

## VICARIANCE AND DISPERSAL IN CARIBBEAN BIOGEOGRAPHY

S. BLAIR HEDGES

*Department of Biology, 208 Mueller Laboratory, Pennsylvania State University,  
University Park, PA 16802, USA*

**ABSTRACT:** The species diversity and phylogenetic relationships of West Indian vertebrates are incompletely known, but several lines of evidence support a dispersal origin for most of the fauna. Crother and Guyer have contested much of that evidence, claiming a far greater role for vicariance. However, it is shown here that none of their criticisms can be substantiated and their paper is dominated by inconsistencies. They have used the irrelevant evidence from intra-Caribbean vicariance events to address the origin of the fauna, failed to discriminate between old and new geologic syntheses by the same authors, chosen molecular estimates of divergence time randomly rather than with respect to phylogeny, attempted to diminish the consequences of a catastrophic event in Earth history (the K–T bolide impact), and have claimed to have discovered a congruent pattern of area relationships when in fact their proposed phylogenetic pattern is present in only a single, unpublished study.

*Key words:* West Indies; Vertebrates; Amphibians; Reptiles; Molecular

THE West Indies harbors a rich biota that has intrigued biogeographers for over a century. The numerous islands, some of which are of great age, and the complex geologic history of the region are factors that have influenced the evolutionary histories of these organisms to varying degrees. In the two decades since Rosen (1975) proposed a vicariance model for Caribbean biogeography, attention has focused on determining the relative roles of vicariance and dispersal in the origin of the West Indian biota. The vicariance model proposes that the present biota represents the fragmented remnants of an ancient proto-Antillean biota that was continuous with those of North and South America in the late Cretaceous. The alternative explanation is that over-water dispersal has been responsible for the origin of the West Indian biota (e.g., Pregill, 1981; Simpson, 1956).

Hedges et al. (1992) tested these two hypotheses using estimates of amino acid sequence divergence in the protein serum albumin across a broad array of West Indian terrestrial vertebrates: bufonid, hylid, eleutherodactyline, and leptodactyline frogs; anoline, iguanine, sphaerodactyline, tropidurine, teiid, and anguid lizards; amphisbaenians; and alsophine and tropidophiid snakes (inter-island divergences also

were examined in those taxa, and in typhlopoid snakes). The chronological properties of albumin immunological distance (ID) data (Hedges et al., 1994) provided the means of estimating times of divergence between Antillean groups and their mainland relatives. All 13 groups examined exhibited lower estimates of divergence than would be predicted by the vicariance model, indicating an origin by over-water dispersal in the mid- to late-Cenozoic.

In an abundance of words, Crother and Guyer (1996) have re-examined our study (Hedges et al., 1992) and concluded that vicariance has been “an important force in shaping diversity within the Caribbean.” This is based on their reinterpretation of geological and molecular data, calculation of tsunami wave heights, and a cladistic biogeographic analysis. Below, I will point out the flaws in their reinterpretation and conclude that **none of these criticisms is valid**. Because the Crother and Guyer (1996) critique is similar in many respects to another published elsewhere (Page and Lydeard, 1994), to which we have replied (Hedges et al., 1994), my response here will be brief, and I direct the interested reader to those papers.

Since the original analysis of 13 groups (Hedges et al., 1992), I have reviewed the

origin of all amphibians and reptiles in the West Indies (Hedges, 1996a), as well as other West Indian vertebrates (Hedges, 1996b). New species continue to be discovered, and the phylogenetic relationships of some major groups still are poorly known. Nonetheless, sufficient data exist to draw some general conclusions. Only a few lineages of West Indian vertebrates, out of more than 500 (representing 1252 known species), appear to be of ancient origin (Hedges, 1996b). This suggests that dispersal from the mainland during the Cenozoic was the primary mechanism that led to the origin of the West Indian vertebrate fauna. This is supported by the reduced higher-taxon diversity of the fauna, the growing fossil record documenting a similar taxonomic composition in the past, widely distributed Cenozoic estimates of divergence time from molecular data, and a predominant South American influence (for the non-volant fauna) consistent with the unidirectional current flow through the West Indies (Hedges, 1996a,b).

