PALEOGEOGRAPHY OF THE ANTILLES AND ORIGIN OF WEST INDIAN TERRESTRIAL VERTEBRATES[1]

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Abstract

The fauna of the West Indies includes more than 1300 native terrestrial vertebrate species and is characterized by high levels of endemism. Several theories have been proposed to explain how these animals arrived to the islands, including dispersal, vicariance, and land bridges. The dispersal theory proposes that most of the West Indian terrestrial biota arrived by flying or by flotsam. The vicariance theory suggests that there was a proto-Antillean land mass, or masses, connecting North and South America in the late Cretaceous that traveled eastward as the Caribbean geologic plate developed and carried an ancient biota with it. One widely discussed land bridge theory proposes that much of the Antillean biota originated by dispersal over an unbroken dry land connection, the Aves Ridge, between South America and the Greater Antilles 35–33 Ma. Geologic evidence cannot unambiguously support or refute any of these models, despite claims to the contrary. Other evidence bearing on these three theories, or mechanisms, comes from the taxonomic composition of the fauna, their phylogenetic relationships, fossil record, paleogeography, ecology, climate, water currents, and divergence time estimates from molecular clocks. This evidence supports an origin by overwater dispersal for most or all of the West Indian terrestrial vertebrate fauna. The strongest support comes from a reduced higher-level taxonomic composition of the fauna (now and in the past), the presence of unusually large adaptive radiations, and the finding of divergence time estimates between island and mainland groups that are not clustered around a particular time. In addition, the majority of terrestrial (non-flying) groups have closest relatives in South America, which is consistent with the direction of water currents and most hurricane tracks. Some of the same evidence in support of dispersal argues against a mid-Cenozoic land bridge from South America. Several ancient, relictual groups (e.g., xantusiid lizards and solenodontoid shrews) may have arisen through proto-Antillean vicariance, and molecular clock analyses—here revisited—provide support for this, but an origin by dispersal can also be argued. No model can be completely discounted. Although the general pattern (dispersal) has emerged, many details remain to be determined concerning the origin of the fauna.

Keywords: animals, biogeography, Caribbean, dispersal, systematics, vertebrates, vicariance, West Indies.

Resumen

La fauna de las Antillas incluye más de 1300 especies nativas de vertebrados terrestres y se caracteriza por altos niveles de endemismo. Se han propuesto varias teorías para explicar cómo estos animales llegaron a las islas, incluyendo dispersión, vicarianza, y corredores terrestres. La teoría de la dispersión propone que la mayoría de la biota terrestre antillana llegó volando o en restos flotantes. La teoría vicariante sugiere que hubo una masa (o masas) de tierra proto-antillana, que conectaba a América del Norte y del Sur en el Cretácico tardío y que se desplazaba hacia el este mientras la placa geológica del Caribe se desarrollaba y llevaba consigo una biota antigua. Una teoría ampliamente discutida acerca del corredor terrestre propone que la mayoría de la biota antillana se originó por dispersión sobre una conexión seca intacta de tierra, el Promontorio de Aves, entre América del Sur y las Antillas Mayores hace 35–33 Ma. La evidencia geológica no puede apoyar o refutar en forma inequívoca cualquiera de estos modelos, a pesar de que se opine lo contrario. Otra evidencia concerniente a estas tres teorías, o mecanismos, proviene de la composición taxonómica de la fauna, de sus relaciones filogenéticas, del registro fósil, de la paleogeografía, la ecología, el clima, las corrientes de agua, y estimados de tiempo divergentes de los relojes moleculares. Esta evidencia apoya un origen por dispersión para la mayoría de la fauna vertebrada terrestre antillana. El apoyo más fuerte proviene de una reducida composición taxonómica de alto nivel de la fauna (en el presente y el pasado), la presencia de radiaciones adaptativas inusualmente grandes y el hallazgo de divergencia en los estimados de tiempo entre grupos de las islas y del continente que no se agrupan alrededor de un tiempo particular. Además, la mayoría de grupos terrestres (que no vuelan) tienen parientes más cercanos en América del Sur, que es consistente con la dirección de las corrientes de agua y de la mayoría de huracanes. Algunas de las mismas evidencias de apoyo a la dispersión argumentan en contra de un corredor terrestre desde América del Sur en el Cenozoico medio. Varios grupos antiguos, relictos (e.g., lagartos xantusiidos y musarañas solenodontoides) pudieron haber surgido a través de vicarianza proto-antillana, y los análisis de relojes moleculares—aquí revistos—dan apoyo a esto, pero también se puede argüir un origen por dispersión. Ningún modelo se puede descartar totalmente. Aunque el patrón general (dispersión) ha sobresalido, todavía quedan por determinar muchos detalles referentes al origen de la fauna.

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Table 1. Taxonomic diversity of native West Indian terrestrial vertebrates.

			Genera			Species		
Group	Orders	Families[a]	Total	Endemic	% Endemic	Total	Endemic	% Endemic
Freshwater fishes	6	9	14	6	43	74	71	96
Amphibians	1	4	6	1	17	173	171	99
Reptiles	3	19	50	9	18	499	478	96
Birds	15	49	204	38	19	425	150	35
Mammals:								
Bats	1	7	32	8	25	58	29	50
Other[b]	4	9	36	33	92	90	90	100
TOTALS	30	97	342	95	28	1319	989	75

[a] Includes one endemic family of birds (Todidae) and four of mammals (Capromyidae, Heptaxodontidae, Nesophontidae, and Solenodontidae).

[b] Edentates, insectivores, primates, and rodents.

The West Indies has captured the attention of biogeographers for over a century (Wallace, 1881). Some of the reasons for this include a large but taxonomically peculiar fauna, high levels of endemism, and an intriguing physiography. For example, there are four large islands, the Greater Antilles, now known to be quite old (ca. 100 million years); a large group of smaller, flat islands on a limestone plateau, the Bahamas Bank; and a textbook-like arc of volcanic islands, the Lesser Antilles. When plate tectonics and past sea-level fluctuations are added, this physical setting presents a complex challenge for the biogeographer. The primary task is to understand how and when the biota arrived. A comprehensive review of Caribbean biogeography is not possible in this limited space, and thus for additional insights see recent reviews by Hedges (1996a, c, 2001), Iturralde-Vinent & MacPhee (1999), Graham (2003a, b), and Santiago-Valentin and Olmstead (2004), some of which will be discussed and contrasted herein. Although models of historical biogeography apply to both plants and animals, examples will be drawn from the latter, and primarily land vertebrates of the West Indies.

