecology.

Ecological biogeography seems broadly to overlap the population biology of ecologists and may thus be in the act of divorcing itself from the objectives of historical biogeography. Vuilleumier (in press) may be quite right in seeing an unbridged gap between ecological (equilibrium) and historical (vicariance) biogeography: as the former is gradually merging with ecology, the latter is becoming increasingly integrated with the objectives of systematics and the historical aspects of earth science.

The sorting process that has been separating traditional biogeography into its ecological and historical ingredients, as its most substantive benefit, will provide opportunities for biologists to discover whether each ingredient can be imbued with its own body of principles and methods. It is my present opinion that equilibrium theory has the same relation to vicariance theory in biogeography that population genetics has to phylogenetic analysis in evolutionary biology. The relation is one of friendly but independent coexistence. A hope for the future reintegration of these divergent interests may be misguided, because current equilibrium theory, although claiming to “explain” how distribution patterns arise, is not designed to study major patterns of monophyletic groups of organisms in the context of long-term earth history. For this reason, I conclude that the present choice of methodology for biogeographers does not include equilibrium theory, but is a choice between the traditional approach with its rules for determining centers of origin and directions of dispersal and the vicariance approach which is attempting to discover the bases for uniting phylogenetic theory, concepts of distributional congruence, and theories of earth history (e.g., Platnick and Nelson, 1978).

The views on vicariance biogeography that I present below were derived directly from Croizat's (1958, 1962) concepts of distributional congruence and from Nelson's (MS.) ideas on component analysis in phylogenetic theory. The relation between these two kinds of ideas is that the components of cladograms (or phylogenetic trees), when viewed in the geographical context of the distributions of taxa within monophyletic groups, provide information for deciding whether distributions of several different monophyletic groups have some general significance greater than, or in addition to, empirically observable geographic coincidence. The greater general significance referred to concerns an estimate of whether congruence of distribution of

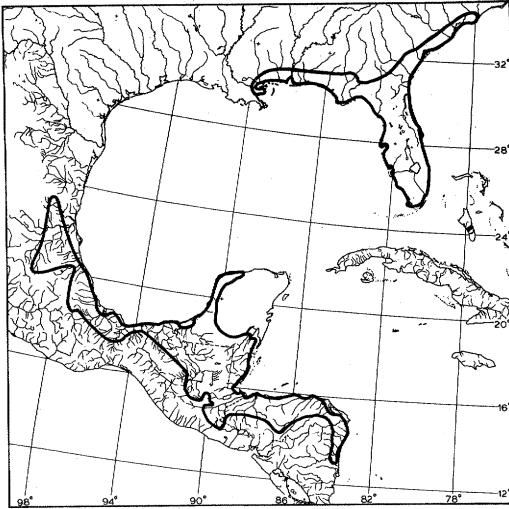


FIG. 1.—Distribution of the species of the poeciliid fish genus *Heterandria* in North and Middle America. The North American *H. formosa* is the sister group of an assemblage including all Middle American forms.

two or more groups could have occurred by chance alone.

This relation extends Croizat's panbiogeographic method by integrating cladistic techniques. I shall attempt to illustrate how vicariance biogeography can be applied in specific cases and to suggest how the results of a vicariance analysis may be compared with theories of earth history.<sup>1</sup>

The plan of this paper is first to illustrate some general distribution patterns which coincide broadly in North and Middle America and which show similar disjunctions within the region. Two earlier thoughtful attempts to explain these



FIG. 2.—Distribution of the species of the poeciliid fish genus *Xiphophorus* in North and Middle America. The North American (Rio Grande) species pair, *X. couchianus* and *X. gordonii*, is the sister group of an assemblage including all Middle American forms.

disjunctions are reviewed. Questions about the significance of these disjunctions are then framed in terms of vicariance theory, followed by a discussion of the relations among vicariant patterns, endemism and different kinds of cladistic statements drawn from elements of the North and Middle American biota. Cladistic statements with and without historical content are contrasted. Next the vicariant patterns are compared with the physical history of North and Middle America to illustrate the kinds of problems, and their solutions, that may be expected when selecting certain historical geologic or geographic events as explanations of the biological patterns. A distinction is, and must be, made between the original, or underlying, causes of biological patterns and the subsequent alterations of these patterns. A failure to make this distinction has led biogeographers to a temporally narrow view of biotic history. Because a temporally narrow view of biotic history focuses attention on taxa of low rank, and because some biogeographers have advocated that only the distributions of species-level-

<sup>1</sup> A frequent complaint about vicariance biogeography (Keast, 1977:285; McDowall, 1978) is that the role of dispersal is ignored, considered irrelevant, or understated. I will therefore clear the decks of such notions by restating what has already been stated emphatically and explicitly before: 1) under the allopatric speciation model, sympatry is evidence of dispersal, 2) for the modern world to show evidences of a fragmented Mesozoic biota it is a necessary assumption that a large-scale dispersal of an ancestral biota, had first to have occurred on a predrift landscape, and 3) that, therefore, both local dispersal and dispersal of biotas (cosmopolitanism) are assumed in the vicariance paradigm (see Platnick, 1976).

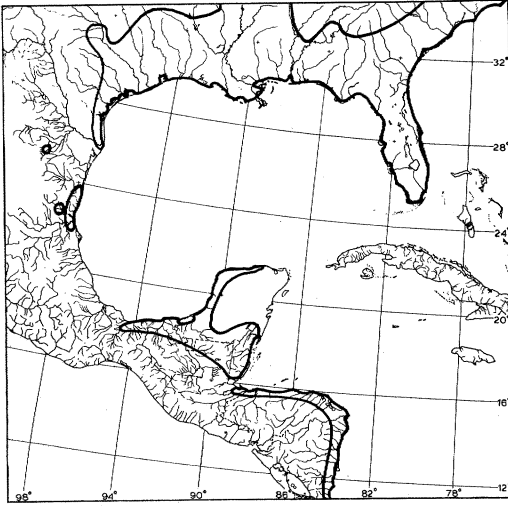


FIG. 3.—Distribution of the poeciliid fishes of the *Gambusia affinis* species group in North and Middle America.

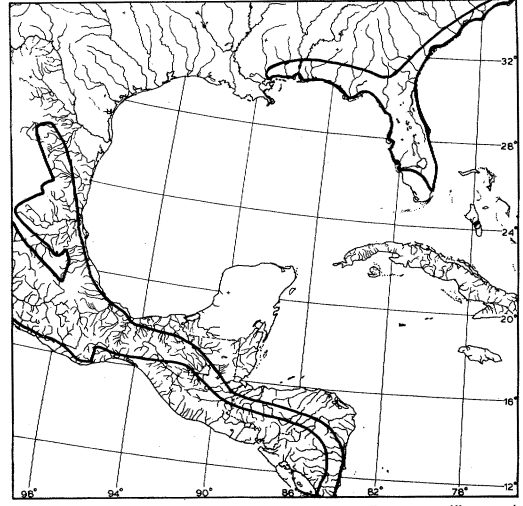


FIG. 5.—Distribution of the species of colubrid snakes, genus *Rhadinaea*, in North and Middle America. South American occurrences, to Ecuador, not shown.

el taxa form the data-base for biogeography, some consideration is also given to the use of concepts of subspecific, specific, and supraspecific taxa in biogeographic analysis. The final discussion, which incorporates ideas developed in the foregoing sections, describes a comparative cladistic method of analysis of

biological distribution patterns and geologic or geographic patterns.

Although many groups of organisms are discussed to exemplify some particular point or method, primary attention is focused on two groups of tropical American fishes—poeciliid fishes of the genera *Heterandria* and *Xiphophorus*.

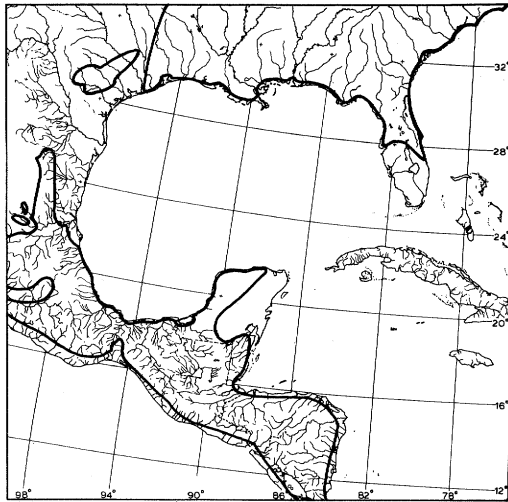


FIG. 4.—Partial distribution in North and Middle America of the lungless salamanders, family Plethodontidae. Western and northeastern North American and South American occurrences not shown.

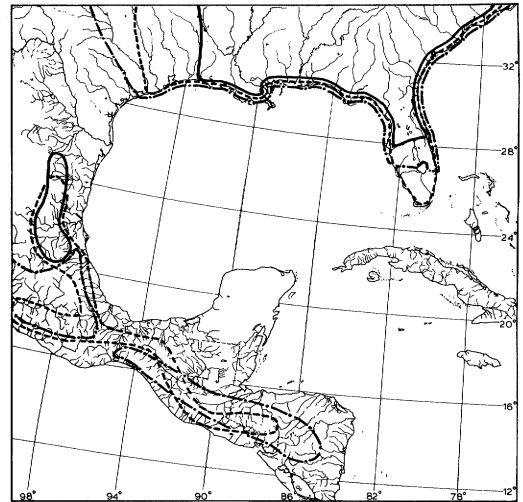


FIG. 6.—Co-occurrences of a red-bellied snake, *Storeria occipitomaculata* (solid), flying squirrel, *Glaucomys volans* (dash), and barred owl, *Strix varia* (dash-dot).

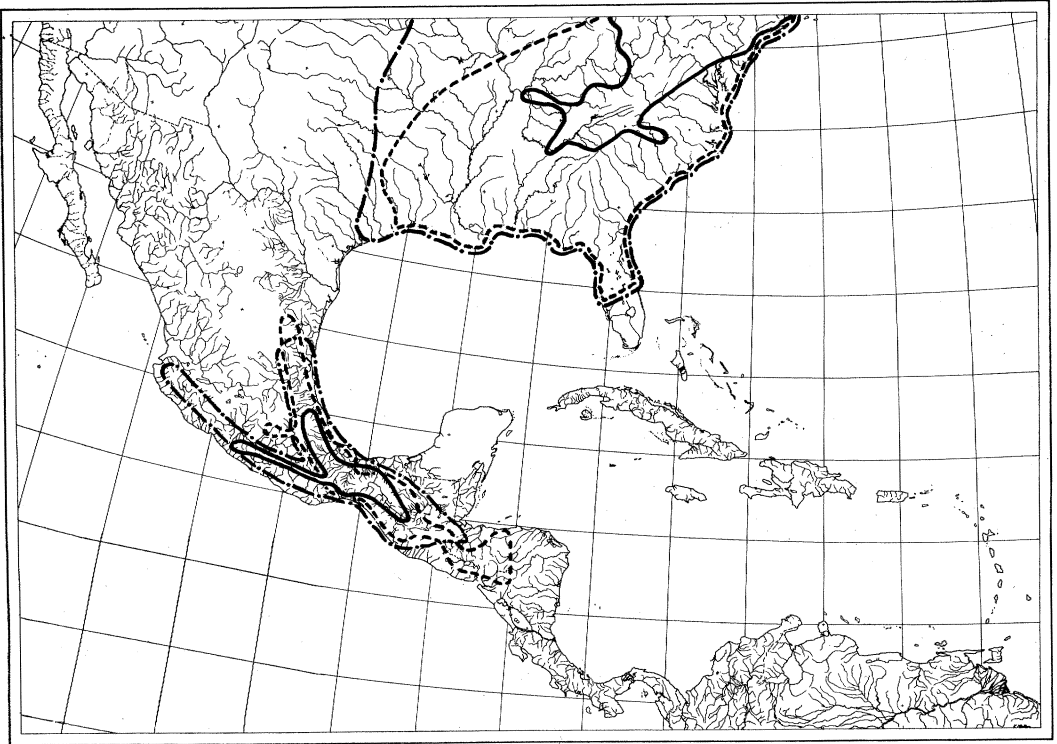


FIG. 7.—Co-occurrences of a pine, *Pinus strobus* (solid), sweet gum, *Liquidambar styraciflua* (dash), and blue beech, *Carpinus caroliniana* (dash-dot).

Poeciliids are tiny, viviparous, freshwater fishes such as the guppy. The two genera were selected because recent revisionary work has been done on both groups (Rosen, in press).

