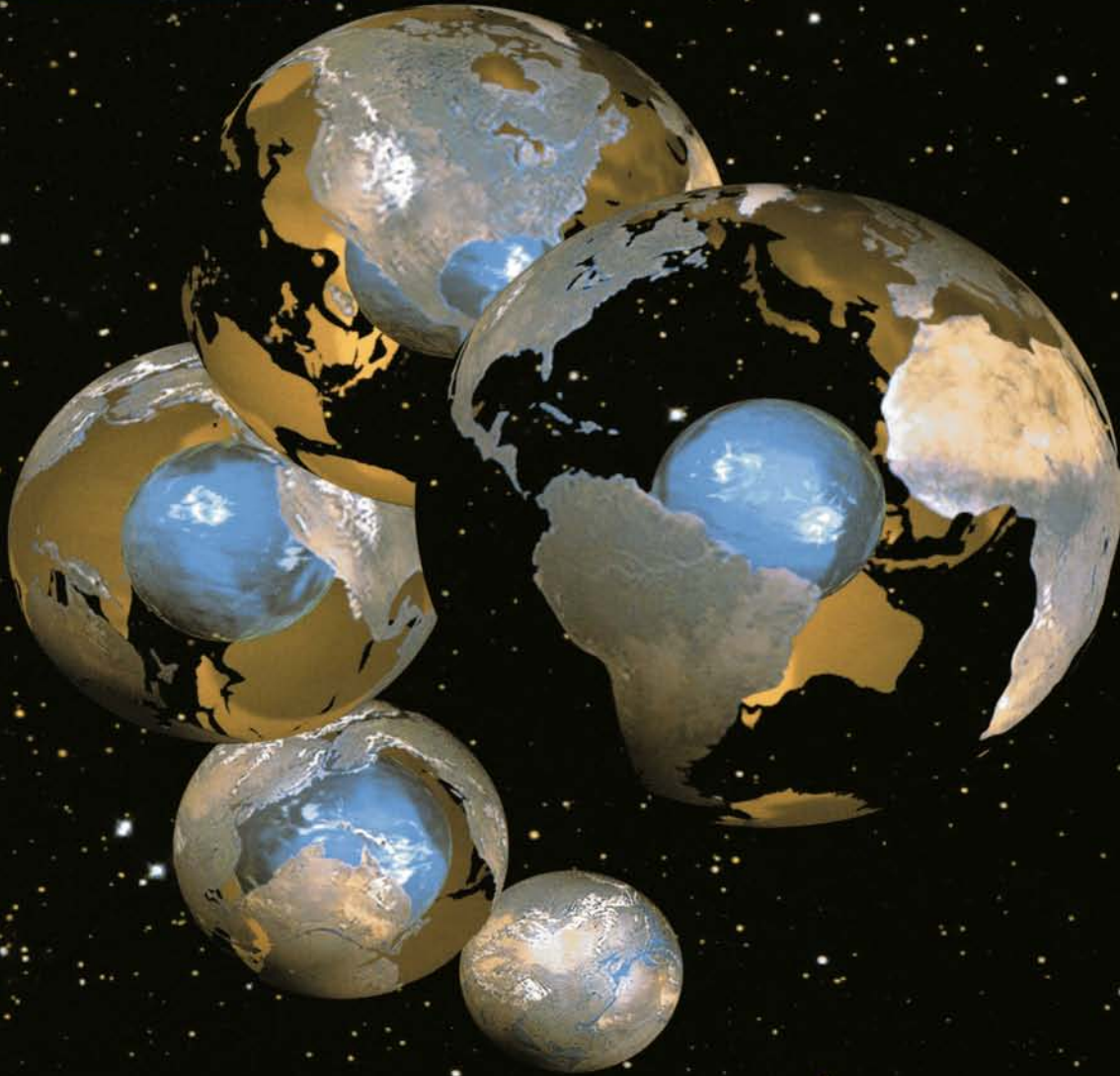


Biogeography in a Changing World



Edited by
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2 Common Cause and Historical Biogeography

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ABSTRACT

The search for a general pattern of area relationships for a group of taxa living in the same region lies at the core of historical or cladistic biogeography. Once a general pattern is discovered, its cause may be inferred. This sequence, first discovering a pattern, then inferring its cause, is the logical foundation of cladistic biogeography. Ignoring this sequence, for example, inferring the causes of a distribution pattern and then using those inferences to reject, or to fail to look for, a pattern, is a rejection of the principles of cladistic biogeography. One reason for ignoring this sequence is misapplication of the principles of phylogenetic systematics in biogeographic analysis. A second reason is inferring *a priori*, using fossil evidence, molecular data, or both, that a taxon is too young or too old to be part of a general pattern and, hence, could not have been affected by the same Earth history events as other taxa. A third reason is assuming that taxa with different dispersal abilities or ecologies are unlikely to be part of the same general pattern, therefore, unlikely to share a distributional history. There are other reasons, many discipline-specific and often correlated with adherence to a center of origin concept. Formation of redundant distribution patterns, with widespread taxa, pruned by extinction, has left some baffling, sometimes seemingly contradictory, distribution patterns worldwide and throughout geologic time. The relationship between Earth history (geology) and phylogeny and distribution patterns (biology) is still under debate. Separating identification of a pattern from inferences about the processes or mechanism that caused it remains a challenge for historical biogeography.

INTRODUCTION

In 1979, the American Museum of Natural History in New York hosted a symposium on *Vicariance Biogeography: A Critique* to "provide a diversified evaluation of the methods and concepts of vicariance biogeography by comparison with other biogeographic concepts such as refuge theory, equilibrium theory, progression rule theory and dispersalism," quoting from the symposium brochure. Gareth Nelson and Donn E. Rosen, then colleagues in the Department of Ichthyology and leaders in the development of vicariance biogeographic theory, methods, and application, were among the symposium organizers and edited the published proceedings

(Nelson and Rosen, 1981). In the Introduction, Rosen, in Nelson and Rosen (1981, p. 5), wrote "It seems doubtful, at least to me, that the notion of congruence between geographical and biological patterns could ever be formulated in a testable way without cladistic information, just as there seems here the promise that the study of cladistic congruence between the earth and its life will be the next 'revolution in the earth sciences' — an integrated natural history of the geological and biological systems." Paleoichthyologist Colin Patterson, of the Natural History Museum, London, a close colleague of both Nelson and Rosen (e.g., Patterson, 1975), also expressed this view (Patterson, 1981).

Donn Rosen died in 1986 at age 57 (see Nelson et al., 1987), just one year before John C. Avise and colleagues (1987) introduced the term "phylogeography" to describe the geographic pattern displayed by intraspecific gene trees — the mitochondrial DNA "bridge" between population genetics and systematics. The subsequent explosion in application of molecular techniques to systematics at the population level and above, as summarized in Avise (2000) and elsewhere, is well known. Application of these techniques to systematics and biogeography has been, on the one hand, invigorating, as it has generated many novel hypotheses of phylogenetic relationships, yet at the same time, detrimental, as it has revived untestable hypotheses of center of origin, recognition of ancestors, and dismissal of the importance of Earth history at all levels, not just plate tectonics, in biogeography (see Ebach, 1999; Humphries, 2004; Nelson, 2004; Parenti & Humphries, 2004; Heads, 2005a; and below).