Most groups of West Indian invertebrates are poorly known. Examples of some groups that have been given taxonomic attention are ants (Wilson, 1985, 1988; Morrison, 1998), termites (Scheffrahn et al., 2003), butterflies (Smith et al., 1994), earthworms (James, 1996), land snails (Gould & Woodruff, 1986; Goodfriend & Gould, 1996), scorpions (deArmas, 1982), mites (Niedbala, 2004), and selected other groups (Liebherr, 1988, 1992). Fossils from Dominican amber have added significantly to the knowledge of West Indian invertebrate diversity. In some cases the amount of information is so detailed and material of such high quality that complex ecological and behavioral interactions can be inferred (Poinar & Poinar, 1999). However, studying the historical biogeography of a group is difficult when a majority of the living species has yet to be discovered. West Indian vertebrates, on the other hand, are better known taxonomically, and therefore most zoogeographic analyses have focused on these animals.

Currently 1319 species of living vertebrates are known from the West Indies (Table 1). Relatively few new species of mammals and birds are being encountered, indicating that knowledge of the species diversity of those two groups is nearly complete. However, amphibians, reptiles, and to a lesser degree freshwater fishes, show more steeply rising discovery curves, suggesting that undescribed species still exist (Hedges, 1996a, c). Amphibians (173 species), reptiles (499 species), and birds (425 species) are the most species-rich groups, although levels of endemicity differ considerably. Only about one-third of bird species (35%) are endemic to the West Indies, whereas nearly all species of amphibians (99%), reptiles (96%), and freshwater fishes (96%) are endemic. That the ability to fly is the reason for this difference is seen clearly in mammals; only 50% of bats are endemic, whereas all non-flying mammals are endemic (Table 1).

Not unexpectedly, most West Indian vertebrate fossils are from the Quaternary, <1.8 million years ago (Ma), and most often are from regurgitated remains of owl meals and victims of natural pitfalls (Pregill & Olson, 1981; Pregill, 1986; Pregill et al., 1992). Approximately 15 to 20 vertebrate taxa are known from the Paleogene (65–1.8 Ma), including those in amber (MacPhee & Iturralde-Vinent, 1994, 1995; MacPhee & Grimaldi, 1996; Poinar & Poinar, 1999). The amber fossils are mostly from the same formation, but the date (30–15 Ma) has been disputed (Grimaldi, 1995; Hedges, 1996a; Iturralde-Vinent & MacPhee, 1996). With such a small number of Paleogene fossils, a clear picture of the Paleogene vertebrate fauna is not available. However, current fossils suggest that the fauna was similar to the Quaternary fauna in higher-level taxonomic composition. For example, fossils of frogs (*Eleutherodactylus* Dumeril & Bibron), lizards (*Anolis* Daudin and *Sphaerodactylus* Wagler), a snake (*Typhlops* Oppel), and a mammal (Solenodontidae) are representatives of vertebrate groups present today on the islands (MacPhee & Grimaldi, 1996; Poinar & Poinar, 1999). Giant megalonychid ground sloths (Order Edentata) underwent a major adaptive radiation in the Antilles, as evidenced from Quaternary fossils, and their fossils are known starting from the Early Oligocene, ca. 33 Ma (MacPhee & Iturralde-Vinent, 1995). Primates are also known from the Paleogene and Quaternary of the West Indies (MacPhee & Iturralde-Vinent, 1995; MacPhee & Horovitz, 2004). No sloths or native primates occur in the West Indies today. A rhinoceros relative (*Hyrachyus* Leidy) is known from the Eocene (ca. 50 Ma) of Jamaica (Domning et al., 1997), but no other ungulates are known from the West Indies subsequent to that record. In fact, *Hyrachyus* may represent a survivor of the proto-Antilles or an early disperser from Central America (Domning et al., 1997; Pregill, 1999; Hedges, 2001).

Although many naturalists have commented on the West Indian fauna over the centuries (e.g., Sloane, 1725; Gosse, 1851; Darwin, 1859), Wallace (1881) was one of the first to discuss the historical zoogeography of the islands. He noticed that the higher-level taxonomic composition of the West Indian fauna was reduced when compared to that of mainland areas, a fact also noted by subsequent zoogeographers (Matthew, 1918; Simpson, 1956; Darlington, 1957; Williams, 1989). Such patterns are characteristic of oceanic islands where the fauna has arrived by dispersal, rather than of islands previously connected to mainland areas (Williams, 1989; Paulay, 1994). However, much of the debate during the first half of the 20th Century concerned the possibility of land bridges (Scharff, 1912; Barbour, 1916; Schuchert, 1935). Since about 1960, knowledge of seafloor topography and the acceptance of plate tectonics have greatly changed the physical backdrop for zoogeographic studies, and rendered the suggestions of those land bridges obsolete. For this reason, I briefly review the current knowledge of geology, water currents, and climate, before discussing contemporary models of Caribbean zoogeography.

GEOLOGIC HISTORY AND PALEOGEOGRAPHY

The Caribbean region was formed when the supercontinent Pangaea broke apart in the Jurassic (200–150 Ma). The initial ocean floor that was created by a spreading center has since been recycled through subduction. The current Caribbean Plate formed in the eastern Pacific in the mid-Cretaceous and has moved east-northeast relative to the American Plate (Dengo & Case, 1990; Donovan & Jackson, 1994; Pindell, 1994; Pindell & Kennan, 2002), although models that do not require high rates of plate movement have been proposed (Meschede & Frish, 1998). The present-day Greater Antilles were formed mostly from subduction, and resulting island-arc volcanism, of the North American Plate under the lighter Caribbean Plate during this eastward movement (Fig. 1). However, collision of this Antillean island arc with the Bahamas Platform in the early Paleogene caused subduction to stop and a fault zone and short spreading center (Cayman Trough) to form south of Cuba, thus fixing Cuba and eventually northern Hispaniola and Puerto Rico to the American Plate. Subduction continued along the leading (east) edge of the Caribbean Plate during the Cenozoic, always feeding an island arc on the overriding (Caribbean) plate. Initially the arc was the Aves Ridge (probably then a chain of islands), but later in the Cenozoic the expression of arc materials (andesitic volcanism) transferred slightly eastward to its present position as the Lesser Antilles. Among the Lesser Antilles, Barbados is an exception, being emergent Atlantic sea floor caused by the buckling of the Atlantic oceanic plate. The northern boundary of the