#### GENERAL PATTERNS AND HISTORICAL PERSPECTIVES

If the Rio Grande basin is taken as a southern geographic limit in North America, the distributions of both *Heterandria* (Fig. 1) and *Xiphophorus* (Fig. 2) show a disjunction between North and Middle American taxa north of the Rio Tamesí basin. The disjunction is especially striking in *Heterandria* where the North American representative is confined to the southeastern states.

A brief survey, based on combined zoological and botanical literature, showed that many other plant and animal distributions are also disjunct between North and Middle American occurrences, al-

though the exact location of the disjunction is somewhat variable. For example:

poeciliid fishes of the *Gambusia affinis* species group (Fig. 3), in part from Rosen and Bailey (1963);

plethodontid salamanders (Fig. 4), in part from Wake and Lynch (1976);

colubrid snakes of the genus *Rhadinaea* (Fig. 5), from Myers (1974);

*Storeria occipitomaculata*, the red-bellied snake (Fig. 6) (this and the following from Martin and Harrell, 1957);

*Strix varia*, the barred owl (Fig. 6);

*Glaucomys volans*, a flying squirrel (Fig. 6);

eight groups or species of mesophytic trees and shrubs and a root parasite (Figs. 7–9).

Apparently the distributions of *Heterandria* and *Xiphophorus* have some generality with respect to their southern lim-

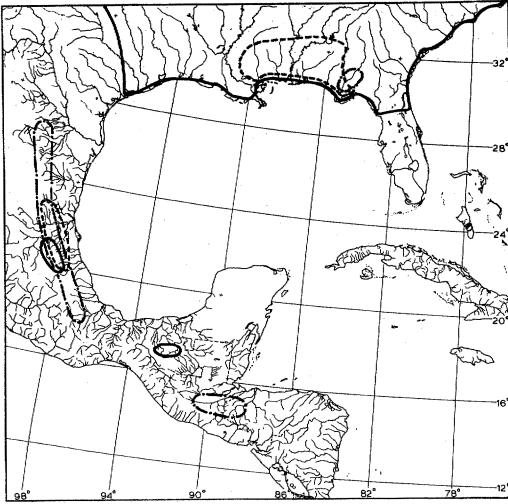


FIG. 8.—Co-occurrences of the sour gum, *Nyssa sylvatica* (solid), and the species pairs of star anise, *Illicium floridanum* and *I. mexicanum* (dash), and yew, *Taxus floridana* and *T. globosa* (dash-dot).

its and the disjunction between Mexican and North American populations (Figs. 10, 11). The confinement of the North American representative of *Heterandria* to the southeast is also found in a few groups, but in most of those illustrated the North American distributions, al-

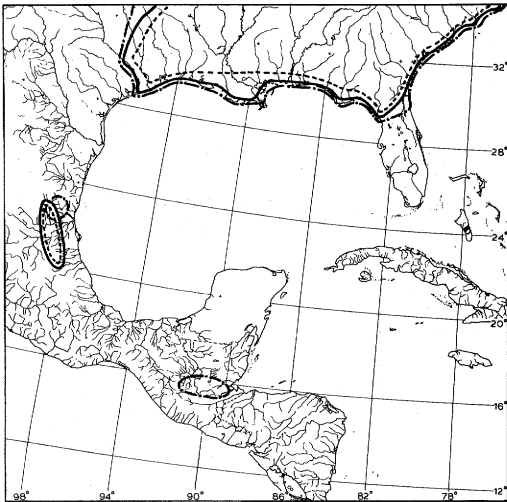


FIG. 9.—Co-occurrences of the beech, *Fagus grandifolia* (solid), and its root parasite, *Epifagus virginiana* (dash), and sugar maples of the *Acer saccharum* species group (dash-dot).



FIG. 10.—Patterns produced by superimposed North and Middle American distributions of three groups of poeciliid fishes, *Heterandria*, *Xiphophorus*, and *Gambusia*.

though eastern, are not confined to such low latitudes. A few groups also have a small western distribution west of the Rocky Mountains. Still other biogeographic literature pertaining to this region suggests that adding more distributions to the analysis would not appreciably change the percentage of



FIG. 11.—Patterns produced by superimposed North and Middle American distributions shown in Figs. 6 to 9.

groups with these somewhat different latitudinal restrictions in eastern North America. In other words, the figured distributions may fairly represent the diversity of North American distributions of extant groups that have eastern North American representatives with Mexican and Nuclear Central American vicariads.

Adding fossils to the analysis shows, however, that the North American representatives of those particular groups that are now tropical and subtropical were formerly both more numerous than now and also generally widespread in the eastern two thirds of North America. For example, crocodiles and giant land tortoises occurred as far north and west as South Dakota in early Pliocene times and in the late Pliocene they occurred at least as far north as Kansas; during interglacial times of the Pleistocene they were still present north to Kansas and Nebraska (Dott and Batten, 1976). Both crocodiles and tortoises did then occur also in the American tropics, including the Antillean islands, as crocodiles still do; crocodiles continue to occupy North America, but now only in the extreme southeast. Among the non-passerine birds formerly present in North America but now confined in the New World to the tropics are such groups as boobies, flamingos, chachalacas, parrots, and barbets, ranging in age from Middle Eocene to late Quaternary (Brodkorb, 1963, 1964, 1967, 1971). Among mammals, Floridian fossils belonging to taxa that are now confined to South America, Central America, Mexico, or the western Gulf States, or some combination of these, include three bats, a gopher, a capybara, a hog-nosed skunk, three cats, a tapir, several peccaries, and several camelids (data from Webb, 1974; Hall and Kelson, 1959).

Twenty years ago Martin and Harrell (1957) attempted to deal with the age of the disjunction between extant eastern North American and Middle American plant communities. They expressed concern with the proposal by various workers that the disjunction developed during late Pliocene–Pleistocene time—a pro-

posal which requires the development of “a Pleistocene forest corridor, or at least a transitory spread of temperate forest, across the plains and isolated mountains of northern Mexico and south Texas,” an area that today is arid grassland and thorn scrub. An additional requirement is that cooler and much wetter climatic conditions would have had to prevail to support a corridor of mixed mesophytic forest with beech, white pine, sugar maple, sour gum, sweet gum, evergreen magnolia, and so on. The alternative proposal is simply that the disjunction is much older, a possibility that is not unrealistic since the modern forest plants of this region were already present in the Eocene.

Martin and Harrell proposed that a rough test of these two phytogeographic views involves examining the fauna of the montane Mexican forests with the expectation of finding “unmistakable faunal evidence” of a Pleistocene forest corridor. They supposed that if the forest connection is more ancient, any residual faunal evidence “should accordingly be less obvious and at a higher taxonomic level.” Their study of an isolated outpost of cloud forest in southwestern Tamaulipas showed that the number of vertebrate species with eastern North American vicariads was only 2% of the vertebrate fauna of their test station as compared with 29% of the flora with eastern North American vicariads. They concluded, therefore, that there is not “impressive faunal confirmation of a Pleistocene forest corridor to the northeast.” Regarding the taxonomic level of Middle and North American faunal disjuncts, Martin and Harrell argued that the plethodontid salamanders are of special importance for this problem because “(1) a continuous forest corridor is necessary for plethodontid dispersal, (2) there is a closer relationship between the Plethodontidae in eastern and western United States, than between either of these and [those of] Middle America, and (3) the morphological development of the genera found south of the Mexican boundary requires the time of separation to antedate the



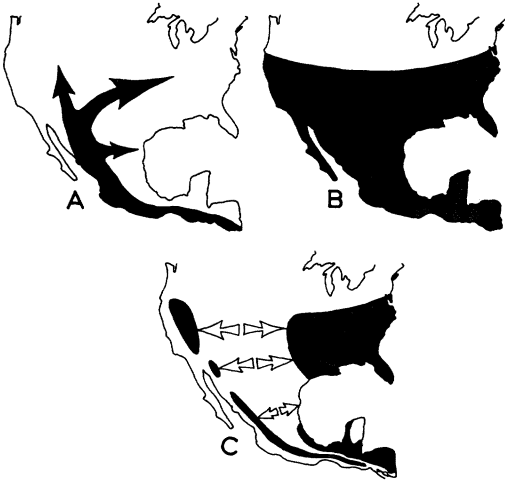


FIG. 12.—Simplified depiction of a theory of the Tertiary history of the Neotropical flora, derived from Axelrod (1975).

Pleistocene.” This general line of argument is, of course, weak and partly flawed, especially the last part which assumes that plants have characteristically different rates of evolution from animals, that levels of taxonomic recognition by different taxonomists are directly comparable and significant, and that there is a known time frame for the evolution of the currently used taxonomic characters of plethodontid salamanders.

Martin and Harrell dealt with the climatic requirements of the Pleistocene-disjunction hypothesis by arguing that “it is not yet possible to correlate low latitude pluvial periods with glacial maxima, although this has been attempted repeatedly (Deevey 1953),” and they cited some data concerning glacial readvances of about 7,000 years BP to infer that, “in fact, the opposite may be true.” Dott and Batten (1971:456) also disputed the necessity of such correlations by pointing out that mild-climate fossils may be found very near obvious glacial moraines. In the view of Dott and Batten “a really harsh climate did not grip most of the United States until the last (Wisconsin) glacial advance.” Moreover, their map (p. 448) of Pleistocene paleogeog-

raphy at the time of the maximum glacial advance shows a hot, dry-climate flora occupying most of central and northeastern Mexico, southern and western Texas and the mountain states. These do not seem to me to be the conditions of a “cooler and a much wetter” climate required for a forest corridor across northeastern Mexico and southern Texas.

Axelrod (1975) dealt with the problem of this biotic disjunction based, to a large extent, on the paleontological evidence. The forest disjuncts considered by him include maple, hornbeam, hickory, redbud, dogwood, beech, witch hazel, holly, sweet gum, sour gum, sweet gale, ironwood, cherry, linden, 125 species of mosses (Crum, 1951) and other bryophytes and ferns, to mention only some of the plant vicariads.

Axelrod’s argument concerns the known distribution of plant megafossils and fossil pollen representing plants closely related to or exactly like those now composing the temperate rain forests of Mexico and Central America. His argument is simple and of two parts. The tropical American rain forests are ancient and were already present in Mexico and Central America at the beginning of the Tertiary at a time when North America was vegetated at middle and low latitudes by a preponderance of tropical species. By the late Eocene the tropical element was reduced to insignificance and the forests were more or less typical of the Mexican temperate rain forests of today (Leopold and MacGinitie, 1972). In essence the evidence now available suggests that, in the Eocene, temperate rain forests dominated by a mixture of evergreen dicots and deciduous hardwoods were continuously distributed from the central United States to Central America along the present axis of the Sierra Madre Occidental (Fig. 12A, B). With drying conditions in the west during the middle Tertiary and the appearance of the Sierra Madre Oriental, the forest shifted to the east in Middle America as it did also in the United States (Fig. 12C). The drought that was moving eastward to northeastern

Mexico and southern Texas caused a floral replacement by xerophyllous woodland which was originally part of a low altitude subtropical forest that lived under a dry winter season. The non-tropical appearance of the Appalachians today was caused by the loss of tropical evergreen dicots following a late Tertiary deterioration in climate that left an impoverished, dominantly deciduous hardwood forest as almost sole reminder of a once more cosmopolitan neotropical flora. Hence, following Axelrod's arguments, there were two Tertiary events affecting the northern extension of the neotropical flora: a middle Tertiary period of increasing aridity in the southwest interrupting a once continuous North and Middle American neotropical forest and a later Tertiary (Miocene-Pliocene) deterioration in climate that eliminated most of the evergreen dicots from temperate eastern North America, leaving prominent signs of a more complete neotropical flora only in certain favorable locations on south-facing or coastal exposures and the Florida peninsula.

Now, whether one argues in favor of Martin and Harrell's, Axelrod's, or some other viewpoint, it is clear that there is a biological relationship between eastern North America and southeastern Mexico and northern Central America and that this relationship may have existed for some of the included taxa for a very long time (i.e., for at least 50–60 million years). One may ask, therefore, to what extent the different components of this inter-American biota have shared the same history and by what method this question might be answered most efficiently? What we are seeking is some statement concerning the included taxa of greater generality than their simple coincidence. That there exists a disjunction between North and Middle American vicariads is one such statement, but this statement (i.e., taxa in area A are related to taxa in area B), lacks complexity and contains no more information than that originally required to recognize the existence of the general problem. However,

if one of the two areas (area A, for example) is subdivided (i.e., a second disjunction is found), a more complex statement becomes possible: A' is more closely related to A'' than either is to B. This three-taxon statement implies a historical component not contained in two-taxon statements, namely, that a speciation event (second disjunction) affecting the ancestor of A' and A'' occurred only after the speciation event (first disjunction) that affected the ancestor of A and B.

