

HISTORICAL BIOGEOGRAPHY OF WEST INDIAN VERTEBRATES

S. Blair Hedges

Department of Biology and Institute of Molecular Evolutionary Genetics, 208 Mueller Laboratory, Pennsylvania State University, University Park, Pennsylvania 16802

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ABSTRACT

The vertebrate fauna of the West Indies (1262 species) exhibits high levels of endemism and has a taxonomic composition characteristic of more isolated oceanic islands. Many groups that are widespread on the mainland are absent in the islands, and some of those present are characterized by large adaptive radiations. The growing fossil record of West Indian vertebrates, including mid-Tertiary amber fossils (considered here to be 20–30 million years old), indicates that this pattern of reduced higher-taxon diversity has persisted for a long period of time. Phylogenetic relationships of nonvolant groups display a strong South American influence, whereas volant groups (birds and bats) and freshwater fish show closer ties with Central and North America. Molecular estimates of divergence times between island taxa and their mainland counterparts indicate a Cenozoic origin (within the last 65 million years) for nearly all groups examined. Together, data from different sources point to an origin by overwater dispersal for a large majority of the vertebrate fauna. The prevailing current direction, from southeast to northwest, and the wide scattering of estimated times of origin suggest that much of the nonvolant fauna arrived by flotsam carried from the mouths of major rivers in northeastern South America. Spatial relationships, especially considering low sea levels during the Pleistocene, appear to better explain the routes of colonization taken by the volant fauna and freshwater fish. Caribbean geologic history does not preclude an origin by late Mesozoic vicariance for several possibly ancient groups, although an early Cenozoic arrival by dispersal also cannot be discounted. An integrative approach to historical biogeography is shown to be more insightful than the current trend in the field, cladistic biogeography, which places prime emphasis only on phylogenetic relationships.

INTRODUCTION

From a biogeographic standpoint, the West Indies includes the Greater Antilles (Cuba, Jamaica, Hispaniola, Puerto Rico), Lesser Antilles, Bahamas, and some peripheral islands. Trinidad, Tobago, and the islands adjacent to Venezuela usually are excluded from this definition because they have a biota more characteristic of South America (11). Among the plants and animals of the West Indies, the vertebrates (1262 species) exhibit some of the highest levels of endemism and therefore have been of considerable interest in biogeographic studies of the Caribbean region. Compared with Madagascar, which has three times the area, there are 60% more species in the West Indies, representing about 5% of all known extant terrestrial vertebrates (Table 1; 197). Sharply rising discovery curves for some West Indian groups indicate that more species remain to be discovered (74). Despite this high species diversity, many major groups are absent when compared with the adjacent mainland, including primary division freshwater fishes, salamanders, caecilians, marsupials, carnivores, ungulates, lagomorphs, and most families of frogs, turtles, and snakes. Instead, exceptionally large radiations characterize some of the groups present, such as eleutherodactyline frogs, anoline and sphaerodactyline lizards, capromyid rodents, and megalonychid edentates.

The focus of this review is the origin of the West Indian vertebrate fauna. Although not an exhaustive survey, aspects of the complex geologic history, fossil record, and biogeographic mechanisms are briefly discussed, and taxon-specific patterns are reviewed. Finally, these data are brought together to elucidate general patterns of historical biogeography for the West Indian vertebrate fauna as a whole.

Table 1 Numbers of orders, families, genera, and species of native West Indian vertebrates^a

Group	Orders	Families ^b	Genera			Species		
			Total	Endemic	% Endemic	Total	Endemic	% Endemic
Freshwater fishes	6	9	14	6	43	74	71	96
Amphibians	1	4	6	1	17	166	164	99
Reptiles	3	19	50	9	18	449	418	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
TOTAL	30	97	342	95	28	1262	922	73

^aFollowing sources listed in subsequent tables.

^bIncluding one endemic family of birds and four of mammals.

GEOLOGIC HISTORY

Tectonic Development of the Caribbean

Only general aspects of the complex geologic history of the Caribbean region are mentioned here. For those interested in more detailed coverage, geologists provide several recent reviews (e.g. 36, 43).

