2 Biogeography of the West Indies: An Overview

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Abstract — The West Indies harbor a diverse flora and fauna with high levels of endemism. This, coupled with a complex geological history, has attracted interest in the historical biogeography of the region. Two major models have been proposed. The vicariance model proposes that a proto-Antillean biota connecting North and South America in the late Cretaceous was fragmented by plate tectonic movement to form the current island biotas. The dispersal model suggests that organisms dispersed over water during the Cenozoic to reach the islands. A variation on the dispersal model proposes that a dry land bridge connected the Greater Antilles with South America for a short time during the mid-Cenozoic, facilitating dispersal into the Antilles. Most biogeographical studies addressing these models have been based on well-studied groups of vertebrates. Two lines of evidence suggest that dispersal, and not vicariance or a mid-Cenozoic dry land bridge, is responsible for the origin of most lineages studied. First, most West Indian groups are characteristically depauperate at the higher taxonomic levels, yet they often have some unusually large radiations of species. This taxonomic pattern, which is reflected in the fossil record, suggests that niches left vacant by groups absent from the Antilles have been filled by other groups present. Second, times of divergence estimated by molecular clocks indicate that most lineages arrived during the Cenozoic at times when there were no continental connections with the islands. These two lines of evidence are congruent with the nearly unidirectional current flow in the West Indies that probably brought flotsam from rivers in South America to these islands throughout the Cenozoic. Despite this general pattern, a few groups appear to have arrived very early and may represent ancient relicts of the proto-Antilles. The geological history and paleogeography of the West Indies is exceedingly complex and different authors have suggested different scenarios based on the same evidence. For this reason, it is too soon to exclude any particular model of Caribbean biogeography. The geological database and fossil record will continue to improve, phylogenetic relationships will become better known, and molecular divergence time estimates soon will be available for a wide diversity of taxa. Therefore, despite shortcomings of the current models, we can look forward, in the near future, to resolving many of these long unanswered questions of Caribbean biogeography.

INTRODUCTION

A significant percentage of the Earth's known terrestrial biota is distributed on islands of the West Indies (Figure 1). Many of those species are endemic to the region, to individual islands, and even to isolated areas within some islands. Dominican amber fossils indicate with great clarity that the West Indies has been a region with high species diversity and endemism for at least 20 million years (Poinar and Poinar, 1999). In addition, the complex geological history of the region has offered many opportunities for dispersal and vicariance to affect biotas. Together, these features have made the West Indies an appealing region for the study of historical biogeography.

This chapter provides a brief outline of the major hypotheses of Caribbean biogeography being debated and the current evidence bearing on them. Because vertebrates are among the best known organisms in the West Indies, they have been the focus of most biogeographical studies and will be the focus of this outline. This is not intended to be a comprehensive review of Caribbean biogeography but rather an update on the current state of the field. Williams' (1989) earlier outline provides a useful history of the field and its personalities, and a recent review (Hedges, 1996a) is more comprehensive than this one in its treatment of West Indian vertebrates and their historical biogeography.
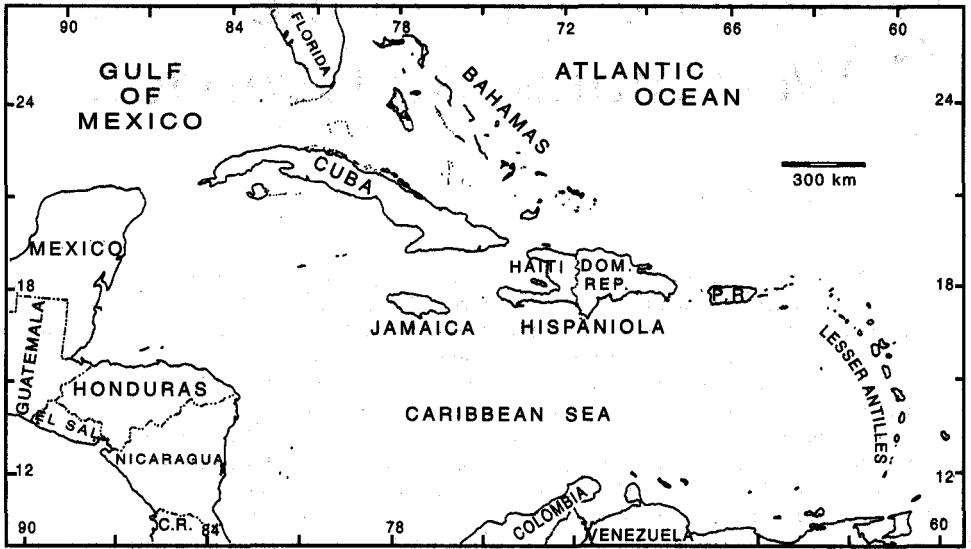
FIGURE 1 The West Indies.

Recently, Iturralde-Vinent and MacPhee (1999) provided a detailed elaboration of their land bridge model of Caribbean biogeography that was proposed earlier (MacPhee and Iturralde-Vinent, 1994; 1995). Their model suggests that a short-lived dry land bridge in the mid-Cenozoic brought land mammals and presumably other aspects of the South American biota to the Greater Antilles. Their paleogeographical reconstructions exclude the possibility of a vicariant origin for the current biota. Moreover, while stopping short of excluding overwater dispersal altogether, they argue that "surface-current dispersal of propagules is inadequate as an explanation of observed distribution patterns of terrestrial faunas in the West Indies" (Iturralde-Vinent and MacPhee, 1999).

A major focus of this outline is to examine the evidence used by Iturralde-Vinent and MacPhee (1999) to support their land bridge model and to show errors and inconsistencies in their argument. In addition, I show that their paleogeographic reconstructions of the Caribbean region have been influenced by the particular biogeographical model that they attempt to support. The current geological evidence does not exclude proto-Antillean vicariance and does not favor a dry land bridge for the mid-Cenozoic Aves Ridge any more than it favors a chain of islands. Finally, I conclude that the same biotic evidence that argues against an origin by vicariance for most lineages also argues against a mid-Cenozoic land bridge.

WEST INDIAN BIOTA

Little is known of the general diversity of bacteria, fungi, and protists in the West Indies or elsewhere (Wilson, 1992; Bayuck, 1999). The flora of the West Indies has not yet undergone a comprehensive review, but there are at least 10,000 species of vascular plants, about one third of which are endemic (Adams, 1972; Gentry, 1992). It is likely that only a small fraction of the invertebrate diversity of the West Indies is known and therefore it is too soon to draw general conclusions. However, the best-known groups tend to exhibit reduced higher-level diversity and have large adaptive radiations of some taxa (Liebherr, 1988; Smith et al., 1994b; Pereira et al., 1997; Schubart et al., 1998).

