Historical Biogeography: An Alternative Formalization

In an attempt to formalize the procedures of Hennig (1966) and Brundin (1966; also Ross, 1974), I argued that, given distributional data for a certain group of descendant species, ancestral distributions could be estimated and episodes of dispersal resolved (Nelson, 1969). Having considered the arguments of Croizat (1964 and other papers), I now believe that dispersal is not realistically resolvable by that formalization. Consider an example of an ancestral species (A) whose range extends over what will become two geographic areas, e.g., continental South America and Africa (Fig. 1). Suppose (1) that a geographic barrier appears within South America and subdivides ancestral species A into two descendant populations: A1 in southwestern South America, and A2 in eastern South America and Africa; (2) that another geographic barrier subsequently appears between South America and Africa, and subdivides population A2 into two descendant populations: A2a in eastern South America and A2b in Africa; and (3) that the three resulting descendant populations (A1, A2a, A2b) differentiate to the point where they might be recognized as species (or monophyletic taxa of whatever rank) and their kinship correctly interpreted. Given the distribution of the three descendant species (A1 in southwestern South America, A2a in eastern South America, A2b in Africa), an attempt to estimate ancestral distributions according to my previous formalization results in propositions (1) that ancestral species A was exclusively South American, (2) that ancestral species A2 occurred both in South America and Africa, and (3) that dispersal (range extension or migration) occurred from South America to Africa, after the splitting (vicariance) of ancestral species A, but before the splitting of ancestral species A2 (Fig. 2, above). With reference to the details of this hypothetical example,1

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1 For a concrete example, see Chardon's (1967) consideration of the geographic history of catfishes, which he believes had their center of origin in South America (also Gosline, 1972).

2 Resolving dispersal when none occurred might be termed a "Type-I error"; not resolving dispersal when dispersal did occur might be termed a "Type-II error." Type-I errors seem to be far more common in biogeography.
recognized, since the theory of hologenesis of Rosa (1918), and has been elaborated in great detail by Croizat in numerous publications during the period 1952–1974 (Nelson, 1973).

I suggest, therefore, that for a given group the distribution of ancestral species can be estimated best by adding the descendant distributions (Fig. 2, below). "Eliminating the unshared element" (Nelson, 1973:314) comes close to assuming that dispersal must occur with the speciation process—an assumption that may be rejected as too restrictive, unnecessary and unrealistic: estimation of ancestral distributions may be considered simply additive (hologenetic). If so, may episodes of dispersal—which no doubt have occurred—be resolved by more efficient means? In the

Fig. 1.—The splitting (vicariance event) of an ancestral species (A) into descendant species A1 and A2, and the subsequent splitting of A2 into descendant species A2a and A2b.

Fig. 2.—Three species (A1, A2a, A2b), their distributions (S.A., S.A., and Af., respectively), and alternative interpretations of the distributions of hypothetical common ancestral species (A, A2). Above, an interpretation that resolves dispersal (arrow, from S.A. to Af.), when no dispersal occurred. Below, an interpretation that does not erroneously resolve dispersal.
manner of Croizat, I suggest that estimation of ancestral distributions must ultimately be reconciled with the history of the biota of which a given analyzed group of species is a part, and that the resolution of dispersal, as evidenced by the general phenomenon of sympatry, is more efficiently accomplished in the context of that synthetic approach (Croizat et al., 1974). I suggest, finally, that my previous formalization—and the procedures of Hennig, Brundin, and Ross—may still have merit, not in estimating ancestral distributions, but rather in estimating where barriers appeared, barriers that caused the splitting (vicariance) of ancestral species. In the above example, therefore, one may estimate that the barrier responsible for the splitting of ancestral species A appeared within South America, and that the barrier responsible for the splitting of ancestral species A2 appeared between South America and Africa.

Estimating where a specific barrier appeared is a step toward localizing and identifying a specific barrier as the cause of a specific vicariant pattern, as, for example, the formation of the Panamanian isthmus has been identified as the cause of the eastern Pacific-western Atlantic vicariance displayed by many shallow-water marine groups. If a specific barrier can be identified, and its time of formation determined (as e.g., Upper Oligocene as the time of formation of the Panamanian isthmus), its time of formation is an estimate of the time of origin of the specific vicariance occurring in relation to the barrier. Its time of formation is, also, an estimate of the absolute time of splitting of the evolutionary lineages displaying that specific vicariance (Hennig, 1948, 1966).

Estimating the time of splitting of lineages through a study of vicariance in relation to dated barriers is an alternative to the traditional approach through paleontology, which tends to underestimate the absolute age, or age of origin, of lineages. It is an alternative, also, to molecular and immunological approaches, which are based on the disputed assumption of constant rates of molecular evolution.

Two considerations emerge immediately from the vicariance approach: (1) that the various populations isolated by a specific barrier will evolve at different rates, such that their descendants, through the vagaries of taxonomic procedure, might be classed as different subspecies, species, subgenera, etc.—all with the same absolute time of origin, and (2) that the known fossil record of the lineages displaying a particular vicariance will vary in completeness, such that some or most of the lineages actually dating from the time of formation of the barrier that caused their vicariance might be unrepresented in the known fossil record, and that few if any lineages would be represented from their time of origin. The above considerations suggest two conclusions: (1) that, as represented in traditional classification, discrepancy of taxonomic rank among lineages displaying a given vicariant pattern is evidence of different rates of evolution—not temporally different origins, and (2) that, as represented in the known fossil record, discrepancy in the known minimum ages among lineages displaying a given vicariant pattern is evidence of sampling variability of the fossil record—not temporally different origins.

In summary, I reject as aprioristic all "clues" or "rules" used to resolve centers of origin and dispersal without reference to general patterns of vicariance and sympathy (Croizat et al., 1974). With many others, I include as a rejectable apriorism Hennig's "Progression Rule" (Ashlock, 1974). Unencumbered by aprioristic dispersal, historical biogeography is the discovery and interpretation, with reference to causal geographic factors, of the vicariance shown by the monophyletic groups resolved by phylogenetic ("cladistic") systematics.

REFERENCES


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