Before replying to the specific criticisms, it must be pointed out that Crother and Guyer (1996) have confounded two very different mechanisms: proto-Antillean vicariance, which explains the origin of the West Indian biota, and intra-Caribbean vicariance, which does not. In their conclusions, they state that "when examined over a variety of geological and evolutionary assumptions, between 30% and 90% of available ID data conform to vicariance. From these observations, we conclude that the bolide impact did not eliminate the ancient biota." But reference to their results (Crother and Guyer, 1996: their Table 2) shows that those numbers quoted include intra-Caribbean vicariant events (and are, themselves, in error; see below), yet they are used in support of proto-Antillean vicariance. Vicariance as a biogeographic mechanism is undisputed, operates at widely varying spatial and temporal scales, and certainly has been an important mechanism in the West Indies (e.g., Hedges, 1989a,b). However, unless one postulates spontaneous generation, only the proto-Antillean (not intra-Caribbean) model of vicariance (Rosen, 1975) can ad-

dress the **origin** of the West Indian biota, and only that model is relevant to the issue (e.g., the "bolide hypothesis") being disputed by Crother and Guyer (1996).

#### CARIBBEAN GEOLOGIC HISTORY

In our study (Hedges et al., 1992), we used divergence times of land masses from the most recent geologic literature. In an attempt to criticize our dates for geologic events, Crother and Guyer have assembled a table of geologic scenarios and dates from studies extending back nearly a quarter of a century, to a time when plate tectonics had just become accepted (Freeland and Dietz, 1971). Moreover, they include studies published by the same authors at different times (e.g., papers by Burke, 1983–1988, and by Pindell, 1982–1991). This is unrealistic, because later reviews by the same author (of the same topic), based upon more data, implicitly supersede earlier reviews by that person. Just as in the biological literature, syntheses are only as good as the data available at the time. For an active area such as Caribbean geology, the most relevant geologic syntheses are those published most recently (e.g., Pindell, 1994). This is not a minor point, because much of Crother and Guyer's claim of vicariance relies on accepting a relatively recent date of 48 mya for a direct land connection between North and South America, a date derived from an older geologic scenario (Sykes et al., 1982) and one (Pindell et al., 1988) which is superseded in their table (Pindell and Barrett, 1990) and even more recently (Pindell, 1994). Furthermore, Crother and Guyer erred in that table entry, because the Middle Eocene (48 mya) window in Pindell et al. (1988:133) shows Cuba fused to the Bahamas, with no land connection between North and South America.

Just as Guyer and Savage (1986) formulated their own unique geologic scenario for the Caribbean (see Williams, 1989a, for discussion), Crother and Guyer (1996) also have made assumptions that go beyond the limitations of the current geologic database. There is no evidence that a continuous dry land connection between North and South America ever existed in

the late Mesozoic or early Cenozoic. The scenarios in the geologic literature are concerned with the relative positions of tectonic structures (e.g., volcanic arcs), not with emergence versus submergence of land. The most recent scenario (Pindell, 1994) places a continuous volcanic arc between North and South America in the Campanian (76 mya), but shows dislocation of that arc, along its northern boundary, by the Maastrichtian (70 mya). Determining if there was ever a dry land connection, and if so, when it fragmented, is a complicated geologic detective story. In the few cases where geologists have tackled this problem, they have found evidence (e.g., pelagic sediments and paleogeography of the Aves Ridge) that the proto-Antilles probably was a chain of islands and not a dry land connection (Donnelly, 1989, 1990; Holcombe and Edgar, 1990). Moreover, the fact that much of southern North America and northwestern South America was submerged during the late Mesozoic and early Cenozoic due to globally high sea levels (Smith et al., 1994) makes a proto-Antillean dry land connection even less likely. Geologic evidence is insufficient to rule out completely the possibility, but Crother and Guyer have gone far beyond existing data in their review (and assumptions) of Caribbean geologic history.