Vertebrates are the best-studied organisms in the West Indies; there are 1,295 described species (Table 1). Of those, endemism ranges from a low of 35% in birds to 99% in amphibians, with an average of 74%. Taxonomic diversity is poor at the higher levels, with many major groups absent,

TABLE 1
Current Diversity of Native West Indian Terrestrial Vertebrates[a]

Group	Orders	Families[b]	Genera			Species		
			Total	Endemic	% Endemic	Total	Endemic	% Endemic
Fishes	6	9	14	6	43	74	71	96
Amphibians	1	4	6	1	17	174	172	99
Reptiles	3	19	50	9	18	474	443	93
Birds	15	49	204	38	19	425	150	35
Mammals								
Bats	1	7	32	8	25	58	29	50
Other	4	9	36	33	92	90	90	100
Totals	30	97	342	95	28	1295	955	74

[a] After Hedges (1996a), updated.
[b] Including one endemic family of birds and four of mammals.

including primary division freshwater fishes, salamanders, caecilians, marsupials, carnivores, lago-morphs, and most families of frogs, turtles, and snakes. On the other hand, some genera have undergone large radiations. For example, the frog genus *Eleutherodactylus* and the lizard genus *Anolis* each contains at least 140 West Indian species and geckos of the genus *Sphaerodactylus* are not far behind with approximately 85 known species.

Most fossils of terrestrial organisms in the West Indies come from Quaternary deposits (Pregill and Olson, 1981; Pregill et al., 1992; Woods and Ottenwalder, 1992; Morgan, 1993) and Hispaniolan amber (Poinar and Poinar, 1999). There is not complete agreement over the dating of the amber (Poinar and Poinar, 1999), although most authors consider the major amber deposits (e.g., La Toca) to be Oligocene or Early Miocene (30 to 15 million years ago [mya]) (Grimaldi, 1995; Hedges, 1996a; Iturralde-Vinent and MacPhee, 1996). Fossils also are known from other times in the Tertiary (Cockerell, 1924; Graham and Jarzen, 1969; Graham, 1993; MacPhee and Iturralde-Vinent, 1994; 1995; Domning et al., 1997; Pregill, 1999). Dominican amber deposits contain the largest fossil assemblage of terrestrial invertebrates in a tropical environment (Poinar and Poinar, 1999). The amber ant fauna has been suggested to be more continental in taxonomic composition (Wilson, 1985) compared with the extant fauna, but such comparisons have not been made for most other invertebrate groups in amber. The fossil vertebrates found in amber are representatives of extant West Indian groups and include frogs of the genus *Eleutherodactylus*, lizards of the genera *Anolis* and *Sphaerodactylus*, a snake of the genus *Typhlops*, a capromyid rodent, a nesophontid insectivore, and a woodpecker (Poinar and Poinar, 1999). In general, these and other fossil vertebrates from the Tertiary of the West Indies reflect the same taxonomic pattern seen in the Quaternary and extant biota. Exceptions include fossil hair in Dominican amber that may have belonged to a carnivore (Poinar and Poinar, 1999) and an Eocene rhinocerotoid ungulate from Jamaica (Domning et al., 1997). The significance of the Jamaican fossil will be discussed below.

GEOLOGICAL HISTORY

The Caribbean region has had a complex geological history (Dengo and Case, 1990; Donovan and Jackson, 1994). This history began when the supercontinent Pangaea separated into Laurasia (north) and Gondwana (south) in the Jurassic (~170 mya). This created the "space" for the Caribbean plate, which formed later in the mid-Cretaceous. Since that time, the Caribbean plate has been moving eastward relative to the North American and South American plates. The Antilles were formed by andesitic volcanism resulting from the subduction of the North American plate beneath the Caribbean

plate. Initially, these were underwater volcanoes (seamounts) that enlarged with time to rise eventually above the water level as islands. It is not known precisely when the islands became emergent, but the proto-Antillean island arc more or less connected North and South America during the late Cretaceous (~100 to 70 mya).

In the early Cenozoic (~60 mya) the proto-Antilles began to collide with the Bahamas platform (part of the North American plate) and fused. This initiated a transform fault south of Cuba and northern Hispaniola, adding to the geological complexity of the region. This newly defined northern edge of the Caribbean plate moved eastward carrying with it Jamaica and the southern portion of Hispaniola (south of Cul de Sac/Valle de Neiba). Eventually the two (or more) portions of Hispaniola fused in the Miocene (~10 mya). Because the Greater Antilles lie along the northern edge of the Caribbean plate where there has been mostly lateral motion during the Cenozoic, there are no active volcanoes on those islands. On the other hand, there are active volcanoes in the Lesser Antilles because they are at the leading edge of the Caribbean plate and directly above the subducting North American plate.

For biogeography, it is critical to know which areas were above sea level during the geological history of the West Indies. Unfortunately, that is one of the most poorly known aspects of Caribbean geological history. This is because the exposure of dry land is the result of three interrelated factors: uplift, erosion, and sea level. Sea level fluctuations alone cannot be used as a guide, because large mountain ranges can be uplifted and eroded away in a relatively short period of time. For example, the present Blue Mountains (>2200 m) of Jamaica were uplifted only 5 to 10 mya (Comer, 1974). Although the nature of sedimentary strata provides clues to whether there was subaerial land nearby, such strata are not exposed at all locations and at all time periods. It has been claimed that no land areas in the Greater Antilles were continuously above sea level before about 45 mya (MacPhee and Iturralde-Vinent, 1994; MacPhee and Grimaldi, 1996; Iturralde-Vinent and MacPhee, 1999). However, the geological history of the region is not known in enough detail to support such speculation. In fact, other authors have claimed the opposite: "The first terrestrial (emergent) centers seem to have been in the Dominican Republic, Puerto Rico, and the Virgin Islands. In these places the date of emergence is sometime during the Albian (about 100–110 million years), and in these places emergence persisted to the present" (Donnelly, 1992). Also, the plutons of Puerto Rico were being uplifted and eroded in the early Tertiary. Larue (1994) noted that "shallow-water limestone facies are found in north- and south-central Puerto Rico, suggesting that the Central Block may have been a topographic high in the Eocene."

Even some of the best-known features of Caribbean paleogeography may need to be revised in the future. For example, it has been claimed for Jamaica that "probably no part of the island was more than a few meters above sea level at any time" between the middle Eocene and middle Miocene (Robinson, 1994). However, it seems unlikely that the major drop (160 m) in sea level at the beginning of the Oligocene (32.2 mya) (Miller et al., 1996) did not subaerially expose a similar elevation of the carbonate platform. If this happened, then most of the island would have been exposed for millions of years, at least until the platform eroded back to sea level (or subsided). Iturralde-Vinent and MacPhee (1999) make a similar point, arguing in addition that eastern Jamaica has been continuously subaerial since the Eocene and was connected at one point to southern Hispaniola. This case illustrates that paleogeographical reconstruction is difficult and that geologists with similar data can arrive at very different conclusions.

The Bahamas platform has remained a relatively stable carbonate block for most of the Cenozoic (Dietz et al., 1970; Dengo and Case, 1990; Donovan and Jackson, 1994). Only barrier reefs and low islands (as seen today) are believed to have existed in the past. However, the compressional forces of the collision with the proto-Antilles during the early Cenozoic may have caused uplift along the southern margin of the Bahamas platform. Because the platform already was near sea level, any uplift would have exposed dry land for colonization by terrestrial organisms. This biogeographical possibility has not yet been explored.