In the *New York Times* report on the 1979 symposium (Webster, 1979), Niles Eldredge, an AMNH curator of invertebrate paleontology, expressed the view of many in attendance: "... the debate here is whether a certain pattern of species distribution was caused by dispersal or vicariance." The importance of process or mechanism — debating between vicariance and dispersal — was fixed in biogeographical thought and remains so today for many biogeographers despite the earlier arguments by Platnick & Nelson (1978), more recent statements by Heads (2005a, b), and many others in between, that this diverts attention away from the principal goal of discovering patterns. McLennan and Brooks (2002, p. 1055), for example, note that over the past 30 years, "... the discipline of historical biogeography has diverged into at least two research programmes. These programmes differ fundamentally in their views about the way biological diversity has been produced ...". Cook and Crisp (2005, p. 744) agree: "Biogeographical problems are concerned with process, typically involving discrimination between vicariance and dispersal ...".

Rosen's anticipated "revolution in the earth sciences" — an integrated natural history of the geological and biological systems — has been realized only to a limited degree (e.g., Ebach & Humphries, 2002). It has been stalled not only by some applications of molecular techniques, but also by an emphasis on inferring mechanisms of biological distributions before, or instead of, discovering shared patterns of biological and geological diversity, an emphasis on centers of origins. Further, it has been stalled by adherence to traditional biogeographic regions or realms when global distribution patterns recognized for over 150 years have supported a drastic overhaul or revision of those regions (e.g., Morrone, 2002). In the

language of Ebach and Humphries (2002), the revolution in biogeography has been stalled by attempts to generate explanations rather than to discover patterns.

CLADISTIC VS. PHYLOGENETIC BIOGEOGRAPHY

Historical biogeography aims to discover shared patterns of distribution among organisms in a biota, rather than explaining distributions one organism at a time. The search for a general pattern of area relationships as specified by the phylogenetic relationships of taxa living in the same region lies at the core of cladistic biogeography. Once a general pattern is discovered, its cause may be inferred. This sequence, first discovering a pattern, then inferring its cause, is the logical foundation of cladistic biogeography (viz. Platnick & Nelson, 1978; Nelson & Platnick, 1981; Humphries & Parenti, 1986, 1999). Ignoring this sequence, for example, inferring the causes of the distribution of taxa in a biota and then using those inferences to reject, or to fail to look for, a pattern, is a rejection of the principles of cladistic biogeography. Chris Humphries and I (Humphries & Parenti, 1986, 1999) deliberately chose "cladistic biogeography" to identify this research program to emphasize discovery of patterns rather than "vicariance biogeography," which implied an emphasis on identification of Earth history events to explain all distribution patterns, or "phylogenetic biogeography" (see Brundin, 1981; Brooks, 2004), which was tied to center of origin and dispersal concepts, or "panbiogeography" (see Craw et al., 1999; Croizat, 1982), which did not integrate phylogenetic relationships. We did not argue that Earth history had no role in forming the patterns, but that hypothesizing a particular mechanism was secondary to discovering a pattern (see also Ebach, et al., 2003).

Phylogenetic biogeography of Brundin (1966, 1972, 1981) and Hennig (1966) revolved around the notions of a center of origin and dispersal away from such a center by progressively more derived taxa (Figure 2.1a). This method, incorporating the deviation and progression rules (Hennig, 1966), persists (e.g., Bremer, 1992, 1995; Briggs, 1992, 1999; Brooks, 2004, among many others) and dominates phylogeographic studies, as it may be applied to one taxon at a time.

Identification of centers of origin was soundly rejected by Croizat *et al.* (1974) as untestable; biogeography is a science based on the proposal of hypotheses of distribution that are tested with additional distribution patterns. In his early writings on historical biogeography, however, Nelson (1969, p. 687) advocated an explicit, untested notion of dispersal: "assuming the relationships [of Figure 2.1b] who could doubt, e.g., that the occurrence of this lineage in area x is a secondary and a relatively late one?" The conclusion of dispersal was made as an observation, not a hypothesis open to test. Five years later, Nelson (1974, Figure 1) recanted in his alternative formalization of historical biogeography, arguing that there was no such evidence for dispersal and that the ancestral area could be estimated by adding together the areas of the descendant taxa. The method described briefly by Nelson (1969) persists, however, and has even been named, cladistic subordinateness (Enghoff, 1993), to denote presumed evidence of secondary dispersal by a taxon with a restricted distribution nested among more broadly distributed derived taxa. Nelson and Ladiges (2001, Figure 1c) reworked Nelson's (1974, Figure 1) example, to demonstrate that