Crother and Guyer (1996) suggest that we were inconsistent by recognizing that Jamaica was submergent in our earlier papers, but not in Hedges et al. (1992). However, they have overlooked the two places where we refer to Jamaica's submergence in the paper that they are critiquing (Hedges et al., 1992:1910–1911). This is in contrast to others who have been inconsistent on this particular issue (e.g., compare Guyer and Savage, 1986, with Crother and Guyer, 1996). As in biological history, many aspects of geological history are not irrefutable facts. The evidence for Jamaica's complete submergence (reviewed in Hedges, 1989*a,b*) is strong but not entirely conclusive; some low islands (e.g., atolls) may have existed. Therefore, we saw no reason to bias our analyses by excluding it from consideration (Hedges et al., 1992).

The relationships of the emergent land masses in the West Indies during the Cenozoic still remains speculative (Draper and Barros, 1994), and this represents a separate issue from proto-Antillean vicariance. The focus of our study was on the origin of the West Indian vertebrate fauna (Hedges et al., 1992). Although we included panels showing the timing of intra-Caribbean vicariant events, and some of the divergence points fell within those time ranges, general conclusions regarding intra-Caribbean vicariance must await better geologic data and additional molecular comparisons.

#### MOLECULAR ESTIMATES OF DIVERGENCE

Crother and Guyer (1996) re-analyze our molecular data and other data in the literature, coming to the conclusion that up to 61% of the data points conform to proto-Antillean vicariance (their Table 2C). However, that value can be easily dismissed because of several methodological errors: (1) using all molecular divergence values instead of the phylogenetically relevant ones, (2) using those data in a circular fashion by recalibrating the albumin clock based on presumed vicariant events in the Caribbean and then using the resulting time estimates to support vicariance, and (3) using a more recent date (48 mya) for a proto-Antillean land connection with North and South America than is supported by the most recent geologic literature (as discussed above).

Crother and Guyer (1996) go to great lengths, with figures and statistical tests, to show that our choice of data points was non-random. But this indicates a major misunderstanding on their part; the comparisons were not supposed to be random. The whole point was to estimate a biogeographic event (dispersal or vicariance) and not some unrelated phylogenetic divergence that occurred much earlier in time. We selected those specific comparisons to represent the "most recent divergence event between the lineages examined" (Hedges et al., 1992:1910–1911). Two examples illustrate how Crother and Guyer's mistake has affected their conclusions. Their claim of support for proto-Antillean

vicariance in sphaerodactyline geckos is based on a published ID of 76 between a West Indian *Sphaerodactylus* and *Gonatodes* (mainland) (Hass, 1991). However, we used the much lower value of 45 between a West Indian *Sphaerodactylus* and *Lepidoblepharis* (mainland) (Hass, 1991), because the two groups are more closely related than either is to *Gonatodes* (Hass, 1991; Kluge, 1995). If the data were available, an even better comparison might be with a mainland species of *Sphaerodactylus*, or with *Coleodactylus* or *Pseudogonatodes* (Kluge, 1995), but such data would only be expected to provide a more recent time of divergence, thus further supporting dispersal.

The second example involves West Indian lizards of the genus *Anolis* (sensu Powell et al., 1996). Crother and Guyer do not dispute the low ID (28) between mainland and West Indian species of *Anolis*, but instead question, at length, one of our inter-island comparisons. Their discussion again illustrates this misunderstanding concerning biogeographic comparisons. We chose the ID (21) between *A. distichus* (Hispaniola) and *A. evermanni* (Puerto Rico) because those two taxa were the closest relatives available, and therefore the divergence might correspond to the vicariance or dispersal event responsible for their separation. Crother and Guyer (1996) consider that selection to be biased and instead have included ID values between more distantly related anoles on these two islands, such as *cybotes* (Hispaniola) versus *crisatellus* (Puerto Rico), and *cybotes* versus *cuvieri* (Puerto Rico). Even considering that relationships of anoline lizards are not yet well resolved (Burnell and Hedges, 1990; Hass et al., 1993; Williams, 1989b), a close relationship between the *cybotes* series and *crisatellus* series is contradicted by molecular and chromosomal data (Wyles and Gorman, 1980), and a close relationship between the *cybotes* series and *cuvieri* series never has been proposed previously (as far as I am aware) and is not supported by molecular, chromosomal, or morphological data.