A large bolide (asteroid, or less likely, a comet) approximately 10 km in diameter struck the Earth in the Caribbean region at 65 mya (Hildebrand and Boynton, 1990). This well-known event almost certainly was responsible for the extinction of the dinosaurs and many other groups. Besides the global effects of the impact, the local effects are of significance to Caribbean biogeography. For example, the proto-Antilles were located only 1 to 3 crater diameters away from the impact site and apparently sustained massive waves (tsunamis) on the order of a kilometer or more in height (Maurrasse, 1991). Gigantic hurricanes (hypercanes) also would have been generated (Emanuel et al., 1994). These local effects of the bolide impact may have destroyed most or all life on the proto-Antilles at that time (Hedges et al., 1992).

OVERWATER DISPERSAL

For islands that have never been connected to other landmasses (e.g., Hawaii, Galápagos), dispersal over water is the only possible biogeographical mechanism. In the case of the West Indies, the complex geological history leaves open the possibility of proto-Antillean vicariance or movement across land bridges. Nonetheless, there is evidence that overwater dispersal was the primary mechanism for the origin of the terrestrial vertebrates (Hedges, 1996a, 1996b). This evidence concerns the taxonomic composition of fauna and molecular clock estimates of divergence time between island lineages and their closest relatives on the mainland.

The unbalanced taxonomic composition of the fauna (see above), with poor representation at the higher levels and enormous adaptive radiations of some groups, has been noted for over a century (Wallace, 1881; Matthew, 1918; Simpson, 1956; Darlington, 1957). This has been termed the "central problem" in Caribbean biogeography (Williams, 1989). Although it is possible to reach such a taxonomic composition by extinction of a pre-existing, diverse fauna, one would expect to see some remnants of that pre-existing complexity in the present fauna. In fact, the great radiation and morphological diversity of such groups as the ground sloths (now extinct) and hystricognath rodents, filling niches normally occupied by other orders of mammals (Morgan and Woods, 1986; Woods, 1990), supports the contention that those other orders were absent during much of the Cenozoic. A similar argument can be made for the gigantism, dwarfism, and unusual adaptations observed in many other West Indian living and extinct groups (Olson, 1978; Morgan and Woods, 1986; Pregill, 1986; Hedges, 1996a).

The other evidence for dispersal as a major biogeographical mechanism comes from molecular clock studies of vertebrates. The number of amino acid differences in the protein serum albumin separating two species can be estimated using the immunological technique of micro-complement fixation (Maxson, 1992). From calibrations with the vertebrate fossil record it has been shown that such immunological distances are correlated with geological time and can be used as a molecular clock. When this method was applied to amphibians and reptiles in the West Indies (Hass, 1991; Hass and Hedges, 1991; Hass et al., 1993; Hass et al., Chapter 11, this volume) it was found that times of origin for West Indian lineages were scattered throughout the Cenozoic and not clustered during one time period (Hedges et al., 1992; Hedges, 1996b). Moreover, nearly all lineages originated more recently than would be predicted based on the vicariance model (see below). This supported an origin by overwater dispersal for most lineages of amphibians and reptiles in the West Indies.

If dispersal is the predominant mechanism, then what was the source area for these lineages? The answer to this question can be obtained from phylogenies, where the source area is inferred from the location of the closest mainland relative to the West Indian lineage. Such an analysis revealed that South America was the major source area for amphibians and reptiles during the Cenozoic (Hedges, 1996b). Although the Greater Antilles, in most places, are closer to North and Central America, this South American origin agrees with the nearly unidirectional water currents in the Caribbean region, flowing from southeast to northwest (Figure 2). Thus, flotsam from rivers in South America that emptied into this current probably carried the ancestors of many Antillean
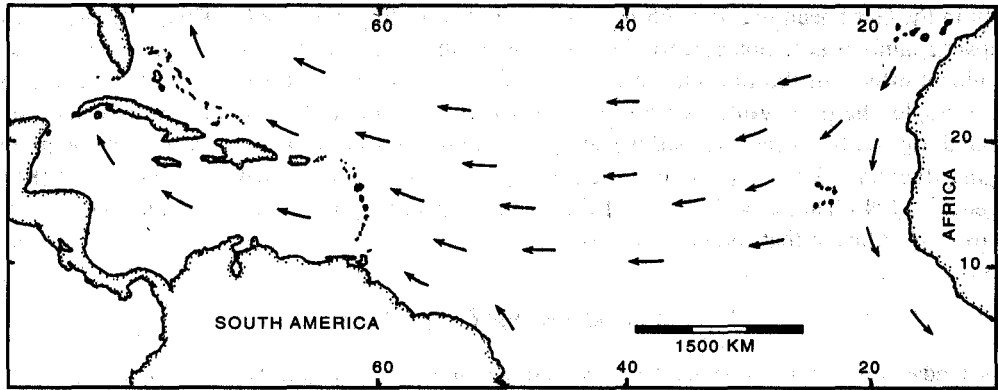
FIGURE 2 The southern half of the North Atlantic Gyre, showing the North Equatorial Current flowing from Africa to South America and the West Indies (after Hedges, 1996b). This same clockwise current flow in the North Atlantic would have operated throughout the Cenozoic because of the Coriolis force.

TABLE 2
The Origin of West Indian Terrestrial Vertebrates[a]

| | | | | | Mammals | | |
Group	Fish	Amphibians	Reptiles	Birds[b]	Bats	Other	Total
Mechanism							
Dispersal	16	8	67	425	42	8	566
Vicariance	0	1	0	0	0	0	1
Undetermined	1	0	1	0	0	1	3
Source							
South America	6	7	35	—	14	7	69
Central America	0	0	8	—	18	1	27
North America	9[c]	0	3	—	2	1	15
Other	2	0	4	—	0	0	6
Undetermined	0	2	18	—	0	0	20

[a] Shown are the numbers of independent lineages (populations, species, and higher taxa), after Hedges (1996a).
[b] The number of lineages in birds is not known, but is >300; the major source area is North America, but the specific number of lineages from each source area is not known.
[c] Some of these lineages of fishes may have arrived from Central America.

lineages (Hedges, 1996b). In some cases, such as the endemic Cuban lizards of the genus *Tarentola*, flotsam probably carried them all of the way from Africa in this same current. Although molecular data generally are lacking for most other vertebrate lineages in the West Indies, some data on relationships and timing can be gleaned from the literature and fossil record. These data showed that overwater dispersal was supported for nearly all (>99%) lineages of West Indian terrestrial vertebrates (Hedges, 1996a). For nonvolant taxa, the primary source area still was South America, but most of the volant taxa (birds, bats) in the West Indies arrived from North and Central America (Table 2).

How could a terrestrial vertebrate such as a frog survive a long journey (several months) across open water? Although floating mats of vegetation (flotsam) have been observed frequently (Guppy, 1917; King, 1962; Heatwole and Levins, 1972), no raft carrying an animal has been seen leaving

a river in South America and later landing in the Greater Antilles. However, flotsam apparently carried green iguanas from Guadeloupe to Anguilla during September and October 1995 and a viable population was established. The entire journey was not verified but lizards were seen on the flotsam as it landed on a beach in Anguilla and circumstantial evidence suggested that the journey began in Guadeloupe at least 1 month earlier as a result of one or two hurricanes (Censky et al., 1998). Those authors elude to the importance of this observation by stating that "for overwater dispersal to be considered a realistic explanation for the distribution of species in the Caribbean, it must be demonstrated that a viable population could be established" (Censky et al., 1998). But this is not so, because many aspects of science are inferred without direct observation (e.g., existence of past life and subatomic particles). In the case of biogeography, the existence of organisms on islands (e.g., Hawaii) that never had connections with continents demonstrates that overwater dispersal must have occurred unless one evokes spontaneous generation. Whether the Greater Antillean fauna owes its origin primarily to dispersal or vicariance is another question. But the fact that dispersal is a "realistic" alternative to vicariance does not rely solely on the observation that green iguanas landed on a beach in Anguilla in 1995.