The complexity of Caribbean geology is due in part to the position of the region, wedged between two major continental and oceanic plates (North and South America), and bounded on the west by Pacific plates. Although rocks as old as Precambrian occur in the Greater Antilles (44), the origin of the Caribbean region is tied to the breakup of Pangaea (mid-Jurassic), when Laurasia began to separate from Gondwana. The initial ocean floor that formed the gap between the two continents subsequently disappeared through subduction. Later, in the mid-Cretaceous, the Caribbean Plate formed in the eastern Pacific and has since moved eastward relative to the North and South American Plates. Volcanic islands formed along the northern and eastern margins of this plate as it moved, due to subduction of the North American Plate beneath the lighter Caribbean Plate, creating the proto-Antilles. In the early Tertiary, the northeastern boundary of the Caribbean Plate (Cuba, Hispaniola, Puerto Rico) collided with the Bahamas Platform (on the North American Plate) and essentially "plugged" the subduction in that region. Subsequently, the plate began to move in a more easterly direction, and a major fault developed to the south of Cuba, along with a small spreading center and associated fault zone (Cayman Trough). Jamaica and the southern portion of Hispaniola moved eastward along the northern edge of the Caribbean plate; eventually southern Hispaniola collided with northern Hispaniola in the Miocene (85). Southeastern Cuba and northern Hispaniola may have been connected in the early Tertiary and separated in the middle to late Eocene (44) or Oligocene (87a). The Bahamas Bank has remained as a carbonate platform fixed to the North American Plate, and the Lesser Antilles have remained as a classical island arc, moving eastward along the leading edge of the Caribbean Plate (36, 43).

Recently, it was suggested that the southern and northern Lesser Antilles have had separate geologic histories that have influenced the evolution of anoline lizards (158). However, a closer examination of the geologic evidence does not support that suggestion. For example, the major evidence was a purported fault zone in the central portion of the Lesser Antilles proposed in the late 1970s and early 1980s (12), but geologists (and others) abandoned that hypothesis in the late 1980s for lack of evidence (13, 84, 121). Also, other geologic studies cited (e.g. 174) do not support a geologic break between Dominica and Martinique.

Instead, the Lesser Antilles would appear to form a classic island arc of volcanic islands built above a subduction zone (184).

PALEOGEOGRAPHY The aspect of Caribbean geologic history of greatest interest to biogeographers, the relationships of emergent land areas, unfortunately is the one that is most poorly understood. There is no place in the West Indies that is known by the presence of a continuous sequence of sediments to have been emergent since the late Cretaceous, although some areas of Cuba, northern Hispaniola, and possibly Puerto Rico, may have been. Current geologic evidence is inconclusive but suggests that the proto-Antilles did not form a continuous dry land connection similar to the present-day Isthmus of Panama; instead it was probably a chain of islands (41, 42, 138). However, the recent suggestion that there were no permanently subaerial landmasses in the Greater Antilles prior to 42 million years ago (mya) (111a, 112a) is speculative; it can be neither refuted nor supported with current evidence.

Karst topography and exposed limestone rock are abundant in the West Indies and reflect the widespread mid-Tertiary inundation of most land areas. Many of the present high mountain ranges are the result of relatively recent (late Tertiary and Quaternary) orogenic activity and cannot be used as a guide to the early or mid-Tertiary physiography of the West Indies. For example, probably no part of Jamaica was more than a few meters above sea level from the middle Eocene to the middle Miocene (2, 20, 155), although subsequent orogenic activity has obliterated part of the evidence (widespread limestone formations). The Blue Mountains of eastern Jamaica, rising to over 2200 m, were uplifted only 5–10 mya (30, 185).

In Cuba, paleogeographic reconstructions suggest that some land areas were emergent throughout the Cenozoic (65–0 mya), possibly forming small islands. Beginning in the early Miocene, the present major upland areas of Cuba probably were large islands, later coalescing in the late Miocene and Pliocene as the present island shape emerged (44, 87).