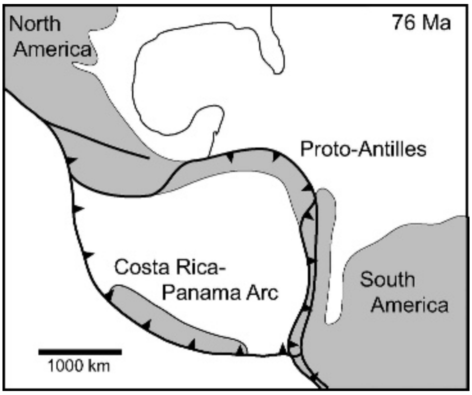

Figure 1. Location of the Proto-Antilles in the late Cretaceous (ca. 76 Ma), redrawn and modified with permission from Pindell (1994). Present coastline of southern North America is shown as narrow line; heavy lines without teeth are transform fault zones; heavy lines with teeth are subduction zones (teeth indicating direction of subduction). Shading denotes continental and arc areas that may or may not have been above sea level. This remains speculative for the Proto-Antilles, which may have been emergent, a chain of islands (as in the current Lesser Antilles), or completely submerged. The Costa Rica-Panama Arc is shown to the west.

plate has remained largely a transform fault and minor spreading center.

The Bahamas Platform has been a stable carbonate block on the North American Plate since the Cretaceous, and reef development has kept the platform near sea level apparently for much of that time. Although Jamaica and the southern portion of Hispaniola were initiated during the development of the proto-Antilles, their histories have been quite different from that of Cuba, northern Hispaniola, and Puerto Rico. They have been attached to the northern boundary of the Caribbean Plate and have moved eastward relative to Cuba and northern Hispaniola during the Paleogene. Jamaica has remained isolated during this time, but southern Hispaniola collided with northern Hispaniola in the Miocene (Huebeck & Mann, 1985), with the zone of attachment being the Cul de Sac-Valle de Neiba of present-day Hispaniola. The similar origin and proximity of Cuba, northern Hispaniola, and Puerto Rico raises the possibility that two, or all three, of these islands were attached at some point during the Paleogene, although that has yet to be firmly established (Pindell, 1994). The close similarity of the fauna of the Virgin Islands and Puerto Rico reflects the fact that they reside on the same bank. A more detailed account of Caribbean geologic history can be found elsewhere (Pindell, 1994; Pindell & Kennan, 2002).

Also of importance for biogeography is the paleogeography of the West Indies. This is a complicated problem because several poorly known variables must be considered simultaneously, such as sea level fluctuations, geologic uplift, and erosion. Some high mountain ranges (e.g., Blue Mountains of Jamaica) were uplifted over a period of only a few million years (late Miocene and Pliocene) and even higher ranges were eroded in less than a million years, as evidenced by the Eocene Wagwater Trough formation of Jamaica (Comer, 1974). Therefore, the current topography is a relatively poor guide of paleogeography during most of the Paleogene. Clearly, at some point between the inception of subduction in the mid-Cretaceous and today, the Antilles became emergent.

Determining when the islands first rose above the sea (and remained above sea level) and how, if at all, they were connected is not a simple task, and is often based on the distribution and type of marine sediments that presumably came from erosion of emergent areas. This type of information has suggested that the proto-Antillean island arc of the late Cretaceous probably was not a continuous (unbroken) land area resembling Central America but rather a chain of islands (Donnelly, 1989; Perfit & Williams, 1989; Donnelly, 1990, 1992; Pindell & Kennan, 2002), although the details are unknown. Some workers have claimed that no land areas in the Greater Antilles were constantly above sea level before 45 Ma (MacPhee & Iturralde-Vinent, 1994; MacPhee & Grimaldi, 1996; Iturralde-Vinent & MacPhee, 1999), although such absolute statements cannot be backed by existing evidence. To support this claim would require having an uninterrupted geologic record from most areas in the Caribbean region, and this is not yet available (Dengo & Case, 1990). In addition, small areas low in elevation would not be expected to yield large quantities of terrestrial sediments.

The claim by Iturralde-Vinent & MacPhee (1999) that no land areas in the Greater Antilles were constantly above sea level before 45 Ma, and their advocacy of a mid-Cenozoic dry land connection (Aves Ridge land bridge) with South America for the purpose of emplacing land mammals to the Antilles (see below), demonstrate that their models are not "paleogeography" but rather biogeography. The distinction is important because it provides the independence needed to falsify or test biogeographic models. For example, if a biogeographic model claims that animals must have walked across land to reach another area, and paleogeographic evidence says that no such land existed, then the biogeographic model can be rejected.

Finally, an important detail of Earth history of relevance to the Caribbean is the Cretaceous-Paleogene bolide impact of 65 Ma. This was one of the largest impacts in the inner solar system since the Precambrian, and is believed to have exterminated the dinosaurs and other groups (Hildebrand & Boynton, 1990). The impact site is in the Caribbean region under sediments of the Yucatan Peninsula (Kring & Boynton, 1992). At the time of impact, the islands of the Greater Antilles were only 1–3 crater diameters away (Pindell, 1994) and undoubtedly experienced massive waves hundreds to thousands of meters in height (Maurrassee, 1991). In addition to the global climatic effects of the impact, these local effects must have resulted in much extinction of the proto-Antillean fauna present on the islands at the time (Hedges et al., 1992).

Water Currents

The direction and speed of water currents is of importance to the dispersal of terrestrial organisms unable to fly. Even those non-piscine vertebrates capable of swimming are unlikely to swim against the current for long distances. For nearly all West Indian vertebrates, this mode of transport would involve rafting on floating vegetation (flotsam) washed into ocean currents from the mouths of rivers following

Figure 2. A floating island of vegetation (ca. 600 m^2) near Santarém, Brazil, at the confluence of the Amazon and Tapajós rivers. The upper photo shows the entire island; the lower photo is a close-up of the left side, with a cattle egret (*Bubulcus ibis*), approximately 50 cm in height. Photograph taken by Pervaze Sheikh in February, 1997 (used with permission).

storms (Fig. 2). This method of dispersal is well known (Guppy, 1917; King, 1962; Heatwole & Levins, 1972), and has been documented for West Indian vertebrates (Henderson et al., 1995; Censky et al., 1998; Knapp, 2000).