If tropical storms and hurricanes have been influential in the transfer of flotsam in the Caribbean, then it is possible that the direction of transfer will not always have corresponded to the generalized water current flow. The strong winds of a hurricane, moving in a counterclockwise vortex, will move current in any direction depending on the specific track of the storm. For example, a westward-moving hurricane passing to the north of Puerto Rico and eastern Hispaniola will bring strong winds and currents from west to east across Mona Passage. Whether this would be sufficient to carry flotsam from Hispaniola to Mona or Puerto Rico is not known, but the likelihood must be considered (also, the hurricane itself may reverse direction). Based on the number of hurricanes following such a track during the previous 50 years, it is likely that hundreds of thousands of dispersal opportunities have occurred over the last 20 million years. Some seemingly anomalous distributions of vertebrates, such as the presence of two reptiles (*Anolis longiceps* and *Tropidophis bucculentus*) with Cuban affinities on Navassa Island, may be the result of such hurricane transport. Although such phenomena may explain local distributions, it is unlikely that hurricanes would modify the direction of movement of flotsam over longer distances.

PROTO-ANTILLEAN VICARIANCE

As an alternative to overwater dispersal, Rosen (1975) proposed a vicariance model of Caribbean biogeography. This model suggests that the present West Indian biota represent the fragmented remnants of an ancient biota that was continuous with those of North and South America in the late Cretaceous. Proto-Antillean vicariance cannot be eliminated on geological grounds because even the most current geological models (Dengo and Case, 1990; Donovan and Jackson, 1994) show a proto-Antillean island arc system connecting North and South America during the late Cretaceous. The question whether that island arc formed a dry land bridge or was a chain of islands has not yet been answered conclusively.

Since it was proposed, the vicariance model has proven difficult to test. The original suggestion that the congruence of "tracks" (lines drawn between areas with shared faunas) supports the model is not upheld because distributional congruence could simply reflect similar patterns of dispersal as would be expected with unidirectional current patterns (Hedges, 1996a; 1996b). The same can be said of using phylogenies and area cladograms (Rosen, 1985), although the added difficulty here is that the details of land connections through time in the Greater Antilles remain poorly understood. Some cladistic biogeographers have considered dispersal to be untestable and unscientific, and have placed it in a secondary role (Nelson and Platnick, 1981; Morrone and Crisci, 1995). However, most biogeographers consider dispersal a major mechanism that cannot be ignored.

The same evidence discussed above as support for overwater dispersal is the evidence that argues against vicariance as the primary mechanism explaining the origin of the West Indian fauna.

The taxonomic composition of the current and known Tertiary fauna is depauperate at higher taxonomic levels and does not reflect a cross section of a continental biota. In addition, the times of divergence between Antillean groups and their mainland relatives suggest a more recent (Cenozoic) origin than would be predicted by vicariance. Nonetheless, several lineages of Antillean vertebrates may be quite old and could possibly date to the proto-Antilles. One is the frog genus *Eleutherodactylus*, which shows a time of origin in the West Indies close to the Cretaceous/Tertiary boundary (Hass and Hedges, 1991, Hedges, 1996b). Another is the xantusiid lizard genus *Cricosaura* that occurs in eastern Cuba. No molecular clock estimate is available for *Cricosaura*, contra Iturralde-Vinent and MacPhee (1999:51), but instead the older age for its lineage is inferred from mainland fossil data and the relationships of xantusiid lizards (Hedges et al., 1991; Hedges and Bezy, 1993). Even if the lineage itself is old, the relictual nature of xantusiid lizards suggests caution in using the current distribution as evidence of past distribution. Among mammals, the insectivores *Solenodon* and *Nesophontes* probably represent old lineages that might date back to the Cretaceous (MacFadden, 1980), but no molecular or fossil data have yet been offered as support of that suggestion.

Even if the current West Indian fauna does not show a predominantly vicariant origin, this is not to say that a vicariant biota did not exist at earlier times. For example, the recent discovery of ungulate (rhinocerotoid) and iguanid lizard fossils from the Eocene (~50 mya) of Jamaica (Domning et al., 1997; Pregill, 1999) may be evidence of such a biota. Ungulates are not known from elsewhere in the West Indies. Whether this lineage reached Jamaica on dry land from the mainland, or dispersed across a water gap, is not known. The Oligocene submergence of Jamaica, if it occurred (see above), presumably would have eliminated most or all of the existing biota. Nonetheless, the Jamaican Eocene fossils indicate that a diverse biota may have existed on some Caribbean islands in the early Cenozoic.

THE LAND BRIDGE MODEL OF MACPHEE
AND ITURRALDE-VINENT

Before plate tectonics provided the mechanism for vicariance, the "land bridge" was the major alternative mechanism to dispersal. Supporters of land bridges (Scharff, 1912; Barbour, 1916; Schuchert, 1935) debated with supporters of overwater dispersal for the first half of the 20th century. The primary argument for land bridges was the seeming impossibility that some groups of organisms, such as freshwater fishes and amphibians, could disperse across salt water (see discussion above). The peninsulas of land that were erected between the islands and the mainland, based on the distributions of organisms, largely were conjectural with little or no geological evidence. After plate tectonics became accepted in the latter part of the 20th century, and paleogeography became better known, most of the proposed land bridges were not supported by geological evidence. However, the refined geological data have suggested new possibilities for past land bridges. One such possibility of a mid-Cenozoic land bridge in the Caribbean region is the Aves Ridge, now almost entirely submerged.

The Aves Ridge, located just to the west of the Lesser Antilles, has long been known to have been the precursor of the present-day Lesser Antilles (Malfait and Dinkelman, 1972; Dengo and Case, 1990; Donovan and Jackson, 1994). As such, it was intimately tied to the geological evolution of the Greater Antilles and connections, in the "island arc" sense, with the adjacent continents. Biogeographers also have noted the importance of the Aves Ridge for Caribbean biogeography (Rosen, 1975; Holcombe and Edgar, 1990; Woods, 1990).

In a detailed discussion of the Aves Ridge, Holcombe and Edgar (1990) stated "between middle Eocene and early Miocene time it is possible that the Aves Ridge may have been a land bridge. To have been a land bridge, the Aves Ridge would have had to have undergone about 2,000 m of subsidence. There is no direct evidence to support subsidence greater than about 1200 m, but

samples of Eocene reef limestone recovered from a well (Marathon SB1) drilled on Saba Bank, which joins Aves Ridge on the north, demonstrate that the bank has subsided about 3000 m since the end of Eocene time." Those authors show a figure of what the present Aves Ridge would look like if it were 600 m and 1000 m higher, exposing many islands, or by inference, a land bridge if subsidence had been even greater. In a separate paper in the same volume, Woods (1990) specifically proposes that this Aves Ridge land bridge (or chain of islands) provided a potential mid-Cenozoic corridor for the entry of mammals to the Greater Antilles. However, geological support for a continuous land bridge vs. a chain of islands does not exist.