It is clear from this lengthy section that forms the core of the Crother and Guyer (1996) critique that they are considering

any ID values between groups separated on two land areas as valid tests of vicariance versus dispersal. Such comparisons must be guided by phylogeny or else they may simply reflect some earlier phylogenetic divergence unrelated to the biogeographic question. Later, in their section on "cladistic biogeographic analysis", Crother and Guyer acknowledge the importance of phylogeny in making comparisons between islands. The reason for this internal inconsistency is unexplained.

Crother and Guyer (1996) suggest that we suppressed information supporting vicariance in *Eleutherodactylus*. To show that is not true, I quote from our paper:

"The only West Indian groups whose pattern of distribution, relationships, and level of molecular divergence are compatible with an ancient origin are a Cuban xantusiid lizard, *Cricosaura typica*, and the frog genus *Eleutherodactylus*. . . In *Eleutherodactylus*, the major split between the subgenera *Euhyas* and *Eleutherodactylus* (*auriculatus* section) may have occurred when the proto-Antilles separated, with *Euhyas* isolated on Cuba and *Eleutherodactylus* on the North Island of Hispaniola (Hedges, 1989a,b). The average ID between these taxa, 117, corresponds to the timing of the break-up of the proto-Antilles (Hass and Hedges, 1991). That comparison was not included here because both taxa are West Indian and are not each others closest relatives [based on morphology]" (Hedges et al., 1992:1911).

A considerable body of literature now exists pertaining to molecular estimates of phylogeny and biogeography of West Indian amphibians and reptiles, and Crother and Guyer (1996) overlook many of those contributions. Several studies on anoline lizards (e.g., Burnell and Hedges, 1990; Gorman et al., 1983; Hedges and Burnell, 1990; Shochat and Dessauer, 1981), eleutherodactyline frogs (Hedges, 1989a), and xantusiid lizards (Hedges et al., 1991) were not mentioned. The latter study is noteworthy because it came to a different conclusion than the re-analysis of published morphological data by Crother et al. (1986). After our study was critiqued by Crother and Presch (1992, 1994), we responded (Hedges and Bezy, 1993, 1994) by re-iterating the statistical significance for the molecular results (basal location of *Cricosaura*) and showing that the two pivotal morphological characters uniting *Crico-*

*saura* and *Lepidophyma* were scored incorrectly by Crother et al. (1986), thus placing into question the conclusions of their study.

Likewise, a similar re-analysis of published data on West Indian anoline lizards (Guyer and Savage, 1986) was shown to have "serious errors and confusions" (Williams, 1989b) and methodological difficulties (Cannatella and de Queiroz, 1989), some of which have been acknowledged (Guyer and Savage, 1992). Unfortunately, that study also is cited by Crother and Guyer (1996) as support for vicariance of anoline lizards, while much of the published molecular evidence is not reviewed.

#### THE BOLIDE IMPACT

A large crater, 170–320 km in diameter, exists about 1 km beneath the surface of the Yucatán peninsula and is believed by most geologists to be the impact site for the Cretaceous–Tertiary (K–T) bolide (e.g., Hildebrand and Boynton, 1990; Kring and Boynton, 1992; Maurrassee and Sen, 1991; Sharpton et al., 1993; Swisher et al., 1992). The fact that the impact occurred in the Caribbean region, only a few crater diameters away from the Antillean islands, suggested to us a possible explanation for the absence of ancient lineages: the local effects, in addition to the global effects, must have been catastrophic and likely caused extinctions (Hedges et al., 1992).