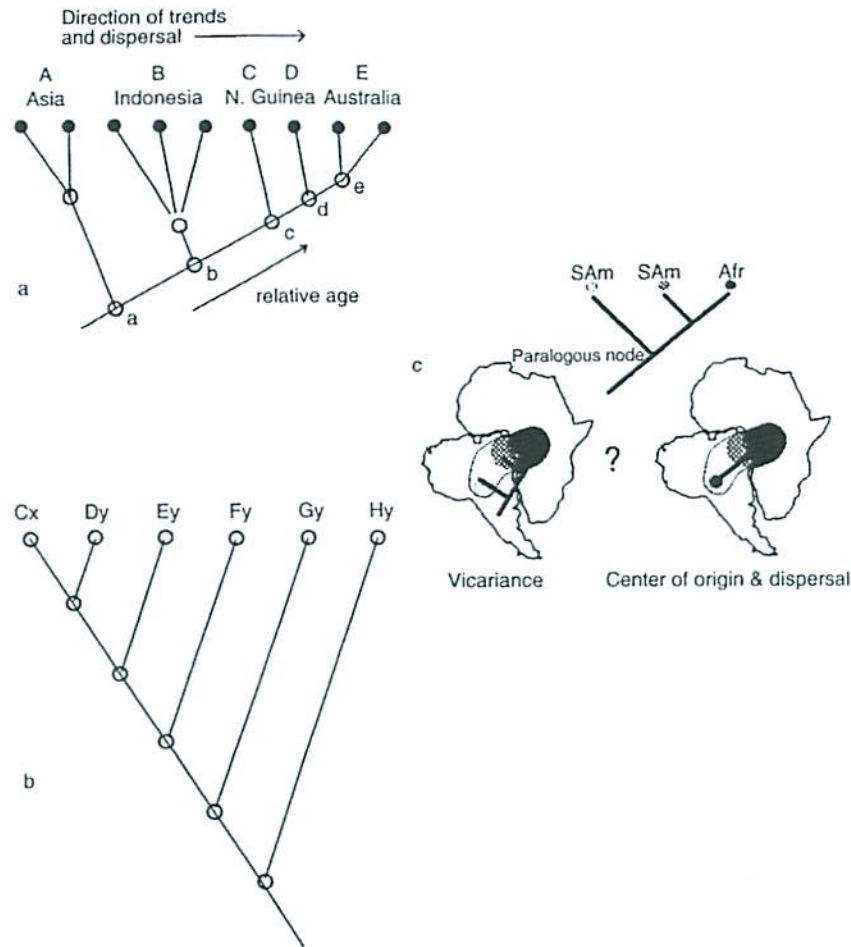


FIGURE 2.1 (a) Phylogenetic biogeographic hypothesis specifying sequential dispersal of increasingly derived taxa away from a center of origin, from Brundin (1972, Figure 3); (b) historical biogeographic hypothesis specifying the dispersal of taxon C from area y to area x, from Nelson (1969, fig. 3); (c) alternative interpretations of a distribution pattern from Nelson and Ladiges (2001, Figure 10), following Nelson (1974).

either a vicariant or dispersal hypothesis may be used to interpret the distribution pattern — in other words, that the paralogous node in Figure 2.1c, repetition of South America, adds no information to area relationships and does not specify a center of origin in South America.

Another kind of center of origin interpretation of single cladograms — optimization of habitat — was made by Rosen (1974) in his study of salmoniform phylogeny and biogeography. The phylogenetic hypothesis of salmoniform fishes (Figure 2.2a) was interpreted as follows (Rosen, 1974, p. 313), "... salmoniforms

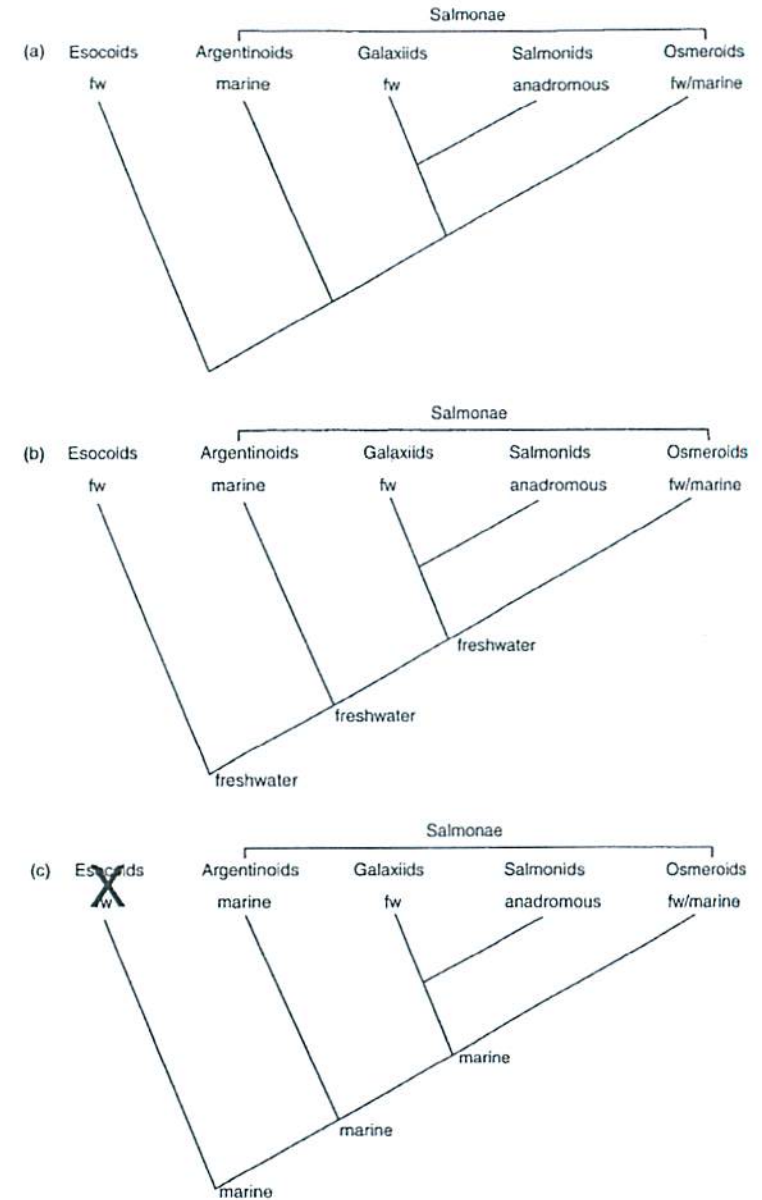


FIGURE 2.2 (a) Cladogram of relationships of the subgroups of the order Salmoniformes (sensu Rosen, 1974, Figure 39), including basic habitat; fw = freshwater; galaxiids are diadromous, but were treated as freshwater by Rosen (1974) because they breed in freshwater. (b) Habitats optimized according to Rosen's (1974) criteria given a freshwater sister group of the Salmonae. (c) Alternate optimization of habitats following Rosen's (1974) hypothetical proposal of a marine sister group of the Salmonae. (d) Reconstruction of ancestral habitat of marine and freshwater for Salmonae.

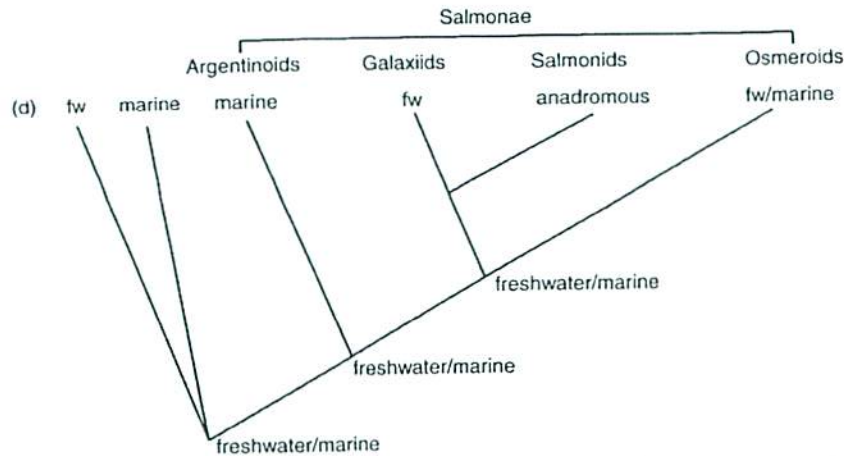


FIGURE 2.2 (Continued)

are therefore primitively freshwater fishes that have twice become secondarily marine ... It should be noted, however, that if esocoids are incorrectly associated in this order and the sister group of Salmonae should prove to be marine instead of freshwater, then the Salmonoidei may be secondarily anadromous [migrating between marine and freshwaters] ... Here, Rosen (1974, Figure 2.2b and 2.2c) treated a cladogram as a phylogenetic tree and habitat (marine vs. freshwater) as a character to be optimized. An alternate interpretation (Figure 2.2d) would entail reconstructing a widespread ancestral habitat for the Salmonae — both freshwater and marine — rather than relying on the present-day habitat of the hypothesized living sister-group to interpret historical habitat distribution (see also Parenti, submitted). Coincidentally, McDowall (1997) also concluded that diadromy is an ancestral condition for the Salmonidae, Osmeridae, and Galaxiidae (Parenti, in press).