#### VICARIANT PATTERNS, CLADISTIC SEQUENCES AND EARTH HISTORY

In order to learn if the distribution of *Heterandria* in the southeastern United States, eastern Mexico, and northern Central America (Fig. 1) has some generality with respect to at least two areas of disjunction, it was compared first with major disjunctions in freshwater fish distributions. The location of faunal disjunctions was derived from a matrix in which the occurrences of all known fish species (data from Meek, 1904) were plotted against river systems of the Atlantic versant of Mexico (Fig. 13). The rivers were ordered in north to south geographical sequence, the most northern being the Rio Grande and the most southern the Rio Papaloapan near the Isthmus of Tehuantepec. Such a matrix, which provides an immediate indication of regions of endemism, allows a more precise resolution of regions of disjunction than is possible by the graphic superimposition of distributions as shown in Figs. 10 and 11. Of 114 taxa shown in Fig. 13, 36 are endemic to the Rio Grande, none is endemic in the next two rivers south, 14 are endemic to the Rio Panuco basin, and 35 occur only in the rivers south of the Rio Panuco. Of the 36 in the Rio Grande, some are the same as, and others are most closely related to, species of the eastern United States (thus showing that the Rio Grande is part of a much larger region of endemism). Of the 35 taxa in six rivers south of the Rio Panuco some are the same as, and others are most closely re-

TAXA	RIO GRANDE	RIO SAN FERNANDO	RIO SOTO LA MARINA	RIO PANUCO BASIN	RIO SAN FRANCISCO	LAS LAGUNAS	BOCA DEL RIO	RIO BLANCO	RIO OTAPA	RIO PAPALOAPAN	TAXA	RIO GRANDE	RIO SAN FERNANDO	RIO SOTO LA MARINA	RIO PANUCO BASIN	RIO SAN FRANCISCO	LAS LAGUNAS	BOCA DEL RIO	RIO BLANCO	RIO OTAPA	RIO PAPALOAPAN
LEPISOSTEUS 1	x		x								CICHLASOMA 2	x	x	x	x						
ICTALURUS 1	x		x	x							NEETROPLUS 1	x	x	x	x						
ICTALURUS 2	x		x		x						GOBIOMORUS 1	x	x	x	x						
ICTALURUS 3	x	x									DORMITATOR 1	x									
ICTALURUS 4	x										XIPHOPHORUS 2			x	x						
LEPTOPS 1	x										LEPISOSTEUS 2			x							
CARPIODES 1	x		x	x							ICTALURUS 5			x					x		
CARPIODES 2	x										ICTALURUS 6			x							
CARPIODES 3	x	x	x								CARPIODES 4			x							
PANTOSTEUS 1	x										ALGANSEA 1			x							
CATOSTOMUS 1	x										HYBOGNATHUS 2			x							
MYZOSTOMA 1	x	x	x								AZTECULA 1			x							
CAMPOSTOMA 1	x										NOTROPIS 9			x							
CAMPOSTOMA 2	x										DOROSOMA 2			x							x
CAMPOSTOMA 3	x										FUNDULUS 3			x							
HYBOGNATHUS 1	x										GOODEA 1			x							
PIMELOCEPHALUS 1	x										GOODEA 2			x							
LEUCISCUS 1	x										POECILIA 4			x							
NOTEMOGONUS 1	x										XIPHOPHORUS 3			x							
COCHLOGNATHUS 1	x										POMADASYS 1			x							x
NOTROPIS 1	x		x								CICHLASOMA 3			x							
NOTROPIS 2	x										CICHLASOMA 4			x							
NOTROPIS 3	x										AWAOUS 1			x	x			x			x
NOTROPIS 4	x										HETERANDRIA 1			x				x	x		x
NOTROPIS 5	x										XIPHOPHORUS 4			x				x	x		x
NOTROPIS 6	x	x									STRONGYLURA 1			x							x
NOTROPIS 7	x										CENTROPOMUS 1			x		x					x
NOTROPIS 8	x										CICHLASOMA 5			x	x	x					x
PHENACOBIOUS 1	x										GOBIUS 1			x	x	x					
RHINICHTHYS 1	x										GOBIUS 2			x	x	x					
HYBOPSIS 1	x	x									OPHISTERNON 1			x							
COUSIUS 1	x										AGONOSTOMUS 1			x						x	x
ASTYANAX 1	x	x	x	x					x		CICHLASOMA 6			x							x
ANGUILLA 1	x		x								CICHLASOMA 7			x						x	x
DOROSOMA 1	x		x	x					x		ELEOTRIS 1			x	x						
FUNDULUS 1	x	x	x								GAMBUSIA 2			x				x		x	x
FUNDULUS 2	x										BELONESOX 1			x				x		x	x
LUCANIA 1	x										SYPHOSTOMA 1			x							
CYPRINODON 1	x		x								RHAMDIA 1								x	x	x
CYPRINODON 2	x										RHAMDIA 2								x		x
GAMBUSIA 1	x		x	x							ASTYANAX 2								x	x	x
XIPHOPHORUS 1	x										ICTALURUS 7									x	
POECILIA 1	x	x	x	x	x	x	x	x	x		DOROSOMA 3									x	x
POECILIA 2	x										POECILIOPSIS 1										x
POECILIA 3	x		x	x							CICHLASOMA 8										x
LEPOMIS 1	x										ARIUS 1										x
LEPOMIS 2	x										ICTIOBUS 1										x
LEPOMIS 3	x										HYPHESSOBRYCON 1										x
LEPOMIS 4	x										RIVULUS 1										x
EUPOMOTIS 1	x										PRIAPELLA 1										x
MICROPTERUS 1	x	x	x								XIPHOPHORUS 5										x
ETHEOSTOMA 1	x										MENIDIA 1										x
ETHEOSTOMA 2	x										POMADASYS 2										x
ETHEOSTOMA 3	x										CICHLASOMA 9										x
APLODINOTUS 1	x		x								CICHLASOMA 10										x
CICHLASOMA 1	x										CICHLASOMA 11										x
											CICHLASOMA 12										x
											ACHIRUS 1										x

CONTINUED IN COLUMN 2

lated to, species in the remainder of southeastern Mexico and northern Central America. Three disjunct regions are thus defined (Fig. 14): (1) eastern North America southwest to the Rio Grande, (2) the Rio Panuco basin near Tampico, and (3) the rivers of southeastern Mexico and Central America south to the Great Lakes of Nicaragua; these three regions correspond with patterns of disjunction within *Heterandria* (Figs. 14, 16).

Comparing the geographical components of the *Heterandria* cladogram with the three areas of endemism shows that the principal dichotomy separates North American from Middle American taxa, or, put another way, the cladogram predicts a closer historical relationship between areas 2 and 3 than between either and area 1. The same pattern is present also in poeciliid fishes of the genus *Xiphophorus* (Figs. 14, 16) and box tortoises of the genus *Terrapene* (Fig. 14).<sup>2</sup> However, poeciliid fishes have their plesiomorph

<sup>2</sup> That is, in *Heterandria*, *Xiphophorus*, and *Terrapene* Middle American taxa in areas 2 and 3 are more closely related to each other than either is to taxa in area 1. This may be seen readily from the more complete cladograms of *Heterandria* and *Xiphophorus* in Figs. 19 and 20. In the case of the forms of *Terrapene carolina*, the cladogram is constructed from data in Milstead (1969): within *T. carolina* seven subtaxa are recognized, five in North America and two in Middle America. In the two Middle American taxa, *yucatanana* and *mexicana*, the carapace has a peculiar shape (posteriorly depressed and somewhat constricted), a shape unusual if not unique in box turtles. This form of the carapace is, therefore, presumably derived and is a synapomorphy uniting *yucatanana* and *mexicana* with each other but not with any of the five North American taxa. *Terrapene c. mexicana* is from southwestern Tamaulipas, northeastern San Luis Potosí and northern Veracruz (area 2), and *yucatanana* is from Campeche, Quintana Roo and Yucatan (area 3).

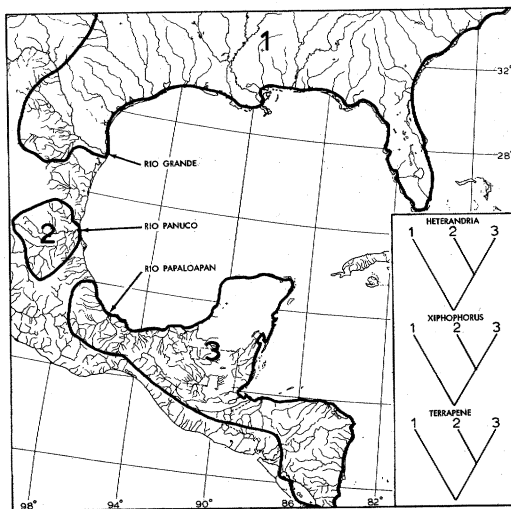


FIG. 14.—Simplified depiction of the geography of principal regions of endemism, derived from the matrix in Fig. 13. Cladograms are described in text.

sister group in South America whereas the three consecutive sister groups to the entirely North and Middle American *Terrapene* (*Emydoidea*, *Emys* and *Clemmys*, in that order; Bramble, 1974) are confined to Laurasia and Africa north of the Atlas Mountains (a detached fragment of southern Europe) (Loveridge and Williams, 1957).

One implication of this difference in extralimital sister-group relationships but identity of vicariance patterns in the study area is that one or both groups of taxa dispersed into the study area and became sympatric prior to the relevant vicariance events and subsequent allopatric speciation.

Other fishes, for example, the alligator gar, show no recognized taxonomic differentiation within the region and are continuously distributed between at least

←

FIG. 13.—Matrix of the geographical occurrences of fish taxa (each numeral following a generic name represents a separate nominal species) for North America (Rio Grande only) and nine major freshwater areas of the Atlantic slope of Mexico (from Meek, 1904). Although there have been taxonomic additions, deletions and changes since Meek's formal survey (Darnell, 1962; Rosen and Bailey, 1963; Miller, 1976), the basic patterns of endemism revealed by the matrix remain substantially unaltered. A few names have been changed to correspond with current usage.

two of the three areas. Forms such as a gizzard shad exhibit the disjunct distributions of the endemic taxa, but show no apparent regional differentiation.

Why some groups show patterns of disjunction and others do not is related to what may be called a species' activity range—the geographic perimeter of occurrence of the individuals of a species during their diurnal, seasonal, or annual movements by active or passive means. For example, a vicariant event separating two once-connected streams will affect the fishes and aquatic invertebrates, but not necessarily the birds that feed on them. This problem might be generalized in the following three statements:

(1) When the geographical extent of an area exceeds the activity ranges of the species of the included taxa, a majority of the taxa should exhibit the same, or components of the same, patterns of vicariance.

(2) When the geographical extent of an area is exceeded by the activity ranges of the species of the included taxa, the taxa should exhibit no vicariant patterns.

(3) When the geographical extent of an area exceeds the activity ranges of the species of some of the included taxa, but not of others, only some of the taxa should exhibit vicariant patterns.

The activity ranges of some of the included taxa (e.g., gars) may in fact be found to exceed the geographical extent of the areas showing biogeographical disjunctions—for example, taxa with continuous distributions which span two or more regions of disjunction. For these taxa, no decision can be reached regarding their age in the study area since they are uninformative with regard to specific historical events.

For the included taxa that did respond in the regions of biogeographical disjunction, but nevertheless show no recognizable taxonomic differentiation in all three regions of endemism, one can only say that they too are cladistically uninformative with regard to the history of the region.

In the example where different groups have the same vicariant patterns, one might hope to associate each pattern with specific events of geographic history. A search for such associations must begin at some time level, and I will take the age of the oldest known fossil representatives of lineages in the modern biota (e.g., gars, lungless salamanders, boid snakes, crocodiles; see Romer, 1966) as a best initial estimate of where to begin the search. This is the Cretaceous.<sup>3</sup>

Since the Cretaceous, North America, Mexico and northern Central America have experienced a succession of major transformations of surface relief, climate, and coastline (Fig. 15). Mountain building in the far west during the Cretaceous and Paleocene was precursor to the Rocky Mountains of North America and the Sierra Madre Occidental of Middle America. Erosional reduction of these features was followed during mid-Tertiary times by an orogeny that uplifted and enlarged the western ranges and gave rise to the Sierra Madre Oriental in eastern Mexico. During the latter part of the Tertiary and continuing to the present day, volcanism contributed lesser ranges along the Pacific versant of Middle America and one that bisected Mexico latitudinally between Tampico and the Isthmus of Tehuantepec.

