

Herpetologists' League

Caribbean Historical Biogeography: Was the Dispersal-Vicariance Debate Eliminated by an Extraterrestrial Bolide?

Author(s): Brian I. Crother and Craig Guyer

Source: *Herpetologica*, Vol. 52, No. 3 (Sep., 1996), pp. 440-465

Published by: Herpetologists' League

Stable URL: <http://www.jstor.org/stable/3892664>

Accessed: 16/09/2008 16:54

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=herpetologists>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



Herpetologists' League is collaborating with JSTOR to digitize, preserve and extend access to *Herpetologica*.

POINTS OF VIEW: A DISCUSSION OF
CARIBBEAN BIOGEOGRAPHY

EDITOR'S NOTE.—The following two papers, by B. I. Crother and C. Guyer and, separately, by S. B. Hedges, are peer-reviewed discussions of Caribbean biogeography.

CARIBBEAN HISTORICAL BIOGEOGRAPHY: WAS THE
DISPERSAL-VICARIANCE DEBATE ELIMINATED BY AN
EXTRATERRESTRIAL BOLIDE?

BRIAN I. CROTHER¹ AND CRAIG GUYER²

¹*Department of Biological Sciences, Southeastern Louisiana University,
Hammond, LA 70402, USA*

²*Department of Zoology and Wildlife Sciences, Funchess Hall,
Auburn University, Auburn, AL 36849, USA*

ABSTRACT: The Caribbean region has been a center for debate about processes that gave rise to current species distributions. This dialogue is of particular interest to herpetologists, because much of the terrestrial vertebrate fauna is composed of amphibians and reptiles. Some workers have examined patterns of evolution and distribution of these organisms and concluded that widespread dispersal is the primary process explaining current biogeography; others have examined these same data and concluded that vicariance associated with complex tectonic movements is the primary biogeographic process. In this essay, we review Caribbean biogeography, focusing on a recent study of albumin immunological data. These data were interpreted as demonstrating that lineages on the Greater Antilles were too recent in origin, relative to the mainland as well as among islands, to be explained by vicariance. A novel hypothesis was presented, drawn from recent geological evidence of an extraterrestrial bolide impacting on the northern coast of the Yucatan at the Cretaceous–Tertiary boundary. The location, timing, and magnitude of the impact as well as concomitant tsunamis were used to explain why recent dispersal appears to explain the origin of current herpetological lineages in the Caribbean.

We re-examine the geological and immunological data that were used to generate the bolide hypothesis. Additionally, we use Brooks Parsimony Analysis to analyze phylogenetic patterns of Caribbean taxa. From these data, we conclude that (1) estimates of timing of Caribbean tectonic events are poorly constrained, (2) considerable immunological data are of sufficient age to conform to the predicted timing of vicariant events associated with the Greater Antilles, (3) dispersal events between the mainland and the Greater Antilles as well as among the Greater Antillean islands can be documented with immunological evidence provided that assumptions of evolutionary rates and direction of travel are examined carefully, (4) consistent patterns of phylogenetic relations of Caribbean taxa suggest a common history for many taxa, and (5) the pattern exhibited in conclusions 2 and 4 are sufficient to invoke vicariance as an important force in shaping current diversity within the Caribbean.

Key words: Cretaceous–Tertiary (K–T) bolide; Tsunamis; Vicariance; Dispersal; Immunological distance clock; Caribbean tectonic history; Cladistic biogeography

DEBATES over explanations for the current geographical distributions of animals and plants are as old as the discipline of biogeography (Nelson, 1978, 1983). Candolle's (1820) essay, considered by Nelson to be the first to define biogeography as an area of study, recognized that some distributions of species were the result of dispersal (only cosmopolitan species) and others were not. Because cosmopolitan species were rare relative to those with restricted

distributions, Candolle thought of dispersal as an exception for explanations of plant distributions. The normal explanation for species' distributions was "Buffon's law" (Buffon, 1761, in Nelson, 1978), which Nelson (1978) succinctly translated into its current form: allopatry. Thus, recognition of two distinct modes of explaining the origins of current distributions is not recent; the debate has only changed as our knowledge of geologic history has changed.

Nearly a century after Candolle's essay, arguments over the origin of the Antillean fauna had already commenced, as marked by the disagreement between Thomas Barbour (1916) and William D. Matthew (in Barbour, 1916). Their concern was whether over-water dispersal or land-bridges were the more plausible explanation for the origin of the Caribbean fauna. For example, Barbour (1914) had written, "... it becomes evident at once that these groups of individuals on each island have been isolated for a long time, and that evolution by isolation would be impossible if individuals were being carried by flotsam and jetsam dispersal. If this has (dispersal) taken place in the past, it should be occurring still, and the fact that it does not now occur is good proof that this method of dispersal has never played a part of any importance in the past." Barbour (1914) obviously took the position that over-water dispersal was untenable (this work emphasized reptiles and amphibians). Matthew, as an advocate of Alfred Wallace's work, frowned on intercontinental connections of any kind and followed the prevailing theory at the time by assuming a permanency of ocean basins; thus, he considered over-water dispersal as the main explanation for animal distributions (1915).

Between the early 1900's and the present, the dispersal position on the origin of the Caribbean biota strengthened, mostly due to the influential writings of Myers (1938), Darlington (1938), and Simpson (1956). By the time of Simpson's (1956) work, the dispersal explanation was so thoroughly entrenched in the minds of the mainstream zoogeographers that Simpson (1956:7) wrote, "When I first drafted the present paper it seemed useless to reopen a question that had been so thoroughly discussed and had, I felt, been settled." Simpson (1956) did address the dispersal question and sufficiently quashed other ideas on distributional origins that it was not until recently that the dispersal position was seriously challenged.

Ernest Williams (1989) summarized the new debate as one of vicariance versus dispersal. The dispersal explanation remained unchanged, but the predominant

alternative hypothesis, vicariance, was born of a marriage between a new geology (plate tectonics: e.g., Dietz and Holden, 1970; Isacks et al., 1968; Morgan, 1968; Wilson, 1966) and a new systematics (cladistics: Hennig, 1966). The vicariance school of historical biogeography was molded by Nelson (1969, 1974), who was inspired by the work of Croizat (e.g., 1958, 1964), and was expanded by Rosen (1976, 1978), Platnick and Nelson (1978), and Nelson and Platnick (1981). The formulation of vicariance theory was important to biogeography, because it attempted to replace untestable scenario construction with testable hypotheses based on cladogram congruence. Although dispersal was never rejected as having occurred by vicarists [e.g., "If so, may episodes of dispersal—which **no doubt have occurred**—be resolved by more efficient means?" (emphasis ours, Nelson, 1974:556)], dispersal was discarded as an a priori explanation for distributions and instead was considered an anomaly discoverable through vicariance methods (Croizat et al., 1974; Nelson, 1974; see Endler, 1982; Mayr, 1982; Williams, 1989, for examples of contrary views). What Nelson said was simply that the proper test in historical biogeographic studies was to test vicariance and not dispersal.

Broadly described, vicariance biogeography entails the construction of cladograms of various faunal and floral elements for the same areas of endemism and the examination of these cladograms for congruence. Congruence implies that the organisms' distributions resulted from common vicariance events (i.e., any type of barrier erection whether geological or climatological in origin). Anomalies in the congruent patterns represent dispersal events, and the absence of any congruence (i.e., random patterns) suggests random dispersal as the main explanation for the distribution. We emphasize random dispersal as distinguishable by congruent patterns, because concordant dispersal could result in congruent patterns indistinguishable from vicariant patterns. An important aspect of vicariance theory is that the biological data, congruent cladograms, need

not be constrained by geological data, because as stated by Rosen (1985), "... biology has an independent story to tell about the history of the world." Thus, non-random congruence can be used at the least to choose among competing geologic hypotheses, but also as a flag pointing to potential problems in geologic hypotheses and in our understanding of the age of organismal lineages.

The Greater Antilles, with its high endemism and complex tectonic history, offers herpetologists, in particular, a tempting region to employ vicariance ideas and methods (see Williams, 1989, for a review). Rosen (1976) constructed the first vicariance model of the Caribbean and refined it (Rosen, 1985) to confront the numerous complex tectonic hypotheses that had been proposed since his first paper. Savage (1982) also proposed a vicariance model of the Caribbean which, in a general way, complemented Rosen's (1976) model. The key difference was that Rosen argued for a proto-Antillean archipelago that was emergent between North and South America from the late Cretaceous to the early Paleocene. The archipelago provided a connection between the two continents and allowed dispersal to occur between them. Savage, on the other hand, argued that the proto-Greater Antilles received its biota exclusively from Nuclear Middle America which was part of North America. The South American component, according to Savage, arrived much later via dispersal through the Lesser Antilles. Both Rosen and Savage argued that the Caribbean archipelago moved east relative to North and South America, theoretically carrying a continental biota with it. Subsequent fragmentation of the archipelago resulted in allopatric speciation creating a non-random pattern recoverable by phylogenetic methods. It is this agreement of cladistic relationships from replicate taxa that is viewed by vicariance biogeographers to be *the* appropriate biogeographic test (Rosen, 1976, 1985; Savage, 1982).

The dispersalist position remains unchanged, even in the face of possibly telling geological data. This position being that the biota currently found in the Antilles is

the result of independent over-water dispersal events occurring over millions of years. For example, Briggs (1984:433) stated, "There is little doubt that the Antilles should continue to be regarded as oceanic islands which have gradually accumulated their terrestrial and freshwater biota by means of overseas dispersal." The main argument for the dispersal hypothesis has been that the lineages currently represented by the Caribbean biota are too young to have participated in the tectonic events required for the vicariance hypothesis. The key evidence for the lineage ages is the fossil record, or better put the absence of a fossil record (Pregill, 1981a; Williams, 1989). Another argument used to support the dispersal hypothesis is the absence of any continental faunas (Williams, 1989). We cite the same passage from Savage (1982:637) as Williams (1989:25) did to address the problem of fossils.

"The absence of groups from the fossil record of an area, especially a lowland tropical one, tells us very little about the history of its biota. There are no fossil records in Central America of marsupials, bats, primates, non-caviomorph rodents, most families of carnivores and almost all families of amphibians and reptiles that occur there today. Does this mean that none of these groups occurred there until very recently? Or tell us at what time they appeared in the region? There are hardly any records of fossil vertebrates from tropical South America, including most families present there today. Does this mean that the missing groups were absent from the region?"

Williams (1989:25) suggested that Savage was "inverting the logic of the fossil record" and added, "Unfortunately, in his rhetorical emphasis of one truth, he has omitted to call attention to its inverse: that absence in the present does not imply presence in the past." We agree with both Savage and Williams, and in our agreement, we translate their stances into the following: absence has nothing to say about implying presence or rejecting vicariance. The absence of fossils is just that; it is the absence of data to accept or reject a hypothesis. Because the fossil record is so poor, fossil absence says nothing about implying past presence nor anything about past absence. In fact, ancient fossils can only support, and not reject, vicariance hypotheses.

Younger fossils cannot reject vicariance because they provide minimum age boundaries, not maximum age. In essence, our view on fossils is a restatement and re-emphasis of the views of Rosen (1976) and Patterson (1981), which were disputed by Williams (1989) and Perfit and Williams (1989).

Williams (1989) supported his argument through the mammalian fossil record, specifically of ungulates. He argued that the absence of ungulates, either extant or as fossils, in the West Indies is evidence for their never having been there and by extension that the only way they could have been there was through vicariance and not over-water dispersal; therefore this is evidence that vicariance did not occur. At the most, it did not occur for ungulates. Hershkovitz (1972:337) interpreted the absence of ungulates and other expected mammals in the West Indies differently:

"The 'imbalance' sometimes noted in the composition of the older West Indian mammalian fauna is misleading. Except for the absence of marsupials, the relict West Indian fauna is representative of what the *sylvan* [emphasis his] fauna of Middle and northern South America must have been during the Tertiary. Judged by this fauna, the West Indies then, as now, lacked suitable natural habitats for establishment of the grazing ungulates and their train of predators known to have occurred in Middle America and northern South America since the Miocene."

Hershkovitz (1972) added that given the resemblance of the West Indian mammal fauna to "refugium of a mainland Tertiary sylvan fauna, it may be necessary to postulate the existence of a land bridge or a Caribbean Land at the time of the invasion." He thus excluded over-water dispersal as the main explanation for the Caribbean mammal distributions. This idea of vicariance for mammals garnered further support from MacFadden's (1980) work on the Greater Antillean insectivores, where he explicitly followed a vicariance model.

