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## ADDITIONAL COMMENTS ON THE ORIGIN OF THE WEST INDIAN HERPETOFAUNA

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IN HIS response to our recent essay (Crother and Guyer, 1996), Hedges (1996a) took issue with each of our major points. Because biogeography represents the ultimate puzzle in biology, it is not surprising that such polar positions could be taken by scientists examining the same data. Our major point was that the sampling regime used by Hedges and his colleagues to assess the roles of vicariance and dispersal in the

Caribbean was biased and, therefore, incapable of arbitrating between these two explanations. As an aid to readers interested in sorting our differing views, we add the following observations associated with specific points raised by Hedges.

Hedges (1996a) complained that we missed significant literature dealing with molecular evolution of Caribbean taxa. In our defense, we note that virtually all of

the references, listed by Hedges as missing from our paper, are present in the citations associated with our text.

Hedges argued that our statistical treatment of a clearly identified pool of immunological data was unnecessary because the appropriate data are the most recently derived sister-taxa that can be found for pairs of sites. This observation by Hedges crystallizes our differing views and, we think, illuminates flaws in methods and logic used by Hedges et al. (1992) and repeated by Hedges (e.g., 1996*b*). The sampling universe now described by Hedges does not reflect pairs of taxa that appeared in Hedges et al. (1992), especially for mainland-island comparisons. Because phylogenies clearly identifying sister taxa for Caribbean taxa are not available, one could not expect to design a sampling protocol for the pool now described. We argue that the sampling pool that we outlined appropriately mimics the one implied by Hedges et al. (1992:Table 1) and, therefore, that immunological distances besides the ones listed by those authors must be considered. The observation that a fossilized anole is known from the Caribbean [Rieppel (1980); upper Eocene (40–36 ma), but may be as young as 30–17 ma (Grimaldi, 1995)] that is older than the divergence events selected by Hedges et al. (1992; 16.8 ma; Table 2) to describe the origination of that lineage within the Greater Antilles provides further support for our contention that immunological data associated with older divergence events must be considered. Hedges and his colleagues admitted that the fossil evidence was problematic but failed to recognize its impact on their sampling universe.

Hedges (1996*a*) claimed that no consistent pattern exists among published phylogenies of Caribbean taxa. Additionally, he asserted that our attempt to extract such a pattern merely reflected the inclusion of currently unpublished data on xenodontine snakes (Crother, 1989). Because the quality of data used to create some published phylogenies has been questioned (e.g., Hass, 1991; Page and Lydeard, 1994), we attempted to include only studies that were at least minimally defensible. Again,

we clearly identified the pool from which we sampled, used a currently recognized analytical tool (Brooks and McLennan, 1991) to describe an overall pattern, and provided a crude test of the significance of that pattern. The same pattern is recovered from our sample of phylogenies when the study by Crother (1989) is eliminated. This pattern is demonstrably non-random, illustrating how easily one's eyes can cause one to conclude, falsely, that phylogenetic trees lack pattern (see also Simberloff, 1989).

Because dispersal between a pair of sites can occur in either direction and at any time, the method championed by Hedges cannot be used to arbitrate between islands containing taxa originating exclusively by overwater dispersal [or nearly so, according to Hedges (1996*b*)] from islands containing taxa originating via vicariance followed by occasional dispersal to and from those islands. We do not believe that Hedges or his collaborators have addressed this point adequately nor do we believe that they can, given the well known problems with determining directionality for dispersal events and determining history from two-taxon statements (Rosen, 1978).

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## 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 porcatius* 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