In Hispaniola, the emergent land areas during the mid-Tertiary quiescent period were the Cordillera Central, Cordillera Oriental, and possibly a portion of the La Selle-Baoruco Range in the south (14, 104, 118, 126). Even in the Cordillera Central, the recent major uplift of that mountain range took place only 3–4 mya (105). Initial uplift of the Massif de La Hotte on the southwestern peninsula of Hispaniola is correlated with the collision between the South Island and northern Hispaniola; this began in the middle Miocene (15 mya), and the entire peninsula emerged in the Pliocene (5 mya) and Pleistocene (105). The major uplift of the Massif de La Selle and Sierra de Baoruco also began in the middle Miocene, although some small portions may have been emergent throughout the mid-Tertiary (118). The Sierra de Neiba and the Sierra Martin

Garcia, which are areas of endemism for vertebrates (164), apparently were not emergent until the late Miocene or Pliocene (5–10 mya; 126).

Most of Puerto Rico, and probably the Virgin Islands, was submerged from the late Eocene to the Pliocene (105). However, several periods of localized uplift occurred, from the late Cretaceous to the late Oligocene, on the Puerto Rican Bank. During one such event (late Eocene to mid-Oligocene), uplift of several kilometers occurred (99), and palynological evidence suggests a high altitude flora at that time (57, 58). These data indicate that some emergent land areas may have persisted on the Puerto Rican Bank throughout the Cenozoic.

The Bahamas Bank has been a carbonate platform since the mid-Mesozoic, gradually subsiding but maintaining near sea-level elevations as carbonate reef-deposits accumulated (39, 131). As such, it has been subject to periodic submergence and emergence, the latter most recently in the Pleistocene. Basement rocks in the northern Lesser Antilles are as old as Jurassic, but the oldest rocks in the southern Lesser Antilles are middle Eocene (184). The Cretaceous date for rocks on Union Island (Grenadines), mentioned in the earlier geologic literature and recently cited for biogeographic purposes (158), was in error (12, 175). The degree to which Lesser Antillean volcanoes have been emergent during the history of the island arc is unknown.

FOSSIL RECORD

Tertiary

AMBER FOSSILS Amber deposits in the Dominican Republic provide dramatic documentation of a mid-Tertiary biota, including (among vertebrates) frogs (*Eleutherodactylus*, seven specimens), lizards (*Anolis*, five specimens; *Sphaerodactylus*, six specimens), mammals (hair and bones), and a bird (feathers) (9, 99a, 111a, 141–143, 154). The mammal hair is believed to be from a rodent, the mammal bones from an insectivore, and one bird feather has been identified as belonging to a woodpecker or relative (Picidae). Critical to understanding the importance and relevance of these amber fossils to Caribbean biogeography is the establishment of their age.

Recent tabulations of dates for Tertiary fossils of West Indian vertebrates (112, 112a) listed two of the lizard fossils as Miocene and a frog fossil as Late Eocene. However, those and several other important vertebrate fossils all came from the same mine (La Toca) in the Cordillera Septentrional and therefore are considered to be of the same age (143). That age was determined to be late Eocene (40 mya) based on microfossils from a locality (El Mamey) west of La Toca in the Altimira Formation (47) and on correlative evidence

from nuclear magnetic resonance spectroscopy (98, 143). Since then, further studies on the geology of the Cordillera Septentrional have distinguished the formation containing the amber mine as the La Toca Formation (38, 40). This formation ranges from Lower Oligocene to lower Middle Miocene and contains massive conglomerates in the lowermost portion and turbiditic sandstones and mudstones in the middle and upper portions (40). Because Dominican amber is found in turbiditic sandstones (45), and because those rocks, within the La Toca Formation, have been dated by nanofossils as upper Oligocene to lower Middle Miocene (40), the age range (minimum to maximum) of the La Toca amber fossils is 15–30 mya. Indirect evidence from nuclear magnetic resonance spectroscopy and hardness (98) would suggest that the older portion of that time interval (20–30 mya) contains the actual age of the fossils, concordant with an upper Oligocene time assigned to amber from the Cordillera Septentrional in a stratigraphic correlation (119).

