Crosscurrents in Biogeography

Vicariance Biogeography. A Critique. Papers from a symposium, May 1979. GARETH NELSON and DONN E. ROSEN, Eds. Columbia University Press, New York, 1981. xviii, 594 pp., illus. $35.

As symposium proceedings go, this one is a tour de force. Its almost 600 pages contain an astonishingly rich and concentrated mix of fact, opinion, theory, and polemics. Nearly all its 41 contributors (this includes the discussants) state their opinions and the reasons for them clearly and persuasively. Readers should consider themselves jurists in what will be a long-drawn-out case. Their task is much harder than merely deciding which side is the winner in the "vicariist" versus "dispersalist" debate, for there appears to be a five-sided (at least) debate in progress. Before considering the sides it is necessary to define the two simple, contrasted theories at the root of it all. Assuming that range disjunction (allopatry) is nearly always the precursor of evolutionary differentiation, dispersalists suppose that disjunctions arise through long-distance dispersals that occur separately and independently in individual taxa; the dispersing organisms are mobile. Vicariists suppose that, on relatively few occasions, simultaneous disjunctions have arisen in all the taxa of a region as a result of abiotic "vicariance events"; the most important vicariance events are the ruptures and separations of tectonic plates, on which organisms are immobile passengers.

The first team of contenders in the five-sided debate mentioned above are a comparatively well-mannered lot. They regard pure dispersal theory and pure vicariance theory as the end points of a continuum (Solem), and when they differ among themselves it is chiefly in their position along the continuum. They would all presumably agree with Tattersall that "to dichotomize biogeographical studies into vicariance versus dispersal would be fatuous." Erwin emphasizes that dispersal and vicariance are both necessary if evolutionary diversification is to take place. "Dispersal promotes cosmopolitanism, not isolation," he writes; then, once a taxon has become widespread because of dispersal, it is possible for a vicariance event to interrupt the dispersal and create allopatry. Erwin seems to be appealing to the two sides in the dispersalist-vicariist battle to make peace because both are right. However, this attempt to pour oil on the waters misses the point. It fails to distinguish between two fundamentally different forms of dispersal, which are so different that for clarity they should have different names. I use the self-explanatory terms "diffusion" and "jump-dispersal" (E. C. Pielou, *Biogeography*, 1979). Vicariists don't dispute the universality of diffusion; what they do argue is that jump-dispersals, unaccompanied by vicariance events, play a negligible role in evolutionary diversification. Failure to discriminate between diffusion and jump-dispersal makes many discussions fuzzy; Slater, for example, criticizes Brundin on this point.

Other players on the first team (they play on other teams too) include Haffer, Hallam, Koopman, Niklas, Prance, and Wolfe. Niklas gives an interesting discussion of the different evolutionary modes of plants and animals, a topic biogeographers too often overlook. Koopman makes the elementary mistake of assuming that any jump-dispersal, however improbable, "given a long enough time . . . becomes very probable." Wolfe, and also Prance, consider the need to ensure a match between the taxonomic rank (hence age) of a pair of vicariads and the time of their disjunction. According to Wolfe, angiosperm diversification came too late for it to be explained by the breakup of Pangea; the generic and specific disjunctions between Africa and South America are at too low a taxonomic level for the breakup of West Gondwana to account for them.

The second team in the five-sided debate consists of uncompromising vicariists who do not concede that their theories differ only in degree from those of the first team. Their leader is Croizat, who revels in his role as enfant terrible, describes Darwin's writings as "piffle," and is entertainingly shocking throughout. The rest of the team are much more solemn. Their favorite word is "paradigm." According to Schuh, the dispute between vicariists and dispersalists is between people whose methods are, respectively, hypothetico-deductive and ad hoc or inductive; thus the dispute "involves different philosophies of science." One is not allowed to sit on the fence; for example, Springer takes Solem to task because "nowhere in his paper does he clearly make a case for or against either paradigm." The uncompromising vicariists seem adamant in the belief that if you reject vicariance as the explanation of some disjunctions then you reject it for all. They appear to think they alone are scientifically rigorous. And they are sticklers for method. Brundin (who would not wish to be lumped with the vicariists since he proposed a vicariance/dispersal paradigm) insists on "rules" and "laws." Parenti is obsessed with parsimony.