Erasing the notion of centers of origin from biogeography became a goal of Nelson and Rosen once teamed with Croizat (e.g., Croizat et al., 1974). Despite explicit, repeated criticism that optimization of nodes in biogeography implies a center of origin hypothesis (e.g., Nelson, 1974, 2004; Platnick & Nelson, 1978; Parenti, 1981, 1991; Parenti & Humphries, 2004), it persists as a method among both neontologists and paleontologists, especially to infer an ancestral habitat (e.g., Brooks & McLennan, 1991; Stearley, 1992; Winterbottom & McLennan, 1993; McLennan, 1994; Lovejoy & Collette, 2001; Thacker & Hardman, 2005, among many others).

METHODS OF HISTORICAL BIOGEOGRAPHY

Methods of historical or cladistic biogeography were developed to interpret the area relationships of three or more taxa in a biota, using the area cladogram, or areogram, in which the names of taxa were replaced by the name of the areas in which they live (e.g., Brundin, 1972; Rosen, 1978). Component analysis was developed by

Nelson and Platnick (1981; Platnick & Nelson, 1978) and programmed by Page (1989, 1993; see also Page, 1990; Morrone & Carpenter, 1994; Crisci et al., 2003). Brooks parsimony analysis (BPA) was developed by Brooks (1981) for host-parasite relationships, following Hennig's (1966) parasitological method, and expanded to encompass a range of historical biogeographic questions by Wiley (1987, 1988), Brooks & McLennan (1991, 2002), Lieberman (2000, 2004), Van Veller et al., (2000) and Van Veller & Brooks (2001), among others. Both methods adopt the simple premise that organism relationships reflect their distributional history, complex in practice because organisms and areas do not act as one, especially through geological time (see discussions in Grande, 1985; Cracraft, 1988; Hovenkamp, 1997). There are other methods of historical biogeographic analysis (see Crisci et al., 2003), but it is not my purpose to review all of them here. Widespread taxa (taxa living in more than one area), extinction (taxa missing from areas) and redundant distributions wreak havoc on patterns of areograms (see Platnick & Nelson, 1978; Nelson & Platnick, 1981; Nelson & Ladiges, 1996). Widespread taxa, missing areas and redundant distributions are analyzed and interpreted differently by component analysis and BPA, and therein lies the basis of a quarter century of debate (compare Ebach et al., 2003 with McLennan & Brooks, 2002, for example). A taxon that lives in two areas, A and B, is interpreted by BPA as indicating that areas A and B share a closer history than either does to another area, say area C. Under component analysis, presence of a taxon in areas A and B does not preclude that either one of those areas shares a closer history with area C. A widespread taxon could have failed to differentiate as the areas it occupied (A and B) diverged (Nelson & Platnick, 1981).

Donn Rosen would have had methods develop in another way, with biologists collaborating with geologists, as he did in formulating his hypotheses of Caribbean historical biogeography (Rosen, 1985, see below). I was privileged to be one of Rosen's graduate students at the American Museum of Natural History from 1975 to 1980. Naturally, I sent him a draft of the proposal for the first edition of *Cladistic Biogeography* (Humphries & Parenti, 1986) for comment. He replied:

I think your and Chris' book outline is fine so far as it goes, but that it lacks a major ingredient — perhaps the most important one if we're concerned with the future development of biogeography. This ingredient is a discussion of cladistic historical geology, without which 'the evolution of the earth and its life' is a pipe dream. Historical geology is analyzable cladistically, and both theoretical and real examples must be presented to explain to geologists how to go about providing the independent data base necessary to demonstrate consilience. I've been consulting recently with knowledgeable geologists and will try to put together a method for dealing with the geology. It's more complicated than I thought it would be, but still workable. My suggestion, therefore, is that you and Chris gather up some of the stray geologists in Britain who can give you some well-documented histories and convert these into cladistic patterns that might be compared with some good biological ones. This is the way to convince geologists that they have much to learn from biology and that they had best set to work producing supportable cladograms. The other important feature of such a chapter is that it would describe a common language for biologists and geologists that would enhance a needed exchange of ideas now sorely lacking. It might even provoke a methodological revolution in historical geology (Donn E. Rosen, *in litt.*, 3 March 1982; italics in original).

Geological cladograms have not been pursued with the same interest and enthusiasm as areagrams derived from taxon cladograms, for better or worse. Better because we, as biologists, are not tied to consensus interpretations of geological hierarchies (see McCarthy, 2003, 2005, for example). Worse because without independent geological cladograms, biologists rely on prevailing geological hierarchies as the best interpretations of Earth history, as in event-based methods (e.g., Sanmartín & Ronquist, 2004), which therefore cannot discover patterns that conflict with current geology (see Heads, 2005a, b). Geologists have provided detailed summaries of the geological histories of complex regions, but not explicit geological cladograms. The detailed reconstructions of Southeast Asian geology over the past 55 million years by Robert Hall, Department of Geology, University of London, and colleagues are notable in this regard (e.g., Hall, 1996, 2002; <http://www.gl.rhul.ac.uk/seasia/>).

In developing methods of historical biogeography using areagrams, the principle of parsimony has been applied to choose among competing hypotheses. The analogy between taxa and characters in phylogenetics and areas and taxa in biogeography is not precise, however, and efforts to make it so have not addressed adequately the above-mentioned differences between the goals of component analysis and BPA with respect to widespread taxa (viz. Kluge, 1988; Wiley, 1988; Brooks & McLennan, 1991; Lieberman & Eldredge, 1996). Further, Nelson & Ladiges (1991, 1993) have developed an areagram-based method termed three-area statements analysis to extract informative statements about area relationships from complex areagrams that are characterized by duplicated or paralogous nodes. Most parsimonious interpretations of area/taxon matrices, as required by BPA, do not necessarily account for geographic paralogy, area hierarchies that are interpreted as contrary to a general pattern because of duplication or overlap in geographic distribution of taxa (Nelson & Ladiges, 1996). The differences in these general classes of methods have been characterized by McLennan & Brooks (2002, pp. 1056–1057) and Brooks (2004) as an emphasis on area relationships (component analysis) vs. speciation processes (BPA). The so-called non-vicariant (i.e., non-Earth history) elements of diversity listed by McLennan & Brooks (2002, p. 1063) as explanations for a pattern such as non-response to a vicariant event (widespread taxa), extinction and lineage duplication were all recognized by Nelson & Platnick (1981), Nelson & Ladiges (1996) and others as common phenomena that all biogeographic methods should address. The two other non-vicariant elements of diversity listed by McLennan & Brooks (2002), peripheral isolates speciation and post-speciation dispersal, are hypotheses that, like all hypotheses, are open to test. They are interpretations, not observations. Proposing them does not necessarily refute allopatric speciation or vicariance (see also Ebach et al., 2003), although it does endorse the philosophy that one aim of historical biogeography is to generate an explanation as well as to discover a pattern.