Explanations for the origins of the herpetofauna (by far the dominant vertebrates in terms of diversity and abundance) in the Caribbean have also been divided. In the following examination of hypotheses, we recognize three distinct

classes of explanations: (1) dispersal dominant, (2) vicariance dominant, and (3) non-committal. Several evolutionary studies on Caribbean herpetofauna were not included in the following list because they did not address the question of historical biogeography (e.g. Gorman et al., 1983; Shochat and Dessauer, 1981). Dispersal dominant explanations have been made for toads in the genus *Peltophryne* (Pregill, 1981*b*); however Pregill cautions that without a phylogeny his hypothesis should be employed carefully: personal communication), eleutherodactyline frogs (Hedges, 1989*a*; this study focused on Jamaican taxa), geckoes of the genus *Sphaerodactylus* (Hass, 1991), anoline lizards (Burnell and Hedges, 1990; Hass et al., 1993; Hedges and Burnell, 1990: this paper focused on Jamaican anoles), xenodontine snakes (Cadle, 1985; Jenner, 1981), and boid snakes of the genus *Epicrates* (Tolson, 1987). Vicariant dominant explanations have been made for eleutherodactyline frogs (Hass and Hedges, 1991; Hedges, 1989*b*; Joglar, 1989), typhlopoid snakes (Thomas, 1989), xantusiid lizards (Crother et al., 1986), anoline lizards (Guyer and Savage, 1986; Roughgarden, 1995), and xenodontine snakes (Crother, 1989). All of these vicariance explanations have elements of dispersal included. The non-committal group is composed of studies in which the authors did not believe enough evidence was available for supporting an explanation in either direction. Included taxa are emydid turtles (Seidel, 1988), anoline lizards (Williams, 1989), tropidurid lizards, genus *Leiocephalus* (Pregill, 1992), xantusiid lizards (Hedges et al., 1991), and boid snakes, genus *Epicrates* (Kluge, 1988). Clearly, there is no consensus on the origins of the Caribbean herpetofauna.

The most recent hypothesis concerning the origins of the Caribbean biota, if correct, makes the debate over dispersal or vicariance moot. Hedges et al. (1992) employed the assumptions of a molecular clock on albumin immunological distances to test whether or not divergence times between pairs of taxa corresponded to ages of known tectonic events. If the ages predated the hypothesized tectonic events,

then vicariance was implicated, but if the ages post-dated the tectonic events, dispersal was implicated. Nearly all of their data post-dated their specified tectonic events, thus being virtually unequivocal in support of dispersal. The "proximate cause" (Hedges et al., 1992:1909) given for the absence of ancient lineages was the impact of an extraterrestrial bolide that may have occurred on the northern edge of the Yucatan peninsula at the Cretaceous-Tertiary boundary (Pope et al., 1991). Further evidence suggested that associated with the impact were giant tsunamis (Bourgeois et al., 1988; Hildebrand and Boynton, 1990; Maurrasse and Sen, 1991; Smit et al., 1992). Based on the bolide hypothesis, Hedges et al. (1992) suggested that if an ancient biota entered the Caribbean via a proto-Antilles moving between North and South America during the late Cretaceous, it must have been exterminated later by the effects of the bolide impact. Or, as Hedges et al. (1992:1909) stated it, "We suggest that the bolide impact at the Cretaceous-Tertiary boundary at 64 Myr and its catastrophic effects explain the virtual absence of ancient lineages in the present fauna." Essentially, the islands were wiped clean of original vicariants and then later colonized during the Tertiary by over-water dispersal: "Because the islands already had separated from the mainland when the impact occurred at 64 Myr, subsequent colonization in the Tertiary only could have occurred by overwater dispersal." (Hedges et al., 1992:1911).

The albumin immunological clock coupled with the hypothesized timing of tectonic events and the possibility of a bolide impact about 65 million years ago (mya) combines into a formidable challenge to a vicariance explanation for the Caribbean biota. The remainder of this paper will examine in some detail the hypothesis of Hedges et al. (1992). We shall (1) review the tectonic hypotheses of the formation of the Caribbean islands, (2) further examine the bolide impact hypothesis, (3) re-evaluate the albumin immunological data set, and (4) employ a cladistic approach to estimate the historical biogeographic patterns emergent from phylogenies of Ca-

ribbean taxa. Our findings suggest that patterns consistent with vicariance are exhibited by the albumin immunological data and the phylogenetic data, and thus that the hypothesized bolide impact did not erase patterns that originated earlier in earth history.

THE GEOLOGIC HYPOTHESES

The Caribbean region has received enormous attention by geologists over the past two decades (e.g., Dengo and Case, 1990, and references within) because of its incredible compositional and tectonic complexity. Of interest to biogeographers is the literature that addresses the timing of geologic events in the region. Numerous hypotheses have been presented, but these can be reduced to essentially three classes: (1) in situ origin, (2) mobilist, and, (3) surge tectonics. The mobilist explanations are the most common and have the most support (see below), whereas the in situ origin hypotheses of the Greater Antilles (e.g., Salvador and Green, 1980) have received little support and appear inconsistent with much of the geological data (Morris et al., 1990; Pindell and Barrett, 1990). The surge tectonic hypothesis is the most recent and is part of a developing theory of global geophysics (Morris et al., 1990). Although the endorsers of the surge hypothesis state that their theory represents the best explanation of the geological data, further details are required before it can be evaluated in terms of possible influence on Caribbean biogeography.

The timing of Caribbean plate movements has been a source of argument between vicariance versus dispersal explanations (e.g., Hedges et al., 1992; Perfit and Williams, 1989; Rosen, 1976, 1985; Savage, 1982). Biogeographers have traditionally relied on one or a few geologic models in the construction of their own hypotheses. This implies that the chosen geologic model is correct, or at least nearly so. Such reliance is especially important in the Hedges et al. (1992) bolide scenario where they used narrow time frames for the various fragmentation events. These time frames were apparently derived from three geologic hypotheses. Citing Burke (1988), Ross and Scotese (1988), and Pin-

dell and Barrett (1990), Hedges et al. (1992) stated a proto-Antilles–Mainland divergence time of 70–80 mya, a Cuba–Hispaniola divergence time of 20–30 mya, a Hispaniola–Puerto Rico divergence time of about the same time: i.e. 20–30 mya, and a Jamaica–proto-Antilles divergence time of 70–80 mya.

In actuality, the timing of these events is not agreed upon, and inspection of the literature reveals a wide range of dates (Table 1). A summary of the ranges of geologic divergence times shows some consistency among the various hypotheses, but the consistency is over broad time periods. For the West Indies–Mainland split, an upper-bound is about 85 mya (Santonian or Campanian, Late Cretaceous) and a lower-bound is about 48 mya (Middle Eocene). The timing of the Cuba–Hispaniola (C–H) and the Puerto Rico–Hispaniola (PR–H) splits are even less clear. The C–H split may have occurred as early as sometime between 85 mya and 66 mya and as late as sometime during the Miocene, between 17 mya and 11 mya; estimates of the PR–H split range from 66 mya–45 mya as an upper-bound and about 20 mya (early Miocene) as a lower-bound.

The relationship of Jamaica to the rest of the Greater Antilles in terms of fragmentation timing is a special problem. Hedges et al. (1992) used an expected divergence date of 70–80 mya between J–H and J–C taxa. However, Ross and Scotese (1988) suggested that Jamaica was the western edge of the Great Arc (=proto-Antilles) and that the island was broken off when the arc collided with the Yucatan, about 84 mya–59.2 mya. The remainder of the arc continued its eastward movement, leaving Jamaica behind (Fig. 1). Subsequent to the collision, Jamaica did not rift from Central America until sometime during the Oligocene (e.g., Burke et al., 1984; Buskirk, 1992; Donnelly, 1989; Rosen, 1985; Smith, 1985) whereas the rest of the Greater Antilles split from the Yucatan at about 50 mya at the very latest. Hedges et al. (1992) tested a model that assumes the J–H/C split occurred at the same time as the Yucatan–H/C split, which as noted above, is contrary to many geological reconstructions. Given these ac-

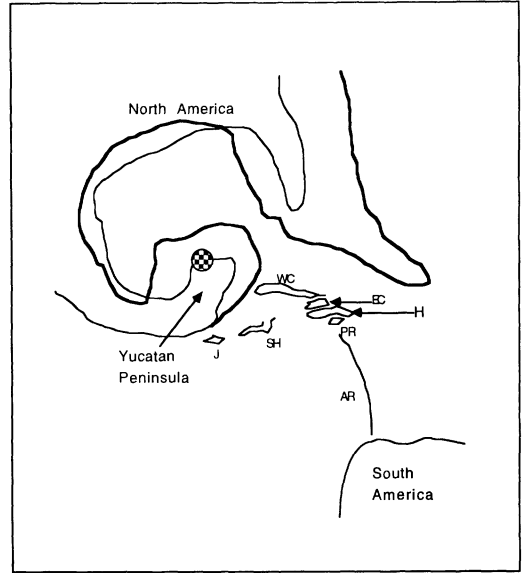


FIG. 1.—Approximate positions of the Greater Antillean arc at the time of the bolide impact on the Yucatan Peninsula. The depicted positions are actually for approximately 59 mya as estimated by Pindell and Barrett (1990: their Plate 12, Fig. E), so the islands at the time of impact were probably west of the figured locations. The dark outline represents the boundary of the continental shelf at the time. The checkered circle is the proposed site of the bolide impact. EC = eastern Cuba, WC = western Cuba, H = Hispaniola, PR = Puerto Rico, AR = Aves Ridge, SH = southern Hispaniola, J = Jamaica. Drawing is not to scale.

counts, a proper test of vicariance would be to examine divergence between Jamaican and Central American sister taxa. In a cladistic test of vicariance then, the expected recurrent area relationships for Jamaican endemics should be Jamaica–Central America.

Another reason why Jamaica's biogeographic history is unique relative to other Greater Antillean islands is because it was submerged from perhaps as early as the upper middle Eocene (~44–40 mya) to the late Oligocene (~30–23 mya) or even the early Miocene (~23–17 mya) (Burke et al., 1980; Buskirk, 1992; Lewis and Draper, 1990; Meyerhoff and Kreig, 1977). Given that these accounts are correct, the duration of Jamaica's submergence seems sufficient to have eliminated any biota that had become previously established via the Central American connection. As such, the predicted vicariance pattern of sister-taxa

TABLE 1.—Estimated times of tectonic fragmentation of the Greater Antilles from a sample of geologic papers. The numbers are millions of years. GA = Greater Antilles, MI = Mainland, C = Cuba, J = Jamaica, H = Hispaniola, PR = Puerto Rico.

Authors	WI-ML	C-J	J-H	C-H	H-PR
Freeland and Dietz, 1971	Already split at 100	—	—	Adjacent at 45	>45
Pindell and Dewey, 1982	<65 > 53	<80 > 65	<80 > 65	<36 > 21	<53 > 36 (?)
Sykes et al., 1982	48	—	—	—	—
Wadge and Burke, 1983	—	—	—	No contact until 20–10	—
Mattson, 1984	85–66	—	—	<85 > 66	<66 > 45
Duncan and Hargraves, 1984	NA-SA bridge present @ 60	—	—	—	—
Burke et al., 1984	Proto-Antilles began moving through NA, SA gap @ 110 for next 50	—	—	—	—
Smith, 1985	Flatly states that the history of the Caribbean plate is very poorly constrained.	—	—	Early to mid Miocene 23–11	—
Pindell et al., 1988	84–48	Never connected	Connection intact ~20 mya, early Miocene	—	pre-early Miocene, >20
Ross and Scotese, 1988	84–59	84–59, Jam. suggested as western edge of proto-Antilles	59–50 or 44	—	36–20
Donnelly, 1988	Latest Cretaceous–early Cenozoic	—	—	—	—
Burke, 1988	Western end collided with Yucatan ~66	—	—	Contact at 30	>30
Donnelly, 1989	<84 > 65	—	—	Not explicit but all three depicted as separated at 38	—
Mann et al., 1990	—	—	—	Post Eocene <36.6	Post Eocene
Lewis and Draper, 1990	? Poorly constrained	—	—	Middle Miocene 17–11	~35 ?
Pindell and Barrett, 1990	80–59 ?	—	—	Miocene 23–6.4	Eocene–Early Miocene, 57–21
Pindell and Draper, 1991	—	—	—	<16 > 6	After or nearly same time as C–H split
Montgomery et al., 1994; Montgomery, personal communication	Entered the gap as early as 125 mya and did not leave until possibly 65 mya.	—	—	—	—

between Jamaica and Central America, as well as any remnant of J-C or J-H patterns, have been erased. Thus, the geological history of Jamaica suggests that over-water dispersal was the main route for colonization and that no cladistic patterns or molecular clock divergence times would be expected to support vicariance explanations for the origin of Jamaica's biota. Interestingly, both Hedges "... Jamaica during the Oligocene ... was completely submerged" (1989:332) and Hass "The south island of Hispaniola and Jamaica ... were submerged completely from 30 to at least 20 mybp" (1991:548) previously recognized Jamaica's submergent history.

To summarize, the tectonic hypotheses of the history of the Caribbean region are very poorly constrained; that is, the geologic data are not present to interpret or explain the origins of many of the geological structures in the Caribbean region (e.g., Lewis and Draper, 1990; Morris et al., 1990; Perfit and Williams, 1989; Pindell and Barrett, 1990; Smith, 1985). Two especially troubling aspects of Caribbean evolution to geologists are **when** the Caribbean islands entered the gap between North and South America and **what** events were associated with tectonic movements (Lewis and Draper, 1990; Pindell and Barrett, 1990). No less troubling are unresolved questions about the nature and timing of the collision of the Greater Antilles with the Bahama Platform and commencement of Tertiary left-lateral tectonics (*ibid*), because these events are associated with island movement, both in terms of fragmentation and accretion. All of these poorly constrained aspects of Caribbean evolution are critical to the testing of species divergences by vicariance. But based on what is known, if we were forced to provide a range of dates for the mainland-Antillean split, we would proffer a range of 60–85 mya, with a strong lean towards the younger dates.