Crother and Guyer (1996) try to diminish the effects of the impact by raising some doubts about its existence, calculating what they consider to be low wave heights, and suggesting that many of the islands were "in the shadow of the Yucatan" and thus would have received smaller waves. While it is true that an alternative explanation has been proposed (volcanism), the evidence for an extra-terrestrial impact is overwhelming (e.g., references cited above). In another respect, Crother and Guyer have misrepresented the geologic literature. Sedimentary evidence of impact ejecta and giant tsunamis came **before** the discovery of the Yucatan crater, and it was the thickness and composition of these tsunami deposits that pointed to the Caribbean region as the likely site of

the impact (Hildebrand and Boynton, 1990; Maurrassee and Sen, 1991). Moreover, the original wave height calculations were based on actual deposits, not just on models. Such deposits in Haiti and in the Colombian basin indicated wave disturbance of sediments that were on the deep ocean floor (>2 km below sea level) at the time, and those at a more proximal Cuban site range up to 450 m in thickness (apparently one depositional event) and contain large boulders (Hildebrand and Boynton, 1990; Maurrassee and Sen, 1991). The discoverers of the Caribbean impact site gave the following interpretation of the Cuban tsunami deposit: "We believe that large waves from the impact swept across the lowlands of the ancient Cuban islands, tearing up boulder-sized pieces of the terrain and dumping them into the trough [on the other side]" (Hildebrand and Boynton, 1991). Crother and Guyer cite several papers that provide "arguments against tsunami generated deposition", but this is misleading because they pertain to a specific disputed site in northeastern Mexico, not to tsunami deposits in general. Because the impact occurred on top of the submerged Yucatan platform, there is no evidence to support Crother and Guyer's statement that the Antilles were "in the shadow of the Yucatan" (with respect to tsunamis). For this to be correct, the impact site would have had to have been in the Bahía de Campeche (it was not). While it is necessary to point out these errors, the fact is that none of the evidence (molecular or otherwise) pertaining to the origin of West Indian vertebrates (Hedges, 1996a,b; Hedges et al., 1992) relies on the existence of the K–T bolide impact or its waves.

#### CLADISTIC BIOGEOGRAPHY

In this section, Crother and Guyer (1996) assume that "if a congruent pattern is present among the cladograms, it suggests that the taxa examined responded by speciation to the same fragmentation events: i.e., a vicariance hypothesis is supported." Although this is a common assumption of cladistic biogeographers, it is incorrect because congruence of phylogenetic relationships also can result from concordant

dispersal (Hedges, 1996a,b; Hedges et al., 1994; Page and Lydeard, 1994; Sober, 1988). Crother and Guyer "rule out the concordant dispersal hypothesis" because they "cannot think of any mechanism that would allow concordant over-water dispersal for disparate groups such as freshwater fish, caddisflies, and snakes." This response is inconsistent, because the trees shown for these groups (Crother and Guyer, 1996: their Fig. 4) are in fact not congruent. Moreover, all of the "freshwater" fish of the Antilles are secondarily freshwater (Myers, 1938) and therefore are salt tolerant, and the wind and ocean currents in the West Indies are not random. Most non-volant West Indian groups show affinities with South America rather than North or Central America, and this is expected based on the unidirectional current flow coming from South America (Hedges, 1996a,b).

Notwithstanding the inability to distinguish vicariance from dispersal by congruence in phylogeny, the cladistic biogeographic analysis of Crother and Guyer is problematic. It did not go without notice that Hass' (1991) study of *Sphaerodactylus* was disregarded because her phylogeny "had no nodes supported by >90%" [bootstrap confidence], yet bootstrap support was not even considered for the other studies used, and only the most-parsimonious trees were considered in Crother and Guyer's analysis. In a similar light, Guyer and Savage (1992) criticized bootstrap values in a molecular study of West Indian *Anolis* (Burnell and Hedges, 1990), yet they did not employ statistical tests in their own analyses. At the least, this is inconsistent.

The final result of Crother and Guyer's (1996) cladistic biogeographic analysis is shown as two consensus trees of a set of most-parsimonious trees exhibiting a common pattern of area relationships: (Jamaica(Cuba(Puerto Rico, Hispaniola)). I was quite surprised to see that such a strong pattern of congruence could be distilled from 11 studies of disparate organisms, until I looked closely at the original trees (Crother and Guyer, 1996: their Fig. 4). That supposedly common pattern of area relationships is present in only one of the

constituent trees: one based on the unpublished dissertation of the senior author (Crother). Clearly, there is a flaw in their analysis, or in their application of this methodology to biogeography. Thus, based on Crother and Guyer's own assumption that congruence implies vicariance, their cladistic biogeographic analysis itself does not support vicariance.