GEOLOGY AND DISPERSAL

Cladistic biogeographers have invoked Earth history explanations for biotic distribution because of the overwhelming congruence between the two, on both local and global scales (e.g., Rosen, 1974, 1976, 1978, 1979, 1985), for both freshwater (e.g., Sparks & Smith, 2005) and marine taxa (e.g., Springer, 1982) and over geological time periods

(e.g., Upchurch, et al., 2002). Such interpretations have been viewed repeatedly as a neglect of, or disdain for, the phenomenon of dispersal (recently, De Queiroz, 2005). By 1978, Rosen (1978, p. 750) had dispensed with this argument in a footnote. Nonetheless, it persists, for example, in BPA coding of matrices for the analysis of “geodispersal”.

“Geodispersal” is a term, coined by Lieberman & Eldredge (1996), that refers to (Lieberman, 2000, p. 22) “... tectonically mediated events such as continental collision [that] can ... bring formerly separated faunas into contact with one another producing a pattern of congruent range expansion in several groups.” As a concept, it has been around at least since the early writings of Alfred Russel Wallace. In 1863, Wallace read a paper at a meeting of the Royal Geographical Society of London, *On the Physical Geography of the Malay Archipelago* (Wallace, 1863). Although Wallace’s understanding of Indonesian geology was rudimentary by today’s standards, and he may not have conceived of areagrams, he understood the potential for mixing of biotas on either side of what was to become known as Wallace’s Line following geological rearrangement and proposed it as a mechanism to produce composite biotas in the Philippines and Sulawesi (Wallace, 1863, pp. 232–233): “The nature of the contrast between these two great divisions of the Malay Archipelago will be best understood by considering what would take place if any two of the primary divisions of the earth were brought into equally close contact Some portion of the upraised land [between two continents] might at different times have had a temporary connection with both continents and would then contain a certain amount of mixture in its living inhabitants.”

Nonetheless, the idea of mixing biotas following geological rearrangement was considered novel by Lieberman (2000) because he interpreted it as having been rejected by cladistic or vicariance biogeographers: “Originally, it was believed that biogeographic patterns in different groups of organisms could only result from vicariance. However ... in addition to vicariance, there is geodispersal. In vicariance, congruence results from the formation of geographic barriers, while in geodispersal it is produced when geographic barriers fall” Lieberman (2000, p. 186).

“Originally” I interpret to mean in the early writings of Nelson, Platnick, and Rosen, rather than during the time of Wallace (viz. Humphries, 2004). But, these three “original” vicariance biogeographers had an explicit concept of mixing of biotas following geologic rearrangement. In what could be interpreted as an effort to implement the “... next ‘revolution in the earth sciences’ — an integrated natural history of the geological and biological systems”, Rosen (1985, pp. 652–653) discussed the history of the Caribbean biota with regard to the potential complexity of biogeographic patterns that would result from accretion and fragmentation. “Biotic mixing” here is dispersal of members of one biota into the range of another following suturing of the respective land masses, or what would later be called “geodispersal”:

... in a general cladogram of areas based on both fragmentation and accretion, land hybridizations would be represented either as reticulations ... or, as in the case of biological hybridizations, as unresolved branches representing the parent taxa and the hybrid ... One might suppose that land hybridization ... would lead to a sharing of biotas by the joined fragments, but that supposition requires the subsidiary idea, probably correct in some instances but not others, that the suture zone represents no obstacle to biotic mixing.”

Lieberman (2000, p. 83) claimed that Platnick and Nelson were opposed to dispersal in the form of range expansion as an explanation for a biogeographic pattern: "Platnick and Nelson (1978, p. 7) also invoked a geological example that produced what I have defined as geodispersal — the collision between India and Australia during the Cenozoic era — and they termed it 'biotic-dispersal.' I consider this term inaccurate and potentially confusing because the range expansion is not caused by biological factors at all ... rather it is related to geological change. Therefore, I prefer the term geodispersal."

He continued (Lieberman, 2000, p. 83): "... what is important is that the existence of the *same phenomenon* [my italics], congruent episodes of range expansion was recognized by Platnick and Nelson (1978), two of the primary architects of the vicariance biogeography approach, although they were generally virulently opposed to invoking traditional dispersal in any explanation whatsoever" Here, Platnick and Nelson's understanding of biotic-dispersal, a senior synonym of geodispersal in taxonomic parlance, is dismissed by the claim that they opposed dispersal in any form. Not so, as Platnick & Nelson (1978, p. 8) were not opposed to a notion of dispersal, but argued that it is the discovery of a pattern, shared area relationships among taxa, that is primary in historical biogeography and an explanation for a pattern, breaking apart of land masses, extinction, dispersal, and so on, that is secondary to that discovery of pattern (see Crother, 2002). Geological rearrangement resulting in biotic mixing has been proposed as an explanation for complex, composite biotas at least since Wallace (1863; see e.g., Carpenter, 1998; Carpenter & Springer, 2005). Integration of non-Hawaiian islands into the Hawaiian Islands was proposed as a mechanism for the mixing of two different biotas and as an explanation for endemism in the Hawaiian Islands (Rotondo, et al., 1981).

Interpreting evolution of the Caribbean biota required complex, reticulate areagrams, according to Rosen (1985), to incorporate adequately the complex patterns over geologic periods. Concurrently, a time control refinement for cladistic biogeography was proposed by Grande (1985) as a method to identify historical biogeographic patterns for fossil biotas from specified geologic periods. This was in response to his conclusion that summarizing complex patterns of vicariance, accretion, and dispersal for a biota in a single areagram would require the cladogram to be either reticulate or unresolved (Grande, 1985, p. 238): "The *Recent* [italics in original] biota of certain geographic areas could be the biota least likely to show a fully resolved biogeographic pattern for a given area because it may contain descendants of older endemic components ... *plus* species ... which later dispersed into the area or were introduced ... *minus* all those species which have become extinct." For the North American fish biota, Grande (1985) concluded that five Green River Eocene taxa have trans-Pacific relationships, whereas this affinity is masked among Recent taxa because of the presence of additional taxa with trans-Atlantic affinities and because of extinction of Australasian taxa. He argued that a series of areagrams, each representing a different time period, would eliminate the conflict that characterizes a single, summary cladogram. Older and younger components to general areagrams have also been dealt with by recognizing that composite areas, for example, South America, could be part of two patterns of possibly different ages

(see Parenti, 1981; Humphries & Parenti, 1986, 1999; Wanntorp and Wanntorp, 2003) despite statements to the contrary (e.g., Donoghue & Moore, 2003).