In the West Indies, the present-day surface current flow is predominantly from the southeast to the northwest, and would have been similar in the past (Fig. 3). This is because the Caribbean is in the southwestern portion of the North Atlantic Gyre, the clockwise flow of water in the Atlantic. The clockwise flow is the result of the differential rotational velocity of the Earth (Coriolis Force). Water currents come from the west coast of Africa across to northeastern South America and then up and across the Caribbean to the southern tip of Florida where they form the Gulf Stream. One of the best documented cases of flotsam dispersal involves a West Indian vertebrate, green iguanas (*Iguana iguana* Linnaeus), and is consistent with this pattern. The distribution of this species and hurricane paths suggest that the iguanas originated in Guadeloupe and were transported to Anguilla, about 250 km to the northwest (Censky et al., 1998).

The closest relatives of most West Indian terrestrial vertebrates (excluding birds, bats, and freshwater fishes) are in South America, a fact that is compatible with the hypothesis that current flow is responsible for most overwater dispersal. The Amazon and many other major rivers in northeastern South America (Guiana Shield) drain into the Guiana Current, which flows into the Caribbean, and presumably carried the ancestors of much of the West Indian biota (Fig. 4). The closest relatives of a few West Indian vertebrates (Hedges, 1996c) and plants (Guppy, 1917) are in Africa. In those cases, the dispersal event would have taken at least several months based on the present rate of current flow (Guppy, 1917).

The West Indies has been north of the equator since the origin of the Caribbean Plate, and therefore the general east-to-west current flow would have been the same in the past, even prior to the emergence of the Isthmus of Panama (Fig. 3). An argument has been made elsewhere (Iturralde-Vinent & MacPhee, 1999) that a dry land bridge between South America and the Greater Antilles in the mid-Cenozoic would have altered that general current flow. In addition, those authors have argued that, based on past ocean current flow, most animals carried on flotsam during that time would not have ended up on islands in the West Indies. However, these suggestions are speculative (see below). Even in the presence of such a land bridge, the North Atlantic Gyre still would have

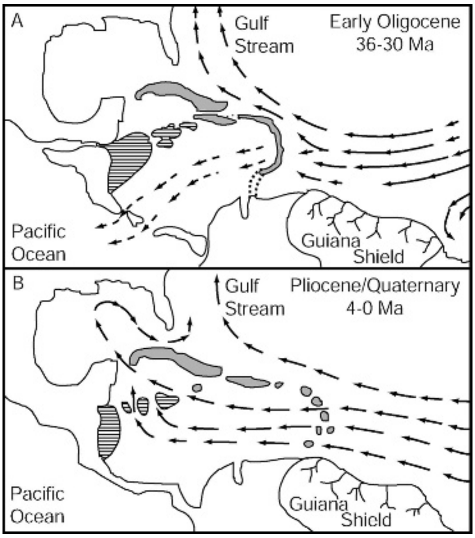

Figure 3. Water current patterns in the West Indies in the (A) Early Oligocene (36–30 Ma) and (B) Pliocene/Quaternary (4–0 Ma), after Hedges (Copyright 2001 from *Biogeography of the West Indies: Patterns and Perspectives* by C. A. Woods & F. E. Sergile (editors). Reproduced by permission of Routledge/Taylor & Francis, LLC.). Current flow along the Guiana Shield (Guiana Current) in the past is inferred given its paleolatitude at that time. Carbonate platforms (horizontal bars) may have affected current flow in the Caribbean (Droxler et al., 1998). —A. Early Oligocene. If the Aves Ridge (shaded crescent) was submerged or was a chain of islands (Droxler et al., 1998) some current flow (dashed arrows) would have passed on to the Pacific Ocean, as it did during the Miocene. If the Aves Ridge were a dry land bridge (dotted lines) the Guiana Current would have been deflected to the northwest along the Antillean landmasses and up to the Gulf Stream. Under both scenarios, rivers in northeastern South America draining into the prevailing current would have provided a source of flotsam for the Antilles. —B. Pliocene/Quaternary. The Guiana current continues to flow along the coast of South America and into the Caribbean, bringing flotsam to the Antilles.

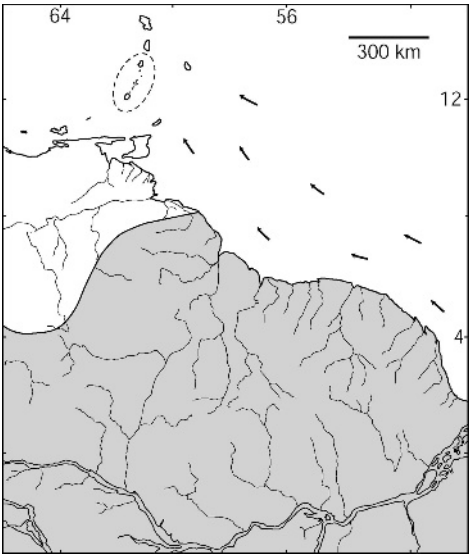

Figure 4. Distribution of a species of snake (*Corallus hortulanus* Linnaeus; shading) in South America and its closest relatives (*C. cooki* Gray and *C. grenadensis* Barbour; dashed lines) in Lesser Antilles (Henderson & Hedges, 1995; Henderson, 1997). Based on their distributions, and the direction of current flow, the island endemics likely arose by dispersal from South America of a snake (or snakes) floating on flotsam in the Guiana current (arrows).

brought currents from northeastern South America to the Antilles (Fig. 3; Hedges, 2001). Also, the focus on where flotsam from particular rivers in South America would go, rather than on where flotsam reaching the Greater Antilles originated, was an error in logic. If lizards riding on flotsam from a river in northwestern South America were carried out to the Pacific in the mid-Cenozoic (Iturralde-Vinent & MacPhee, 1999), that was their unfortunate luck. To understand the origin of the Antillean fauna, the hits are important; the misses do not count. If the Antillean hits are still mostly from South America, as opposed to Central and North America, those arguments concerning misses are of no consequence. Even if the implication is that fewer hits would occur, that also is of little consequence when the odds being discussed already are as low as one in 65 million years.

HURRICANES

Hurricanes are important for Caribbean biogeography because flotsam usually is the result of storm action (King, 1962) which affects air and water currents. For geographic and climatic reasons, the West Indies represents a hot spot for hurricanes, and most storm tracks are similar in direction to the surface current flow (Fig. 5). Thus, hurricanes and current flow work together to give a strong directionality for over-water dispersal in the West Indies. For example, it would be difficult for flotsam (or organisms) to travel from Cuba to the Lesser Antilles; the reverse would be much more likely. Although hurricanes may generate at least some flotsam in the West Indies (Censky et al., 1998), thunderstorms probably are responsible for nearly all flotsam emanating from rivers in South America.