## CONCLUSIONS

None of the criticisms of Crother and Guyer (1996) can be substantiated, and their paper is dominated by inconsistencies. The title of their paper and focus of their criticisms concern our hypothesis for the origin of the West Indian biota (Hedges et al., 1992), yet they use the irrelevant data from intra-Caribbean vicariant events as the primary basis of their argument. Their extraction of critical information from the geologic literature fails to discriminate between old and new reviews of Caribbean geologic history published by the same geologists. They criticize and disregard some phylogenetic studies based on bootstrap results, while refraining from using that same (or any) statistical test in their own phylogenetic analyses. Although they claim that the result of their cladistic biogeographic analysis of 11 diverse Caribbean groups yields a congruent set of area relationships, careful inspection shows that only one of the 11 groups exhibits that pattern. Their review of the K-T bolide literature is misleading, implying that there is more doubt among geologists than actually exists for these events. Finally, they have incorrectly assumed that congruence of phylogenetic relationships implies vicariance; concordant dispersal provides an equally plausible explanation. Although reinterpretations and re-analyses of published data are important, and can sometimes lead to startling new conclusions, this is not such a case.

*Acknowledgments.*—I thank C. Hass for providing helpful comments on the manuscript and the National Science Foundation for its support of my research.

## LITERATURE CITED

- BURNELL, K. L., AND S. B. HEDGES. 1990. Relationships of West Indian *Anolis* (Sauria: Iguanidae): An approach using slow-evolving protein loci. *Caribb. J. Sci.* 26:7-30.
- CANNATELLA, D. C., AND K. DE QUEIROZ. 1989. Phylogenetic systematics of the anoles: Is a new taxonomy warranted? *Syst. Zool.* 38:57-69.
- CROTHER, B. I., AND C. GUYER. 1996. Caribbean historical biogeography: Was the dispersal-vicariance debate eliminated by an extraterrestrial bolide? *Herpetologica* 52:440-465.
- CROTHER, B. I., M. M. MIYAMOTO, AND W. F. PRESCH. 1986. Phylogeny and biogeography of the lizard family Xantusiidae. *Syst. Zool.* 35:37-45.
- CROTHER, B. I., AND W. F. PRESCH. 1992. The phylogeny of xantusiid lizards: The concern for analysis in the search for the best estimate of phylogeny. *Mol. Phylo. Evol.* 1:289-294.
- . 1994. Xantusiid lizards, concern for analysis, and the search for the best estimate of phylogeny: Further comments. *Mol. Phylo. Evol.* 3:272-275.
- DONNELLY T. W. 1989. History of marine barriers and terrestrial connections: Caribbean paleogeographic inference from pelagic sediment analysis. Pp. 103-118. *In* C. A. Woods (Ed.), *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- . 1990. Caribbean biogeography: Geological considerations bearing on the problem of vicariance vs. dispersal. Pp. 595-609. *In* A. Azzaroli (Ed.), *Biogeographical Aspects of Insularity*. Accadem. Nazionale dei Lincei, Rome, Italy.
- DRAPER, G., AND J. A. BARROS. 1994. Cuba. Pp. 65-86. *In* S. K. Donovan and T. A. Jackson (Eds.), *Caribbean Geology: An Introduction*. University of the West Indies Publishers' Assoc., Kingston, Jamaica.
- FREELAND, G. L., AND R. S. DIETZ. 1971. Plate tectonic evolution of the Caribbean-Gulf of Mexico region. *Nature* 232:20-23.