Only BPA can reconcile the differences among areagrams over geologic time periods, however, according to Lieberman (2000, 2004). In implementations of the method, geodispersal is coded as an ordered, multistate character. Range expansion of a taxon from areas A, B, and C to areas A, B, C, and D, for example, is coded as state 1 in areas A through C and state 2 in area D. The difficulty with such *a priori* coding to implement geodispersal is that the distribution of a single taxon is used to infer the mechanism or process by which it became distributed. That is, a taxon found in areas A through C at one time period that is found in areas A through D at a later time period is interpreted as having expanded its range. This might be true, but an alternate interpretation, for example, that the taxon lived in area D during the earlier time period but has not been found in that epoch, cannot be rejected. Lieberman (2000, p. 148) acknowledges this problem and appeals to completeness of the fossil record. Nonetheless, coding the state as ordered specifies a direction or episode of dispersal — an extension of Hennig's (1966) and Brundin's (1966) progression rule — rather than asks if that inferred dispersal is a hypothesis supported by the distributions of the taxa in the biota.

Coding for geodispersal also does not take into account that some nodes may be paralogous. Paralogy or redundancy in an areagram may be caused by (Nelson & Ladiges, 1996, pp. 11–12): "... tectonics, dispersal, sympatric speciation, mistaken relationships among organisms, imprecise characterizations of geographic areas, and so on." The relationship of a paralogous area conflicts with itself because of overlap or redundancy; sympatric areas are paralogous. For example, an area A may in one portion of an areagram be related to area B, and in another portion of the cladogram be related to area C because of redundancy and extinction. Neither set of area relationships, (A,B) or (A,C), conflicts with a general pattern of (((A,B),C),D), as (A,C) may result from redundancy and extinction in one portion of the biota.

Eliminating paralogous nodes identifies informative statements of area relationship. Eliminating uninformative data has been interpreted as violating the principle of parsimony and therefore as scientifically invalid (see Van Veller & Brooks, 2001). Yet, if a widespread taxon in areas A and C, above, does not mean necessarily that areas A and C share a close history, then it matters little whether there are 1, 10, or 1000 such distributions; each is equally uninformative. Interpretation of informative data, not misapplication of parsimony, is the issue. I offer another analogy. Using the number of species in a monophyletic lineage to support a biogeographic hypothesis about that lineage is analogous to using the number of specimens examined to support a phylogenetic hypothesis of that lineage. That is, coding a morphological character from one specimen or one hundred does not affect the coding of the character in a phylogenetic analysis; it may give one more confidence in the results, but no more explanatory power.

MOLECULES AND TIME

Common causes of congruent distribution patterns have been rejected outright because of the assumption that one or another taxon is too young to have been affected by Earth history events proposed to have affected another taxon (e.g., Lundberg, 1993, for fishes, Voelker, 1999, for birds; De Queiroz, 2005, for oceanic

organisms; see Nelson & Ladiges, 2001 for a historical review). Many of the reasons why it would be folly to ignore a wealth of biogeographic congruence in favor of dispersal and assume molecular data suggest the relative youth of many taxa, as advocated by De Queiroz (2005), are detailed by Heads (2005a) in a cogent review. I comment here on two applications of molecular data to historical biogeography, both from the marine realm, to warn against a rejection of biogeographic patterns using estimates of divergence times based on molecular data.

For some 60 years, coelacanth, basal sarcopterygian fishes, were believed to be represented by just one living species, the western Indian Ocean *Latimeria chalumnae* Smith, 1939. In 1997, a second population was discovered off the coast of Sulawesi, Indonesia, in the western Pacific, and described as a new species, *Latimeria menadoensis* Pouyaud *et al.* (1999). Systematic ichthyologists, a paleontologist (Forey, 1998) and a neontologist (Springer, 1999), predicted that the two populations would be found to be distinct based on several factors, including the widespread distribution of the populations, present-day ocean current patterns, the narrow habitat of the deep-sea, lava-tube dwelling coelacanth and the prevailing understanding of the geological history of the Indo-Pacific region. At first, independent studies using partial mitochondrial gene sequences estimated that the two species diverged from each other between 6.3 and 4.7 Mya (Holder *et al.*, 1999) or as recently as 1.3 mya (Pouyaud *et al.*, 1999). The latter authors equivocated about the type and amount of molecular differentiation between the two populations, but nonetheless described the Sulawesi population as a new species, effectively proposing a hypothesis that the differences between the two populations would be corroborated. A third estimate of divergence time of 40 to 30 mya, based on whole mitochondrial genomes (Inoue *et al.*, 2005) is more in line with Springer's (1999) hypothesis that the collision of India with Eurasia 50 mya bisected the widespread, ancestral range of the coelacanth and, therefore, with the hypothesis that there are two living species. Coelacanth species may be younger or older than the inferred collision of India with Eurasia, or that event may not have caused separation of the ancestral population (*viz.*, Heads, 2005a, b). Estimate of the species' divergence times compared with an estimate of the timing of a major geological event, however, may be used to formulate a hypothesis of the evolution of living coelacanths that incorporates our best, current understanding of speciation and of geology. That there are three different estimates of divergence times based on the application of molecular sequence data is but one indication of how questionable still are these methods, in large part because of their reliance on fossils for calibration (see also Graur & Martin, 2004).

Astralium rhodostomum (Lamarck) is a wide-ranging, reef-dwelling, Indo-west Pacific turbinid gastropod with a short planktonic larval stage (Meyer *et al.*, 2005). Mitochondrial DNA evidence supports an interpretation that the species complex comprises two widespread, overlapping, deeply divergent clades with a high degree of endemism. There are hypothesized to be at least 30 geographically isolated clades throughout islands and island groups ranging from Phuket and Cocos Keeling in the Indian Ocean to Rapa in the western Pacific (Meyer *et al.*, 2005, Figure 1). This high level of diversity and endemism has been viewed as expected for terrestrial species throughout the region, but not for marine taxa which are generally interpreted as having wide-ranging species throughout the Indo-west Pacific that have been distributed by long-range dispersal (Meyer *et al.*, 2005). Notable exceptions to this interpretation come from Springer

(1982), who documented the coincidence of species limits with tectonic plate boundaries for fishes and select other marine taxa, and Gill (1999) and Gill and Kemp (2002), who hypothesized that many currently recognized widespread marine fish species comprise two or more allopatric, cryptic species with endemic distributions.

The two clades of *Astralium rhodostomum*, Clade A and Clade B (Meyer *et al.*, 2005, Figure 3), each repeat in four areas: Ryukyu, New Caledonia, Marianas, and Tonga, Samoa, Niue, and Fiji. The last group, Tonga, Samoa, Niue and Fiji are sister areas in both clades and therefore treated as one area here. The areagram for Clade A is reproduced, along with that portion of the areagram for Clade B that includes the repeated areas (Figure 2.3a and 2.3b).