Patterson describes two important vicariist methods. The first of these is the Croizat-Rosen method of looking for "generalized tracks" and the second that of comparing taxonomic cladograms with area cladograms. In my opinion neither method stands up to close scrutiny. Take the first: a "track" is a line linking the geographic ranges of a pair of vicarious (sister) taxa, and a generalized track is a sheaf of roughly (how roughly?) coincident tracks. But nobody has explained how to define, uniquely, the one appropriate line of the infinitely many lines that can be drawn so as to link two areas. The second method (also discussed by Platnick) is that of searching for congruent taxonomic and area cladograms. The results would be convincing only if museum taxonomists were to construct taxonomic cladograms without being aware of the geographic sources of the specimens they were examining.

The preoccupation of this team with their methods also emerges in Patterson's remark that "fossils are of subsidiary importance in vicariance biogeography but of cardinal importance in dispersal biogeography" and Platnick's restrictive definition (p. 149) of what vicariists attempt to discover. They imply that results obtained by other methods are no concern of theirs and fail to notice that to pick the evidence they want and reject the rest hardly squares with scientific rigor.

The third set of entrants in the debate is made up of people who accept vicariist theory, with plate tectonics as the mechanism, but who espouse their own, heterodox, paleogeography. Its chief feature is a paleocontinent, Pacifica, whose fragments now form part of the Pacific rim. Supporters of Pacifica are Melville and, independently, Nur and Ben-Avraham. Their discussants, and also Hallam, are unenthusiastic; Haugh regards Pacifica as geologically impossible. Whether this bodes well or ill for the theory who can say? New theories often

become popular because their very unpopularity lures mavericks. An interesting comment by McKenna (in discussing Melville's paper) and by Tedford (in discussing Nur and Ben-Avraham's) is that small continental blocks would soon slide below sea level as they drifted away from the rift sundering a once-united Pacifica; a mid-ocean ridge must have formed at the site of the rift, with the ocean floor sloping down on either side. Millions of years would have passed before the blocks emerged as dry land at the periphery of Panthalassa, by which time all air-breathing passengers on the blocks would have breathed their last.

In the fourth team of debaters I put those biogeographers who regard vicariance as fundamentally important but who acknowledge the existence of many kinds of vicariance events and do not, like devout vicariists, consider only the vicariance caused by drifting tectonic plates. Hallam, and also Howden, stress vicariance events caused by pre-Quaternary eustatic changes in sea level. Rising and falling epicontinental seas alternately separated and united terrestrial habitats while they simultaneously united and separated shelf habitats. Hallam presents a splendid (and believable?) table correlating stratigraphic subdivisions, age, plate-tectonic events, eustatic events, and biotic consequences (it prompts McKenna to accuse him of laying down the law). He comments, too, on the range expansions that warmth-loving plants presumably underwent in epochs of equable climate; not discussed, however, is the vegetation in high latitudes at times when atmospheric circulation continually brought warm air masses into places experiencing long, dark winter nights.

Vicariance events can be on enormously varied scales, as Solem remarks; events as small as beating a path through the bush or as great as the breakup of Pangea may cause vicariance. Haffer deals with the effects of fluctuating climate on the vegetation mosaic, and hence the avifauna, of the Amazon basin; shrinking grassland refugia in a sea of forest alternated with shrinking forest refugia in a sea of grassland; as well, erosion led to fragmentation of upland habitats. As Tattersall says, "The fragmentation of ranges into refugia is a vicariant [*sic*] event par excellence." Unfortunately nobody discusses habitat fragmentation due to isostatic sea level changes in the Quaternary. It will be interesting to see whether dedicated, card-carrying vicariists, whose basic tenet is that "general patterns of distribution exist as a result of the forces of earth history" (Schuh, p. 233), will dilute the satisfying grandeur of the concept by admitting the importance of second-order vicariance events. A demand that biogeographic conclusions be "satisfying" (Schuh, p. 231) suggests a preoccupation with aesthetics rather than scientific truth.