NONAMBER FOSSILS There are several other pre-Quaternary fossils of vertebrates: a cichlid fish (*Cichlasoma*) from Haiti (28), ground sloths from Cuba (112) and Puerto Rico (112a), and a capromyid rodent and platyrrhine primate from Cuba (112a). All are early Miocene except the Cuban sloth (early Oligocene). Two reptilian vertebrae are known from Miocene deposits on Puerto Rico and are believed to belong to a boid snake and an iguanid lizard (114). All of these nonamber fossils belong to extant (or recently extinct) Antillean families.

Quaternary

The best fossil record for West Indian vertebrates comes from Pleistocene and Holocene cave and fissure deposits. During the glacial maxima, the West Indies experienced much drier conditions than they do now, and arid-adapted species flourished (149). The reason for the relatively large number of vertebrate extinctions since the Pleistocene is not well established, but it is likely a combination of several factors: reduction in arid habitats, reduction of land area by elevated sea levels, and human-associated causes (128, 129, 134, 148, 149, 176). Humans colonized the West Indies about 7000 years ago (159), and it is probable that many Holocene extinctions were the result of contact by Amerindians and Europeans (129).

BIOGEOGRAPHIC MECHANISMS

Early Ideas

Darwin (34) used the West Indian mammal fauna as an example of how islands surrounded by deeper water exhibit greater endemism, but otherwise he offered

no speculation as to the origin of the fauna. Wallace (186), however, was one of the first to discuss, albeit briefly, the zoogeography of West Indian vertebrates. He made special note of the impoverished nature of the fauna (at higher taxonomic levels), an observation that would be repeated often (33, 117, 172) and one that has been appropriately termed "the central problem" (189). Because such a pattern of taxonomic composition is exactly what one sees on remote, oceanic islands (137a), this has been interpreted as evidence of overwater dispersal. However, land bridges between the islands and the continents also were proposed to explain the same patterns of distribution and faunal composition (5, 162, 163), launching a lengthy debate (33). Deep water now is known to surround many of the islands in the Greater and Lesser Antilles, precluding dry land connections due to recent sea-level changes, and therefore the "land bridge hypothesis" is no longer viable. However, vicariance, through the mechanism of plate tectonics, essentially has replaced the land bridge hypothesis as one of the two primary theories (with overwater dispersal) for the origin of the West Indian biota.

Vicariance and Dispersal

PHYLOGENY The vicariance theory of Caribbean biogeography suggests that the present West Indian biota represents the fragmented remnants of an ancient biota that was continuous with those of North and South America in the late Cretaceous (156, 157). Plate tectonic reconstructions still have not "stabilized" to a single well-supported scenario for the Caribbean region (71, 139, 140), but the proto-Antillean island arc required in the vicariance hypothesis is, nonetheless, a common theme in most reconstructions. Thus, proto-Antillean vicariance cannot be eliminated on geological grounds.

The primary evidence used to support the vicariance theory has come from cladistic (vicariance) biogeography (86, 133). The basic premise of this approach is that congruence among organismal phylogenies, and between those phylogenies and area relationships, supports vicariance. The early proponents of cladistic biogeography considered dispersal to be untestable and unscientific (133), a viewpoint that has not changed significantly (130). Even the less extreme viewpoints place dispersal in a secondary role: "dispersal should be a last resort for explaining modern distributions and used only after all vicariance possibilities have been considered" (60). Following this approach, cladistic biogeographers have claimed considerable support for a vicariant origin for West Indian vertebrates (32, 62, 63, 93, 94, 135, 156, 157, 160, 161).

However, this fundamental tenet of cladistic biogeography recently was called into question (79). The claim that phylogenetic evidence alone can provide such support of vicariance is rejected for the simple reason that dispersal

can produce the same phylogenetic patterns (173a). Fully congruent phylogenies, even those congruent with a geological scenario, can be produced through concordant dispersal. Geographic proximity, air currents, water currents, and other factors all combine to produce higher probabilities of dispersal from some areas than others. In the West Indies, this is especially true because ocean currents flow almost unidirectionally from southeast to northwest (see Figure 1). Therefore, dispersal to the West Indies by rafting on currents is much more likely from South America than from Central or North America (74).