IMMUNOLOGY AND CARIBBEAN BIOGEOGRAPHY

Despite obvious uncertainty regarding tectonic events in the Caribbean, the problem of explaining the origin of the current

faunal diversity of the area remains an attractive scientific endeavor. The use of immunological data by Hedges et al. (1992) to reject vicariance as a general explanation for Caribbean biogeography coupled with the bolide impact hypothesis represents a novel entry into the Caribbean biogeography debate. In evaluating the immunological distance (ID) data, the authors made three key assumptions. These were that (1) ID is measured without significant error, (2) the conversion factor for estimating divergence time from distance data [$1 \text{ ID} = 0.6 \text{ million years (my)}$] is constant among systematic groups and measured without significant error, and (3) ID values predicted for vicariance events are within the known useful range of microcomplement fixation.

The first two assumptions are known to be violated with immunological data. Immunological distance values do vary among runs within a laboratory (but only slightly: Maxson and Maxson, 1990), among laboratories (again, only slightly: Wyles and Gorman, 1980a), and between reciprocal estimates of a pair of species (non-reciprocity: Maxson and Maxson, 1990). Measurement error from these sources is approximately 10% (Maxson and Maxson, 1990), but this should alter the confidence with which divergence times are estimated from ID. The constant used to convert immunological distance to time since divergence comes from regression of ID on date of origin estimated from the fossil record. The value traditionally used for analysis of vertebrates is unchanged from that reported for mammals by Carlson et al. (1978) even though many authors have noted altered rates of evolution within and among vertebrate groups (e.g., Cadle, 1988; Wayne et al., 1991; Wyles and Gorman, 1980a). Additionally, variation exists in the estimates of divergence times. This variation is usually expressed as an earliest and latest date based upon fossil evidence with the midpoint being used for regression analyses. Variance in divergence date is problematic in that the most commonly used regression tool (least squares) requires that the independent variable be measured without error. Some papers (e.g., Wayne

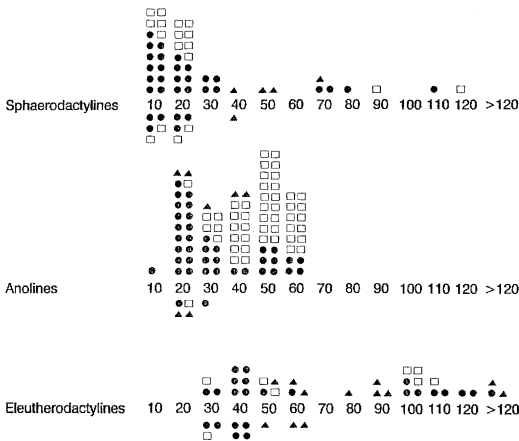


FIG. 2.—Histogram of immunological distance (ID) estimates for three radiations of tetrapods. The scale represents lower bounds of ID categories (e.g., 10 = 10.0–19.9 ID units). Symbols are for comparisons between Jamaica and Cuba, Hispaniola, or Puerto Rico (solid circle), any pairing of Cuba, Hispaniola, and Puerto Rico (open square), and mainland and any Greater Antillean island (solid triangle). Data presented above ID scales are published values; data presented below ID scales are values used by Hedges et al. (1992).

et al., 1991) reported this variation so that its effect on conclusions might be evaluated, but others (e.g., Maxson, 1992) do not. Again, accounting for such variation should inflate confidence limits associated with predicting divergence time based on ID.

The third assumption (ID values within known useful range) may be violated by the data associated with Caribbean taxa, because the predicted ID values for vicariant divergence of island and mainland forms (117–133; Hedges et al., 1992) fall within the nebulous boundary separating informative from uninformative micro-complement fixation data (Maxson, 1992; Fig. 2). This loss of information in large ID values results from the increased probability of amino acid change at previously modified sites (multiple hits; Maxson and Maxson, 1990). We know of no method that clearly identifies informative and uninformative ID values. However, Wayne et al. (1991) examined transformations that might improve predictions made from the larger ID values.

These and other sources of error have

been explored by Hillis and Moritz (1990: 511) who concluded that 95% confidence limits about albumin immunological estimates of divergence time can be too wide to be of any predictive value. Nevertheless, in the following discussion we accept assumptions and methods traditionally used in evaluating such data and use these to examine the proportion of variance in ID attributable to vicariance versus that left over to be explained by dispersal. The existence of a large set of ID data for Caribbean amphibians and reptiles should allow some ability to overcome problems of statistical uncertainty and independence. Additionally, the approaches traditionally used to evaluate ID data are not untenable as long as assumptions are recognized and tested where possible. Below, we address two basic questions: (1) are the data used by Hedges et al. (1992) an unbiased sample of appropriate available data and (2) are the results of their analyses sensitive to potential variation in rates of albumin evolution or estimates of geological divergence events?

Many more ID values than appeared in Hedges et al. (1992: their Table 1) were available to them. The advantage of their restricted data set is that for each inter-island comparison, one (or at most two) ID value was given per genus. This should assure that the data represent independent contrasts (Felsenstein, 1985). However, the restricted data set represents a fair test of vicariance versus dispersal only if these data are an unbiased sample of available contrasts and if the available contrasts are unbiased relative to the sampling universe. To test this, we created a complete data set of published values for three well-studied groups, sphaerodactylines, anolines, and eleutherodactylines (data from Hass, 1991; Hass et al., 1993; Hass and Hedges, 1991). In creating this data set, we tried to mimic the apparent selection regime of Hedges et al. (1992). The pattern of entries in their Table 1 indicated that ID values were chosen if they were representative of (1) species allopatric on island pairs or island and mainland areas, (2) species pairs related at the generic or familial level, and (3) one-way or reciprocal comparisons. This

created a sampling universe of reciprocal comparisons of all possible pairs of species at the intrafamilial level endemic to the Greater Antillean islands as well as those endemic to the Central and South American mainland. We were unable to test whether available data were unbiased relative to the sampling universe. The only evidence indicating that these data are representative of the total pool is the observation that attempts were made to generate antisera from disparate lineages within each group. Thus, the available published data should reflect major patterns of evolution in sphaerodactylines, anolines, and eleutherodactylines. If this assumption is false, then *any* conclusion relative to overall patterns of immunological divergence will be flawed.

In some cases Hedges et al. (1992) presented pooled data. For reciprocal data, the mean of the two-way comparisons was used; for some closely related taxa found on one island, all ID values comparing those taxa with a taxon (or taxa) from a second source were averaged and presented as a single value. For example, the entry labeled *Eleutherodactylus planirostris* versus *E. gossei*/*E. nubicola* in their Table 1 lists a single ID value of 41. This datum is the mean (range: 32–45) of two sets of reciprocal ID's listed in Table 1 of Hass and Hedges (1991). In recreating the data set used by Hedges et al. (1992) and in determining the pool of data available to them, we recorded each ID value separately (raw data entered rather than pooled data). We followed their dichotomous categorization of each datum as being either larger (or equal to) or smaller than that expected of a predicted divergence time; ID data large enough to be as old as or older than the divergence date failed to reject vicariance; data too small to conform to the divergence date rejected vicariance in favor of dispersal.

The distribution of values used by Hedges et al. (1992: their Table 1) differs from the data available to them (Fig. 2); values presented by those authors are biased towards smaller distances for anolines and eleutherodactylines (Mann-Whitney *U*-tests; $z = 2.7, P = 0.008$ and $z = 3.7, P$

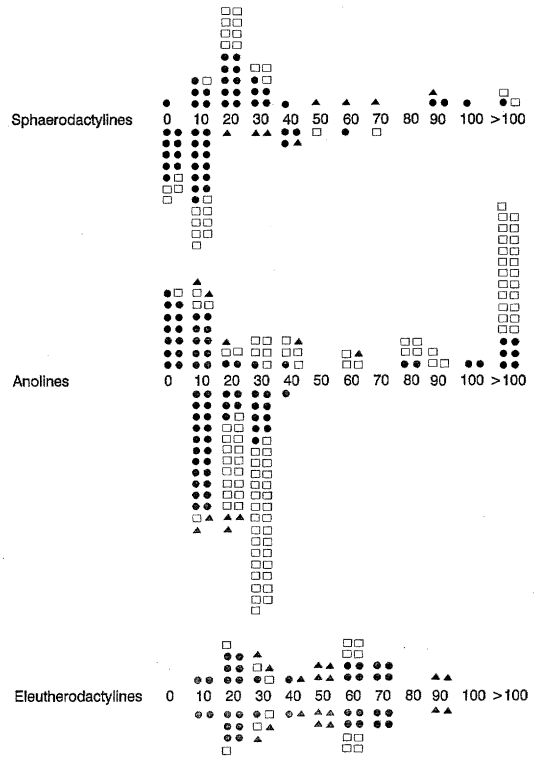


FIG. 3.—Histogram of estimated divergence times for species pairs. The scale represents lower bounds of time categories (e.g., 10 = 10.0–19.9 MYBP). Symbols are for comparisons between Jamaica and Cuba, Hispaniola, or Puerto Rico (solid circle), any pairing of Cuba, Hispaniola, and Puerto Rico (open square), and mainland and any Greater Antillean island (solid triangle). Data presented below divergence scales were calculated with a constant conversion factor; data presented above divergence scales were calculated with separate conversion factors for each taxonomic group.

= 0.0002, respectively; island comparisons pooled). A marginally significant difference in ID values was observed for sphaerodactylines ($z = 1.8, P = 0.07$). To account for potential problems arising from our inclusion of replicate estimates of the same species pairs and the fact that only a few species pairs had reciprocal estimates, we repeated the three tests on data restricted to single, one-way values for each species pair. This reduction of data does not mimic the sample universe implied by Hedges et al. (1992) as faithfully, but it eliminates some problems of independence and does not affect the statistical results substantially (anolines: $z = 2.6, P = 0.01$; eleuth-

erodactylines: $z = 2.1$, $P = 0.03$; sphaerodactylines: $z = 1.6$, $P = 0.10$).

The source of the bias is not obvious in the text of Hedges et al. (1992). The most likely explanation is that taxa within the smallest possible supraspecific category were chosen over pairs representing larger categories. The data for anoles illustrate this. Of the 27 published ID values comparing Puerto Rican with Hispaniolan species (Hass et al., 1993), Hedges et al. (1992) selected a value for *Ctenonotus* (= *Anolis*) *distichus* versus *C. evermanni*. Both species are members of the *acutus* species group (Savage and Guyer, 1989). Seven species of this group are Hispaniolan endemics (*distichus* is also found in the Bahamas) with three species occurring on Puerto Rico and the Virgin Islands. The *acutus* species group is one of two groups within the *crisatellus* series (Savage and Guyer, 1989); the other group (*crisatellus* species group) has a Puerto Rican distribution. Many ID values are available (Shochat and Dessauer, 1977; Wyles and Gorman, 1980a,b) that compare species within the *cybotes* series, an entirely Hispaniolan radiation, with Puerto Rican members of the *crisatellus* series. All of these values are between 34 and 54 ID units, placing them within the limits for vicariance established by Hedges et al. (1992). Thus, if the ID data for these anoles are taken at face value, they indicate a vicariant split of *Ctenonotus* into the *cybotes* and *crisatellus* series on Hispaniola and Puerto Rico, respectively, with subsequent dispersal of an *acutus* species group member to Hispaniola. This scenario requires a monophyletic genus *Ctenonotus* and relatively recent divergence of the *crisatellus* series into monophyletic *acutus* and *crisatellus* species groups, features supported by accumulating evidence (Gorman et al., 1980; Guyer and Savage, 1992). Admittedly, the data comparing *cybotes* and *crisatellus* series anoles are not independent, because all comparisons were made to antiserum from one species (*Ctenonotus cybotes*). However, a similar pattern is obtained for comparisons of the Puerto Rican *Xiphosurus* (= *Anolis*) *cuvieri* with Hispaniolan taxa from the *cybotes*

series within *Ctenonotus* (Gorman et al., 1980; Shochat and Dessauer, 1981; Wyles and Gorman, 1980a).

We suspect that similar sampling bias in favor of dispersal occurs throughout the Hedges et al. (1992) data. This is clearly the case for eleutherodactylines, where many published ID values (Hass and Hedges, 1991: their Tables 1 and 2) conform to Hedges et al.'s (1992) stated expectation for vicariance. Those authors stated (p. 1911) that, because they were unsure of the systematic relationships of the island (*Euhyas* and part of *Eleutherodactylus*) and mainland (*Craugaster* and part of *Eleutherodactylus*) subgenera of *Eleutherodactylus*, they did not include any values associated with these taxa in their Table 1. However, they also stated (p. 1911) that such known sister-taxon status was not a requirement for inclusion of data in their table. Additionally, a value associated with these taxa was used to calibrate an albumin clock in Hass and Hedges (1991), and this calibration was used as justification for the use of the conversion factor that they selected. Thus, data that were deemed sufficient to justify patterns of ID associated with vicariance were not deemed useful in assessing the overall role of vicariance in the Caribbean. Instead, Hedges et al. (1992:1909) concluded that "All albumin ID's between West Indian and mainland (Central and South America) taxa are considerably less than the ID's predicted by the geological history." Their statement that "The [ID] comparisons . . . indicate that the genus *Eleutherodactylus* has dispersed among the islands and between the West Indies and the mainland subsequent to any vicariant event that may have occurred" (p. 1911) may explain certain enigmatic values [all Jamaican comparisons (Hass and Hedges, 1991) and some comparisons with *Syrrhopus* (Hedges, 1991)] but is not supported by the weight of evidence exhibited in available data (Fig. 2).