- GORMAN, G. C., D. G. BUTH, M. SOULE, AND S. Y. YANG. 1983. The relationships of the Puerto Rican *Anolis*: Electrophoretic and karyotypic studies. Pp. 626-642. *In* A. G. J. Rhodin and K. Miyata (Eds.), *Advances in Herpetology and Evolutionary Biology*. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
- GUYER, C., AND J. M. SAVAGE. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). *Syst. Zool.* 35:509-531.
- . 1992. Anole systematics revisited. *Syst. Zool.* 41:89-110.
- HASS, C. A. 1991. Evolution and biogeography of West Indian *Sphaerodactylus* (Sauria: Gekkonidae): A molecular approach. *J. Zool.* 225:525-561.
- HASS, C. A., AND S. B. HEDGES. 1991. Albumin evolution in West Indian frogs of the genus *Eleutherodactylus* (Leptodactylidae): Caribbean biogeography and a calibration of the albumin immunological clock. *J. Zool.* 225:413-426.
- HASS, C. A., S. B. HEDGES, AND L. R. MAXSON. 1993. Molecular insights into the relationships and biogeography of West Indian anoline lizards. *Biochem. Syst. Ecol.* 21:97-114.
- HEDGES, S. B. 1989a. An island radiation: Allozyme evolution in Jamaican frogs of the genus *Eleutherodactylus* (Anura, Leptodactylidae). *Caribb. J. Sci.* 25:123-147.
- . 1989b. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: Slow-evolving loci and the major groups. Pp. 305-370. *In* C. A. Woods (Ed.), *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- . 1996a. The origin of West Indian amphibians and reptiles. Pp. 95-128. *In* R. Powell and R. W. Henderson (Eds.), *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*. Society for the Study of Amphibians and Reptiles, Ithaca, New York.
- . 1996b. Historical biogeography of West Indian vertebrates. *Ann. Rev. Ecol. Syst.* 27:In press.
- HEDGES, S. B., AND R. L. BEZY. 1993. Phylogeny of xantusiid lizards: Concern for data and analysis. *Mol. Phylo. Evol.* 2:76-87.
- . 1994. Xantusiid lizards and phylogenetic inference. *Mol. Phylo. Evol.* 3:275-278.
- HEDGES, S. B., R. L. BEZY, AND L. R. MAXSON. 1991. Phylogenetic relationships and biogeography of xantusiid lizards, inferred from mitochondrial DNA sequences. *Mol. Biol. Evol.* 8:767-780.
- HEDGES, S. B., AND K. L. BURNELL. 1990. The Jamaican radiation of *Anolis* (Sauria: Iguanidae): An analysis of relationships and biogeography using sequential electrophoresis. *Caribb. J. Sci.* 26:31-44.
- HEDGES, S. B., C. A. HASS, AND L. R. MAXSON. 1992. Caribbean biogeography: Molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proc. Nat. Acad. Sci. USA* 89:1909-1913.
- . 1994. Towards a biogeography of the Caribbean. *Cladistics* 10:43-55.
- HILDEBRAND, A. R., AND W. V. BOYNTON. 1990. Proximal Cretaceous-Tertiary boundary impact deposits in the Caribbean. *Science* 248:843-847.
- . 1991. Cretaceous ground zero. *Nat. Hist.* 1991:47-53.
- HOLCOMBE T. L., AND N. T. EDGAR. 1990. Late Cretaceous and Cenozoic evolution of Caribbean ridges and rises with special reference to paleogeography. Pp. 610-626. *In* A. Azzaroli (Ed.), *Biogeographical Aspects of Insularity*. Accadem. Nazionale dei Lincei, Rome, Italy.
- KLUGE, A. G. 1995. Cladistic relationships of sphaerodactyl lizards. *Am. Mus. Novit.* 3139:1-23.
- KRING, D. A., AND W. V. BOYNTON. 1992. Petrogenesis of an augite-bearing melt rock in the Chicxulub structure and its relationship to K/T impact spherules in Haiti. *Nature* 358:141-144.
- MAURRASSE, F. J-M R., AND G. SEN. 1991. Impacts, tsunamis, and the Haitian Cretaceous-Tertiary boundary layer. *Science* 252:1690-1693.
- MYERS, G. S. 1938. Freshwater fishes and West Indian zoogeography. *Smithsonian Year Annu. Rep. Smithsonian Inst.* 1937:339-64.
- PAGE, R. D. M., AND C. LYDEARD. 1994. Towards