Because many West Indian vertebrate groups have their closest relatives in South America (see below), the methodology of cladistic biogeography would dictate that a vicariant event must have separated South America from the West Indies. However, concordant dispersal provides an equally valid explanation. The data that can distinguish between these two possibilities are the times of divergence of West Indian taxa from their closest relatives on the mainland (74, 78, 79). Groups that diverged at the same time as the geologic separation can be inferred to have arisen by vicariance. Those groups that arose after the geologic separation can be inferred to have arisen by dispersal. Thus, phylogeny can help to establish whether a pattern exists and to identify the source area, but it is the timing of the divergence that allows one to distinguish between these alternative explanations (74, 79).

TIMING Information on the time of divergence of West Indian vertebrate groups from their mainland relatives has come from the fossil record and from the use of molecular clocks. The presence of mid-Tertiary fossils has been used both for (143) and against (147) the vicariance theory. In the former case, an Eocene (40 mya) date for the amber fossils was used to suggest that a diverse fauna was present in the Antilles at an earlier date than generally proposed (143). However, those fossils now are considered to be younger (15–30 mya; see above), and dispersal could have occurred at any time (189). Although the fossil record continually is improving, it is at present of limited value in providing the crucial times of origin for West Indian lineages.

More than 65 studies have been published involving protein electrophoretic, immunological, and DNA sequence divergence among West Indian vertebrates, mostly amphibians and reptiles (145). Of those, the data most frequently used to obtain times of divergence are immunological estimates of amino acid sequence divergence of a protein, serum albumin (23, 56, 64, 66, 69, 78, 169). The rate of evolution in this gene is remarkably constant in studies where geological and paleontological calibration was possible (122).

To draw some general conclusions regarding the origin of the West Indian vertebrate fauna, albumin immunological data from diverse lineages of amphibians and reptiles were assembled (78). In all 13 comparisons between West Indian