In eastern North America at the beginning of the Tertiary, the Appalachian chain was represented by an area of gentle relief, having been eroded down into a vast and low, undulating plain, the Schooley Peneplain. The Appalachians were later rejuvenated by a general uplift of the plain which caused renewed erosional activity. The present relief in this region is the result of persistent erosional sculpturing and rejuvenation throughout the Tertiary (Dott and Batten, 1976).

Climate, during Cretaceous and Paleocene times, was subtropical into Canadian latitudes, with no evidence, from

<sup>3</sup> Although a majority of the principal modern lineages of animals and plants are known from the Eocene, starting at that point would exclude those which are known to be older.

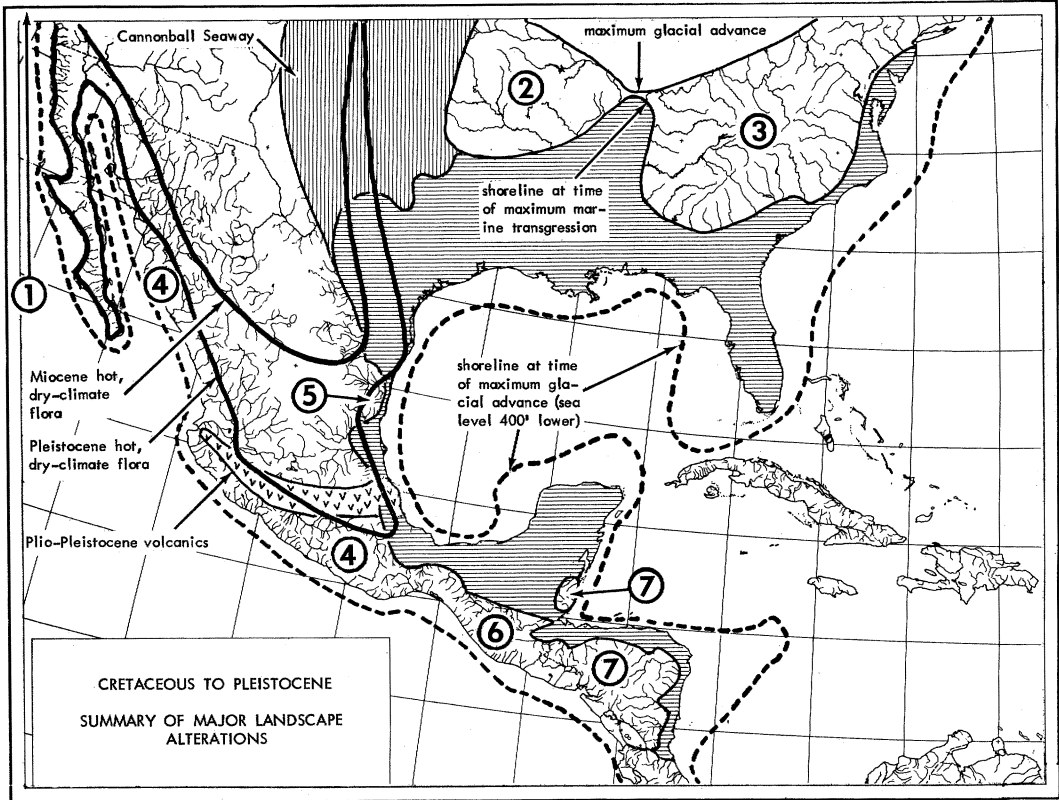


FIG. 15.—Summary of the broad features of Cretaceous-Pleistocene historical geology of North and Middle America. Lower Central America and West Indies omitted. North-south trending mountains not shown. Circled numbers represent areas remaining relatively stable.

geochemistry or the paleofloras, of significant seasonality. Beginning in the early Eocene, however, seasonally drier climate appeared in the western and central Cordilleras, conditions that gradually spread to most of the Cordilleras between Canada and northern Mexico by the mid-Tertiary and finally to the west coast and Great Plains and southward almost to the Isthmus of Tehuantepec in Mexico by the Pleistocene. As the drier conditions were developing in the west and extending gradually eastward toward the Great Plains in North America and toward the Sierra Madre Oriental in Mexico, there was a gradual southward recession of subtropical conditions, until, by about 40,000 years ago, the northern limit of the subtropics came to lie astride the

central Florida peninsula. At the time of the maximum Pleistocene glacial advance, ice sheets, forming a V-shaped wedge, extended down to southern Illinois and paralleled the present courses of the Missouri and Ohio rivers (Dott and Batten, 1976).

Changes in the configuration of the coastline were also dramatic. In Cretaceous times, major portions of the Atlantic versant of North and Middle America were drowned (in North America, as far north as southern Illinois) and a shallow sea extended across North America from the Gulf to the Canadian Arctic—a sea which had retreated south to become the Cannonball Sea of Paleocene times. By the end of the Paleocene the Cannonball Sea had withdrawn farther south, leaving

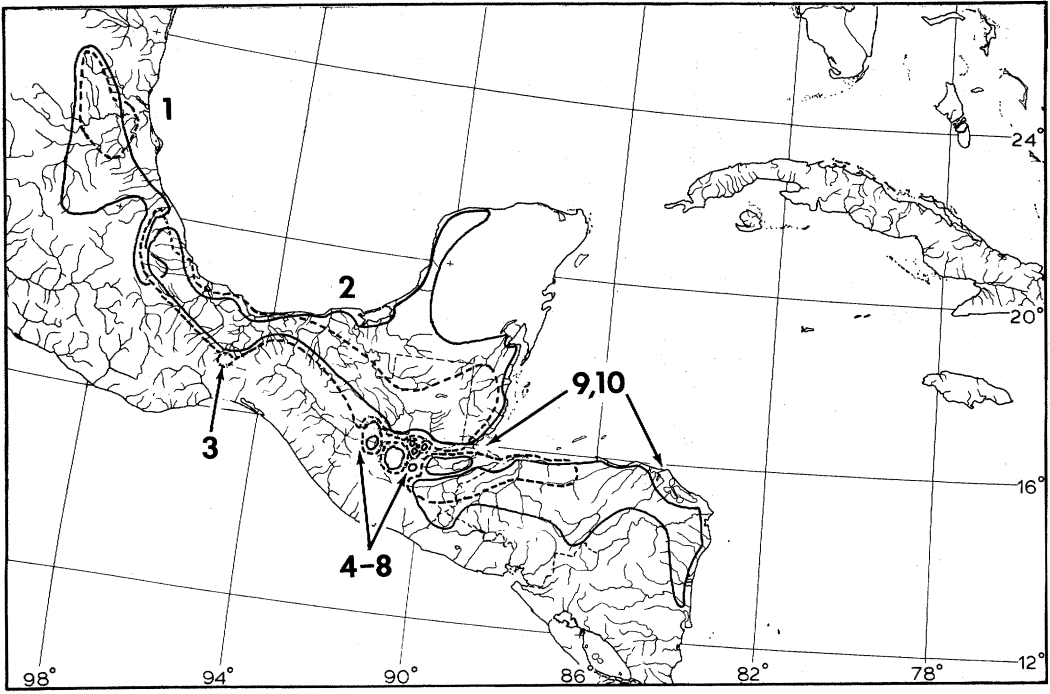


FIG. 16.—Co-occurrences of the Middle American species and recognizable populations of *Heterandria* (solid) and the swordtail species of *Xiphophorus* (dashed) within 10 subregions.

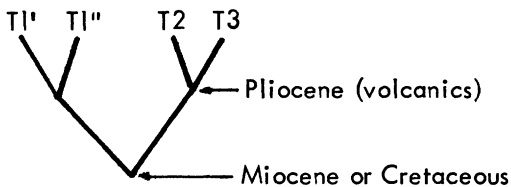
some dry land at middle latitudes. During the mid-Tertiary, Oligocene and Miocene times, the seaway gradually disappeared, there was a slight withdrawal of the marine transgression along the Gulf coast, and parts of the Florida and Yucatan peninsulas had emerged. By the end of the Tertiary, during the period of maximum glacial advance, the present coastline was fully exposed—and more, for the water locked up in the world's glaciers had contributed to a 400-foot lowering of sea level so that almost the entire continental shelf had become subaerial (Dott and Batten, 1976).

Thus, during the roughly 100 million year history just summarized, relatively few areas had remained both continually accessible to nonmarine life and relatively undisturbed by orogenic, volcanic or general tectonic activity: these relatively stable areas (Fig. 15) are 1) parts of extreme western North America, 2) the region of the Ozark Uplift, 3) parts of the

middle latitudes of eastern North America, including the Appalachians, 4) scattered areas of western and central Mexico, 5) the area just north of Tampico in eastern Mexico, 6) most of the base of the Yucatan Peninsula from the Isthmus of Tehuantepec eastward, and 7) the highlands of Belize, Honduras and northern Nicaragua on the Atlantic versant. These relatively stable areas are of special interest because they coincide with the generalized distribution patterns formed by the combined individual distribution patterns of many different components of the biota. To the extent that the different components of the biota shared a common history, their sequences of phylogenetic branching in relation to geography should also correspond. Conversely, a theory of the geographic history should predict the sequences of phylogenetic branching. The prediction should be in the form of a statement that *if* component groups of the biota had responded

to two or more geographical vicariant events, the relative ages of these events should correspond with the branching sequence in their cladograms of relationships.

In relation to cladograms, such as those derived for *Heterandria*, *Xiphophorus*, or *Terrapene*, in which taxa in area 1 are the sister group of those in areas 2 and 3 (Fig. 14), an initial vicariant event is predicted for the region between the Rio Grande and the Rio Panuco basins and a subsequent vicariant event for the region between the Rio Panuco and southern Mexico. At the level of resolution of the geographic history presented above, the initial event could have been either a marine transgression of Cretaceous age or a climatologically induced shift in edaphic conditions (affecting the abundance of surface waters) of middle to late Tertiary times. The subsequent vicariant event providing opportunity for allopatric speciation south of the Panuco basin is attributed most simply to the Pliocene volcanics that bisected Mexico in this region. If the latter is accepted, it carries with it the implication that the initial vicariant event to the north of the Panuco basin had become effective in pre-Pliocene times or at least earlier than the Pliocene volcanics. Whether to accept as the effective agent Miocene edaphic conditions or a Cretaceous marine transgression can be resolved by another cladogram. For example, given the cladogram:



in which T1' is a fossil taxon of older than Miocene age or in which T1' and T1'' are both extant taxa associated with a pre-Miocene vicariance in area 1, the Miocene edaphic factors might be rejected in favor of the Cretaceous marine transgression. I have not attempted to resolve such a cladogram but I will provisionally

adopt the more conservative view that the initial vicariance in this instance is mid-Tertiary simply because the paleofloras associated with the region of disjunction are at present not known to be older than the Middle Eocene.

Assuming that each of the cladograms in Fig. 14 is correct, two historical explanations seem possible. One is that the ancestors of the poeciliids and box turtles had dispersed into the area prior to the Pliocene via coastal drainages that were still unaffected by eastward spreading aridity, and the other is that they were all already present. The discovery of a fossil *Heterandria*, *Xiphophorus*, or *Terrapene* in the Miocene or earlier deposits from the region south of the Rio Grande would cause us to reject the post-Miocene dispersal theory. The poeciliids, however, occur in the rivers that traverse the Cretaceous limestones of the Yucatan Peninsula and members of each genus are also found in the isolated intermontane, karst basins along the foothills of the northern Sierras in Guatemala—the northern limits of the stable land at the base of the Yucatan Peninsula. Living together with them in these karst basins are some endemics with their nearest relatives remote from the region (e.g., in the Great Lakes of Nicaragua and in southeastern South America), and this suggests a long period of isolation. If the age of isolation of the karst basins from the main river could be shown to be Miocene or earlier, this would also be sufficient to reject the post-Miocene dispersal theory. The time of isolation of these karst basins is not yet known and, I suspect, would be extremely difficult to document considering the plasticity of karst topography. A paleontological discovery is therefore likely to provide the most readily available test of the theory.