In a recent series of papers, MacPhee and Iturralde (1994; 1995; 1999) have championed the possibility that the Aves Ridge was a mid-Cenozoic land bridge. They refer to it as a "landspan" defined as "a subaerial connection (whether continuous or punctuated by short water gaps) between a continent and an off-shelf island (or island arc)." But for Caribbean biogeography, the distinction between a dry land bridge and an island chain is a major one. A dry land bridge will allow a cross section of the continental fauna to enter the Greater Antilles whereas an island chain will act as a filter, permitting only selected lineages to enter. Most authors discussing Caribbean biogeography have assumed that the Aves Ridge was an island chain, much like the adjacent Lesser Antilles, during the Cenozoic (Rosen, 1975; Perfit and Williams, 1989; Hedges, 1996a). This concept is not new and it fits with the taxonomic composition of the Antillean fauna. However, the suggestion of a dry land bridge would not agree with the taxonomic composition of the fauna or with molecular time estimates (see below). Although there is no geological evidence yet available to distinguish between a dry land connection and a chain of islands, the paleogeographic diagrams illustrated by Iturralde-Vinent and MacPhee clearly show a dry land connection from 35 to 33 mya, and that is the model that they emphasize.

Iturralde-Vinent and MacPhee (1999) acknowledged that evidence against a dry land connection is provided by molecular clock studies and taxonomic composition of the fauna, and therefore considerable attention was given to a critique of studies supporting overwater dispersal, especially that of Hedges (1996b). The different issues that they raise will be discussed separately below.

DIVERGENCE TIMES

A prediction of a dry land bridge connection is that times of divergence between Antillean groups and their mainland counterparts should cluster around 35 to 33 mya, according to the model of Iturralde-Vinent and MacPhee (1999). Molecular clock studies of West Indian vertebrates do not show this pattern, but instead show a scattering of divergence times throughout the Cenozoic (Hedges et al., 1992; Hedges, 1996b). Iturralde-Vinent and MacPhee criticize several aspects of these studies, with emphasis on the most recent study (Hedges, 1996b). None of these criticisms is valid, and I will respond to each of them below. Ironically, the evidence that they have erred in their criticisms was provided, in most cases, in the original paper (Hedges, 1996b).

Number of Lineages Analyzed

The first criticism of Iturralde-Vincent and MacPhee is that the number of evolutionary lineages was not correctly counted. This is not true. Information on time of origin was unavailable for 4 of the 77 lineages in my study, and the concern of Iturralde-Vinent and MacPhee (1999) was that the readers were misled into thinking that such information was available and supported dispersal. But the relevant table (Hedges, 1996b: table 3) and text are clear about information available and not available: "At least some information is available for nearly all lineages (73/77 = 95%), and of those all but one (99%) are in the Cenozoic" (Hedges, 1996b:113) (note the fraction given in the original text). Even that statement was conservative because the four lineages in question also probably arose by dispersal: "Of the four lineages for which no data on the time of origin are available (*Hyla heilprini*, *Phyllodactylus wirshingi*, *Mabuya lineolata*, and the *Leptotyphlops*

bilenata group), all have congeneric species on mainland Central or South America and none have highly divergent morphologies that would suggest a long period of isolation. Therefore all four of those lineages likely arose in the Cenozoic by dispersal" (p. 113).

In a footnote, Iturralde-Vinent and MacPhee (1999:41) comment that there were three "errors" in my tabulation of data. Again, these were not errors but confusions on the part of Iturralde-Vinent and MacPhee. Regarding the first purported error, they state that "*Crocodylus intermedius*, known from only one or two individuals, cannot be considered to be established in the West Indies." But my criteria (Hedges, 1996b) did not consider the number of individuals — after all, some West Indian species are known only from the holotype. I excluded lineages known to be introduced by humans and *C. intermedius* was not in that category. Schwartz and Henderson (1991) considered *C. intermedius* to be part of the West Indian herpetofauna and I do not disagree with their interpretation. The second purported error involves one of the four populations of the lizard *Iguana iguana*. Iturralde-Vinent and MacPhee state that *I. iguana* "does not occur on the Cayman Islands." This is incorrect. Schwartz and Henderson (1991) included it as part of the endemic (not introduced) Cayman herpetofauna, and its continued presence in the Cayman Islands has been confirmed (A. Echternacht, personal communication). If it is later found that it was introduced by humans (a possibility), then it would be removed from consideration as a native lineage, but in any case the statement by Iturralde-Vinent and MacPhee, that it does not occur on the Cayman Islands, is incorrect. The third purported error mentioned in the footnote concerns another lizard. Iturralde-Vinent and MacPhee state that "*Mabuya bistriata* is presumably a lapsus for *Mabuya mabuya*; *M. bistriata* is a Brazilian species." There was no lapsus. As detailed in the checklist of West Indian amphibians and reptiles (Powell et al., 1996) in the same volume as my study, a taxonomic problem with *M. mabuya* led to the recognition of the West Indian populations as *M. bistriata*. Thus the use of the name *M. bistriata* was not an error but followed current usage.

Mixture of Morphological and Immunological Data

The second criticism by Iturralde-Vinent and MacPhee (1999) is that I mixed morphological and immunological (not immunodiffusion, which is another method) data, and that this obscures biogeographical inference. They state that, in the case of 40 lineages (56%), morphological data are used as a "proxy measure" of divergence time. This is not true. In a relatively small number of cases involving endemic West Indian species with congeners on the mainland, my stated assumption (see above) was that the divergence between two closely related species in the same genus (of these particular vertebrates) probably occurred in the Cenozoic and not in the Cretaceous. However, nearly all of the 40 lineages noted by Iturralde-Vinent and MacPhee involve species that have populations both in the West Indies and on the mainland. As stated in the methods, I assumed that populations of the same species most likely diverged in the Quaternary (2 to 0 mya) regardless of their morphological divergence; published support for this assumption was mentioned. Moreover, none of those time estimates was used in the figure showing times of origin (Hedges, 1996b: figure 2). Iturralde-Vinent and MacPhee were aware of this because they used this large number of nonendemics as a separate criticism (see below).

Taxa Are Not Discriminated in Terms of Interpretative Significance

Here, Iturralde-Vinent and MacPhee explain that different organisms disperse differently. For example, some lizards would be expected to raft rather than swim, whereas large crocodilians may not have required a raft. Of course this is true, but it is unclear why it is mentioned as a criticism because I made no claims to the contrary. However, it is worth noting that nearly all West Indian amphibians and reptiles are much smaller than a crocodilian and would most likely have dispersed by rafting.

Overrepresentation and Ambiguous Significance of Nonendemics

Iturralde-Vinent and MacPhee claim that I have overrepresented the number of nonendemic lineages, but they justify their claim by mentioning only three such species. However, I discussed each of the 77 lineages (including those three) separately (Hedges, 1996b) and, again, it appears that they have apparently overlooked that discussion. For *Gonatodes albogularis*, I mentioned that the Jamaican and Hispaniolan populations are recognized as an endemic subspecies suggesting that they are not the result of human introduction. For *Hemidactylus brooki haitianus*, I mentioned that the West Indian populations are considered to represent an endemic species, *H. haitianus*, in the accompanying checklist (Powell et al., 1996) and therefore are also not the result of human introduction. The origin of the third species in question, *H. mabouia*, is less clear, but that ambiguity is mentioned in the account of that species. Moreover, none of these three taxa is included in the figure of divergence times (Hedges, 1996b: figure 2).