Each areagram is completely resolved. The shared information in each can be extracted easily either through reduced area-cladograms or three-area statements analysis (Nelson & Ladiges, 1996). There are four three-area statements specified by the areagram for Clade A, and three three-area statements for Clade B (Figure 2.3c and 2.3d). There is one three-area statement common to both (Figure 2.3d), which specifies a set of area relationships that the two clades share. Therefore, not only is there a high degree of endemism in the overlapping clades, but a repeated, inferred shared, history. Molecular data have the potential to unravel additional fine-scale patterns of relationship among endemic areas, especially throughout the marine realm where they have not been expected.

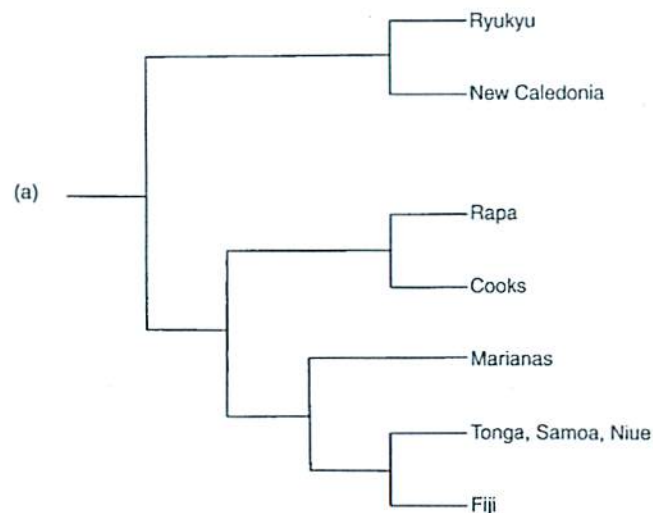


FIGURE 2.3 (a) *Astralium rhodostomum*, Clade A areagram (following Meyer, Geller, and Paulay, 2005, Figure 3). (b) Clade B, groups B1 and B2 areagram. "Philippines" comprises Palawan and Central Visayas; "Eastern I-A Archipelago" comprises: Papua New Guinea/Queensland, Sulawesi, Manus, and New Britain. (c) The four three-area statements specified by the areagram for Clade A. (d) The three three-area statements specified by the areagram for Clade B, groups B1 and B2. There is one shared three-area statement, starred and shaded in Figure 2.3c and 2.3d.

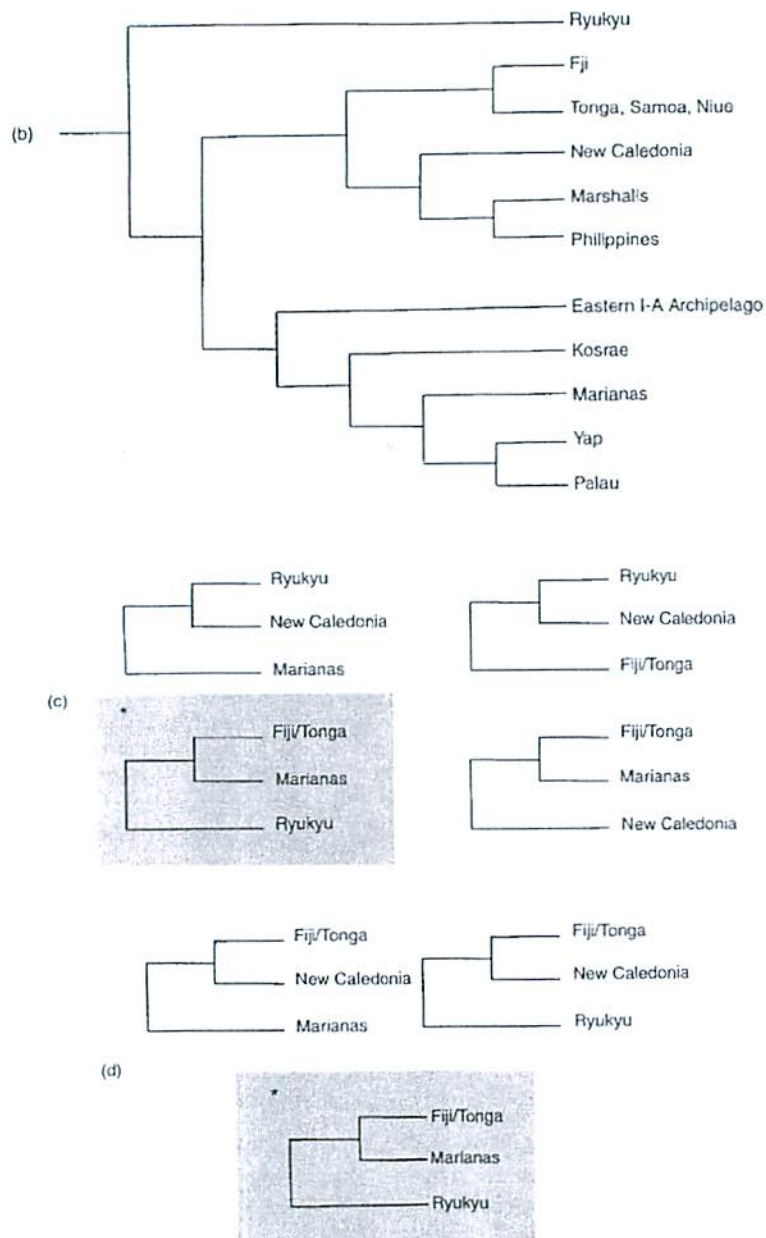


FIGURE 2.3 (Continued)

GLOBAL BIOGEOGRAPHIC PATTERNS VS. BIOGEOGRAPHIC REALMS OR REGIONS

Nearly 150 years ago, Sclater (1858) divided the world into six terrestrial biogeographic regions to describe the distribution of birds: Nearctic, Palearctic, Neotropical, Ethiopian, Oriental, and Australian (see Humphries & Parenti, 1999, Figure 1.9). These were considered useful by Wallace (1876) to describe the world's fauna and have been so used ever since, despite the fact that it has been known for as long that they omit some of the most distinctive and intriguing patterns of plant and animal distributions: pantropical and antitropical distributions. In 1866, Murray published a lavishly illustrated monograph on the distribution of the world's mammal fauna (Murray, 1866). Murray's map 53 colorfully outlines the antitropical distribution of whale bone whales, map 51 the pantropical distribution of Sirenia. South and Central America has been considered nearly synonymous with the Neotropical region despite its composite biota, part tropical and part austral, part Ostariophyan and part austral Salmoniformes, according to Rosen (1974, Figure 45). Repeatedly, historical biogeographic analyses recognize the "two South Americas" (Parenti, 1981; Humphries & Parenti, 1986, 1999; Carpenter, 1993; Arratia, 1997; Vari & Weitzman, 1990), and Nelson & Ladiges (2001) imply "three South Americas": trans-Pacific, trans-Atlantic, and austral. Further, the unjustified separation of marine and freshwater taxa in biogeography has led to description of at least eight marine regions in addition to Sclater's six classic regions (see Mooi & Gill, 2002). A reclassification of global biogeographic regions is long overdue.