By way of a summary, the following points are offered:

1. A major biotic relationship exists across a disjunction between eastern North America and Middle America, implying a former biotic continuity.



2. Many of the earliest known representatives of this biota in North America are from Eocene deposits.

3. Many components of this widespread Tertiary tropical biota became extinct in temperate parts of North America during the latter half of the Tertiary and the Quaternary.

4. The major disjunction between eastern North American and Middle American elements in northeastern Mexico is a prominent and well-recognized feature of the modern remnants of this Tertiary biota.

5. By identifying areas of endemism (regions where populations have evolved in isolation), an additional area of disjunction (between the Rio Panuco of east-central Mexico and rivers to the south) was recognized. This finer subdivision of the biota permitted three-taxon cladistic statements that are capable of differentiating between groups with different histories. The cladistic components predict what patterns of interrelationship one might expect to find in other taxa, but impose some constraints on the time levels for certain allopatric speciation events. This contrasts with earlier attempts to deal with neotropical history such as those by Martin and Harrell and Axelrod which, by considering only the disjunction between North and Middle American elements, were limited to a kind of two-taxon problem that is incapable of resolving historical differences between different monophyletic groups included in both areas. One of the purposes of the discussion thus far is to show, by a simple example, how to avoid that limitation.

#### PROGENERATIVE AND EPIGENERATIVE ASPECTS OF DISTRIBUTION PATTERNS

In modern evolutionary theory, the vicariance history of every polytypic group is a history of allopatric speciation events, and this will be so whether the history is underlain by bouts of dispersal, in situ fragmentation of an ancestral species, or both. This process of diversification of an ancestral taxon into geograph-

ically discrete descendent populations (cladogenesis) is estimated by constructing a character-state tree, or cladogram, which specifies a hierarchical scheme of relationships among the descendent taxa that may be interpreted as corresponding with a sequence of speciation events.<sup>4</sup> If the causal explanation of cladogenesis is sought in the interpretations of earth history, then one would hope to discover a sequence of geologic or geographic changes (vicariant events) that correspond in relative ages with the relative positions of taxa in a cladistic sequence and in geographic position with the geographic disjunctions between taxa. The events that were associated with the breakup of the ancestral taxon into descendent taxa are the original, or *progenerative*, causes of the vicariant pattern. Each vicariant pattern is subject to subsequent modification involving expansion, contraction, alteration in shape of the distributions or extinctions of descendent taxa (the vicariant segments) in response to changing ecology, climate, and so forth. These subsequent, or *epigenerative*, influences will, therefore, be highly correlated with the ecologic and physiographic conditions of the modern landscape.

The distinction between progenerative and epigenerative factors is not meant to imply that Quaternary or recent landscape changes and climatic fluctuations cannot cause speciation, but only that progenerative causes provide the opportunities for allopatric speciation and that epigenerative causes affect the boundaries and dimensions of vicariant segments. The importance of this distinction is that usually it isn't made. Müller (1973:185), for example, observed the strong, but expected, correlation of his

<sup>4</sup>I consider the character-state tree as a primary concept expressing perceived natural order, the cladogram as a derivative concept which expresses inferred relationships of taxa with the ordering data of the character-state tree stripped away, and the phylogeny as a further removed derivative concept which interprets the cladogram in an evolutionary context.

“dispersal centers” with Quaternary climate and vegetational fluctuations. He then concluded (p. 203) that “strong displacements of the biochores have taken place during the Quaternary period and these displacements led to the formation of refuges,” and that “this is an essential reason for the richness of the tropical rain forest of Central and South America in species.” Perhaps so, but to accept this conclusion we would also have to agree that the coincidence of a distributional center with an ecological regime is a sufficient correlation.

But let us suppose that cladistic sequences were worked out for several groups of taxa in several of Müller’s “dispersal centers” and it happened that these sequences showed little or no congruence. Would this not suggest that these several groups of taxa had different histories of cladogenesis (allopatric speciation events)? And what then would be the significance of Müller’s correlation? Or, suppose that their cladistic sequences were all perfectly congruent, but that the sequence of establishment of the refugia or “dispersal centers” was quite different. And, again, what then would be the significance of Müller’s correlation? I submit that the observed correlation, under either of these hypothetical circumstances, could only be judged epigenerative. In turn, that judgment would mean that the progenerative causes (the vicariant events leading to allopatric speciation) lay elsewhere, in a more remote time. The problem with Müller’s presentation, and with many others like it, is that Müller assembled, arranged and summarized a great deal of information in a useful and interesting fashion, but he stopped short of analysis. In place of analysis he substituted a scenario based on the assumption that he had actually found the progenerative factors to be part of Quaternary history. The kinds of correlations noted by Müller seem no more significant than the statement that fishes are found in water and that where the water goes, so go the fishes.

#### SPECIES CONCEPTS AND BIOGEOGRAPHY

To the extent that biogeography searches for patterns and their historical explanation, the choice of a species concept by the practicing biogeographer is crucially important. This is so only because conventional taxonomic practice regards the species as a fundamental evolutionary unit. A concept such as the biological species, however, appears to be inapplicable to observable nature, because it incorporates criteria that are generally undiscoverable. It requires that we identify noninterbreeding sympatric units (I have discussed the reproductive criterion elsewhere: Rosen, in press). But in practice what are these units—crabs and fishes, lions and zebras? Or, does the sympatry refer to more closely related groups and, if so, how closely related? Must they have a sister-group relationship to each other—that is, must they be each other’s closest living relatives which, under the allopatric speciation model, are the least likely groups to occur sympatrically? Even if so, the sympatry of closest living relatives (the only nonarbitrary choice of sister-taxa) couldn’t be shown to meet the requirements of the concept, because the ‘closest living relatives’ may be only the surviving plesiomorph and apomorph members of a formerly speciose group (e.g., man and the chimpanzee within the Homininae). The only way we can postulate that there were no extinctions of cladistically intermediate taxa is that the surviving forms have contiguous ranges which together estimate the range of their ancestral taxon, and that these allopatric distributions coincide with the distributions of other pairs of some groups of other plants and animals, i.e., are part of a general pattern that can be shown to have some historical integrity. In other words, information needed to satisfy the requirements of the ‘biological species’ concept for reproductive incompatibility of sympatric sister-taxa is provided only by allopatric distributions!

What about the evolutionary species concept, which requires that the natural unit be an evolutionary lineage? Presumably this could refer to a population or several populations. A decision about how many populations are to be included depends entirely on the discovery and distribution of apomorphic character states among the populations. If two or more populations share some derived character they are lumped together because, only together, can they be defined by an apomorphic character. If subsequently each population is discovered to have a unique and recognizable apomorphic character, then each population can be recognized. The populations, both grouped and singly, are evolutionary lineages in the sense of being defined by uniquely derived character states, but the decision about whether the populations constitute one or several species has sometimes been, in practice, an arbitrary one dictated by whether a taxonomist has wanted to apply a polytypic species concept. It is the polytypic species concept (which is a logical necessity of the biological species concept) that has required an arbitrary decision about how many species to recognize within a cluster of diagnosable populations in order to avoid monotypic species—making the polytypic species operationally equivalent to the genus. When the choice has been made to confer species status on each unit (of one or more populations) that can be clearly diagnosed with apomorphic characters, the recognized species are those of everyday taxonomy which, when interpreted as lineages, are equivalent to evolutionary species. Thus, the evolutionary species appears to conform, in practice, with Regan's (1926) definition that a species is what a competent taxonomist says it is.

Both of the above species concepts have in common a requirement for the discovery of discontinuous variation; the type of variation which not only permits sharp definition of geographically isolated clusters of individuals (populations) but which also makes possible the adop-

tion of a stable nomenclatural system that requires a type specimen to conform with all the individuals in a reasonable sample of the population (or at least the assumption that it will so conform).

What about two or more geographically isolated clusters of individuals (populations) showing overlapping variation with statistically different modes? They are generally absorbed within the taxonomy of discontinuous variants (species), treated as subdivisions of species (subspecies or races), or ignored taxonomically.<sup>5</sup> This unequal treatment of populations showing overlapping and discontinuous variation involves an assumption that these two aspects of variability are fundamentally different and of different levels of significance from the standpoint of evolutionary history. What is the basis for this assumption? Both are the presumed results of genetic processes operating under conditions of geographic isolation. For the many kinds of organisms in a biota that has undergone geographic fragmentation, the conditions of isolation for all individuals will be the same although their responses to it may differ in accordance with their different genetic histories. Thus, some kinds of organisms will differentiate at what some taxonomists have called the generic or higher levels, some at the level of species, subspecies, race, or statistically recognizable population. The point is that *they have differentiated* and are potentially informative with respect to the relationships of their area to other areas, a quality that is independent of a taxonomist's particular bias concerning what amount of differentiation deserves species recognition.

I conclude, therefore, that a species, in the diverse applications of this idea, is a unit of taxonomic convenience, and that the population, in the sense of a geographically constrained group of individuals with some unique apomorphic characters, is the unit of evolutionary sig-

<sup>5</sup> This may be true mostly of vertebrate taxonomy, especially in ornithology and mammalogy.

nificance.<sup>6</sup> Some populations, whether recognized as species or not, are informative with respect to a history of geographic isolation because they have differentiated. Others are uninformative either because they haven't differentiated, because they are parts of larger populations that span two or more areas (are insensitive to existing barriers), or because taxonomists have thus far failed to detect the ways in which differentiation has occurred (physiologically, developmentally, behaviorally, etc.).

The problems that have beset biogeography by the casual application of species concepts are easily seen in center or origin-dispersal models of biotic history. Mayr and Phelps (1967), for example, have explained the occupation of the Pantepui highlands of northern South America by birds of different taxonomic rank as the result of a series of invasions of different ages, the oldest colonizations being represented by the taxa of highest rank. These authors have, of course, assumed that the bird taxa are evolving at a more or less constant rate so that differences in rank can accurately reflect differences in age. They also have assumed that certain degrees of difference are reliable indicators of certain taxonomic ranks, and they have assumed that the different taxonomic judgments of different taxonomists studying different bird groups are comparable. Presumably their 'colonization' theory was also influenced by prior acceptance of a center of origin-dispersal paradigm which neatly interlocked with their special uses of taxonomic rank.

But suppose Mayr and Phelps had considered the alternative theory that the different bird taxa of the Pantepui were the fragmented remains of an old occupation of these highlands? They would also presumably have allowed for different rates of differentiation of assorted character states in the different groups of

birds. In fact, at some very general level such theories may be the only way we have of crudely estimating differences in evolutionary rates,<sup>7</sup> an option that is denied us by arbitrary application of the center of origin-dispersal model of biotic history. A choice between that and the vicariance theory could be made by asking which groups of birds, at whatever rank, yield congruent area cladograms by the method described below (pp. 178-182). Congruence would naturally suggest a single history for all such taxa, just as more than one pattern of congruence would suggest more than one history for the Pantepui bird fauna. I judge that such an approach is at least a concrete analytical beginning in the elucidation of what must be a complex historical problem. The alternative approach, used by dispersalists, has so many built-in apriorisms that it consists of little more than narrative invention. The absence in traditional biogeography of cladistic methodology and concepts of distributional congruence, as well as the application of doctrinal species concepts, seem to be largely responsible for the lack of rational choices between conflicting narratives.

The following, and final, section discusses a method for choosing between alternative theories of biogeographic history, using examples of two fish groups in Middle America and some groups of insects and fishes in the southern hemisphere.

#### CLADISTIC CONGRUENCE AND HISTORICAL EXPLANATION

In Middle America the two groups of poeciliids, *Heterandria* and *Xiphophorus*, show many detailed similarities in their general patterns of occurrence (Fig. 16). Both have species represented in and around the Rio Panuco basin (area 1

<sup>6</sup> If this view is accepted, it renders superfluous arguments about whether a 'biological species' is an individual or a class (see, e.g., Hull, 1976).

<sup>7</sup> A fossil, of course, provides only an estimate of how young its assigned lineage is. The rare continuous stratigraphic sequences of related fossils provide an estimate of the rate of change in that sequence, but are of no value in concepts of relative rates of change as would be provided by the many components of a single biota.