No one in the vicariance versus dispersal debate has denied that dispersal occurs. Therefore, anyone addressing this topic must consider that both processes probably occurred and impacted the origination and

diversification of taxa. Because the paired-comparisons method of Hedges et al. (1992) was used to demonstrate that dispersal played an important role and that vicariance played an unimportant role in Caribbean biogeography, those authors needed to show a remarkable number of unequivocal dispersal events (ID data too recent to conform to vicariance) and remarkably few such events associated with the timing of the putative vicariance event. The sampling method used by Hedges et al. (1992) will identify unequivocal dispersal events, provided the assumptions of their methods are met. This is because vicariance took place so long ago for Caribbean taxa, thereby providing extensive time for more recent dispersal events to accumulate. Such dispersals will involve taxa that have had limited time for both protein and morphological change to accumulate. We recognize that there are fantastic cases of biochemical divergence with little morphological alteration (e.g., Hillis, 1988; Knowlton, 1993; Miyamoto, 1983) as well as of morphological modification with little biochemical change (e.g., Avise et al., 1980, 1992). However, morphology and molecules should be coupled on average (e.g., Hillis, 1987; Hubby and Throckmorton, 1968). Therefore, if taxa are selected from the least inclusive supraspecific categories (as in Hedges et al., 1991) and if these categories are based on morphological similarity (e.g., see Williams, 1976), then divergence events too recent to be associated with vicariance events will be sorted from the pool of all possible divergences. However, this sampling procedure will be incapable of evaluating the role of vicariance because it fails to consider ID data associated with older events. These data are necessary to evaluate whether remarkably few divergence events are associated with tectonic events. The fact that large ID values exist for other monophyletic taxa shared by island pairs or between the islands and the mainland suggests the presence of vicariance "signal" at a deeper phylogenetic level than examined by Hedges et al. (1992).

They conclude (p. 1911) that refinement of the data set to include only closest sister

TABLE 2.—Number of ID values conforming versus not conforming to models of Caribbean vicariance. (A) Constant clock calibration; Hedges et al. (1992) divergence dates. (B) Recalibrated clocks; Hedges et al. (1992) divergence dates. (C) Recalibrated clocks; revised divergence dates. HI = Hispaniola, CU = Cuba, PR = Puerto Rico, JA = Jamaica.

	Conform	Does not conform	Percent
A.			
Mainland-Island	2	16	11%
HI-CU-PR	56	13	81%
JA-All others	4	77	5%
Overall	62	106	37%
No JA	58	29	67%
B.			
Mainland-Island	4	14	22%
HI-CU-PR	64	5	93%
JA-All Others	17	64	21%
Overall	85	83	51%
No JA	68	19	78%
C.			
Mainland-Island	11	7	61%
HI-CU-PR	68	1	98%
JA-All Others	17	64	21%
Overall	96	72	57%
No JA	79	8	91%

taxa for island-mainland comparisons will only increase the level of support for dispersal. This is true only in the sense that the data allowed in the analysis will become more biased. Only well corroborated phylogenies of replicate groups will allow proper interpretation of the roles of vicariance and dispersal in explaining the ID data (see also Page and Lydeard, 1994). Nevertheless, a crude estimate of support for vicariance versus dispersal can be made from ID values if they are dichotomized as in Hedges et al. (1992); ID data sufficiently small conform to dispersal, those sufficiently large conform to vicariance. If one accepts their geological model and assumes that all taxa have evolved at a rate of 1 ID = 0.6 my, then 37% of published ID data for sphaerodactylines, anolines, and eleutherodactylines conform to vicariance (Table 2). Because there is evidence to suggest that Jamaica was not land positive until approximately 25 mya (e.g., Arden, 1975; Kasfi, 1983; Meyerhoff and Krieg, 1977), inclusion of comparisons involving Jamaica may unfairly bias tests of vicariance in favor of dispersal. If pairs of

ID values involving Jamaica versus other Greater Antillean islands are eliminated from consideration, then 67% of sampled ID values conform to vicariance (Table 2).

In evaluating evolutionary patterns of ID's for Caribbean amphibians and reptiles, Hedges et al. (1992) accepted a constant rate of evolution (1 ID = 0.6 my) among taxa within the region. This value was selected because it conformed to a value calculated for Caribbean *Eleutherodactylus* (Hass and Hedges, 1991:442) and to one published for other vertebrates (Maxson, 1992). The determination of evolutionary rate for *Eleutherodactylus* was made from three calibration points: (1) divergence of Antillean taxa from mainland forms via separation of the proto-Greater Antilles (dated at 70 mya), (2) emergence of Jamaica (dated at 25 mya), and (3) uplift of the Blue Mountains in Jamaica (dated at 7.5 mya). At least two other possible calibration points exist. One is the separation of components of the proto-Greater Antilles. This complicated geological event involved parts of at least three current islands (Cuba, Hispaniola, and Puerto Rico). We have chosen to focus on a split between Hispaniola and Puerto Rico, because it has been discussed extensively in the geological literature (dated at 20–30 mya by Hedges et al., 1992, dates that conform roughly to Pindell et al., 1988, and Ross and Scotese, 1988; we will use 25 mya in the following analysis). The final putative calibration point is the separation of the northern Lesser Antilles from Puerto Rico by tectonic opening of the Anegada Passage, a biogeographic event noted by Roughgarden (1990) and dated at mid-Miocene (we will use 15 mya) by Pindell and Barrett (1990).

In the following discussion, we examine the assumption that albumin evolution has proceeded at a constant rate among taxa. We use the same analytical tool (least squares linear regression) used by previous authors (e.g., Cadle, 1988; Hass and Hedges, 1991; Maxson, 1992) to calibrate evolutionary rate (slope of a regression line through the origin). We do this for heuristic purposes recognizing that previous analyses often are flawed by a lack of in-

dependence among data points (Hillis and Moritz, 1990; Wayne et al., 1991). Because we are interested only in estimates of rates of albumin evolution for vicariance in the Caribbean, our use of replicate taxa from the same divergence events represents replication and not pseudoreplication.

In addition to the estimate for *Eleutherodactylus*, evolutionary rates are calculable for anoles and sphaerodactylines (Table 3). The sphaerodactyline data conform to a significant regression ($R^2 = 0.99$, $P = 0.01$) which, when forced through the origin, has a slope of 0.80, approximately half that of *Eleutherodactylus* (Hass and Hedges, 1991:422). This supports evolutionary change of albumin proteins in a strict clocklike fashion for Caribbean sphaerodactylines but at a reduced rate relative to eleutherodactylines. The anole data are curvilinear but can be transformed to linear ($R^2 = 0.83$, $P = 0.09$) by taking the log of divergence time. The slope of these transformed data (forced through the origin) is 11.7. This result indicates that albumin evolution may not have proceeded in a strictly clock-like fashion in anoles. Nevertheless, the regression can be used to predict divergence times for anole ID values by backtransformation.

These data indicate that albumin clocks of Caribbean amphibian and reptile species might not be running at a constant speed [the anole clock appears to be slowing down at a constant rate as taxa diverge (see also Wayne et al., 1991)]. Additionally, for those taxa displaying clocklike change, rates can differ by at least a factor of two. To examine these effects on conclusions regarding samples of ID data, we recalculated putative divergence times for all ID data of sphaerodactylines, anolines, and eleutherodactylines in the Caribbean. These estimates (Fig. 3) show an increase in their conformance to the Hedges et al. (1992) model of vicariance; overall, 51% of the data conform to that model, a figure that increases to 78% if Jamaican comparisons are eliminated (Table 2). The data for sphaerodactylines, when corrected for altered evolutionary rate, changed most dramatically in relation to vicariance. Thus, for a taxon that previously had been as-

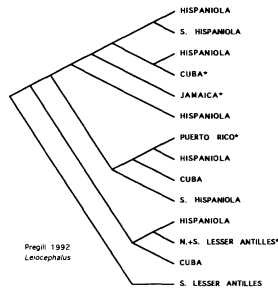
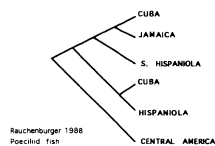
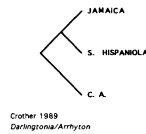
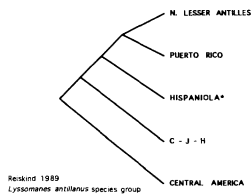
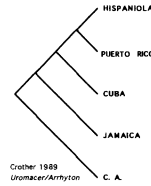
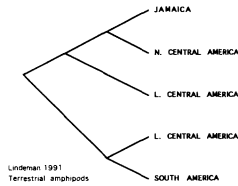
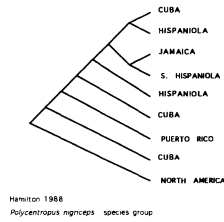
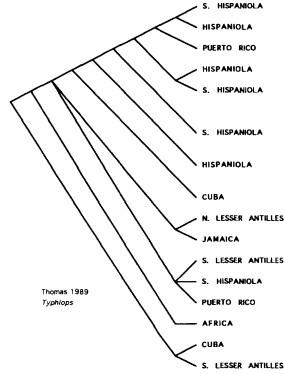
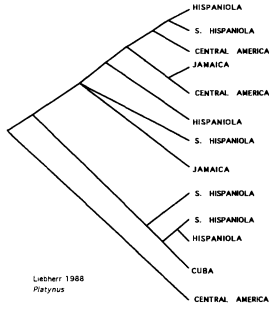
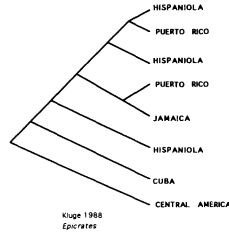
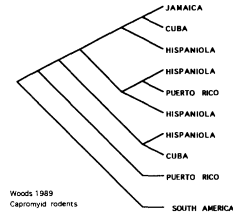
sumed to be a good and recent disperser (Hass, 1991; but see Page and Lydeard, 1994), we find evidence for a more ancient origin (as indicated by Kluge, 1995:19) and considerable conformance to vicariance predictions.

As a final analysis, we used the data modified to allow for unequal rates of albumin evolution and compared these to an alternative set of vicariance dates. Our review of the geological literature (Table 1) indicates that separation of Caribbean islands from the mainland may have occurred as late as 48 mya and that the breakup of Cuba, Hispaniola, and Puerto Rico might have occurred as late as 11 mya. If these dates are substituted for those used by Hedges et al. (1992), then between 60% (all data) and 91% (Jamaican comparisons eliminated) of the ID data from sphaerodactylines, anolines, and eleutherodactylines conform to vicariance.

Our review of the ID data was done with the purpose of demonstrating that the interpretation of them must be done with care and that an unintentional bias occurred in the data presented by Hedges et al. (1992). We conclude that many divergences estimated from ID data are sufficiently old to conform to vicariance. We do not think that this proves vicariance, nor do we conclude that it disproves dispersal. We do not believe that the ID data alone are necessary and certainly not sufficient to arbitrate this debate. One could argue that our examination of the ID data confused the origin of the Caribbean herpetofauna with subsequent vicariance. Such a scenario would propose that, after being eliminated by an event like a large tsunami, the ancestral biota colonized the proto-Greater Antilles from the mainland via concordant overwater dispersal. In such a scenario comparisons of mainland and island taxa should conform to divergence dates more recent than 65 mya, assuming the bolide induced tsunami was the event that scoured the islands, rather than dates as old as 75 mya as predicted by the vicariance hypothesis (both dates from Hedges et al., 1992). All subsequent divergence events in the Caribbean would conform to both vicariance and dispersal,

TABLE 3.—Proposed Caribbean divergence events. Event refers to vicariant separation known from geological literature. Age is the estimated time (mya) of the divergence event. Taxa refer to the species and/or species groups putatively separated by the divergence event. ID and *n* are the mean ID and sample size used to calculate the mean. Source is the reference for the geological age and ID data.