- a cladistic biogeography of the Caribbean. *Cladistics* 10:21-41.
- PINDELL, J. 1994. Evolution of the Gulf of Mexico and the Caribbean. Pp. 13-39. *In* S. K. Donovan and T. A. Jackson (Eds.), *Caribbean Geology: An Introduction*. University of the West Indies Publishers' Assoc., Kingston, Jamaica.
- PINDELL, J., AND S. F. BARRETT. 1990. Geological evolution of the Caribbean region: A plate-tectonic perspective. Pp. 405-432. *In* G. Dengo and J. E. Case (Eds.), *The Geology of North America*. Vol. H. The Caribbean Region. Geological Society of America, Boulder, Colorado.
- PINDELL, J., S. C. CANDE, W. C. PITMAN III, D. B. ROWLEY, J. F. DEWEY, J. LABRECQUE, AND W. HAXBY. 1988. A plate-kinematic framework for models of Caribbean evolution. *Tectonophysics* 155: 121-138.
- POWELL, R., R. W. HENDERSON, K. ADLER, AND H. A. DUNDEE. 1996. An annotated checklist of West Indian amphibians and reptiles. Pp. 51-93. *In* R. Powell and R. W. Henderson (Eds.), *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*. Society for the Study of Amphibians and Reptiles, Ithaca, New York.
- PREGILL, G. C. 1981. An appraisal of the vicariance hypothesis of Caribbean biogeography and its application to West Indian terrestrial vertebrates. *Syst. Zool.* 30:147-155.
- ROSEN, D. E. 1975. A vicariance model of Caribbean biogeography. *Syst. Zool.* 24:431-464.
- SHARPTON, V. L., K. BURKE, A. C.-ZANOQUERA, S. A. HALL, D. S. LEE, L. E. MARIN, G. S.-REYNOSO, J. M. Q.-MUÑETON, P. D. SPUDIS, AND J. U.-FUCUGAUCHI. 1993. Chicxulub multiring impact basin: Size and other characteristics derived from gravity analysis. *Science* 261:1564-1567.
- SHOCHAT, D., AND H. C. DESSAUER. 1981. Comparative immunological study of albumins of *Anolis* lizards of the Caribbean islands. *Comp. Biochem. Physiol.* 68A:67-73.
- SIMPSON, G. G. 1956. Zoogeography of West Indian land mammals. *Am. Mus. Novit.* 1759:1-28.
- SMITH, A. G., D. G. SMITH, AND B. M. FUNNEL. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press, Cambridge, U.K.
- SOBER, E. 1988. The conceptual relationship of cladistic phylogenetics and vicariance biogeography. *Syst. Zool.* 37:245-253.
- SWISHER, C. C., J. M. G.-NISHIMURA, A. MONTANARI, S. V. MARGOLIS, P. CLAEYS, W. ALVAREZ, P. RENNE, E. C.-PARDO, F. J.-M. R. MAURASSE, G., H. CURTIS, J. SMIT, AND M. O. MCWILLIAMS. 1992. Coeval  $^{40}\text{AR}/^{39}\text{AR}$  ages of 65.0 million years ago from Chicxulub crater melt rock and Cretaceous-Tertiary boundary tektites. *Science* 257:954-958.
- SYKES, L. R., W. R. MCCANN, AND A. L. KAFKA. 1982. Motion of Caribbean plate during last 7 million years and implications for earlier Cenozoic movements. *J. Geophys. Res.* 87:10656-10676.
- WILLIAMS, E. E. 1989a. Old problems and new opportunities in West Indian biogeography. Pp. 1-46. *In* C. A. Woods (Ed.), *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- . 1989b. A critique of Guyer and Savage (1986): Cladistic relationships among anoles (Sauria: Iguanidae): Are the data available to reclassify the anoles? Pp. 433-478. *In* C. A. Woods (Ed.), *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- WYLES, J. S., AND G. C. GORMAN. 1980b. The classification of *Anolis*: Conflict between genetic and osteological interpretation as exemplified by *Anolis cybotes*. *J. Herpetol.* 14:149-153.

Accepted: 23 March 1996

Associate Editor: Henry Mushinsky

DATE OF PUBLICATION

*Herpetologica*, Vol. 52, No. 2, was mailed 4 June 1996.