Panbiogeographers (Croizat, 1958, 1964; Craw et al., 1999) have argued for a classification of the world's biotic regions centered on ocean basins, not continents, to reflect the composite nature of continental biotas. Other biogeographers have agreed (e.g., Parenti, 1991; Morrone, 2002; Humphries, 2004). The relationships among these areas has been interpreted by Humphries and Parenti (1986, 1999) and Nelson and Ladiges (2001, Figure 8) who proposed a cladistic summary of Croizat's (1958, Figure 4a) and Craw et al.'s (1999) global distribution patterns. These patterns endlessly repeat, and extinction has pruned them (Figure 2.4b). Nonetheless, if they are to be useful, patterns must have explanatory and predictive power. This may be demonstrated for the atherinomorph Scomberesocidae, a family of epipelagic marine fishes distributed broadly in temperate and tropical oceans (Hubbs & Wisner, 1980). Scomberesocids have been classified in four genera, *Scomberesox* and its miniature sister genus, *Nanichthys*, and *Cololabis* and its miniature sister genus, *Elassichthys*. Their relationships and distribution pattern (Figure 2.5) reflect the global pattern (Figure 2.4a), with some pruning. *Nanichthys*, in the tropical Atlantic and Indian oceans is sister to *Scomberesox* in the North Atlantic and in austral seas. *Cololabis* is boreal in the northern Pacific; *Elassichthys* is tropical in the eastern central Pacific. Such patterns can be used to make predictions about where closely related taxa may be found: 'is there an austral *Cololabis*?', for example.

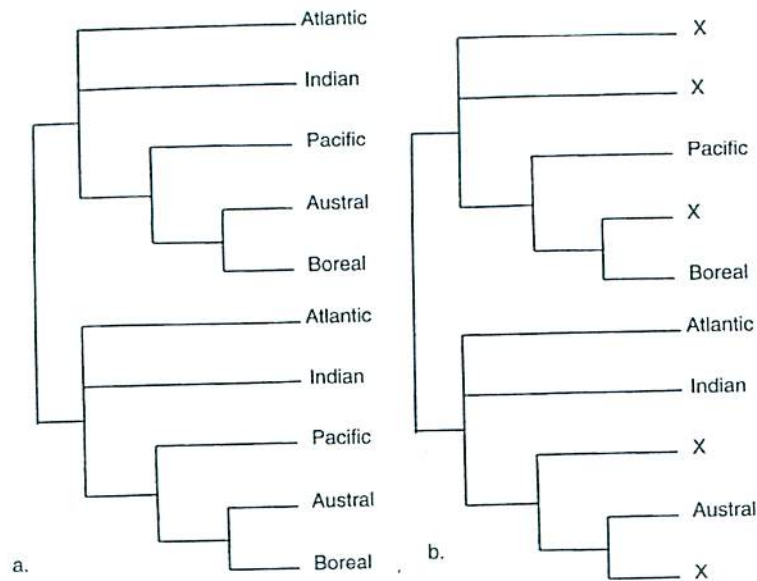


FIGURE 2.4 (a) Cladistic summary of Croizat's (1958) and Crow, Grehan, and Heads's (1999) global distribution patterns, from Nelson and Ladiges (2001, Figure 8), drawn to demonstrate repetition. (b) The pattern of 2.4b pruned by hypothesized extinction events marked by an X.

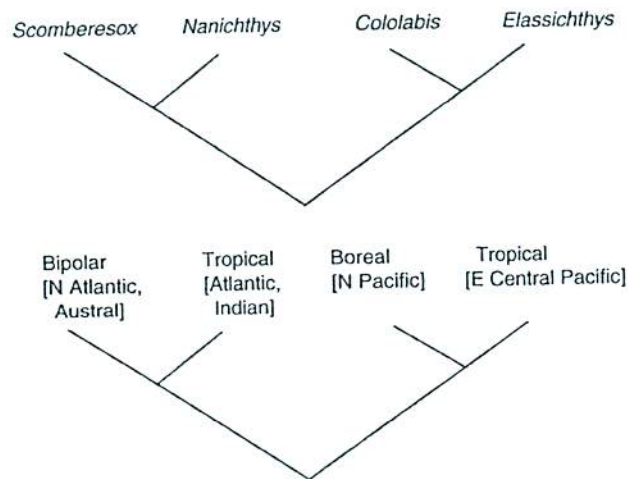


FIGURE 2.5 Classification of the genera of the epipelagic marine atherinomorph fish family Scomberesocidae, following Hubbs and Wisner (1980), expressed in a taxon cladogram, above, and areogram, below.

CONCLUSIONS

Incorporating center of origin explanations into the methods of historical biogeography has resulted in the generation of untestable hypotheses rather than the discovery of testable patterns. The principle of a center of origin was part of the early formalizations and implementations of historical biogeography (e.g., Nelson, 1969), but subsequently rejected (Croizat *et al.*, 1974; Nelson, 1974). Discovery of patterns is primary in biogeography — identifying the mechanism by which the pattern was produced is secondary. This was stated clearly in early formalizations of vicariance biogeography (e.g., Platnick & Nelson, 1978), but it has been misinterpreted or ignored. These and many of the other papers cited here are reproduced in the immensely valuable volume by Lomolino *et al.* (2004), which makes them more accessible and available for study and interpretation of methodological developments.

Many intriguing biogeographic patterns remain to be discovered based on analysis of phylogenetic relationships using morphology and molecules, on specimens collected through field exploration, or on revision of museum and herbarium collections. Molecular estimates of divergence times are as yet unable to reject the ancient differentiation of lineages as predicted from biogeographic patterns. Recognition of a high degree of endemism among marine populations is one example of how molecular data can be used to demonstrate diversity over broad geographic scales.

Global biogeographic realms/regions that have been used uncritically for over 150 years need to be replaced to recognize realistic, definable, repeatable areas. They should incorporate both terrestrial and marine components, hence, ocean basins (*viz.* Croizat, 1958). They need to incorporate major biogeographic patterns such as pantropical and antitropical distributions and acknowledge that continental biotas are composite. This will be the start of the "revolution" in biogeography that is long overdue.

ACKNOWLEDGEMENTS

I am grateful to Malte Ebach and Ray Tangney for inviting me to participate in the Fifth Biennial Conference of the Systematics Association where a version of this paper was presented. Chris Humphries and Dave Williams kindly read and commented on a previous manuscript that incorporated some of the ideas expressed here. Gary Nelson provided references.

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