Event	Taxa	Age	ID	<i>n</i>	Source
Mainland/Island	roquet sp. gp./all other anoles <i>Lepidoblepharis-Gonatodes/Sphaerodactylus</i>	70	51.6	66	1, 2
Hispaniola/Puerto Rico	Subgenus <i>Eleutherodactylus</i> /Subgenus <i>Euhyas</i>	30	57.2	4	3
	<i>C. cybotes</i> sp. gp./ <i>C. cristatellus</i> sp. gp.		116.7	6	3
	<i>S. asterulus, copei/S. klauberi, macrolepis, roosevelti, townsendi</i>		42.5	14	2
			17.5	4	3
Cuba/Jamaica	<i>E. planirostris/E. gossei, nubicola</i>	25	41.0	4	3
	<i>C. cristatellus</i> series/ <i>C. bimaculatus</i> series	20	36.1	16	2
Puerto Rico/N. Lesser Antilles Blue Mts, Cockpits/Lowland Jamaica	<i>E. nubicola/E. cundalli</i> and <i>jamaicensis</i> sp. gps.	7.5	11.8	4	3
	<i>S. semastops/S. argus</i>		1.0	1	3
	<i>N. reconditus/N. ineotopus</i>		6.0	1	4



under this scenario. We did not consider this possibility because Hedges et al. (1992) did not. In fact, four of the five general categories used by these authors to evaluate the role of vicariance were of relatively recent inter-island comparisons. Only one of their general categories involved island-mainland comparisons. If the debate is reduced to a consideration of concordant dispersal of taxa to an ancient proto-Antilles attached to the mainland versus a strictly vicariant scenario involving concordant dispersal to a proto-Antilles attached to the mainland (as in Guyer and Savage, 1986), then we see more similarities than dissimilarities in the positions being taken. Additionally, we see little hope that the ID data can test between these two possibilities because of problems with sampling such data (as outlined above and in Page and Lydeard, 1994), problems with distinguishing dates so close to each other and so close to the limits of ID utility (Maxson, 1992), problems with two taxon comparisons (as outlined by Rosen, 1978), and problems with distinguishing concordant dispersal from strict vicariance (Savage, 1982). We believe that other methods, like those that optimize distribution patterns on phylogenetic trees (e.g., Brooks and McLennan, 1991:242), are more appropriate for identifying dispersal events.

THE BOLIDE IMPACT HYPOTHESIS

The biogeographic hypothesis of Hedges et al. (1992) used an extraterrestrial bolide to explain the apparent absence of ancient taxa in the Caribbean. Their basic explanation was that the impact triggered tsunamis that were large enough to have exterminated the terrestrial Caribbean biota: "A wave of such proportions almost certainly would have decimated much of the biota existing on the islands at that time" (Hedges et al., 1992:1911). Evidence indeed exists for parts of this scenario, but

there remains some skepticism. An impact site dated to the Cretaceous-Tertiary boundary (about 64 mya) has been identified on the north coast of the Yucatan peninsula (e.g., Hildebrand and Boynton, 1990; Penfield and Camargo, 1981; Pope et al., 1991; Sharpton et al., 1993; Smit et al., 1992). Some workers suggest that the tektites studied to identify impact localities are the result of terrestrial processes (volcanic), not extraterrestrial processes (e.g., McCartney et al., 1990, and references within). Even the Yucatan site has been disputed as an impact site (Keller, 1992), and more recently Meyerhoff et al. (1994) suggested that the structure is of volcanic origin. Regardless of the process that created the Yucatan crater, some major geologic event did take place in the region about 65 mya. This event (impact?) has been implicated as the event responsible for possible tsunami deposits of the same age in parts of the Caribbean and North America (e.g., Bourgeois et al., 1988; Habib et al., 1996; Maurrasse and Sen, 1991; Smit et al., 1992, 1996; but see the following for arguments against tsunami generated deposition: Adatte et al., 1996; Lopez-Oliva and Keller, 1996; Stinnesbeck and Keller, 1996).

Assuming that there was a bolide impact on the north coast of the Yucatan that triggered tsunamis, just how large were these waves? Maurrasse and Sen (1991) suggested a 2-km tall wave was required to leave the deposits in southern Hispaniola. Hedges et al. (1992) followed Hildebrand and Boynton (1990) and stated that the initial wave height (at the impact site) may have been 4-5 km, diminishing to 500 m when it reached Cuba. These numbers were based on an impact in an oceanic basin (Colombian), not the continental shelf waters of the northern Yucatan, as they were at the end of the Cretaceous (Ward et al., 1985). Oceanic basin impact sites

←

FIG. 4.—Area cladograms used in the Brooks Parsimony Analysis. Some of the cladograms are condensed from the original. For example a ((H,H)H)C) clade = (H,C). Certain areas, such as the Bahamas and the Cayman Islands, were deleted from the area cladograms because of their tectonically unrelated geologic history. Eastern and Western Cuba were combined into the area Cuba. Asterisks indicate fossil data. See text for further explanation of the areas used in the study.

have been entertained, but the composition of the tektite glasses indicates that the impact occurred on continental crust, not ocean basin (Sigurdsson et al., 1991): in other words in shallow water, not deep water. Tsunamis generated from large bolides (radii of kilometers) may be only as tall as the water depth of the impact site (Bourgeois et al., 1988:569; Gault and Sonett, 1982:90–91). According to Ward et al. (1985), the waters at the age and location of the impact were inside the 600-foot (182-m) depth contour. If the maximum height of the tsunami is constrained by water depth, then the initial wave size would be approximately 180–200 m. This wave height fits well with the suggested wave height of 50–100 m required for the Bourgeois et al. (1988) tsunami scenario near the Brazos River in Texas (due to reduction in wave amplitude associated with distance traveled: Gault and Sonett, 1982).

The position of the Greater Antilles at 65 mya is also important. If we follow a relatively fast mobilist model (one which depicts the Cuba–Bahamas collision in the Paleocene, ~66–57 mya: e.g., Pindell and Barrett, 1990) of the Caribbean, the tsunami would have had only an indirect hit on the islands, except for perhaps extreme western Cuba (Fig. 1). The rest of the islands would have been further south and west, essentially in the shadow of the Yucatan. The distance traveled coupled with refraction and barriers probably reduced the wave significantly in height (Gault and Sonett, 1982) and consequently reduced the wave's potential of cleansing the islands of their ancient fauna.

CLADISTIC BIOGEOGRAPHIC ANALYSIS

As noted previously, vicariance biogeographers have always maintained that congruence (taxonomic or character) was the appropriate test for their hypotheses. A vicariance hypothesis can be falsified through incongruence among cladograms of taxa endemic to the areas in question, and in turn, vicariance can be supported by congruence. If a congruent pattern is present among the cladograms, it suggests that the taxa examined responded by spe-

ciation to the same fragmentation events: i.e., a vicariance hypothesis is supported (see Page, 1988, for an alternative formulation of cladistic biogeography). Importantly, a minimum of three areas are required: two-taxon, or two-area comparisons carry no information.

Is a vicariance pattern recoverable for Caribbean taxa? When working within a cladistic framework, any historical pattern is theoretically recoverable given that synapomorphies (uniquely derived characters) are available and that they covary with a higher frequency than homoplasies (convergences, parallelisms, reversals). In historical biogeography, the synapomorphies are sister taxa in endemic areas that resulted from a fragmentation event; the sister taxon pattern should covary at a high frequency throughout the biota of the two endemic areas. The homoplasies reflect random dispersal events; the sister taxon pattern should not covary but should exhibit random qualities (see Sober, 1988, for a discussion on the relationship between cladistic phylogenetics and vicariance biogeography). Given these assumptions (really only a single assumption), if a vicariance pattern is present in the Caribbean biota, it should be recoverable via a cladistic method.

Several cladistic methods for inferring historical biogeographic relationships are currently used (three-taxon trees: Nelson and Ladiges, 1991; component analysis/consensus: Humphries and Parenti, 1986; Nelson and Platnick, 1981; parsimony: Brooks, 1990; Kluge, 1988; Wiley, 1988). The relative efficacy of these methods has not been adequately tested, although they have all been criticized (e.g., Brooks and McLennan, 1991; Harvey, 1992; Kluge, 1993; Ladiges et al., 1992; Page, 1990). We employed the parsimony method (BPA: Wiley, 1988) to document non-random patterns of Caribbean biogeographic history. The BPA method is straightforward and was detailed in a lucid fashion by Brooks and McLennan (1991), so we will not review the details here.

We created a BPA data matrix from 11 area cladograms derived from a diverse assemblage of Caribbean taxa including

TABLE 4.—The BPA data matrix derived from the area cladograms in Fig. 4. These data were analyzed with PAUP 3.1.1 (Swofford, 1993). Specifically, these data were analyzed as unordered, the ACCTRAN optimization option (convergences favored over reversals) was employed, and the BRANCH and BOUND algorithm was used to obtain the most parsimonious trees. An all "0" outgroup was included to root the trees. The letter symbols across the top designate the specific clades which the data were derived from. T = *Typhlops*, R = capromyid rodents, A = amphipods, P = poeciliid fish, N = *Polycentropus* (caddisflies), C = *Platynus* (carabid beetles), L = *Letocephalus*, S = *Lysosomes* (salticid spiders), E = bold snakes, X and D = xenodontine snakes.

OTU'S	Characters												
	T	R	A	P	N	C	L	S	E	X	D		
Cuba	0000001001111	110011111	????	11111	101111111	000000011111	0111101110111	0011	000011	011	??		
S. Hispaniola	111111011101	000000000	????	01010	011111111	110111111111	1011100110011	?????	101111	???	11		
Hispaniola	111111001101	011111111	????	00111	10111111111	111111111111	111111111111	0111	101111	111	??		
Puerto Rico	010111011101	001110111	????	?????	00000111	??????????????	000001110011	1111	111111	111	??		
Jamaica	000000101101	110010111	1101	11011	011111111	001111000111	0001100010011	0011	011111	???	11		
N. Lesser Antilles	000000101101	???????????	????	?????	???????????	??????????????	00000001111	1111	???????	???	??		
S. Lesser Antilles	?????????????	???????????	????	?????	???????????	000000000111	??????????????	?????	???????	???	??		
Nuclear C.A.	?????????????	???????????	1101	00001	???????????	011111000111	???????????????	0001	000001	001	01		
Lower C.A.	?????????????	???????????	????	?????	???????????	011111000111	???????????????	0001	000001	001	01		
North America	?????????????	???????????	????	?????	00000001	???????????????	???????????????	?????	???????	???	??		
South America	?????????????	000000001	0011	?????	???????????	???????????????	???????????????	?????	000001	???	??		
Africa	000000000101	???????????	????	?????	???????????	???????????????	???????????????	?????	???????	???	??		
Outgroup	000000000000	000000000	0000	00000	00000000	000000000000	000000000000	0000	000000	000	00		

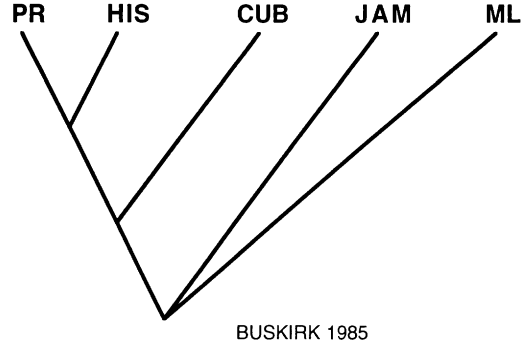


FIG. 5.—Greater Antillean area relationships proposed by Buskirk (1985) based on geologic history.

arthropods, fish, mammals, and reptiles (Fig. 4, Table 4). Because evolutionary patterns can be obscured by including phylogenies with weak character support (e.g., Guyer and Slowinski, 1991), we excluded some obvious reptilian and amphibian phylogenies from the analysis; specifically, phylogenies of *Eleutherodactylus*, *Sphaerodactylus*, and anoline lizards were not used because of serious conflict and/or lack of resolution (conflict: e.g., Hedges', 1989b, and Joglar's, 1989, hypotheses for *Eleutherodactylus*; Guyer and Savage's, 1986, and Williams', 1989, hypotheses for anoles). The phylogeny of *Sphaerodactylus* (Hass, 1991) proved to be intractable and unusable because of the severe lack of resolution. No consensus trees were shown for the character analysis, but Hass (1991:536) stated that the strict consensus tree (P. 534) gave very similar results to the bootstrap tree (which had no nodes supported by >90%), which showed the relationships of West Indian *Sphaerodactylus* as nearly totally unresolved except for a few species pairs. We must point out that the taxa we excluded from the BPA analysis were the same groups that we used in the immunological distance (ID) analyses. We used them in the ID section because (1) Hedges et al. (1992) used them extensively in their study (i.e., they must have trusted the ID data and we merely followed this assumption) and (2) the ID analysis (comparing island pairs of taxa) relies less heavily (if at all) on precise tree structure, whereas BPA does. The BPA analysis was restricted to the following en-

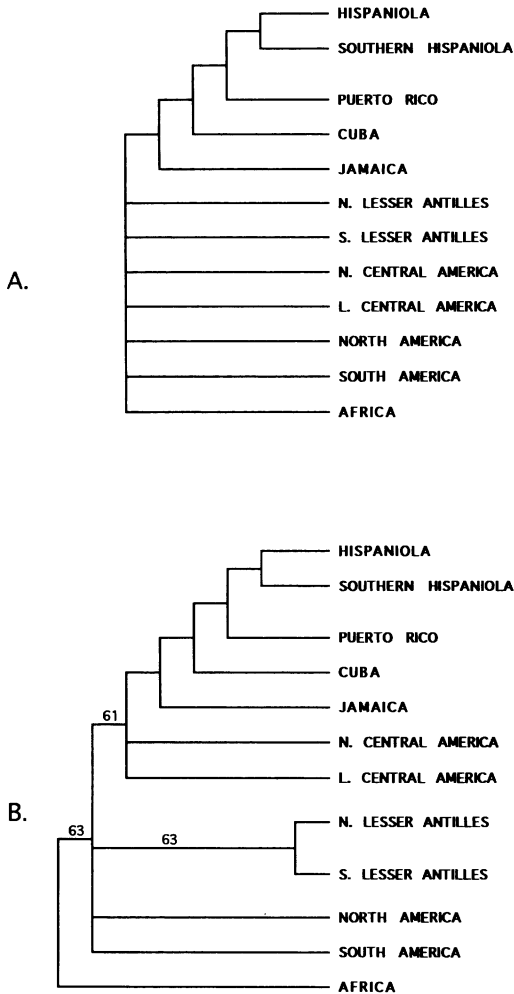


FIG. 6.—Consensus trees derived from the 208 most parsimonious trees that resulted from the BPA. (A) strict consensus, (B) 50% majority rule consensus. The numbers represent the percentage that the clades are found in the 208 trees. Unnumbered clades are represented in 100% of the trees, and polytomies indicate components represented in less than 50% of the trees.

demarcated areas: Cuba, southern Hispaniola, Hispaniola (exclusive of southern Hisp.), Puerto Rico, Jamaica, northern Lesser Antilles, southern Lesser Antilles, Nuclear (=northern) Central America, Lower Central America, North America, South America, and Africa.