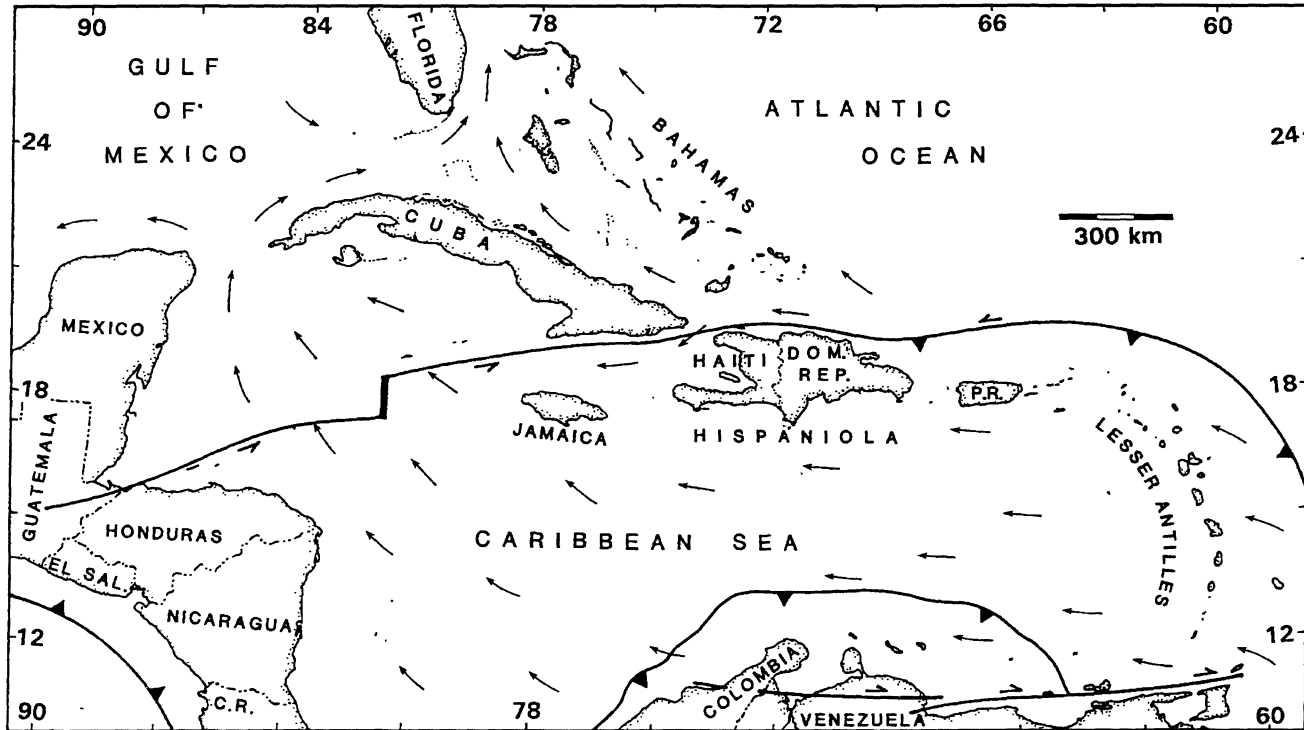


Figure 1 The West Indies, showing direction of water currents (long arrows). The geologic features, indicated by thick lines, are faults (short arrows indicate direction of plate movement), subduction zones (teeth indicate direction of subduction), and a spreading center (double-thick line).

lineages and their closest relatives on the mainland, the estimated divergence times were later than predicted by vicariance, indicating mid-Tertiary rather than late Cretaceous origins (78, 79). Since then, other molecular and non-molecular data were used to examine the remaining 64 independent lineages of West Indian amphibians and reptiles (74). With the possible exception of the frog genus *Eleutherodactylus* and the xantusiid lizard *Cricosaura typica*, all lineages appear to have originated in the Cenozoic. Phylogenetic analyses indicate that most West Indian groups have affinities with South American taxa, suggesting overwater dispersal from that continent. It was proposed that the nearly unidirectional (southeast to northwest) ocean currents have carried flotsam (e.g. 70, 91) from the mouths of major rivers in South America to islands of the West Indies throughout the Cenozoic era (74).

The Bolide Impact

Given the geologic possibility for vicariance, the virtual absence of an ancient West Indian vertebrate fauna suggests that numerous extinctions may have occurred since the formation of the proto-Antilles in the late Cretaceous. Because most of the mid-Tertiary fossils are of groups extant in the Holocene, an ancient West Indian biota—if it existed—would appear to have become extinct earlier in the Tertiary. To explain this, it was proposed that the impact of the Cretaceous-Tertiary (K-T) asteroid or comet (bolide) at 65 mya probably devastated the ancient West Indian biota because of its very close proximity to that region (78).

A large crater (Chicxulub) about 1 km beneath the surface of the Yucatán peninsula is believed by most geologists to be the impact site for the K-T bolide (81, 96, 120). The size of the crater is not agreed upon, but it is between 170 km and 320 km in diameter, making it the largest known impact structure in the inner solar system during the last 4 billion years (82, 166, 167). At the time of impact, the Greater Antilles were the closest land masses, located only 1–3 crater diameters away (139). It was, in fact, the local effects of this impact that helped locate the crater (81). Giant wave deposits found in Haiti and Cuba indicated disturbances in sediments that were at least 2 km below sea level at that time (120). “Megawave” deposits also have been found in deep water (> 400 m) sediments in northeastern Mexico, containing leaves, wood, and terrestrial debris (173), and in the southern United States (81) and the Gulf of Mexico (1). Gigantic hurricanes (hypercanes), resulting from local heating of sea water, also have been proposed (48). Besides the devastating global effects of the impact, these catastrophic local effects would almost certainly have caused widespread extinctions of many organisms that might have existed in the Caribbean region at that time.

Table 2 Numbers of families, genera, and species of native West Indian freshwater fishes^a

Order and family ^b	Genera			Species		
	Total	Endemic	% Endemic	Total	Endemic	% Endemic
Luganoiiformes						
Lepisosteidae	1	0	0	1	1	100
Ophidiiformes						
Bythitidae	1	1	100	4	4	100
Cyprinodontiformes						
Poeciliidae	5	3	60	46	45	98
Cyprinodontidae	2	1	50	8	8	100
Fundulidae	1	0	0	1	0	0
Rivulidae	1	0	0	7	7	100
Atheriniformes						
Atherinidae	1	1	100	1	1	100
Synbranchiformes						
Synbranchidae	1	0	0	1	0	0
Perciformes						
Cichlidae	1	0	0	5	5	100
TOTAL	14	6	43	74	71	96

^aAfter Burgess & Franz (17); but including the Miocene cichlid (28) and some recently described taxa.