Iturralde-Vinent and MacPhee also claim that the nonendemics, in general, are overrepresented "relative to their importance." My intention was to be objective and identify all independent lineages no matter when they arrived to the West Indies, as long as it was by natural means. A dispersal event in the Pleistocene could be just as important as a dispersal event in the Eocene. Although in my analysis these data were given equal importance, Iturralde-Vinent and MacPhee have the option not to consider them to be important. In any event, this is not an error or misrepresentation.

Low Number of Nonendemic Lineages in the Greater Antilles

This criticism is similar to the previous one in that Iturralde-Vinent and MacPhee place greater importance on some aspects of my analysis than others. In this case, their focus was on the Greater Antilles, so they were sensitive to the fact that Lesser Antillean lineages were included. But my study concerned the biogeography of the West Indies and therefore I was interested in the Lesser Antilles as well as the Greater Antilles. Again, there is no error or misrepresentation.

Unknown Shaping Influence of Extinction

The effect that the extinction of lineages has had on shaping the past and present composition of the West Indian fauna is unknown. The major problem is that there are very few Tertiary fossils. My analysis was not concerned with this question and therefore it is unclear why this was mentioned in this section of Iturralde-Vinent and MacPhee (1999).

Finally, Iturralde-Vinent and MacPhee consider one possible source of error in the time estimation: phylogenetic error. This might happen when the closest mainland relative of an Antillean group is actually more distantly related, resulting in an overestimation of the divergence time. We mentioned this source of error in our original paper (Hedges et al., 1992) and noted that, because nearly all times were younger than the predicted time for vicariance, that this type of error, even if present, would not affect our conclusion. Iturralde-Vinent and MacPhee (1999) state that "it actually does matter because filling a matrix with overestimates can obscure whatever pattern — including any concentration of splits — that may exist within the phylogeny" (p. 45). Again, they have taken this out of context and misinterpreted the point. Our studies were not focused on testing a dry land bridge hypothesis in the Oligocene but rather proto-Antillean vicariance (Cretaceous) vs. dispersal (Cenozoic). So we were correct in stating that such error did not affect "our conclusion." But at the same time, acknowledging that this source of error is a possibility is not the same as saying that our entire data set was full of this type of error. The latter is not true.

Iturralde-Vinent and MacPhee further speculate that the "pre-28" mya splits might represent overestimates, in which case the absence of data points clustering at that time would not bear negatively on their model. However, all comparisons were chosen carefully, and I discussed each separately in the text (Hedges, 1996b). While a few pre-28 mya comparisons (e.g., *Osteopilus*,

Typhlops, *Amphisbaena*) may be influenced by such phylogenetic error, most probably are not because other data were available to guide choice of sister group.

WATER CURRENTS

Iturralde-Vinent and MacPhee (1999) claimed that some of the past current flow patterns "are incompatible with the history of faunal emplacement in the Caribbean region as envisaged by Hedges" (1996a, 1996b). They note that I gave "little attention to the varying paleogeographical configurations of the Caribbean region on current flow" (p. 45). This is not true, as I noted "because the Caribbean always has been north of the equator during geological history, the Coriolis Force would have produced the same clockwise current flow in the past, even while a water connection to the Pacific was in existence" (Hedges, 1996b:118). As will be seen below, the existence or not of the Aves Ridge land bridge would not alter this primary mechanism for the transport of flotsam from South America to the Antilles.

Iturralde-Vinent and MacPhee (1999) present reconstructions of marine surface current patterns for four time periods during the Cenozoic (since latest Eocene) based on "slight modifications" of several primary sources. However, reference to those primary literature sources indicates that these purported slight modifications were in reality major modifications. For example, their reconstruction of 35 to 33 mya shows the Aves dry land bridge fully exposed, completely blocking current flow between the Atlantic and Pacific Oceans. However, their reference (Droxler et al., 1998) shows a continuous current flow from Atlantic to the Pacific, noting that "the Aves Swell might have been shallow enough for at least part of a 35 m.y. long interval to have modified the circulation of oceanic waters in the western North Atlantic and to have formed a partially or fully developed barrier to circulation" (p. 172). The two alternatives depend on whether there was a continuous dry land bridge (Iturralde-Vinent and MacPhee, 1999) or an island arc (Pindell, 1994).

Even if the two alternatives were equally plausible (see discussion of geological evidence above), the water current flow patterns presented by Iturralde-Vinent and MacPhee are influenced by their need to explain how mammals got to the Greater Antilles. In this sense, it is circular reasoning to use such biased interpretation of surface current patterns to argue in favor of the same biogeographical model. Even Droxler et al. (1998) eluded to the influence of mammal fossils in their assessment of water current patterns: "very strong supporting evidence for this possibility [of a land bridge] comes from the islands of the Greater Antilles where fossil skeletal remains of early Miocene land mammals with South American affinities, including sloths, have been discovered" (MacPhee and Iturralde-Vinent, 1994, 1995; Iturralde-Vinent et al., 1996). However, they concluded that the part played by the exposure of the Aves Swell in "modifying the oceanic circulation and the regional and global environment is much more speculative" (p. 186).