Despite the directionality of dispersal mechanisms in the West Indies, some exceptions exist. For example, in 1999, the rare west-to-east Hurricane Lenny began near the Cayman Islands and ended near Nevis in the Lesser Antilles (Fig. 5). This unusual direction gave it the nickname “Lefty.” Although west-to-east tracks are rare (only two others during the last five years), this indicates that some unusual distribution patterns might be explained by atypical hurricanes. Another possible factor is the counter-

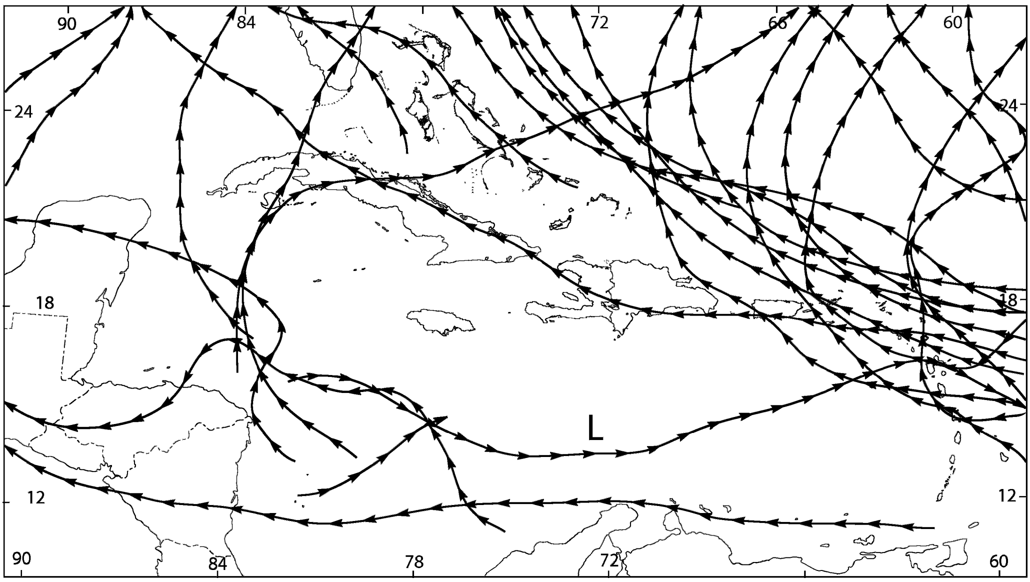

Figure 5. Hurricane tracks in the West Indies (1995–1999). The hurricane track labeled "L" is Lenny (also called "Lefty") of 1999. Source of hurricane track data: National Oceanic and Atmospheric Administration.

clockwise airflow of the hurricane vortex itself. Although the hurricane track may be moving in a westerly direction, strong surface winds to the south of the storm will be moving in the opposite (easterly) direction. This would not explain dispersal over long distances but might be a factor for short (tens of kilometers) distances, such as between islands (Powell, 1999).

Contemporary Models of Historical Zoogeography

In the several decades since plate tectonics became accepted, zoogeographers have had to consider the complexities introduced by past movements of islands. Early on, a new biogeographic theory was proposed suggesting that much of the West Indian biota originated on a proto-Antillean land area connecting North and South America in the late Cretaceous (Rosen, 1975, 1985). According to this vicariance model, the present-day Antillean fauna did not arrive by dispersal but instead was carried on the islands as they drifted, tectonically, to their current positions. Subsequent geologic models for the Caribbean differ considerably in details but not in the general notion of a proto-Antillean arc. However, as discussed above, the paleogeographic details concerning which land areas were emergent (and when), critical for this vicariance model, are still poorly known.

Advocates of the vicariance model have used phylogenetic relationships of organisms, almost exclusively, as evidence (Guyer & Savage, 1986; Crother & Guyer, 1996). This has been done with the assumption that the historical pattern of land area relationships should be reflected in the phylogeny of organisms that underwent vicariance (Rosen, 1975, 1985). A similar application of this approach was attempted for West Indian mammals (Dávalos, 2004). However, dispersal patterns often have directionality, as in the Caribbean, and can yield concordant phylogenies of groups (Hedges et al., 1994; Hedges, 1996b, c, d). Also, reconstruction of land area relationships in the West Indies is not yet possible because of uncertainty in details of the geologic history and paleogeography.

Other approaches to clarifying the vicariance vs. dispersal problem integrate multiple sources of information, including times of divergence of species and groups. The fossil record has been used in an indirect manner to show that times of divergence (i.e., the origin of West Indian groups) are too recent to support an origin by vicariance (Pregill, 1981). However, fossil-based divergence times are always minimum estimates. Time estimates from molecular data pertain to the actual splitting event because genetic differences begin to develop immediately following speciation. The most extensive molecular data available for testing these competing models of Caribbean biogeography have been immunological estimates of protein sequence divergence in serum albumin of West Indian vertebrates (Fig. 6). Generally, time estimates from these data have been too recent to support proto-Antillean vicariance (Hass,