The fifth team are at one in their attempts to devise and apply objective tests to biogeographic hypotheses. They wrangle among themselves on how this should be done, but at least they try; thus they do more than merely pay lip service to the need for falsifiable theories in biogeography. Simberloff, Heck, McCoy, and Connor, in a joint paper, describe tests for simple null hypotheses in two contexts: (i) they derive the expected number of species common to two islands, on the hypothesis of random colonization from a common species pool; and (ii) they derive the probability distributions of distinguishably different cladograms, given various null hypotheses. Their discussants take issue with them on several points. Terborgh, discussing the first context, argues that a random-colonization hypothesis is unrealistic. This is probably true, but the trouble with a realistic hypothesis is that if a test leads to its "acceptance" (actually, "non-rejection") the probability of error is unknown. Farris makes this point clearly and emphatically. He also discusses the second context and the arbitrariness that is unavoidable when one must choose among competing null hypotheses. The discussion neatly demonstrates how strongly dependent on assumptions, as well as on data, conclusions always are. At any rate, Simberloff and co-workers make a valiant attempt to unite, if only in methods of approach, the disparate fields of island biogeography and historical biogeography.

The symposium proceedings conclude with a summary by Nelson, in which he presumes to correct "well intentioned authors who nevertheless mislead" and to instruct "well intentioned readers who nevertheless misconstrue." The condescension is breathtaking. However, dyed-in-the-wool vicariists would be wise not to make their views absolutely clear to the rest of us, for if they do they will have to give up the ploy of fending off criticism with the complaint that their critics haven't really understood them.

My own conclusion after reading the book is that the vicariists have not succeeded in making their case and that an explanation for any given disjunction is more likely to be obtained by commonsense investigation than by abstract theorizing. For instance, why has the test for vicariance versus dispersal proposed by Edmunds (p. 296) been so little used? Concerning angiosperm disjunctions, he argues that associated and coevolved organisms would be expected to share a disjunct pattern if the disjunction were caused by vicariance but not to share such a pattern if it were caused by dispersal. Edmunds gives one example of each of these two types of disjunction; there seem to be few parallel examples in the literature, which is surprising.

The last word should go to McKenna. He pleads (p. 336) for greater "interchange and synthesis among the so-called subjects of botany, zoology, and geology" so that all three pursuits lead to congruent results. To that I say "Hear, hear."

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Elementary Particles

Quarks and Leptons. Proceedings of an institute, Cargèse, Corsica, July 1979. MAURICE LÉVY, JEAN-LOUIS BASDEVANT, DAVID SPEISER, JACQUES WEYERS, RAYMOND GASTMANS, and MAURICE JACOB, Eds. Plenum, New York, 1980. xvi, 720 pp., illus. $75. NATO Advanced Study Institutes Series B, vol. 61.

In recent years we have witnessed the discovery of several new species of elementary particles and the birth of elegant field theories of weak, electromagnetic, and strong interactions. As experiments have probed smaller distances, their findings have inspired rapid theoretical progress. Now, with a new generation of very-high-energy accelerators being readied for operation, further exciting discoveries are being anxiously awaited. The proceedings of the 1979 Cargèse summer institute, *Quarks and Leptons* presents a collection of up-to-date reviews that provide good introductions to some areas of current experimental and theoretical work.

A particularly nice discussion of quantum chromodynamics (QCD), the field theory of strong interactions, is presented by J. Ellis and C. T. Sachrajda. They emphasize the perturbative high-energy successes and predictions of QCD. I found their paper basic enough to serve as a self-contained introduction for students yet detailed enough to be a useful reference for workers in the field. Additional aspects of QCD are described in the experimental papers by H. Bøggild, J. M. Gaillard, and F. Muller, which