Even if the Aves Ridge formed a continuous land bridge that blocked marine current flow between the Atlantic and Pacific, this would not have prevented flotsam from reaching the Antilles. The North Atlantic Gyre would have functioned the same then as it does now, bringing currents up along the northeast coast of South America to the Caribbean (Figure 3). An equatorial counter-current may have affected some areas along the northeast coast of South America because that region was not very far north of the equator at that time (Figure 3). However, even if this were true, at least some flotsam from northeastern South America would have been deposited on the Aves Ridge land bridge (i.e., part of the Antilles) and directly on the Greater Antilles. The attention given by Iturralde-Vinent and MacPhee to the rivers of northwestern (rather than northeastern) South America is misleading because, even today, they are less likely to be major contributors of flotsam to the Greater Antilles. Similarly misleading is the counterclockwise current direction, east of the Aves Ridge land bridge, shown by Iturralde-Vinent and MacPhee (1999: figure 10) in their water current reconstructions. Presumably this represents the Equatorial Countercurrent, but it was not illustrated in Droxler et al. (1998) — whose primary concern was paleocurrent flow in this region — and would be unlikely considering the Coriolis force (resulting in clockwise flow) and the fact that the Caribbean always has been north of the equator.
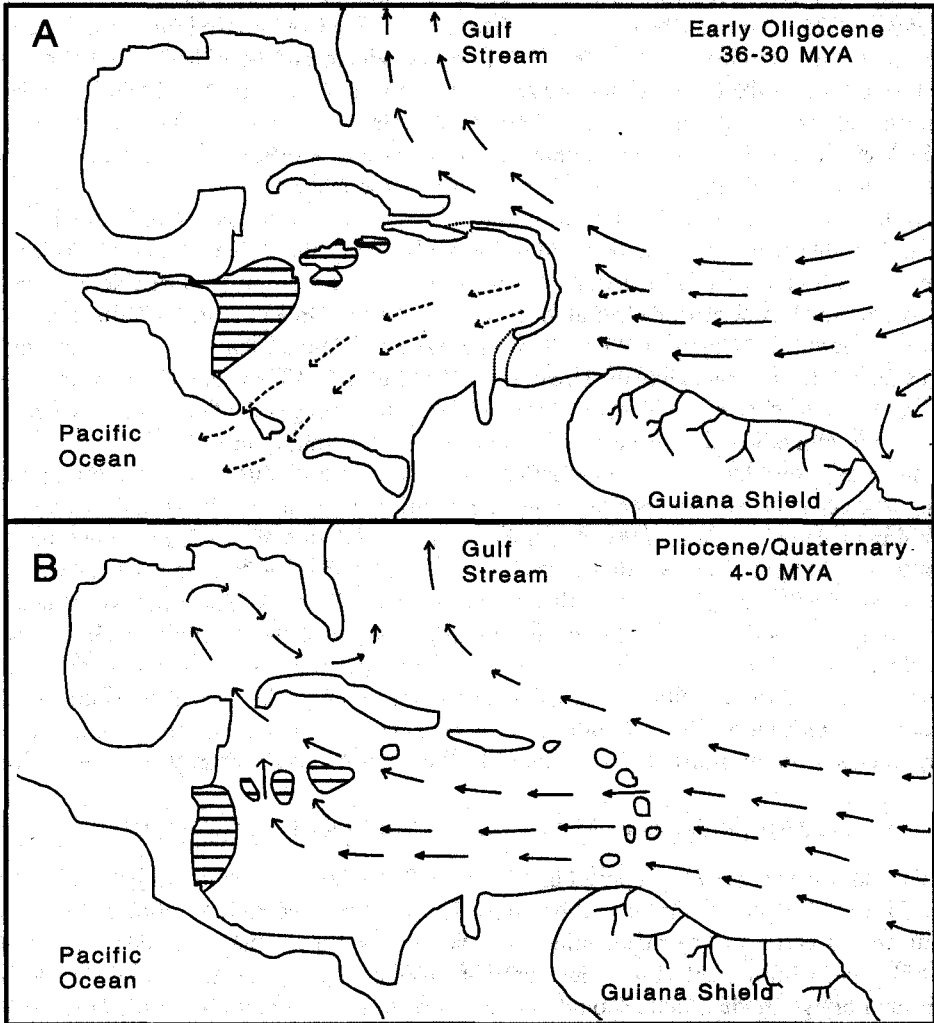
FIGURE 3 Water current patterns in the Caribbean region at two different times in the Cenozoic. Most features are based on Droxler et al. (1998), although more of the northeastern coast of South America is shown. Water current flow along the Guiana Shield (Guiana Current) is based on present-day water current patterns (Droxler et al., 1998) and inferred patterns in the past based on paleolatitude (Smith et al., 1994a). Carbonate platforms that may have affected current flow in the Caribbean are indicated with horizontal hatching. (A) Early Oligocene (36 to 30 mya). There are two possibilities. If the Aves Ridge were a dry land bridge (Iturralde-Vinent and MacPhee 1999; shown by dotted lines) the Guiana Current would have been deflected to the northwest along the Antillean landmasses and up to the Gulf Stream. If the Aves Ridge were a chain of islands (Droxler et al., 1998), then some current (dashed arrows) would have passed by the islands and on to the Pacific Ocean (as it did during the Miocene). In either case, rivers in northeastern South America draining into the Guiana Current would have provided a source of flotsam for the Antilles. (B) Pliocene and Quaternary (4 to 0 mya). The Guiana Current continues to flow along the northeastern coast of South America and into the Caribbean, bringing flotsam to the Antilles.

Most of northeastern South America, between the present-day Orinoco and Amazon Rivers, forms the Guiana Shield, and drainage from this region, because of its location southeast of the Lesser Antilles, is an important source of flotsam in the Caribbean (Guppy, 1917). The importance of this potential source region, and adjacent current patterns, is highlighted by the distribution and

relationships of species occurring in northeastern South America and the Lesser Antilles (Henderson and Hedges, 1995; Hedges, 1996b: figure 4). This region also would have drained into the Atlantic during the Tertiary (Hoorn et al., 1995), but Iturralde-Vinent and MacPhee suggest that flotsam "would have been as likely to drift toward Africa as the West Indies" (p. 51). Even if true, it would only mean that about half of the millions of potential rafting organisms might be diverted elsewhere than the West Indies. However, to explain the origin of one Antillean lineage (e.g., tropidophiid snakes) requires only a single, very fortuitous rafting experience.

Iturralde-Vinent and MacPhee take a similar approach in their discussion of bottle drift studies. For example, they conclude that the results "strongly imply that, given existing surface-current patterns, flotsam emitted from the Orinoco and Amazon rivers is much more likely to end up in southeastern North America or Central America than in the Greater Antilles." But this has been known for some time (Guppy, 1917) and no one has ever claimed that all flotsam leaving South America automatically ends up in the Greater Antilles! Iturralde-Vinent and MacPhee may consider the rate of one out of every seven drift bottles released (on average) landing in the Greater Antilles to be low, but others would consider this number to be surprisingly high.

In summary, Iturralde-Vinent and MacPhee do not consider that the number of rafts potentially carrying animals from South America to anywhere during the Cenozoic must have been very large (i.e., millions). This is because flotsam is quite common and animals, including amphibians, have been observed riding on flotsam (Guppy, 1917; Boyd, 1962; King, 1962; Heatwole and Levins, 1972; Censky et al., 1998). The particular destination of rafts from South America that do not land on the Greater Antilles is not of interest to understanding the origin of the Antillean fauna. It is already assumed that the vast majority of rafts and their occupants perish, and it is already known that some currents do not lead to the Antilles. For Caribbean biogeography, the most likely source of flotsam that reaches the Greater Antilles is South America, considering both past and present current patterns. The arguments given by Iturralde-Vinent and MacPhee (1999) do not change that conclusion.

INCONSISTENCIES AND PROBLEMS IN MODEL OF MACPHEE AND ITURRALDE-VINENT

MacPhee and Iturralde (1994) proposed that the Aves Ridge became a land bridge in the Oligocene at 30 to 27 mya. The precise timing was based partly on uplift of the region (followed by subsidence at 27 mya) and partly on the major mid-Cenozoic sea level drop that occurred at about 30 mya (Haq et al., 1987). Presumably, this sudden drop of ~160 m fully exposed the Aves Ridge. According to their land bridge model, fauna should not have arrived prior to that time if the land bridge was the primary explanation for the origin of these endemic mammals. However, the discovery of a 34 to 33 mya sloth in Puerto Rico (MacPhee and Iturralde-Vinent, 1995) created a conundrum because it predated the land bridge. Rather than reject the land bridge as an explanation for the presence of the Puerto Rican sloth, MacPhee and Iturralde modified their model by making the land bridge an earlier event (35 to 33 mya). As an explanation, they stated "either the sea level drop is not accurately dated or was not global, or for some other reason did not affect GAARlandia [land bridge] in the way originally imagined" (MacPhee and Iturralde-Vinent, 1995:20). In the most recent version of their model, Iturralde-Vinent and MacPhee (1999:27) claim that "general tectonic uplift coincided with a major eustatic sea level drop at ca. 35 Ma" (Miller et al., 1996). However, the sea level drop shown by Miller et al. (1996) at 35 mya was not a redating of the major Oligocene drop (Haq et al., 1987) used by MacPhee and Iturralde (1994), now considered to be 32.2 mya (Miller et al., 1993), but rather another sea level drop altogether. This inconsistent use of evidence shows that their paleogeographical model was influenced by their biogeographical model (i.e., the need to have the land bridge in place before the sloth fossil date).