As noted above, the geologic history of the Caribbean has been an exceedingly complex series of fragmentations, accretions, orogenies, and subsidences. As such, a single hypothesis of area relationships

may be unrealistic to propose. Rosen (1985) derived 19 possible four-area cladograms (excluding Puerto Rico but including the Bahamas and eastern and western Cuba) based on accretions and fragmentations. All of these may possibly reflect a vicariance history, but we believe that a simpler, single pattern of vicariance should be discoverable through the complexity. Buskirk (1985) depicted the pattern based on the fragmentation of the main blocks of the Greater Antilles. Her hypothesis suggested (((Hispaniola, Puerto Rico)Cuba)Jamaica, Mainland) (Fig. 5). If there was an original concordant dispersal onto the proto-Antilles and these taxa responded to subsequent island fragmentations through speciation, that pattern depicted by Buskirk should be present in the current Caribbean biota. Although the complexity of the history means several vicariance signals may be present (Page and Lydeard, 1994; Rosen, 1985), this single, simple pattern should have a strong signal (barring extensive extinction). This pattern is the only one that would encompass the entire history of the Greater Antilles, from the first fragmentation to the last, and as such we believe it is the most meaningful pattern in the vicariance/dispersal debate.

A branch and bound analysis yielded 208 most parsimonious trees (out of over 10^{10} possible trees) of 117 steps with a CI = 0.635 (excluding uninformative characters; CI = consistency index: Kluge and Farris, 1969) and an RI = 0.648 (RI = retention index: Farris, 1989). A tree-length frequency distribution analysis of 50,000 random trees (Hillis, 1991) strongly indicated that the data contains phylogenetic signal ($g1 = -0.63$, $P = 0.01$; Hillis and Huelsenbeck, 1992). This suggests that the characters (trees in this case) show non-random congruence. The strict consensus tree shows (((southern Hispaniola, Hispaniola)Puerto Rico)Cuba)Jamaica) with all the other areas unresolved (Fig. 6). The 50% majority-rule consensus tree suggests a Central America relationship congruent between the BPA result and the pattern suggested by Buskirk (1985). The differences are the inclusion of southern Hispaniola in our data set and the resolved

basal position (relative to the other Greater Antilles) of Jamaica. The results suggest that a vicariance pattern is present among the sample of taxa in this analysis.

Interpretation of the pattern in terms of fragmentation history is straightforward. The following description is based on tectonic evidence discussed earlier. The Greater Antilles as a block fragmented from mainland sources initially with Jamaica subsequently separating from the rest of the Greater Antilles first. Cuba split off next from the Hispaniola/Puerto Rico amalgamation, and then Puerto Rico separated from Hispaniola. Southern Hispaniola accreted to the main Hispaniola island and dispersal ensued. Subsequent inundation separated the south and north islands and the widespread populations, which responded by allopatric speciation. Evidence to support the southern Hispaniola-Hispaniola scenario comes from the deposition of a carbonate shelf sequence (limestone) over most of southern Hispaniola from the Eocene to the mid-Miocene and repeated seawater incursions into the Enriquillo Valley post-Miocene through Pleistocene (Mann et al., 1984). The unresolved non-Greater Antillean areas may suggest that the original biotic source units for the Greater Antilles were varied and cosmopolitan (not surprisingly).

Instead of vicariance, could the recovered pattern be explained equally well by concordant dispersal? Concordant dispersal could in fact result in recurrent patterns that may be indistinguishable from vicariance. However, we rule out the concordant dispersal hypothesis because we cannot think of any mechanism that would allow concordant over-water dispersal for disparate groups such as freshwater fish, caddisflies, and snakes.

What of the biotic history of Jamaica? Buskirk (1985) plotted Jamaica as a basal polytomy in her relationships of the Greater Antilles and further noted its biotic uniqueness by examining presence and absence of taxa (Buskirk, 1992). As Buskirk (1985, 1992), Hedges et al. (1992), and we have noted, there is a plethora of data to suggest that Jamaica was submerged for an extended period after its separation from

northern Central America. Could a small portion of Jamaica perhaps have remained emergent with a biota and consequently retain a biological connection to the early fragmentation of the Greater Antilles? We would suggest that the absence of any recurrent pattern of sister taxa area relationships indicates a dispersal history for Jamaica's current biota. Of the taxa that we surveyed with Jamaican residents, there is a varied assortment of sister area relationships (Fig. 7) including southern Hispaniola, Central America, Puerto Rico, Bahamas, Cayman Islands and/or Cuba/Cayman Islands, Mexico, northern Lesser Antilles, and more inclusive clades such as Cuba-Hispaniola-Bahamas. Although our BPA cladogram also supports four different sister relationships for Jamaica that are consistent with the vicariance cladogram, the presence of several other sister relationships in our short list suggests dispersal as the probable explanation for the origin of Jamaica's biota. However, the resolved position of Jamaica is also concordant with the order of tectonic fragmentation events, and thus may be considered a refutation of dispersal. Superficially, one would imagine that an island biota the origins of which were via dispersal would perhaps not be resolved and its relationship to other areas would be ambiguous and conflicting. The full resolution in this case is not because of a reflection of vicariance, but because of the way BPA handles dispersal data (Page, 1990). What is indicated in the resolved position of Jamaica is that most of its current biota (at least within our taxonomic groups) were derived from other Greater Antillean sources.

The molecular clock could also be used to support or reject the claims of Jamaica as a dispersal depository. Given that Jamaica became land positive 25 mya, any pair of *sister* species ID's should be less than the equivalent of 25 mya. Unfortunately, these comparisons were not restricted to sister species, and any comparisons between non-sister species would be expected to result in divergence times >25 mya. An examination of Fig. 3 shows 30% of the Jamaica-other Greater Antilles comparisons to be older than 25 mya, but

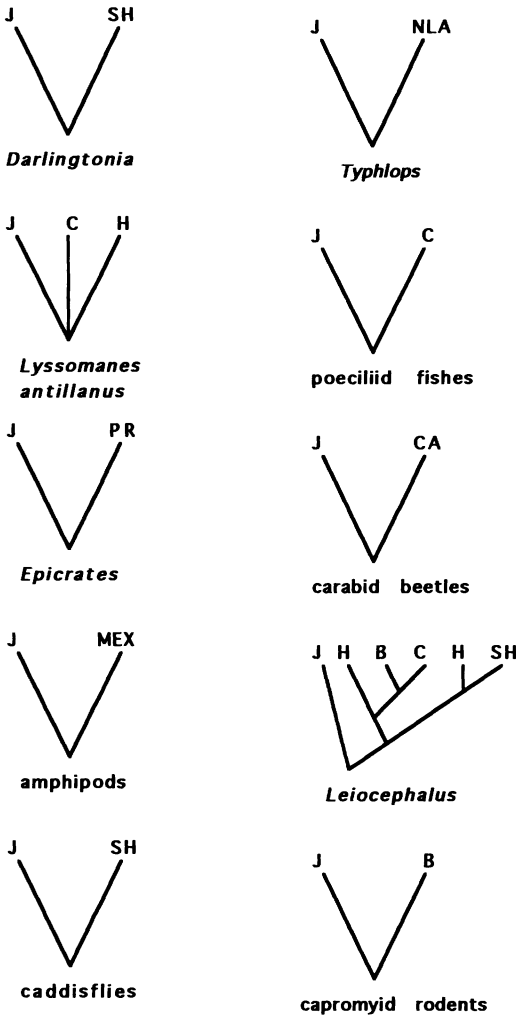


FIG. 7.—Sister area relationships of various Jamaican taxa from clades used in this study. The trichotomy for *Lyssomanes* represents a taxon found in three areas. C = Cuba, J = Jamaica, SH = southern Hispaniola, H = Hispaniola, PR = Puerto Rico, MEX = Mexico, B = Bahamas, NLA = northern Lesser Antilles (above 17°N), CA = Central America.

because of the uncertainty of sister species in these comparisons, the older divergence estimates are equivocal in rejecting dispersal. The presence of pre-emergence dates in the Jamaican taxa are probably attributable to non-sister species comparisons.

CONCLUSIONS

Although much is known about the geologic history of the Caribbean region, sev-

eral key areas remain in debate, especially the timing and sequence of events as the proto-Antilles passed between North and South America, and the later events associated with the accretions and fragmentations of Cuba, Hispaniola, and Puerto Rico. Given these uncertainties, we conclude that studies of historical biogeography should account for this variation (this point is not restricted to Caribbean problems: Cox, 1990).

There seems little doubt that a significant geologic event (either exogenous or endogenous) occurred on the northern coast of the Yucatan about 65 mya, apparently creating a series of tsunamis. Consideration of paleo-bathymetry suggests that the tsunamis were restricted in maximum wave height, thus precluding the possibility that the early islands were scoured and their fauna was washed away. This conclusion is bolstered by immunological data. 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. Instead, a consistent pattern of divergence among Caribbean endemics emerges. This pattern is congruent with at least one vicariance hypothesis and indicates that earth history is at least as important as dispersal in explaining the current distribution of Caribbean organisms.

A consensus finally has emerged among the three data sets used in this study, geology, immunological distances, and phylogeny (sister relationships), to recognize firmly that Jamaica has had a history separate from the rest of the Greater Antilles. The idea is not new (e.g., Simpson, 1956; Vaughan, 1918), but maybe now Caribbean biogeographers will seriously consider the fact that Jamaica is a dispersal depository, and as such represents noise in a vicariance pattern. Lastly, the potential of the cladistic approach to studying historical biogeography is beginning to be realized with the increased availability of cladistic hypotheses. Skepticism concerning the number of phylogenies and the robustness of phylogenies remains (e.g.,

Williams, 1989), and debate continues among the different schools of cladistic biogeography. However, we predict that as cladograms accumulate, the different methods of cladistic biogeography will converge on the same answers.

Acknowledgments.—The following people are thanked for their comments and discussion on the subject: R. Anderson, R. A. Crother, D. R. Frost, A. G. Kluge, A. Knight, J. B. Slowinski, K. Toal, and M. E. White. Aspects of this work were funded by grants from the National Geographic Society (3649-87) and National Science Foundation (DEB-9207751).