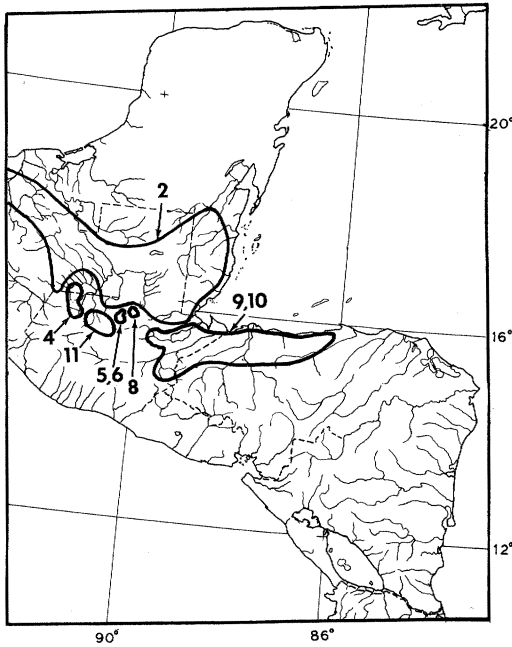


FIG. 17.—Distributions in southern Mexico and northern Central America of the swordtail species and recognizable populations of *Xiphophorus*. The samples from subregion 11 are intermediate between the taxon in subregions 4, 5, and 6 and that in subregion 2, and are provisionally interpreted (Rosen, in press) as intergrades.

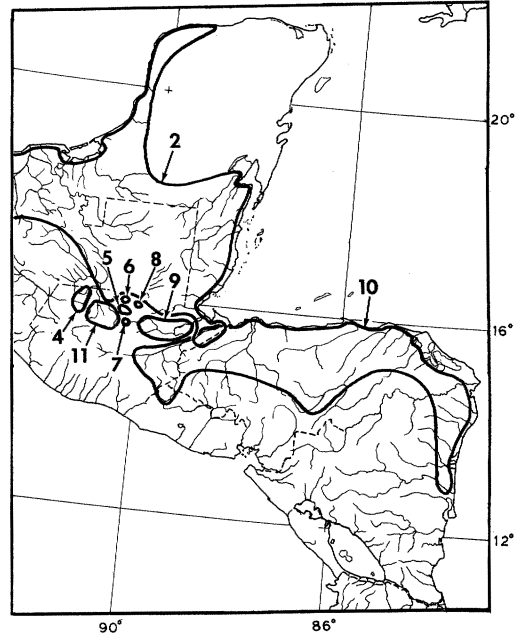


FIG. 18.—Distributions in southern Mexico and northern Central America of the species and recognizable populations of *Heterandria*. The samples from subregion 11 are intermediate between the taxon in subregions 4 and 5 and that in subregion 2, and are provisionally interpreted (Rosen, in press) as intergrades.

in Fig. 16) and both groups have a complex of species and recognizable populations southeast from the Panuco to Honduras and Nicaragua. Within the region south of the Panuco, each group has a widespread taxon or group of related taxa occupying most of the Atlantic versant southeast to Belize and eastern Guatemala (area 2), each has a form in the Rio Motagua basin and the rivers of coastal Honduras related to the widespread taxon (area 10), and each has a complex of species or populations ranged along the foothills of the Sierras in northern Guatemala (areas 4 to 8). Each group is also represented by an upland population in west-central Guatemala that is morphologically intermediate between a Sierran form and the widespread taxon (an area 11, not identified in Fig. 16). There are some dissimilarities, too. For example,

only the swordtail group of *Xiphophorus* is represented by a distinct endemic taxon in the headwaters of the Rio Coatzacoalcos basin of Mexico (area 3), and only *Heterandria* is represented by endemic species or differentiated populations in the Rio Polochic basin of Guatemala (area 9) and in certain isolated basins along the Sierras (areas 6 and 7, Figs. 17 and 18). Furthermore, *Heterandria* is, in general, of wider occurrence than the swordtail group of species south of the Rio Panuco basin, on the Yucatan Peninsula, in southeastern Guatemala, southern Honduras, and in extreme northeastern Nicaragua.

By replacing the named taxa or populations on cladograms derived for *Heterandria* and *Xiphophorus* (Figs. 19, 20) with numerals representing one or more of the 11 subregions, the cladograms of

species or populations may be converted into cladograms of areas. The justification for this procedure is the underlying assumption that the history of all life has some generality with respect to the history of the earth's geography; hence, the search for general distribution patterns is equivalent to the search for related geographic areas. Inspection of the area cladograms for the two groups shows that *Heterandria* has a unique component in area 7 and that the two are incongruent with respect to three areas (3, 6 and 9). In relation to the question of whether each cladogram shows some generality with respect to the other, it is evident therefore that it is not with respect to area 7 (the unique component of *Heterandria*), or areas 3, 6 and 9. Deletion of unique area components and those which are incongruent because only one group has endemic taxa in certain areas (Fig. 21), shows that there is a residual congruence involving five main areas (1, 4-5, 10, 8 and 2). The significance of the identity of the two reduced area-cladograms is not the fact that they each includes the same areas, but that each includes the same areas in the same cladistic sequence.<sup>8</sup>

What is the probability that the geographically transformed and reduced cladogram of *Xiphophorus* will coincide with the transformed and reduced clado-

<sup>8</sup> One may, of course, ask questions about the significance of the unique or incongruent elements in the original cladograms. Assuming that the original, unreduced cladograms truthfully represent real phylogenies and that the unique or incongruent elements have no generality with respect to other as yet unanalyzed components of the Middle American biota, the incongruent elements would be most simply explained as dispersals. Because of the assumptions required, however, it is evident that such explanations have little scientific merit. In other words, such explanations are without significance at the level of general explanation. Mayr (1965), and others, have curiously continued to view biogeographic explanation almost wholly as a search for unique explanations of unique events. Mayr has written: "As a result of various historical forces, a fauna is composed of unequal elements, and no fauna can be fully understood until it is segregated into its elements and until one has succeeded in explaining the separate history of each of these elements."

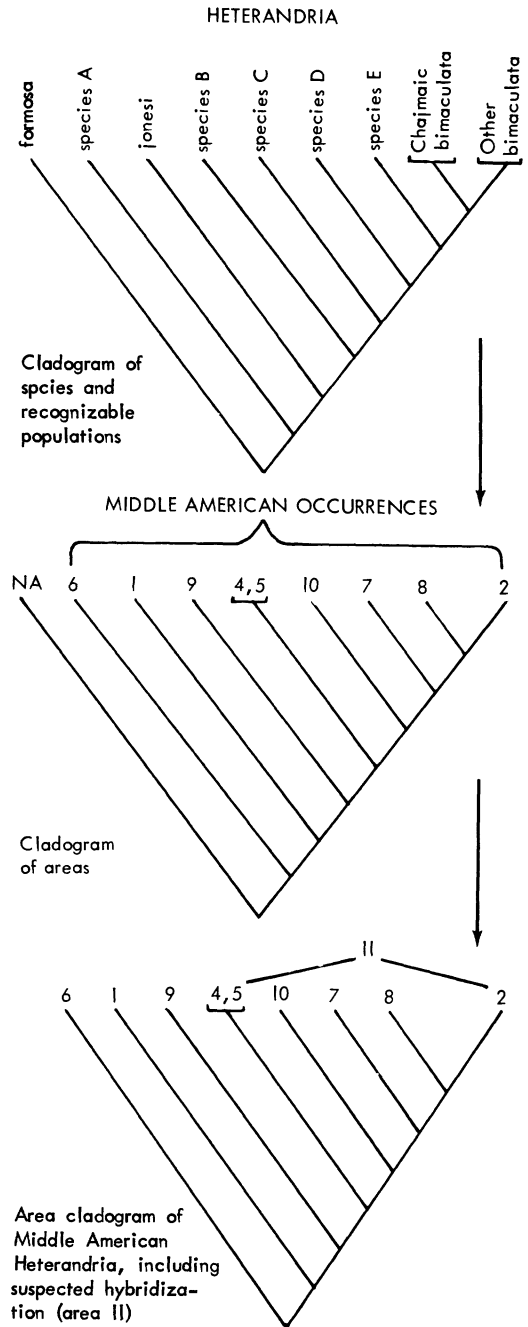


FIG. 19.—Conversion of cladogram of species and recognizable populations of *Heterandria* (derived from a character-state tree in Rosen, in press) into cladograms of areas. Species referred to here by letters (A to E) are described as new in Rosen (in press). Numbers refer to areas in Figs. 16 to 18; NA = North America.

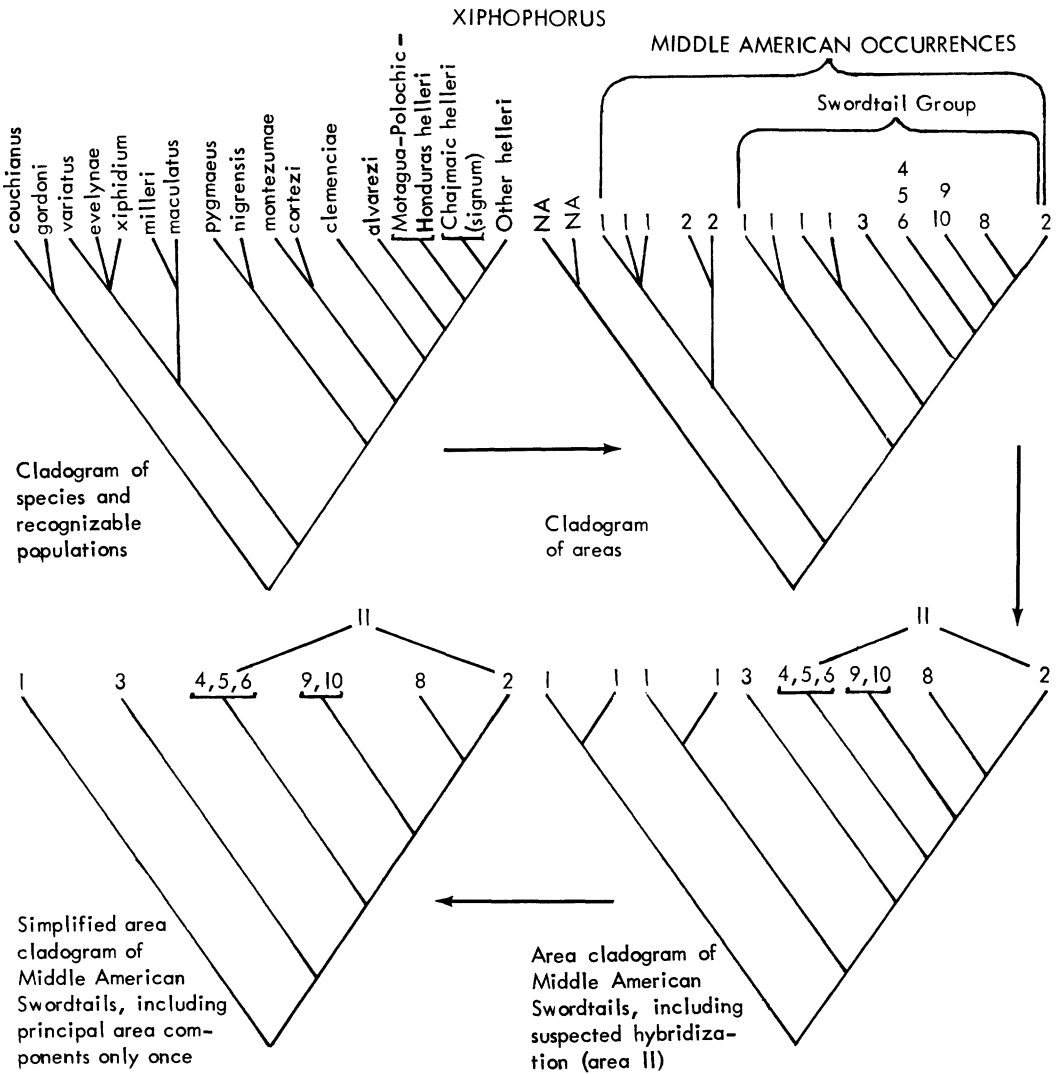


FIG. 20.—Conversion of cladogram of species and recognizable populations of *Xiphophorus* (derived from a character-state tree in Rosen, in press) into cladograms of areas. The first area cladogram is reduced to that part relevant to Middle American swordtails, which is in turn reduced to an area cladogram specifying only the cladistic sequence of principal area components (primary branch points). Numbers refer to areas in Figs. 16 to 18; NA = North America.