Another inconsistency involves the definition of the land bridge itself. It is defined as a "subaerial connection (whether continuous or punctuated by short water gaps) between a continent and an off-shelf island (or island arc)" (Iturralde-Vinent and MacPhee, 1999:52). This definition is consistent with a textual description earlier in the paper (p. 31): "we argue that exposure of the ridgecrest

created, for a short time ca 33–35 Ma, a series of large, closely spaced islands or possibly a continuous peninsula stretching from northern South America to the Puerto Rico/Virgin Islands Block." However, in other places the Aves Ridge land bridge is considered to be continuous: "central to the hypothesis is the argument, sustained at length in this paper, that the Cenozoic paleogeography of the Caribbean region strongly favored emplacement over land (as opposed to over water) only once in the past 65 Ma" (p. 53). Moreover, they clearly illustrate the land bridge as a fully continuous dry land connection, with no water gaps, much like the current Isthmus of Panama (Iturralde-Vinent and MacPhee, 1999:figures 6 and 12).

The difference between an island chain and a continuous land bridge is fundamental for biogeography. The former will behave as a biotic filter allowing only selected taxa to cross, whereas the latter will permit a greater diversity of terrestrial life (a cross section of a biota) to enter. But, in addition, the existence of a single water gap implies that all organisms that crossed that gap must have done so by swimming or floating on flotsam (i.e., overwater dispersal). As noted above, that the Aves Ridge was at least a chain of islands during the mid-Cenozoic is normally assumed in discussions of Caribbean biogeography and is not a new concept. The possibility that it was a continuous land bridge also has been raised previously (Woods, 1990) but, as discussed elsewhere in this chapter, the current biological evidence does not support that alternative.

Finally, Iturralde-Vinent and MacPhee (1999:56) acknowledge that the taxonomic composition of the West Indian fauna, including the Tertiary mammal fossil record, supports an origin by dispersal ("low initial diversity model") and not the transfer over land of a diverse fauna in the Oligocene. They also acknowledge that at least some sloths were adapted to marine habitats (Muizon and McDonald, 1995). This raises the question, that if the faunal evidence favors a filter and not a dry land bridge, and the geological evidence is equivocal, then why is the dry land bridge favored?

EVIDENCE AGAINST A MID-CENOZOIC LAND BRIDGE

As with the proto-Antillean vicariance model, evidence against a mid-Cenozoic dry land bridge connection between South America and the Antilles is the depauperate nature of the Antillean fauna and molecular clock estimates of divergence times for terrestrial vertebrates. With regard to faunal composition, Iturralde-Vinent and MacPhee (1999) concede that "all Tertiary [mammal] taxa recovered to date from these islands appear to be closely related to clades known from the Quaternary, which favors the low initial diversity model [overwater dispersal]" (p. 56). They acknowledge that the presence of a more diverse fauna on Jamaica during the Eocene (Domning et al., 1997) is not relevant to the Aves Ridge land bridge model because Jamaica was isolated and underwent submergence during the Oligocene. Concerning the available molecular clock time estimates, the data do not support a clustering of divergences around 35 to 33 mya as would be predicted by the land bridge model. Instead, divergence times are scattered throughout the Cenozoic (Hedges, 1996b). Geological data neither support nor refute the suggestion of a fully continuous dry land bridge.

DISCUSSION AND CONCLUSIONS

It is tempting to consider a complex problem such as the historical biogeography of the West Indies in terms of several alternative mechanisms. However, there is no reason to exclude any of the three models discussed above based on purely geological grounds. Nonetheless, the evidence reviewed in this chapter suggests that most lineages of West Indian vertebrates arrived by overwater dispersal during the Cenozoic. If most arrived by proto-Antillean vicariance in the late Cretaceous or by a land bridge (Aves Ridge) in the mid-Cenozoic, one would expect to see a more diverse fauna resembling a cross section of the continental fauna. However, the present fauna exhibits reduced higher-level diversity, and the fossil record suggests that this pattern was similar in the past. Molecular time estimates also indicate that nearly all lineages examined arrived in the Cenozoic and not the Cretaceous. They also do not support a mid-Cenozoic land bridge because they are

scattered throughout the Cenozoic, rather than clustered. Finally, phylogenetic evidence points to an origin from South America for most nonvolant lineages examined, and this is congruent with water current patterns in the Atlantic and Caribbean today and throughout the Cenozoic.

While there is sufficient evidence now to indicate that overwater dispersal is the general pattern, it is not possible to exclude other mechanisms. For example, it is quite possible that an early Antillean fauna, now extinct (Domning et al., 1997), arose through vicariance. Also, the frogs of the genus *Eleutherodactylus* appear to represent an ancient lineage in the West Indies that may have originated in the late Cretaceous or early Cenozoic (Hedges et al., 1992; Hedges, 1996b). Other extant lineages such as the xantusiid lizards and insectivores also may have arrived early in the history of the Antilles.

Geological data and paleogeographical reconstructions will continue to be refined and contribute to our understanding of biogeography. Nonetheless, when such reconstructions of Earth history are influenced by particular biogeographical models, that bias affects their utility. Unfortunately, the most extensive work on paleogeography of the West Indies (Iturralde-Vinent and MacPhee, 1999) falls into this category. It shows a continuous dry land bridge in the mid-Cenozoic and no land connections prior to the late Eocene. However, as discussed above, geological evidence is inconclusive with regard to both major features of their reconstruction. In this case, the paleogeographical reconstructions of Iturralde-Vinent and MacPhee, taken literally, exclude proto-Antillean vicariance and offer a dry land corridor for emplacement of a mid-Cenozoic biota. In this sense, their biogeographical model and "paleogeographical reconstruction" are one and the same. It is more useful for biogeographers to base their conclusions on unbiased reconstructions of Earth history.

Although some important Tertiary vertebrate fossils have been discovered in recent years in the Antilles, these represent only a small fraction of the endemic extant lineages. In addition, fossils provide only a minimum time of origin of a lineage. The major gap in our knowledge of Caribbean biogeography is not the fossil record — which will always remain fragmentary and biased — but the phylogeny and divergence times of the extant biota. If most lineages arrived in the late Cretaceous, vicariance is a strong possibility, whereas a mid-Cenozoic arrival could be explained by a land bridge. An origin during the last 25 million years would indicate an arrival only by overwater dispersal. Unfortunately, molecular time estimates are known only for selected lineages of vertebrates, and in most of those cases, they are based on an indirect measure of time from one gene (serum albumin). Ideally, we would like to know the relationships and times of origin from multiple nuclear and mitochondrial genes for all Antillean groups of organisms. Given the limited resources for systematics, this information may not be available for all groups even in the future. Nonetheless, a major advance should come in the next decade when such sequence data become more generally available. With these data and new fossil discoveries, we can look forward in the near future to resolving many of these long-unanswered questions in Caribbean biogeography.

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