

## MORE ON WEST INDIAN ZOOGEOGRAPHY

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GUYER AND Crother (this issue) have offered some additional comments in defense of two points that I raised in my recent response (Hedges, 1996b) to their critique (Crother and Guyer, 1996). Although it is tempting to view this debate as differences of opinion, it in fact involves basic differences in methodology. Here I will address their additional comments and illustrate the major error in their method of analysis.

The first and most important point involves divergence times estimated from molecular data that were used to address the origin of the West Indian taxa. We selected the island/mainland comparisons based on **phylogeny** so that the estimated time could correspond to either vicariance or dispersal (Hedges et al., 1992). In their re-analysis, Crother and Guyer (1996) acknowledged that they did not consider phylogeny but instead chose the **oldest dates among all available divergence times**. Unfortunately, besides being explicitly biased (vicariance was their null hypothesis), such a method is unable to distinguish between vicariance and an unrelated lineage-splitting that occurred on the mainland (Fig. 1). In my response (Hedges, 1996b), I used the gecko example (*Sphaerodactylus*) from our original study to show how their method fails and why it is important to consider phylogeny.

Crother and Guyer (1996) suggested that

we used a method of data selection that biased our results in favor of dispersal, but that is incorrect. We selected "the most recent divergence event between the **lineages** examined" (Hedges et al., 1992) and not the "most recently derived sister taxa" (Guyer and Crother, this issue). If we had done the latter, then we would have inferred, for example, that West Indian anoline lizards arose only 3-5 million years ago (mya) because that corresponds to the separation of *Anolis porcatus* from Cuba and *A. carolinensis* from North America (Buth et al., 1980). Even given that anole relationships are controversial, no one disputes that a green anole clade (*carolinensis* series) is only one of many distinct lineages in the West Indies and thus phylogeny dictates that such a comparison would be inappropriate.

Our early Miocene date for anoline lizards was from a comparison between representatives of a mainland clade and a major clade in the West Indies (Shochat and Dessauer, 1981). Even using Crother and Guyer's method, the largest estimated divergence time between a West Indian and mainland species of *Anolis* still is only Oligocene (Hass et al., 1993), much too recent for vicariance. Moreover, an Oligocene-Miocene divergence time is compatible with the presence of fossil anoles in Dominican amber during that time period (Hedges, 1996a). Likewise, our divergence

time for the endemic West Indian lizard genus *Cyclura* was based on the assumption that *Cyclura* is monophyletic and that *Iguana* is a close relative, if not the closest relative, on the mainland (e.g., Norell and de Queiroz, 1991). Our other comparisons were similarly guided by phylogeny.

The second point raised in the preceding commentary (Guyer and Crother, this issue) involves intra-Caribbean biogeography and therefore is not directly relevant to the origin of the West Indian fauna. Guyer and Crother (1996) performed a cladistic biogeographic analysis that attempted to distill a common pattern of area relationships based on 11 phylogenies of animal groups that occur in the West Indies (Crother and Guyer, 1996). Although their analysis was far from comprehensive, my primary criticism was that the resulting consensus pattern of area relationships (((southern Hispaniola, Hispaniola) Puerto Rico) Cuba) Jamaica), oddly, was present only in one of the constituent trees, that of some xenodontine snakes. Moreover, the data used to construct that tree are available only in an unpublished dissertation (B. I. Crother, University of Miami, 1989).

In response, Guyer and Crother (this issue) removed both trees taken from Crother's dissertation and claimed that their new analysis yielded the same consensus pattern of area relationships. But now I have even greater doubt when a consensus pattern claimed to be significant is not found in any of the constituent trees. And this is not a simple case of missing taxa (= areas). The input trees used by Crother and Guyer (1996: their Fig. 4) have major internal conflicts, such as: (((((Jamaica, Cuba) Hispaniola) ((Hispaniola, Puerto Rico) Hispaniola)) (Hispaniola, Cuba)) Puerto Rico) versus ((((((Cuba, Hispaniola) Jamaica, southern Hispaniola)) Hispaniola) Cuba) Puerto Rico) Cuba) versus (((((Hispaniola, Puerto Rico) Hispaniola)(Puerto Rico, Jamaica)) Hispaniola) Cuba), to mention just three of those trees. The fact that islands appear multiple times in a single tree suggests dispersal, and this is supported by reference to some of the original studies, the fossil record, and molecular data for

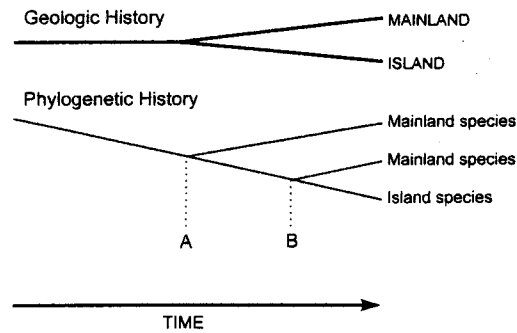


FIG. 1.—Method of Crother and Guyer (1996) to infer an origin by vicariance for groups of amphibians and reptiles in the West Indies. All available pairwise divergence times are used (for simplicity, only two times are shown here) and phylogeny is not considered. Any divergence time "as old as or older" than the geologic divergence time fails to reject vicariance (Crother and Guyer, 1996:449). In this example, because divergence time A corresponds to the known time of land separation, vicariance is supported under their model. However, when phylogeny is considered, that assumption is shown to be incorrect because the divergence at time A was between two lineages on the mainland and not relevant to the geologic event. The actual biogeographic event was dispersal at time B.

those groups. The issue here is not whether congruence exists among any phylogenies of West Indian taxa; I have shown elsewhere that West Indian terrestrial vertebrate taxa have a strong South American influence probably attributable to water current patterns (Hedges, 1996a,c). I only question the usefulness of this particular analysis performed by Crother and Guyer given the striking disparity between the input phylogenies and their output consensus tree.

Vicariance has played a major role in shaping the evolutionary history of organisms, including perhaps the ordinal diversification of birds and mammals (Hedges et al., 1996). Also, the possibility remains that some West Indian groups (e.g., *Eleutherodactylus*) originated by vicariance in the late Cretaceous (Hedges, 1996a,c). But the point of our original study (Hedges et al., 1992), supported in expanded analyses (Hedges, 1996a,c), was to show that enough information is at hand to implicate over-water dispersal as the major agent in the origin of West Indian vertebrates.

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