gram of *Heterandria* by chance alone? This question is related to the number of dichotomous configurations that are possible in groups containing different numbers of taxa (see Schlee, 1971). Going back for a moment to the simpler three-taxon system (Fig. 14), although only one pattern was found, there are three theoretically possible dichotomous area-

cladograms (areas 1 and 2 versus area 3, 2 and 3 versus 1, and 1 and 3 versus 2). The probability that a second group sympatric with the first will duplicate the branching sequence of the first group is one out of three or 33% that such congruence will occur by chance alone. Such a relatively high probability (in fact, the highest *P* value possible in three-taxon

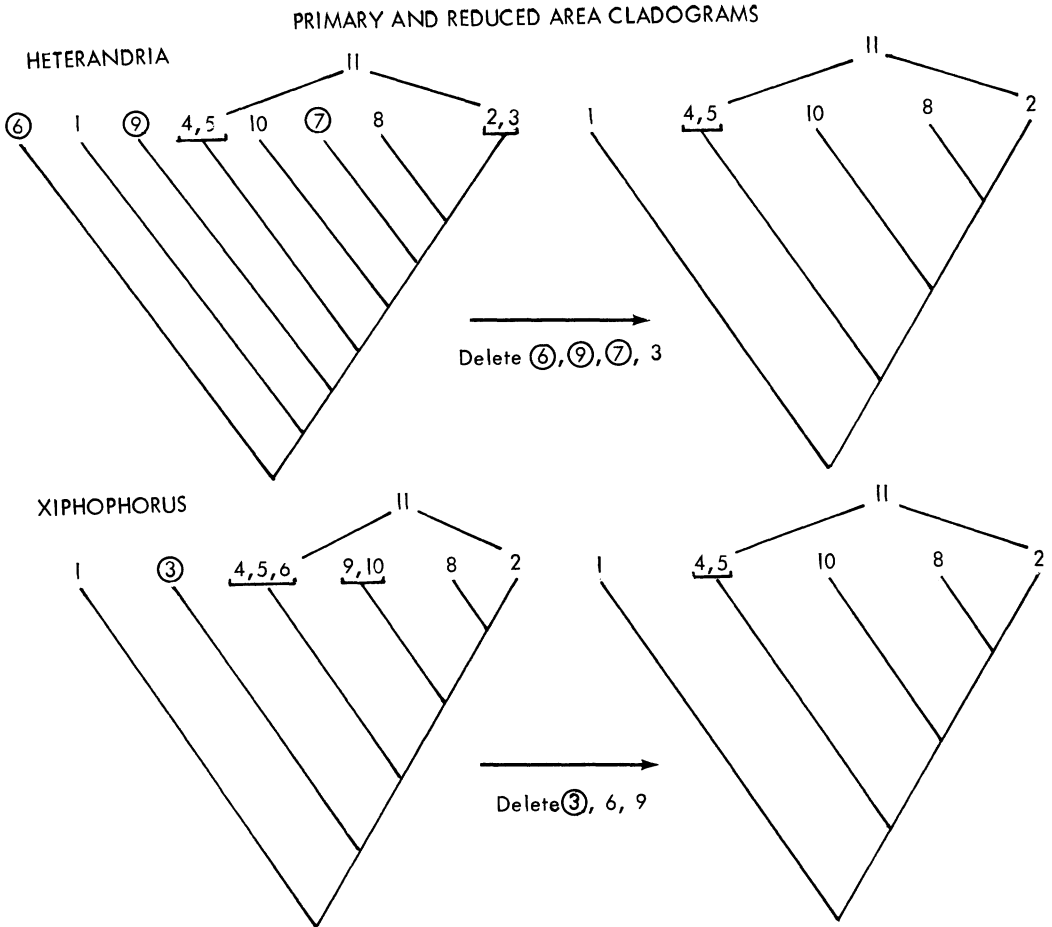


FIG. 21.—Method of reduction of primary cladograms (from Figs. 19 and 20) for *Heterandria* and *Xiphophorus* to produce cladograms representing residual congruence. Deleted unique or incongruent elements are shown below arrows. Circled numbers represent incongruent areas with endemic taxa in each genus.

comparisons) casts some doubt on the significance of finding two congruent three-taxon area-cladograms such as those for *Heterandria* and *Xiphophorus* in North and Middle America. But if a third congruent three-taxon area-cladogram is added to the system, for example the forms of *Terrapene carolina*, then the probability that two three-taxon cladograms will be congruent with the first one is one out of  $3^2$ , or 11% probability that such congruence will occur by chance alone. For a five-taxon area-cladogram, such as those for *Heterandria* and the

swordtail species of *Xiphophorus* in Middle America (Fig. 21), the probability of duplicating a given dichotomous pattern by chance alone is one in 105 (the number of possible dichotomous cladograms for five taxa), or 0.9%. If the individuals in area 11 are correctly interpreted as hybrids (Figs. 19, 20), these putative hybrids, by representing a distinct historical event, could be treated as the equivalent of a sixth taxon in both *Heterandria* and *Xiphophorus*. The probability that the two five-taxon configurations with the sixth reticulate element



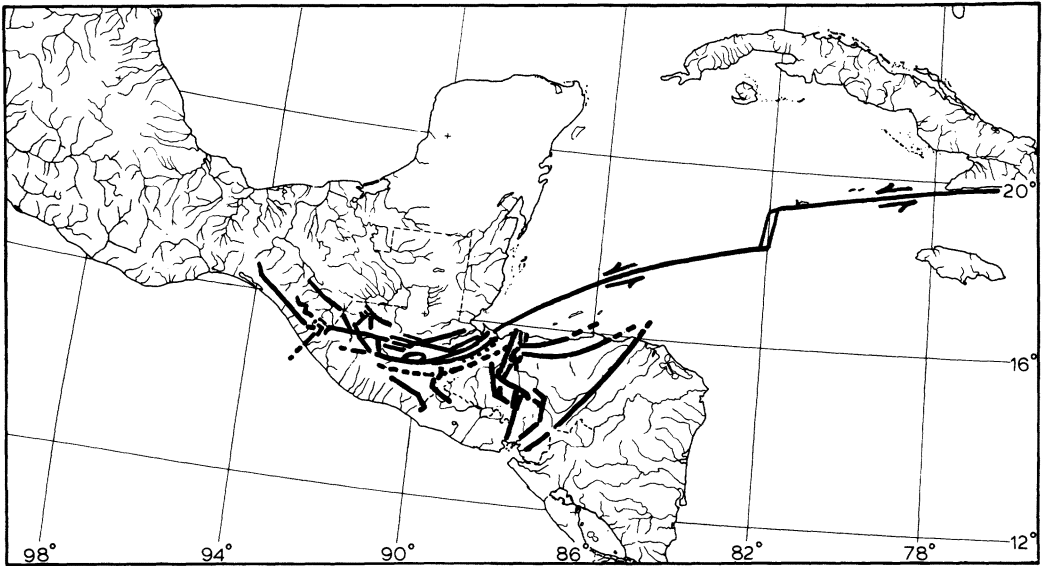


FIG. 22.—Distribution of major fault zones in southern Mexico and northern Central America. The strike-slip fault shown extending into the Caribbean (the Cayman Trench) has its landward extension in the Motagua and Polochic faults of Guatemala, and, according to one geophysical theory, represents the northern boundary of the Caribbean plate (see Muehlberger and Ritchie, 1975).

(area 11) related in the same manner to areas 4, 5, and 2 are congruent by chance alone is only one in 945, or 0.1%.

It appears, therefore, that the coincidence of *Heterandria* and *Xiphophorus* in Middle America can be said to be due to nonrandom factors that affected both equally in five, possibly six, subregions of Middle America (at the 99% confidence level), but that the coincidence of *Heterandria*, *Xiphophorus*, and *Terrapene* in North and Middle America can be said to be nonrandom only at the 89% confidence level. The discovery by random search within other monophyletic groups distributionally coincident in North and Middle America of another cladogram that coincides with those three would alter the estimate of nonrandomness to the 96% confidence level, and of still one more to the 99% level. This is merely another way of saying that the discovery of additional cladistically congruent distributions can only reduce the probability or likelihood that the observed coincidence has resulted from random historical factors.

What might the historical factors have been in Middle America, and on what basis might they be compared with the given biological distributions? The idea that biotic and historical geologic patterns can be compared requires two assumptions: that geologic or geographic change is the cause of biotic fragmentation and that the fragmentation of an ancestral population by the formation of barriers will result in heritable differences among the descendent populations. In such a cause and effect relationship, where the earth and its life are assumed to have evolved together, paleogeography is taken by logical necessity to be the independent variable and biological history, the dependent variable. Drawing a mathematical simile, a set of biological relationships  $y$  (dependent variable) is a function of a set of geological or geographic relationships  $x$  (independent variable), as in a simple regression of effect  $y$  on cause  $x$  where we are given no free choice as to which is the independent variable. Such a view implies that any specified sequence in earth

history must coincide with some discoverable biological patterns; it does not imply a necessary converse that each biological pattern must coincide with some discoverable paleogeographic pattern, because some biological distributions might have resulted from stochastic processes (chance dispersal).

These assumptions do not require either that all components of a biota need respond to a given barrier or that heritable differences resulting from isolation need be recognizable by the taxonomist. Groups that either fail to respond to a barrier or have differentiated at an undetected level are simply uninformative with respect to the history of their area. The significance of endemism, then, is simply that some differentiation has occurred that can be viewed cladistically and therefore used to formulate statements about nested sets of distribution patterns. This is illustrated in the example where the Polochic and Motagua faults of eastern Guatemala (Fig. 22), elements of the tectonic history of the Caribbean region, are correlated with two detectable responses in *Heterandria* at the level of recognizable taxa and with one detectable response in *Xiphophorus* at the population level.

The extent to which detectable differentiation has proceeded is unimportant (e.g., recognizable taxa versus recognizable populations), but the *number of cases* of detectable allopatric differentiation is important since more kinds of differentiation make possible more complex cladograms which in turn make possible more predictions about the history of an area. Thus, *Heterandria* is more informative than *Xiphophorus* with respect to the historical distinctions between the Polochic and Motagua basins because only *Heterandria* has endemic species in both basins; furthermore, because of the plesiomorphic position of the species in area 9 relative to that in area 10 in the cladogram for *Heterandria* (Fig. 21), the branching pattern of the cladogram predicts that the events which isolated the Polochic basin preceded those which iso-

lated the Motagua basin and coastal Honduras drainages from northern Guatemala. In this regard *Xiphophorus* is simply uninformative, for, although its populations in northern Guatemala and those in the Polochic, Motagua, and Honduras are slightly differentiated from each other, no detectable differences have been found between those from the Motagua-Honduras region and from the Polochic.

The idea that a biological area-cladogram predicts something about the sequence of geological events in the region under study requires that geological data are capable of being arranged in nested sets or in the form of a cladogram of related areas now separated by discontinuities (such as water gaps, disrupted river channels, rifts along fault zones, mountains, etc.). Within an historical context, related geological areas are two or more areas that arose by the disruption or fragmentation of an ancestral one. The classic example of such a history is the disruption of Pangaea followed by continental drift, a cladistic representation of which is shown in Fig. 23 based on data from McKenna (1973), Rich (1975) and Ballance (1976). There is nothing fundamentally different between geological and biological cladograms since both incorporate the idea of nested sets of things that are grouped by special similarities (synapomorphies), such as the unique patterns of glacial ridges in the rocks of Gondwanian fragments or the uniquely matching contours of the margins of some of the fragments. Hence, in a geological cladogram, the "taxa" are the separate areas or physical features of the landscape which are united as sister-taxa by the common possession of some special property not known elsewhere, and the origin of the separate areas is inferred to have been the disruption of a formerly continuous area. The relative ages of the different branch points in such a cladogram would be determined by radiometric, paleomagnetic and other physical data pertaining to the actual or relative ages of the various disruptive geographic events (the phenomena that become vi-

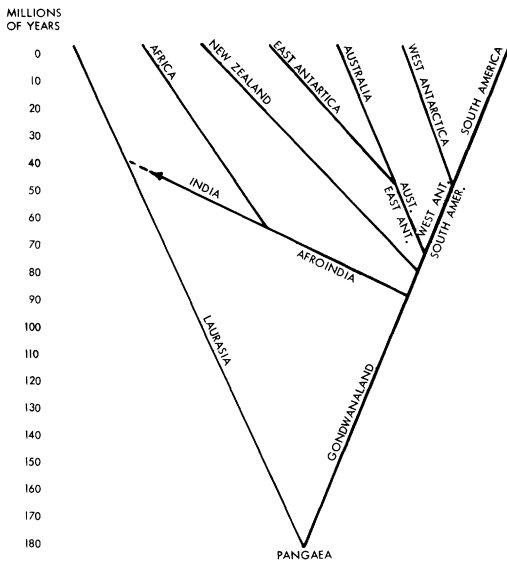


FIG. 23.—Cladistic representation of the history of the breakup of Pangaea greatly simplified, with an approximate time scale of the bifurcations (fragmentation events) and one conjunction (of India and Laurasia).

carian events for the affected biota). The resulting geological cladogram representing related areas arranged according to their relative ages of origin can then be converted into an area-cladogram. As in the comparison of the two area-cladograms for *Heterandria* and *Xiphophorus*, the unique components of the geological area-cladogram are deleted so that the components of the geological area-cladogram are geographically comparable with those of a biological area-cladogram. The two kinds of reduced area cladograms are congruent to the extent that the component areas are interrelated in the same sequence.