LITERATURE CITED

- ADATTE, T., W. STINNESBECK, AND G. KELLER. 1996. Lithostratigraphic and mineralogical correlations of near K/T boundary clastic sediments in NE Mexico: Implications for origin and nature of deposition. In press. In G. Ryder, D. Fastovsky, and S. Gartner (Eds.), *The Cretaceous-Tertiary Event and Other Catastrophes in Earth History*. Geol. Soc. Am. Spec. Pap. 307.
- ARDEN, D. D. 1975. The geology of Jamaica and the Nicaraguan Rise. Pp. 617-661. In A. E. M. Nairn and F. G. Stehli (Eds.), *Ocean Basins and Margins. 3: Gulf Coast, Mexico and the Caribbean*. Plenum Press, New York, New York.
- AVISE, J. C., J. C. PATTON, AND C. F. AQUARDO. 1980. Evolutionary genetics of birds II. Conservative protein evolution in North American sparrows and relatives. *Syst. Zool.* 29:323-334.
- AVISE, J. C., B. W. BOWEN, T. LAMB, A. B. MEYLAN, AND E. BERMINGHAM. 1992. Mitochondrial DNA evolution at a turtle's pace: Evidence for low genetic variability and reduced microevolutionary rate in the testudines. *Mol. Biol. Evol.* 9:457-473.
- BARBOUR, T. 1914. A contribution to the zoogeography of the West Indies, with especial reference to amphibians and reptiles. *Mem. Mus. Comp. Zool.* 44:209-359.
- . 1916. Some remarks upon Matthew's Climate and Evolution, with supplementary note by W. D. Matthew. *Ann. New York Acad. Sci.* 27:1-15.
- BOURGOIS, J., T. A. HANSEN, P. L. WIBERG, AND E. G. KAUFFMAN. 1988. A tsunami deposit at the Cretaceous-Tertiary boundary in Texas. *Science* 241:567-241.
- BRIGGS, J. C. 1984. Freshwater fishes and biogeography of Central America and the Antilles. *Syst. Zool.* 33:428-435.
- BROOKS, D. R. 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. *Syst. Zool.* 39:14-30.
- BROOKS, D. R., AND D. H. MCLENNAN. 1991. *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. University of Chicago Press, Chicago, Illinois.
- BURKE, K. 1988. Tectonic evolution of the Caribbean. *Ann. Rev. Earth Planet. Sci.* 16:201-230.
- BURKE, K., J. GRIPPI, AND A. M. C. SENGOR. 1980. Neogene structures in Jamaica and the tectonic style of the northern Caribbean plate boundary zone. *J. Geol.* 88:375-386.
- BURKE, K., C. COOPER, J. F. DEWEY, P. MANN, AND J. L. PINDELL. 1984. Caribbean tectonics and relative plate motions. Pp. 31-64. In W. E. Bonini, R. B. Hargraves, and R. Shagam (Eds.), *The Caribbean South American Plate Boundary and Regional Tectonics*. Geol. Soc. Am. Mem. 162.
- 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.
- BUSKIRK, R. E. 1985. Zoogeographic patterns and tectonic history of Jamaica and the northern Caribbean. *J. Biogeog.* 12:445-461.
- . 1992. Zoogeographic and plate tectonic relationships of Jamaica to Mesoamerica. Pp. 9-16. In S. P. Darwin and A. L. Welden (Eds.), *Biogeography of Mesoamerica*. Tulane University, New Orleans, Louisiana.
- CADLE, J. E. 1985. The neotropical colubrid snake fauna (Serpentes: Colubridae): Lineage components and biogeography. *Syst. Zool.* 34:1-20.
- . 1988. Phylogenetic relationships among advanced snakes. *Univ. California Publ. Zool.* 119:1-77.
- CANDOLLE, A.-P. DE. 1820. *Geographie botanique*. *Dict. Sci. Nat.* 18:359-422.
- CARLSON, S. S., A. C. WILSON, AND L. R. MAXSON. 1978. Do albumin clocks run on time? *Science* 200:1183-1185.
- COX, C. B. 1990. New geological theories and old biogeographical problems. *J. Biogeog.* 17:117-130.
- CROIZAT, L. 1958. *Panbiogeography*. Published by the author. Caracas, Venezuela.
- . 1964. *Space, Time, Form: The Biological Synthesis*. Published by the author. Caracas, Venezuela.
- CROIZAT, L., G. NELSON, AND D. E. ROSEN. 1974. Centers of origin and related concepts. *Syst. Zool.* 23:265-287.
- CROTHER, B. I. 1989. *Phylogeny and Biogeography of the West Indian Xenodontine Snakes: A Biochemical Perspective*. Ph.D. Dissertation, University of Miami, Coral Gables, Florida.
- CROTHER, B. I., M. M. MIYAMOTO, AND W. F. PRESCH. 1986. Phylogeny and biogeography of the lizard family Xantusiidae. *Syst. Zool.* 38:37-45.
- DARLINGTON, P. J., JR. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. *Q. Rev. Biol.* 13:274-300.
- DENGO, G., AND J. E. CASE (EDS.) 1990. *The Caribbean Region. The Geology of North America*. Geological Society of America, Boulder, Colorado.
- DIETZ, R. S., AND J. C. HOLDEN. 1970. Reconstruction of Pangea: Breakup and dispersion of continents, Permian to present. *J. Geophys. Res.* 75:4939-4956.
- DONNELLY, T. W. 1988. Geologic constraints on Caribbean biogeography. Pp. 15-37. In J. K. Liebherr (Ed.), *Zoogeography of Caribbean Insects*. Comstock, Ithaca, New York.

- . 1989. Geologic history of the Caribbean and Central America. Pp. 299–321. In A. W. Bally and A. R. Palmer (Eds.), *The Geology of North America—An Overview*. Geological Society of America, Boulder, Colorado.
- DUNCAN, R. A., AND R. B. HARGRAVES. 1984. Plate tectonic Caribbean evolution in the mantle reference frame. Pp. 81–84. In W. E. Bonini, R. B. Hargraves, and R. Shagam (Eds.), *The Caribbean—South American Plate Boundary and Regional Tectonics*. Geol. Soc. Am. Mem. 162.
- ENDLER, J. A. 1982. Problems in distinguishing historical from ecological factors in biogeography. *Am. Zool.* 22:441–452.
- FARRIS, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5:417–419.
- FELSENSTEIN, J. 1985. Phylogenetics and the comparative method. *Am. Nat.* 125:1–15.
- FREELAND, G. L., AND R. S. DIETZ. 1971. Plate tectonic evolution of the Caribbean–Gulf of Mexico region. *Nature* 232:20–23.
- GAULT, D. E., AND C. P. SONETT. 1982. Laboratory simulation of pelagic asteroidal impact: Atmospheric injection, benthic topography, and the surface wave radiation field. Pp. 69–92. In L. T. Silver and P. H. Schultz (Eds.), *Geological Implications of Impacts of Large Asteroids and Comets on the Earth*. Geol. Soc. Am. Spec. Pap. 190.
- GORMAN, G. C., D. G. BUTH, AND J. S. WYLES. 1980. *Anolis* lizards of the eastern Caribbean: A case study in evolution. III. A cladistic analysis of albumin immunological data, and the definitions of species groups. *Syst. Zool.* 29:143–158.
- GUYER, G., AND J. M. SAVAGE. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). *Syst. Zool.* 35:509–531.
- . 1992. Anole systematics revisited. *Syst. Biol.* 41:89–110.
- GUYER, G., AND J. B. SLOWINSKI. 1991. Comparisons of observed phylogenetic topologies with null expectations among three monophyletic lineages. *Evolution* 45:340–350.
- HABIB, D., R. K. OLSSON, C. LIU, AND S. MOSHKOVITZ. 1996. High resolution biostratigraphy of sea level, low biotic extinction, and chaotic sedimentation at the Cretaceous/Tertiary boundary in Alabama, north of the Chicxulub crater. In press. In G. Ryder, D. Fastovsky, and S. Gartner (Eds.), *The Cretaceous–Tertiary Event and Other Catastrophes in Earth History*. Geol. Soc. Am. Spec. Pap. 307.
- HAMILTON, S. W. 1988. Historical biogeography of two groups of Caribbean *Polycentropus* (Trichoptera: Polycentropodidae). Pp. 153–182. In J. K. Liebherr (Ed.), *Zoogeography of Caribbean Insects*. Comstock, Ithaca, New York.
- HARVEY, A. W. 1992. Three-taxon statements: More precisely, an abuse of parsimony? *Cladistics* 8:345–354.
- HASS, C. A. 1991. Evolution and biogeography of West Indian *Sphaerodactylus* (Sauria: Gekkonidae): A molecular approach. *J. Zool., London* 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., London* 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* (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*. Sandhill Crane Press, Gainesville, Florida.
- 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. *Carib. 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. Natl. Acad. Sci. USA* 89:1909–1913.
- HENNIG, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana, Illinois.
- HERSHKOVITZ, P. 1972. The recent mammals of the neotropical region: A zoogeographic and ecological review. Pp. 311–431. In A. Keast, F. C. Erk, and B. Glass (Eds.), *Evolution, Mammals, and Southern Continents*. State University of New York Press, Albany, New York.
- HILDEBRAND, A. R., AND W. V. BOYNTON. 1990. Proximal Cretaceous–Tertiary boundary impact deposits in the Caribbean. *Science* 248:843–847.
- HILLIS, D. M. 1987. Molecular versus morphological approaches to systematics. *Ann. Rev. Ecol. Syst.* 18:23–42.
- . 1988. Systematics of the *Rana pipiens* complex: Puzzle and paradigm. *Ann. Rev. Ecol. Syst.* 19:39–63.
- . 1991. Discriminating between phylogenetic signal and random noise. Pp. 278–294. In M. M. Miyamoto and J. Cracraft (Eds.), *Phylogenetic Analysis of DNA Sequences*. Oxford University Press, New York, New York.
- HILLIS, D. M., AND J. P. HUELSENBECK. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. *J. Heredity* 83:189–195.
- HILLIS, D. M., AND C. MORITZ. 1990. *Molecular Systematics*. Sinauer, Sunderland, Massachusetts.
- HUBBY, J. L., AND L. H. THROCKMORTON. 1968. Protein differences in *Drosophila*. IV. A study of sibling species. *Am. Nat.* 102:193–205.
- HUMPHRIES, C. J., AND L. PARENTI. 1986. *Cladistic Biogeography*. Academic Press, London, U.K.
- ISACKS, B., J. OLIVER, AND L. R. SYKES. 1968. Seismology and the new global tectonics. *J. Geophys. Res.* 73:5855–5899.
- JENNER, J. V. 1981. *A Zoogeographic Study and the*

- Taxonomy of the Xenodontine Colubrid Snakes. Ph.D. Dissertation, New York University.
- JOGLAR, R. L. 1989. Phylogenetic relationships of the West Indian frogs of the genus *Eleutherodactylus*: A morphological analysis. Pp. 371–408. In C. A. Woods (Ed.), *Biogeography of the West Indies*. Sandhill Crane Press, Gainesville, Florida.
- KASHFI, M. S. 1983. Geology and hydrocarbon prospects of Jamaica. *Bull. Am. Assoc. Petrol. Geol.* 67: 2117–2124.
- KELLER, G. 1992. Anti-impactors have their day in K–T court. *Sci. News* 142:310.
- KLUGE, A. G. 1988. Parsimony in vicariance biogeography: A quantitative method and a Greater Antillean example. *Syst. Zool.* 37:315–328.
- . 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* 38:7–25.
- . 1993. Three-taxon transformation in phylogenetic inference: Ambiguity and distortion as regards explanatory power. *Cladistics* 9:246–259.
- . 1995. Cladistic relationships of sphaerodactyl lizards. *Am. Mus. Novit.* 3139:1–23.
- KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18:1–32.
- KNOWLTON, N. 1993. Sibling species in the sea. *Ann. Rev. Ecol. Syst.* 24:189–216.
- LADIGES, P. Y., S. M. PROBER, AND G. NELSON. 1992. Cladistic and biogeographic analysis of the 'blue ash' eucalypts. *Cladistics* 8:103–124.
- LINDEMAN, D. 1991. Phylogeny and zoogeography of the New World terrestrial amphipods (landhoppers) (Crustacea: Amphipoda: Talitridae). *Can. J. Zool.* 69:1104–1116.
- LEWIS, J. F., AND G. DRAPER. 1990. Geology and tectonic evolution of the northern Caribbean margin. Pp. 77–140. In G. Dengo and J. E. Case (Eds.), *The Caribbean Region*. Geological Society of America, Boulder, Colorado.
- LIEBHERR, J. K. 1988. Biogeographic patterns of West Indian *Platynus* carabid beetles (Coleoptera). Pp. 121–152. In J. K. Liebherr (Ed.), *Zoogeography of Caribbean Insects*. Comstock, Ithaca, New York.
- LOPEZ-OLIVA, J. G., AND G. KELLER. 1996. Age and stratigraphy of near-K/T boundary clastic deposits in NE Mexico. In press. In G. Ryder, D. Fastovsky, and S. Gartner (Eds.), *The Cretaceous–Tertiary Event and Other Catastrophes in Earth History*. *Geol. Soc. Am. Spec. Pap.* 307.
- MACFADDEN, B. J. 1980. Rafting mammals or drifting islands? Biogeography of the Greater Antillean insectivores *Nesophontes* and *Solenodon*. *J. Biogeog.* 7:11–22.
- MANN, P., F. W. TAYLOR, K. BURKE, AND R. KULSTAD. 1984. Subaerially exposed Holocene coral reef, Enriqueillo Valley, Dominican Republic. *Geol. Soc. Am. Bull.* 95:1084–1092.
- MANN, P., C. SHUBERT, AND K. BURKE. 1990. Review of Caribbean neotectonics. Pp. 307–338. In G. Dengo and J. Case (Eds.), *The Caribbean Region*. Geological Society of America, Boulder, Colorado.
- MATTSON, P. H. 1984. Caribbean structural breaks and plate movements. Pp. 131–152. In W. E. Bonini, R. B. Hargraves, and R. Shagam (Eds.), *The Caribbean–South American Plate Boundary and Regional Tectonics*. *Geol. Soc. Am. Mem.* 162.
- MATTHEW, W. D. 1915. *Climate and Evolution*. *Ann. New York Acad. Sci.* 24:171–318.
- MAURRASSE, F. J.-M. R., AND G. SEN. 1991. Impacts, tsunamis, and the Haitian Cretaceous–Tertiary boundary layer. *Science* 252:1690–1693.
- MAXSON, L. R. 1992. Tempo and pattern in anuran speciation and phylogeny: An albumin perspective. Pp. 41–57. In K. Adler (Ed.), *Herpetology: Current Research on the Biology of Amphibians and Reptiles*. Proceedings of the First World Congress of Herpetology. Society of the Study of Amphibians and Reptiles, Oxford, Ohio.
- MAXSON, L. R., AND R. D. MAXSON. 1990. Proteins II: Immunological techniques, Pp. 127–155. In D. M. Hillis and C. Moritz (Eds.), *Molecular Systematics*. Sinauer, Sunderland, Massachusetts.
- MAYR, E. 1982. Vicariance biogeography. *Auk* 99: 618–620.
- MCCARTNEY, K., A. R. HUFFMAN, AND M. TREDoux. 1990. A paradigm for endogenous causation of mass extinctions. Pp. 125–138. In V. L. Sharpton and P. D. Ward (Eds.), *Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*. *Geol. Soc. Am. Spec. Pap.* 247.
- MEYERHOFF, A. A., AND E. A. KREIG. 1977. Jamaican petroleum potential; 2, five major cycles make up Jamaican tectonic and structural history, Part 2. *Oil Gas J.* 75:141–146.
- MEYERHOFF, A. A., J. B. LYONS, AND C. B. OFFICER. 1994. Chicxulub structure: A volcanic sequence of late Cretaceous age. *Geology* 22:3–4.
- MIYAMOTO, M. M. 1983. Biochemical variation in the frog *Eleutherodactylus bransfordii*: Geographic patterns and cryptic species. *Syst. Zool.* 32:43–51.
- MONTGOMERY, H., E. A. PESAGNO, AND J. L. PINDELL. 1994. A 195 ma terrane in a 165 ma sea: Pacific origin of the Caribbean plate. *GSA Today* 4:1–4.
- MORGAN, W. J. 1968. Rises, trenches, great faults, and crustal blocks. *J. Geophys. Res.* 73:1959–1982.
- MORRIS, A. E. L., I. TANER, H. A. MEYERHOFF, AND A. A. MEYERHOFF. 1990. Tectonic evolution of the Caribbean region; Alternative hypothesis. Pp. 433–457. In G. Dengo and J. E. Case (Eds.), *The Caribbean Region*. Geological Society of America, Boulder, Colorado.
- MYERS, G. S. 1938. Fresh-water fishes and West Indian zoogeography. *Ann. Rep. Smithsonian Inst.* 1937:339–364.
- NELSON, G. 1969. The problem of historical biogeography. *Syst. Zool.* 18:243–246.
- . 1974. Historical biogeography: An alternative formalization. *Syst. Zool.* 23:555–558.
- . 1978. From Candolle to Croizat: Comments on the history of biogeography. *J. Hist. Biol.* 11:269–305.
- . 1983. Vicariance and cladistics: Historical perspectives with implications for the future. Pp. 469–492. In R. W. Sims, J. H. Price, and P. E. S.