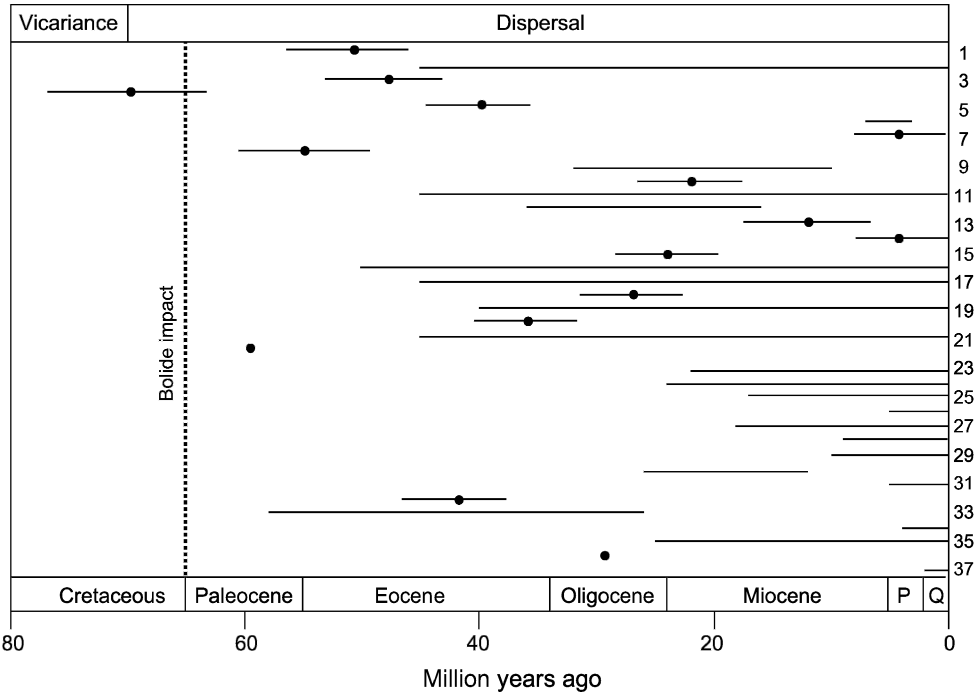

Figure 6. Times of origin for the 37 independent lineages of endemic West Indian amphibians and reptiles, mostly from immunological estimates of sequence divergence in the protein serum albumin (redrawn and modified with permission from Hedges, 1996c). Means and error estimates (in some cases, ranges) are shown. The lineages (indicated by numbers at right) are: (1) *Bufo peltocephalus* Tschudi group, (2) *Colostethus chalcopis* Kaiser, Coloma & Gray, (3) *Osteopilus* Fitzinger, (4) *Eleutherodactylus* Duméril & Bibron, (5) *Leptodactylus albilabris* (Gunther) Boulenger, (6) *Leptodactylus fallax* Müller, (7) *Crocodylus rhombifer* Cuvier, (8) *Amphisbaena* Linnaeus, (9) *Celestus* Gray, (10) *Diploglossus* Wiegmann, (11) *Gymnophthalmus pleei* Bocourt, (12) *Anolis* Daudin, (13) *Cyclura* Harlan, (14) *Iguana delicatissima* Laurenti, (15) *Leiocephalus* Gray, (16) *Aristelliger* Cope, (17) *Phyllodactylus pulcher* Gray, (18) *Sphaerodactylus* Wagler, (19) *Tarentola* Gray, (20) Antillean *Ameiva* Meyer, (21) *Cnemidophorus vanzoi* Baskin & Williams, (22) *Cricosaura typica* Gundlach & Peters, (23) *Epicrates* Wagler, (24) *Chironius vincenti* Boulenger, (25) *Mastigodryas bruesi* (Barbour) Schwartz & Henderson, (26) *Clelia errabunda* Underwood, (27) *Liophis cursor* Schwartz & Henderson group, (28) *Coniophanes andresensis* Schwartz & Henderson, (29) *Tretanorhinus variabilis* Duméril, Bibron & Duméril, (30) alsophine snakes, (31) *Leptotyphlops columbi* Klauber, (32) *Tropidophis* Bibron in de la Sagra, (33) *Typhlops* Oppel, (34) *Bothrops* Wagler, (35) *Trachemys* Agassiz, (36) pelomedusid turtles, and (37) *Geochelone* Fitzinger. Note: P = Pleistocene, Q = Quaternary.

1991; Hedges et al., 1992; Hass et al., 1993; Hedges et al., 1994; Hedges, 1996c; Hass et al., 2001). Also, those divergence time estimates are not strongly clustered at one particular point in time but tend to be more spread out, as one would expect from the action of a random mechanism such as over-water dispersal (Hedges, 1996c). One possible exception is the frog genus *Eleutherodactylus*, which may have arrived in the West Indies in the late Cretaceous or early Paleogene (Hass & Hedges, 1991; Hedges, 1996c). It is widespread, abundant, and diverse (i.e., not relictual), and the divergence times estimated between mainland and Antillean species are in the late Cretaceous or early Paleogene (Hass & Hedges, 1991; Hedges et al., 1992).

The phylogenetic relationships of West Indian vertebrates reveal that most have their closest relatives in South America (Hass, 1991; Hedges, 1996a, c). Among the exceptions are organisms that actively disperse, such as most freshwater fishes, bats, and birds. In those cases, geographic distance rather than current patterns appear to be more important since such organisms show closer affinities with Central and North American faunas.

The reduced higher-level taxonomic diversity remains a major piece of evidence in the comparison of contemporary models. The vicariance model predicts that the Antillean fauna should be a cross section of the continental fauna. Extinction is not excluded under the vicariance model, but no evidence exists in the fossil record that many major continental groups ever were present. For example, no primary freshwater fishes (intolerant of salt water), salamanders, caecilians, marsupials, carnivores, or lagomorphs are known to have occurred in the islands. Most families of frogs, turtles, and snakes are also missing. Ungulates with their large bones fossilize well, yet no record of any ungulate exists aside from the early ca. 50 Ma rhinocerotoid from Jamaica, as noted above.

Other evidence that this peculiar taxonomic composition extended into the past comes from the unusually large radiations of some groups, such as ground sloths, capromyid rodents, eleutherodactyline frogs, and anoline and sphaerodactyline lizards. This is to be expected when niches are left vacant and is characteristic of oceanic islands never connected to continents (Williams, 1989; Woods, 1990; Hedges, 1996a). Probably as a result of these open niches, some of the largest and smallest species of various groups occur on islands, including the West Indies (Estrada & Hedges, 1996; Hedges & Thomas, 2001).

In addition to dispersal and vicariance, organisms may have reached the Greater Antilles by way of a land bridge (Rosen, 1975; Holcombe & Edgar, 1990; Woods, 1990; MacPhee & Iturralde-Vinent, 1994, 1995; Iturralde-Vinent & MacPhee, 1999). Unlike earlier land bridge models, proposed before plate tectonics, this land bridge is based on modern geology. It proposes that the Aves Ridge, now below sea level, formed a chain of islands or dry land connection between northern South America and the Greater Antilles in the mid-Cenozoic. However, the difference between a stable (unbroken) land bridge and a chain of islands is important for biogeography. Even narrow land bridge corridors, such as the current Isthmus of Panama, allow a major interchange of faunas (Stehli & Webb, 1985; Williams, 1989). A chain of islands, on the other hand, acts as a filter selecting for species with more optimal dispersal abilities. The Aves Ridge has been assumed to have been at least a chain of islands, much like the Lesser Antilles, that enhanced the over-water dispersal of organisms to the Greater Antilles (Rosen, 1975; Perfit & Williams, 1989). Thus, the recent assertion that the Aves Ridge was a dry and unbroken land bridge (Iturralde-Vinent & MacPhee, 1999) is of interest here. This model proposes only a narrow window of time (35–33 Ma) when this terrestrial corridor existed (Iturralde-Vinent & MacPhee, 1999).