The nature and method of comparison of biological and geological area-cladograms is most simply illustrated by reference to the Pangaeon model of earth history (Fig. 23). We observe in Brundin's (1966) revision of chironomid midges that, within the subfamily Podonominae, Australian and South American taxa are more closely related to each other than any of them are to African taxa;

this may be reduced to the three-taxon statement, in the form of a biological area-cladogram, shown in Fig. 24B. The nature of any question about the generality of this distribution has therefore been specified with reference to three geographical regions. A comparison of reduced cladograms derived for the other two subfamilies treated by Brundin, the Aphroteniinae and Diamesinae, shows that they, too, have Australian and South American taxa more closely interrelated than are any of them to the taxa in Africa. Similarly, in galaxiid fishes of the subfamily Galaxiinae, Australian, and South American taxa may be more closely interrelated than are any of them to the single southern African species, *Galaxias zebratus*.<sup>9</sup> In order to compare these four coincident and cladistically congruent distributions with a cladistic representation of Gondwanian history, the Pangaeon area-cladogram in Fig. 23 is reduced by the deletion of components that are unique with reference to a problem that specifies only Australia, South America and Africa. When the unique components of the unreduced Pangaeon area-cladogram (Laurasia, India, New Zealand, and East and West Antarctica) are deleted, the remaining figure (Fig. 24A) is directly comparable with the biological cladograms and is seen to be congruent with them. Since the four biological area-cladograms are congruent and may be said to have resulted from nonrandom historical factors at the 96%

<sup>9</sup> This species, sometimes referred to a separate genus by itself or together with other non-African species, differs from all other galaxiines in the anterior extent of the dorsal fin insertion. Given the anterior position of the dorsal fin in the sister group of the galaxiines, the aplochitonines, and the equally advanced dorsal fin position in the sister group of both, the Salmonidae, it appears the *G. zebratus* has retained a primitive fin position and that all other galaxiines are united by the relatively more posterior location. Scott (1966) has suggested that the fin position of *zebratus* and certain other species results from a specific pattern of relative growth that causes a foreshortening of the anterior half of the body; although this may be so, such growth patterns have not been studied in a majority of galaxiine species or in the Aplochitoninae.

confidence level, and since they are congruent with a (presumably) corroborated cladistic representation of the relevant components of Gondwanian history, the ancient fragmentation of Australia, South America, and Africa can be taken as our best current estimate of the progenerative cause of the biological patterns.

McDowall (1978), in a lengthy effort to rebutt the view that galaxiid distribution patterns might have ancient roots, offered in evidence the widespread (South America, New Zealand, and Australia) *Galaxias maculatus* which, according to him, is taxonomically undifferentiated in its different outposts. If McDowall is correct in his taxonomic judgment, it appears that the most one can say about *Galaxias maculatus* is that it is uninformative with respect to the history of Australia, South America, and Africa and to the history of other galaxiids in those regions. Yet McDowall insisted that the distribution of *G. maculatus* and another widespread species freed him from any constraints to consider the possibility of an ancient origin for the group. What he claimed to be reasonable is that the distributions of these two widespread taxa permit one "to assume that early dispersal of galaxiid fishes could have been through the sea." Although McDowall emphasized the necessity of phylogenetic argument in biogeography, he provided none, but seemed intent, instead, on rescuing dispersal at the expense of an arguable position.

Congruence of a biological area-cladogram with a geological area-cladogram

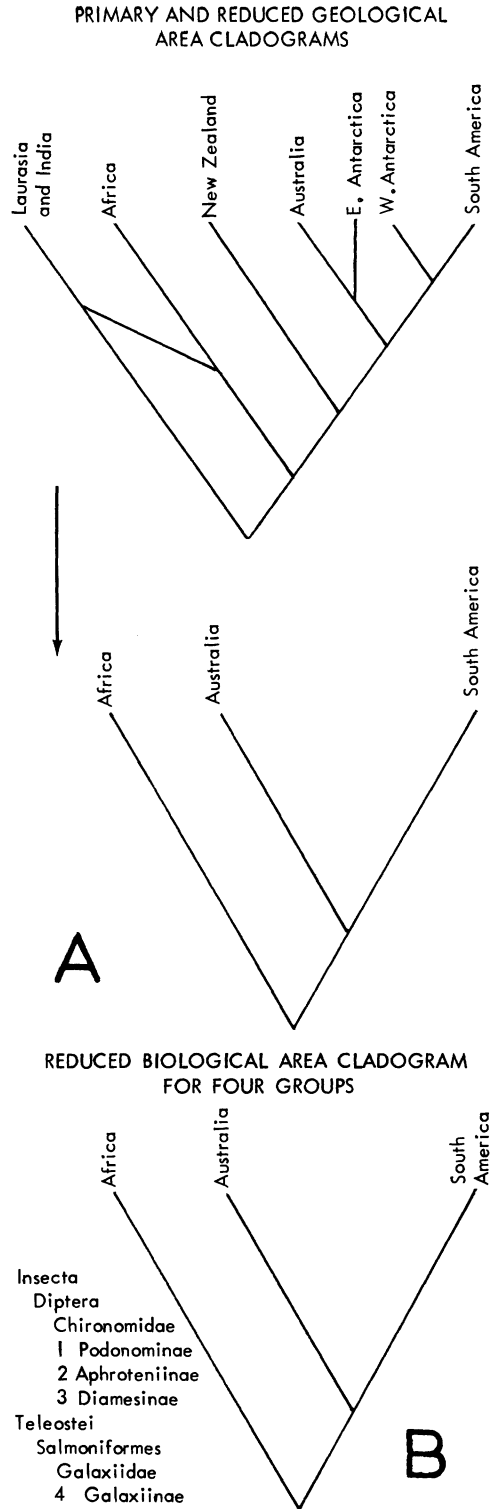


FIG. 24.—Comparison of geological and biological area-cladograms in relation to four monophyletic animal groups in the southern hemisphere. Taken as an explanation of the generalized biological pattern, the geological cladogram specifies an age of about 85 my BP for the first dichotomy (between the taxa in Africa and Australia-South America) and about 70 my BP for the second (between the taxa in Australia and South America). Many other examples of these intercontinental relationships have been discussed by Keast (1973).

does not test the reality of vicariance versus dispersal. However, it does provide a best estimate of a sequence of geological events implied by the geological relationships that might have been involved in the speciation events implied by the biological relationships. Hence, the probability that a five-term geological area-cladogram will correspond with a five-taxon biological area-cladogram by chance alone is one in 105 (about 1%); and, as in the Gondwanian example, above, the probability that four three-taxon biological area-cladograms will be congruent with a three-term geological area-cladogram by chance alone also is about 1%. A decision concerning the nature of this correspondence whether by dispersal or vicariance or some combination of the two, must be a parsimony decision concerned with minimizing the number of separate assumptions entailed by the different types of explanations. Interestingly, a parsimony decision only becomes possible when a given distribution pattern (a biological area-cladogram) can be shown to have some significant generality expressed as a low probability that a given pattern will have occurred in more than one monophyletic group by chance alone. McDowall looked with small favor on a remark by Croizat et al. (1974) that galaxiid distribution "might itself be interpreted, perhaps even credibly, as an example of transoceanic dispersal from some center of origin. But when galaxiid distribution is compared with that of other southern hemisphere organisms, many of which have similar distributions but different means of dispersal . . . 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. . . . The problem is one of different realities: the reality of long-distance dispersal versus the reality of a pan-austral biota." The clear implication and certainly the intent of that remark, which McDowall ignored in his own view of the problem, is that general patterns demand

general explanations. As noted above, cladograms congruent at a very high confidence level only specify that the groups involved have probably shared a common history. Whether that was a history of dispersal or vicariance seems to depend on other considerations. If, for example, a group of perching birds and a group of earthworms had congruent six-taxon area-cladograms (where  $P = 0.1\%$  that the two were congruent by chance alone), would we assume that the earthworms dispersed with the birds or that the birds vicariated with the earthworms? I wonder which alternative McDowall would choose, and why.

A final, and most necessary, observation is that a geological area-cladogram neither tests nor in any way affects the generality of a biological area-cladogram. A geological area-cladogram differing from the biological pattern does not refute the pattern—it is simply irrelevant to it because it contains no explanatory information regarding the biological pattern. A geological area-cladogram that corresponds in part or whole with a biological pattern is simply adopted as an "explanation" of the pattern in the sense of providing a best current estimate of the historical factors that induced the biological pattern. A conflict of geological explanation could only arise, then, if, for the same geographic region, another series of geological relationships of entirely different chronology were shown to have the same cladistic structure.<sup>10</sup> With two congruent but allochronic geological area-cladograms for the same region, only appropriate fossil occurrences could resolve which one to accept as the relevant

<sup>10</sup> If, as logic demands, each set of historical relationships has its own unique properties due to its unique spacio-temporal coordinates, the correspondence between any two allochronic series of events would simply reflect the low resolution of that level of analysis. At the same time, it is the logical uniqueness of historical relationships that makes the comparison of generalized distribution patterns with geological or geographical patterns inherently reasonable, even if we now (and will continue to) face the severe practical problems of inadequate data.

explanation of a particular biogeographic history (e.g., by showing that a relevant part of the biological history is too old for one geological sequence but not for the other).

Returning now to the problem of the geographic history of *Heterandria* and *Ziphophorus* in Middle America: the region has been tectonically active since the end of the Mesozoic, and although a great deal has been written on the historical geology of this region, I am unable to obtain enough precise information to produce a cladistic statement that is relevant to the area extending from the Rio Panuco basin southeastward to Nicaragua. This does not mean that I consider a search for such historical explanation fruitless, but only that, as a nongeologist, I am unable to pick and choose among the varied and sometimes conflicting geological interpretations of the Tertiary history of Middle America.

On the other hand, I could abandon the pursuit of a cladistic synthesis of geographic history and simply try to find an event here and there that coincides with some biological disjunction: for example, the fault zones of northern Central America or the east-west oriented Pliocene volcanic zone south of the Rio Panuco basin in Mexico.

Or, I could renounce my responsibility altogether and simply assume that the biological patterns have been caused by Quaternary events, as Deevey (1949) said we should assume.

Or, I could do something else, which I am inclined to favor. This is to recognize that geology and biogeography are both parts of natural history and, if they represent the independent and dependent variables respectively in a cause and effect relationship, that they can be reciprocally illuminating. But for there to be reciprocal illumination between these two fields there must be a common language. This language must be the language of nested sets, i.e., hierarchical systems of sets and their subsets united by special similarities, i.e., synapomorphies. In short, taxonomists should be

encouraged to continue the current salutary trend to organize their data cladistically, and geologists should be encouraged to begin. At least until the geological data pertaining to Middle America are so ordered I am forced to draw the limited conclusion that the observed biological patterns have formed during a period spanning all or part of the last 80 million years.

#### ACKNOWLEDGMENTS

To my friend and colleague of many years, Gareth Nelson, I offer special thanks for the countless hours, adding up, I am certain, to months, of enjoyable and informative discussion of systematic and biogeographic theory. Appreciated criticism of the typescript was received from James Atz, Daniel Axelrod, Roger Batten, Niels Bonde, Sadie Coats, Leon Croizat, Jürgen Haffer, David Hull, Malcolm McKenna, Gareth Nelson, Lynne Parenti, Norman Platnick, and E. O. Wiley. Helpful discussions of Mexican fish distributions were offered by Robert R. Miller, and information concerning tropical American herpetology was supplied by Eugene Gaffney, Charles Myers, and Richard Zweifel.

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