- Whalley (Eds.), *Evolution, Time and Space: The Emergence of the Biosphere*. Academic Press, London, U.K.
- NELSON, G., AND N. I. PLATNICK. 1981. *Systematics and Biogeography*. Columbia University Press, New York, New York.
- NELSON, G., AND P. Y. LADIGES. 1991. Three-area statements: Standard assumptions for biogeographic analysis. *Syst. Zool.* 40:470-485.
- PAGE, R. D. M. 1988. Quantitative cladistic biogeography: Constructing and comparing area cladograms. *Syst. Zool.* 37:254-270.
- . 1990. Component analysis: A valiant failure? *Cladistics* 6:119-136.
- PAGE, R. D. M., AND C. LYDEARD. 1994. Towards a cladistic biogeography of the Caribbean. *Cladistics* 10:21-41.
- PATTERSON, C. 1981. Methods of paleobiogeography. Pp. 446-497. In G. Nelson and D. E. Rosen (Eds.), *Vicariance Biogeography—A Critique*. Columbia University Press, New York, New York.
- PENFIELD, G. T., AND Z. A. CAMARGO. 1981. Definition of a major igneous zone in the central Yucatan platform with aeromagnetism and gravity. *Soc. Explor. Geophys. Tech. Program, Abstracts and Biographies* 51:57.
- PERFIT, M. R., AND E. E. WILLIAMS. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean sea and its islands. Pp. 47-102. In C. A. Woods (Ed.), *Biogeography of the West Indies*. Sandhill Crane Press, Gainesville, Florida.
- PINDELL, J. L., AND J. F. DEWEY. 1982. Permian-Triassic reconstruction of western Pangea and the evolution of the Gulf of Mexico, Bahamas, and proto-Caribbean Sea. *Tectonics* 4:1-39.
- PINDELL, J. L., S. C. CANDE, W. C. PITMAN, III, D. B. ROWLEY, J. F. DEWEY, J. LABREQUE, AND W. HAXBY. 1988. A plate-kinematic framework for models of Caribbean evolution. *Tectonophysics* 155:121-138.
- PINDELL, J. L., 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 Caribbean Region*. Geological Society of America, Boulder, Colorado.
- PINDELL, J. L., AND G. DRAPER. 1991. Stratigraphy and geological history of the Puerto Plata area, northern Dominican Republic. 1991. Pp. 97-114. In P. Mann, G. Draper, and J. F. Lewis (Eds.), *Geologic and Tectonic Development of the North America-Caribbean Plate Boundary in Hispaniola*. *Geo. Soc. Am. Spec. Pap.* 262.
- PLATNICK, N. I., AND G. NELSON. 1978. A method of analysis for historical biogeography. *Syst. Zool.* 27:1-16.
- POPE, K. O., A. C. OCAMPO, AND C. E. DULLER. 1991. Mexican site for K/T impact crater? *Nature* 351:105.
- PREGILL, G. K. 1981a. An appraisal of the vicariance hypothesis of Caribbean biogeography and its application to West Indian terrestrial vertebrates. *Syst. Zool.* 30:147-155.
- . 1981b. Cranial morphology and the evolution of West Indian toads (Salientia: Bufonidae): Resurrection of the genus *Peltophryne* Fitzinger. *Copeia* 1981:273-285.
- . 1992. Systematics of the West Indian lizard genus *Leiocephalus* (Squamata: Iguania: Tropiduridae). *Misc. Pub. Univ. Kansas Mus. Nat. Hist.* 84:1-69.
- RAUCHENBERGER, M. 1988. Historical biogeography of poeciliid fishes in the Caribbean. *Syst. Zool.* 37:356-365.
- REISKIND, J. 1989. The potential use of amber fossils in the study of the biogeography of spiders in the Caribbean with the description of a new species of *Lyssomanes* from the Dominican amber (Araneae: Salticidae). Pp. 217-228. In C. A. Woods (Ed.), *Biogeography of the West Indies*. Sandhill Crane Press, Gainesville, Florida.
- ROSEN, D. E. 1976. A vicariance model of Caribbean biogeography. *Syst. Zool.* 24:431-464.
- . 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* 27:159-188.
- . 1985. Geological hierarchies and biogeographic congruence in the Caribbean. *Ann. Missouri Bot. Gard.* 72:636-659.
- ROSS, M. I., AND C. R. SCOTESE. 1988. A hierarchical tectonic model of the Gulf of Mexico and Caribbean region. *Tectonophysics* 155:139-168.
- ROUGHGARDEN, J. 1990. Origin of the eastern Caribbean: Data from reptiles and amphibians. Pp. 10-26. In D. K. Larue and G. Draper (Eds.), *Transactions of the 12th Caribbean Geological Conference*, St. Croix, U.S.V.I. Miami Geological Society, Miami, Florida.
- . 1995. *Anolis* lizards of the Caribbean. *Ecology, Evolution and Plate Tectonics*. Oxford University Press, New York, New York.
- SALVADOR, A., AND A. R. GREEN. 1980. Opening of the Caribbean Tethys. In *Geologie de Chaines Alpines Issues de la Tethys*. *Mem. Bur. Rech. Geol. Minières* 115:224-229.
- SAVAGE, J. M. 1982. The enigma of the Central American herpetofauna: Dispersals or vicariance? *Ann. Missouri Bot. Gard.* 69:464-547.
- SAVAGE, J. M., AND C. GUYER. 1989. Infrageneric classification and species composition of the anole genera, *Anolis*, *Ctenonotus*, *Dactyloa*, *Norops*, and *Semiurus* (Sauria: Iguanidae). *Amphibia-Reptilia* 10:105-116.
- SEIDEL, M. E. 1988. Revision of the West Indian emydid turtles (Testudines). *Am. Mus. Novit.* 2918:1-41.
- SHARPTON, V. L., K. BURKE, A. CAMARGO-ZANOGUERA, S. A. HALL, D. S. LEE, L. E. MARIN, G. SUAREZ-REYNOSO, J. M. QUEZADA-MUNETON, P. D. SPUDIS, AND J. URRUTIA-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 study of albumins of *Anolis* lizards of the Caribbean islands. *Comp. Biochem. Physiol.* 68A:67-73.
- SIGURDSSON, H., S. D'HONDT, M. A. ARTHUR, T. J. BRALOWER, J. C. ZACHOS, M. VAN FOSSEN, AND J.

- E. T. CHANNELL. 1991. Glass from the Cretaceous/Tertiary boundary in Haiti. *Nature* 349:482-487.
- SIMPSON, G. G. 1956. Zoogeography of West Indian land mammals. *Am. Mus. Novit.* 1759:1-28.
- SMIT, J., A. MONTANARI, N. H. M. SWINBURNE, W. ALVAREZ, A. R. HILDEBRAND, S. V. MARGOLIS, P. CLAEYS, W. LOWRIE, AND F. ASARO. 1992. Tektite-bearing, deep-water clastic unit at the Cretaceous-Tertiary boundary in northeastern Mexico. *Geology* 20:99-103.
- SMIT, J. A., TH. B. ROEP, W. ALVAREZ, A. MONTANARI, P. CLAEYS, J. M. GRAJALES-NISHIMURA, AND J. BERMUDEZ. 1996. In G. Ryder, D. Fastovsky, and S. Gartner (Eds.), *The Cretaceous-Tertiary Event and Other Catastrophes in Earth History*. *Geol. Soc. Am. Spec. Pap.* 307.
- SMITH, D. L. 1985. Caribbean plate relative motions. Pp. 17-48. In F. G. Stehli and S. D. Webb (Eds.), *The Great American Biotic Interchange*. Plenum, New York, New York.
- SOBER, E. 1988. The conceptual relationship of cladistic phylogenetics and vicariance biogeography. *Syst. Zool.* 37:245-253.
- STINNESBECK, W., AND G. KELLER. 1996. K/T boundary course-grained clastic deposits in northeastern Mexico and northeastern Brazil: Evidence for megatsunami or sea-level changes? In G. Ryder, D. Fastovsky, and S. Gartner (Eds.), *The Cretaceous-Tertiary Event and other Catastrophes in Earth History*. *Geol. Soc. Am. Spec. Pap.* 307.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- 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.
- THOMAS, R. 1989. The relationships of Antillean *Typhlops* (Serpentes: Typhlopidae) and the description of three new Hispaniolan species. Pp. 409-432. In C. A. Woods (Ed.), *Biogeography of the West Indies*. Sandhill Crane Press, Gainesville, Florida.
- TOLSON, P. J. 1987. Phylogenetics of the boid snake genus *Epicrates* and the Caribbean vicariance theory. *Occas. Pap. Mus. Zool. Univ. Michigan.* 715:1-68.
- VAUGHAN, T. W. 1918. Geologic history of Central America and the West Indies during Cenozoic time. *Geol. Soc. Am. Bull.* 29:615-630.
- WADGE, G., AND K. BURKE. 1983. Neogene Caribbean plate rotation and associated Central American tectonic evolution. *Tectonics* 2:633-643.
- WARD, W. C., A. E. WEIDIE, AND W. BACK. 1985. Geology and hydrogeology of the Yucatan and Quaternary geology of northeastern Yucatan peninsula. *New Orleans Geol. Soc.* 1-19.
- WAYNE, R. K., B. VAN VALKENBURGH, AND S. J. O'BRIEN. 1991. Molecular distance and divergence time in carnivores and primates. *Mol. Biol. Evol.* 8:297-319.
- WILEY, E. O. 1988. Parsimony analysis and vicariance biogeography. *Syst. Zool.* 37:271-290.
- WILLIAMS, E. E. 1976. West Indian anoles: A taxonomic and evolutionary summary. 1. Introduction and species list. *Breviora* 440:1-31.
- . 1989. 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.
- WILSON, J. T. 1966. Did the Atlantic close and then reopen? *Nature* 211:676-681.
- WOODS, C. A. 1989. The biogeography of West Indian rodents. Pp. 799-826. 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. 1980a. The albumin immunological and Nei electrophoretic distance correlation: A calibration for the saurian genus *Anolis* (Iguanidae). *Copeia* 1980:66-71.
- . 1980b. The classification of *Anolis*: Conflict between genetic and osteological interpretations as exemplified by *Anolis cybotes*. *J. Herpetol.* 14:149-153.

Accepted: 29 December 1995

Associate Editor: Henry Mushinsky