In the process of providing evidence for their dry land bridge model, Iturralde-Vinent & MacPhee (1999) eliminated the possibility of proto-Antillean vicariance and gave arguments against over-water dispersal. They suggested that the Aves Ridge land bridge played a major role in the origin of West Indian terrestrial vertebrates. However, the same evidence that supports over-water dispersal for much of the West Indian fauna and argues against proto-Antillean vicariance also argues against the Aves Ridge land bridge model. This includes a reduced higher-level taxonomic diversity (now and in the past), unusually large adaptive radiations of groups present, and divergence time estimates that are not strongly clustered at one point in time. The existence of a land bridge would instead predict a more continental-like fauna (at least in the Paleogene fossil record) and divergence time estimates clustered strongly around 35–33 Ma. Nevertheless, because the Aves Ridge was probably a chain of islands, it should be expected to have enhanced dispersal at different times in the Cenozoic, e.g., mid-Cenozoic, much like the Lesser Antilles in the Late Cenozoic. In that respect it may have facilitated dispersal of mammals and other groups from South America to the Greater Antilles, as suggested by previous researchers (Holcombe & Edgar, 1990; Woods, 1990). However, this is different from the dry land connection claimed by Iturralde-Vinent & MacPhee (1999), which would have permitted a diverse cross section of the South American biota to enter the Antilles. Such a diverse cross section is not seen in the fauna.

The dry land bridge initially was proposed as a way to explain the origin of Antillean land mammals (MacPhee & Iturralde-Vinent, 1994, 1995). For example, Iturralde-Vinent & MacPhee (1999: 58) stated that they “doubt that the sloths swam the distance.” Yet, as they acknowledge, some species of ground sloths were highly adapted to marine life (Muizon & McDonald, 1995), thus removing this proposed biological need for a dry land bridge. Unfortunately, the creation of a dry land bridge also has implications for other aspects of the paleogeography of Iturralde-Vinent & MacPhee (1999); as previously mentioned it is used to suggest the direction of water current flow in the past and its influence on dispersal.

Iturralde-Vinent & MacPhee (1999) also claim that no permanent landmasses were present in the Caribbean prior to the middle Eocene, eliminating the possibility of proto-Antillean vicariance. Although the absence of direct evidence for an uninterrupted land occurrence is used as support of that claim, there is also an absence of direct evidence *against* uninterrupted land occurrence. In fact, such evidence would be difficult to obtain, as it would require nearly continuous sedimentation present from all areas and sampled at all time intervals. Because some land areas were at least close to the ocean surface (sea level) during part of that time, as acknowledged by Iturralde-Vinent & MacPhee (1999), the possibility of uninterrupted land areas cannot be completely ruled out. Moreover, organisms are surprisingly resilient to changing landscapes and are known to survive as continuous lineages for millions of years in island chains such as the Hawaiian Islands and Galapagos

Islands (Sequeira et al., 2000). In these cases, temporal continuity in the long term is likely accomplished by dispersal among ephemeral islands in the short term. Thus, the biota of an archipelago can be maintained over time even while individual islands rise and fall.

The Problem of Relictual Groups

Two endemic groups of West Indian animals, the giant shrews (*Solenodon* Brandt) and Cuban night lizards (*Cricosaura* Gundlach and Peters), have been suggested to have arisen through proto-Antillean vicariance (MacFadden, 1980; Hedges et al., 1991; Hedges et al., 1992; Roca et al., 2004). However, the distributions of both groups, including mainland relatives, have receded through time (i.e., are relictual), which presents a problem for interpreting their biogeographic history. Before discussing these biogeographic implications, some clarification is needed concerning the estimated time of divergence for the Cuban night lizards from their closest relatives in the family Xantusiidae.

The lizard family Xantusiidae occurs in North and Central America and the West Indies. Only one species is known from the West Indies, *Cricosaura typica* Gundlach and Peters, restricted to a small region of eastern Cuba. In the original studies reporting the xantusiid lizard sequence data (Hedges et al., 1991; Hedges & Bezy, 1993), the authors suggested that *Cricosaura* might represent a remnant of the proto-Antillean fauna, based on molecular phylogeny and fossil data. Although a molecular clock analysis was not explicitly used, they demonstrated phylogenetically that the West Indian lineage (*Cricosaura*) was the most ancient in the family, and its divergence from other xantusiids must have logically predated fossils of *Palaeoxantusia fera* Hecht (ca. 60 Ma) assigned to the other lineage (Savage, 1963; Schatzinger, 1980; Hedges et al., 1991).

Those sequence data were reanalyzed later by Vicario et al. (2003), who recovered the same topology and performed a molecular clock analysis, arriving at a different conclusion concerning the time of origin of the *Cricosaura* lineage. Although much emphasis was given to this difference, it was the sole result of those authors removing the ca. 60 Ma fossils of *Palaeoxantusia fera* from consideration, without explaining why they disagreed with earlier authorities concerning that fossil. Using the next earliest fossils (ca. 43 Ma) for calibration of a mainland divergence (*Xantusia* Baird/*Lepidophyma* Duméril), their molecular clock time interval for the *Cricosaura* divergence from other xantusiids was 64.9–43 Ma. They stated that this estimate "is not consistent with the Hedges et al. (1992) proposal that the *Cricosaura* line survived the bolide impact at the K/T (Cretaceous/Paleogene) boundary at 65 MYBP, as the earliest limit of our estimate is nearly 100,000 years after that momentous event" (Vicario et al., 2003: 257). However, there are several problems with this interpretation: (1) they ascribed considerably more accuracy to molecular clocks than is justified (e.g., the difference between 64.9 and 65.0 Ma is only 0.15%), especially given the modest sequence data set, (2) they conceded that the calibration could be off by 17 million years, which nullifies the difference of 100,000 years, and (3) they interpreted the divergence date as a fixed time estimate, when it is more correctly interpreted as a minimum (Hedges & Kumar, 2004).

The same data were reanalyzed more recently by Roca et al. (2004), who disagreed with Vicario et al. (2003) and supported the earlier (Cretaceous) divergence for *Cricosaura*, at 76 Ma. They used a different method of time estimation (Thorne et al., 1998) with the same calibration point (43 Ma for *Xantusia/Lepidophyma*) as minimum and added *Palaeoxantusia fera* (60 Ma) as maximum. To explore the effect of calibration point on this time estimate, I reanalyzed the data using the same methods but used instead *Cricosaura*/non-Caribbean divergence for calibration (a Bayesian estimate can be obtained even for calibrated nodes). Regardless of whether that node is treated as a fixed calibration or minimum calibration, at 43 Ma or 60 Ma, and regardless of the ingroup root prior (50–100 Ma), the confidence interval in all cases extends into the Cretaceous. If *Palaeoxantusia fera* is correctly assigned to the *Xantusia/Lepidophyma* lineage, then a fixed calibration of 60 Ma for the *Cricosaura*/non-Caribbean split is the preferred method, yielding a time of 75 Ma (60–116 Ma) using an ingroup prior of 75 Ma, similar to the result of Roca et al. (2004). This date should then be interpreted as a minimum time estimate and not a mean time estimate in drawing conclusions.

The time of divergence of the West Indian shrews (*Solenodon*) from their closest relatives on the mainland was estimated to be 76 Ma (72–81 Ma) using a large sequence data set of 16 nuclear and three mitochondrial genes (Roca et al., 2004). A direct interpretation of this ancient divergence for the shrews and for xantusiid lizards is that the West Indian representatives originated by vicariance on the proto-Antilles in the late Cretaceous, whether it was dry land or an island chain, and survived the bolide impact in that region at 65 Ma. However, both of these groups appear to be relictual, which means that alternative hypotheses should be considered. Xantusiid lizards are patchy in distribution and have clearly receded from a wider distribution in the past (Hedges et al., 1991; Sinclair et al., 2004). As noted by Roca et al. (2004), there is uncertainty regarding the identification of the closest relatives of West Indian shrews. Nonetheless, some North American soricomorphs (e.g., *Apternodus* Matthew), all extinct, have been proposed, and the general conclusion is that solenodontoids and their relatives represent a relictual group of animals (MacFadden, 1980).

The primary alternative hypothesis raised by these relictual groups, such as West Indian shrews and xantusiid lizards, is that they arose by dispersal from the mainland in the early Paleogene and not by vicariance in the late Cretaceous (Hedges, 1996a). According to this hypothesis, the phylogenetic divergence still occurred in the Cretaceous, as estimated by molecular clocks, but it resulted in descendant lineages that initially occupied only mainland areas. At some later time, in the Paleogene, dispersal occurred from the mainland to the West Indies, with the mainland representatives of those "West Indian" lineages later becoming extinct. Advantages of this hypothesis are that it does not require the presence of emergent land in the Antilles since the Cretaceous and survival of the local effects of the bolide impact (65 Ma) by the Antillean group. Nonetheless, a better fossil record of mainland relatives would help to distinguish between this hypothesis and one of vicariance. Currently, neither hypothesis can be strongly favored.

Dispersal from Islands to Mainland

In discussions of island biogeography, dispersal is usually considered to be in one direction: from the mainland to the island or islands (Cox & Moore, 2005). However, the Greater Antilles are large and old land masses capable of being source areas for dispersal. At least three Antillean groups appear to have colonized mainland areas. At some time during the mid-Paleogene, estimated as 37 Ma with a molecular clock, one or more frogs (*Eleutherodactylus*) dispersed from Cuba to the adjacent mainland of Central America (Hedges, 1989; Hass & Hedges, 1991; Hedges et al., 1992). The founders evolved into a clade of *Eleutherodactylus* species recognized today as the subgenus *Syrrhophus* Cope (Hedges, 1989). Some Central American pond turtles of the genus *Trachemys* Agassiz (Seidel, 1988, 1996) and a large clade of anoline lizards (Nicholson et al., 2005) are also considered to have originated by dispersal from the Antilles to the mainland. The West Indies was probably the source for other mainland groups as well, and this should be considered in any discussions of Caribbean biogeography.

Conclusions

This brief overview of West Indian biogeography focuses on the major competing models. Anyone familiar with the literature will admit that this field generates contrasting opinions. In part, this is because of the complexity of the problem and evidence that is often limited. All agree that over-water dispersal can and has occurred, but some dispute the degree of the contribution of this mechanism. The paleogeographic basis for the other two proposed mechanisms, proto-Antillean vicariance and a mid-Cenozoic land bridge, has not yet been confirmed. In the author's opinion, both of those mechanisms remain as possibilities, however remote, and the author disagrees with the assertion that proto-Antillean vicariance must be ruled out (Iturralde-Vinent & MacPhee, 1999). At the same time, paleogeographic evidence does not currently support the Aves Ridge land bridge model, in contrast to claims by its strongest advocates Iturralde-Vinent and MacPhee (1999). In their advocacy of that model, with the corresponding need to construct a mid-Cenozoic walkway for land mammals, they have blurred the distinction between paleogeography (past landscapes) and historical biogeography (past distributions of organisms). They refer to their model as "paleogeography" but in reality it is a biogeographic model biased by their desire to create a corridor for mammals when there is no physical evidence to support such an unbroken corridor of land. Biologists and biogeographers need unbiased paleogeographic reconstructions to evaluate their evidence from organisms.

As noted here, and in more detail elsewhere (Hedges, 1996a, c, 2001), the weight of the evidence supports an origin by over-water dispersal for most of the West Indian vertebrate fauna. This conclusion stems from (1) the reduced higher-level taxonomic composition of the fauna (now and in the past), (2) the presence of unusually large adaptive radiations, (3) the finding that closest relatives of most Antillean groups are from South America (passive dispersers) or Central and North America (active dispersers), and (4) the finding of divergence time estimates that are not strongly clustered. The first point was noted over a century ago and has been dubbed more recently as the central problem (Williams, 1989). The second point is related to the first, and infers that existing groups have taken over niches of the missing groups (thus suggesting that the missing groups have been missing for a long time and not just recently extinct). The third point is consistent with the directionality of water current flowing through the region (now and in the past). The fourth point follows the prediction of over-water dispersal.

Despite this general (major) pattern, several Antillean groups may have originated on the proto-

Antilles in the Late Cretaceous or dispersed there in the early Paleogene. These include the Cuban gars (fish), eleutherodactyline frogs, the xantusiid lizard *Cricosaura*, and the insectivore mammals. Additional data are needed for these and other so-called ancient groups. In the future, divergence time estimates will be based on sequence data from multiple genes, rather than immunological estimates from a single protein, and therefore will increase in precision. Such time estimates from many Antillean groups will permit a more accurate test of these competing models.

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