^bThere are no endemic families.

TAXON-SPECIFIC PATTERNS

Freshwater Fishes

There are six orders and nine families of freshwater fishes in the West Indies (Table 2). Although no families are endemic, 6 of the 14 genera (43%) and 71 of the 74 species (96%) are endemic to the West Indies. Most of those species are restricted to a single island, portion of an island, lake, or even sinkhole. Species diversity is correlated with island area; Cuba (28 species) and Hispaniola (35 species) have the most species, with relatively few on Jamaica (6 species), the Bahamas (5 species), Cayman Islands (4 species), and Martinique (1 species). There are no endemic species on Puerto Rico. Relationships still are not well known for many groups, but approximately 17 independent lineages of West Indian freshwater fishes can be identified: 9 with North (or Central) American affinities, 6 with relationships to South American taxa, and 2 of marine origin (17).

Discussion of the historical biogeography of West Indian fishes has included both vicariance and dispersal as mechanisms for the origin of the fauna (16, 17, 156). However, the Tertiary fossil record consists of only one fossil cichlid from the early Miocene of Haiti (28), and there are no molecular data

that would permit dating of divergences. While it is a reasonable assumption that the few non-endemic species arrived by dispersal in the Quaternary, the time of origin for the remainder of the species cannot be inferred. All of the species are secondary not primary freshwater species, which means that they are to some degree tolerant of salt water. This fact has led previous workers (e.g. 132) to consider secondary freshwater species as inadequate indicators of biogeographic patterns. With the possible exception of the Cuban gar, there is no evidence to indicate that any of the West Indian lineages of freshwater fishes are of ancient (Cretaceous) origin.

The Cuban gar, *Atractosteus tristoechus*, is a lepisosteid and the only luganiform in the West Indies. It is believed to be most closely related to species in the same genus inhabiting North and Central America (17). The oldest lepisosteid fossil is early Cretaceous, and fossils of *Lepisosteus* range back to the late Cretaceous (80 mya) in North America and Europe (54). Four species of brotulas or cusk-eels (Ophidiiformes) occur in the West Indies and are placed in an endemic genus, *Lucifuga*. They inhabit freshwater sinkholes on Cuba and a brackish water cave system in the Bahamas, and they are believed to have had a marine origin (17, 101).

The largest component of the West Indian freshwater ichthyofauna (84% of species) belongs to the order Cyprinodontiformes. Most of those species are in the family Poeciliidae. There is disagreement over the relationships of West Indian *Gambusia* (10 species), although there appear to be at least three species groups representing three separate colonizations, most likely from North or Central America (17, 106, 150, 151). Species in the endemic Cuban genera *Girardinus* (8 species) and *Quintana* (1 species) together form a monophyletic group with affinities to *Carlhubbisia* of Guatemala (151, 156). The endemic genus *Limia* (24 species) and the three species of *Poecilia* (monophyletic subgroup) are each believed to represent a single colonization from South America (17, 150). There are no documented pre-Quaternary fossil poeciliids, although there is an undocumented report of an early Tertiary (Paleocene) fossil from Argentina in the literature (137).

Eight species of killifishes (Cyprinodontidae) are found in the West Indies (17; and those subsequently described). *Cubanichthys* (3 species), a West Indian endemic, is believed to have arrived by dispersal from North or Central America (17). At least two dispersals from North or Central America, probably in the Quaternary, are required to explain the origin of West Indian *Cyprinodon* (5 species). The oldest fossil cyprinodontid is mid-Tertiary (Oligocene), although some early Tertiary (Paleocene) scales, possibly belonging to this family, exist (137). A single, non-endemic, species of fundulid (*Fundulus grandis*) occurs in northern Cuba; it has affinities to populations in southern

Florida. Dispersal from North America during the Quaternary has been postulated to explain its origin (17). Seven species of rivulids (*Rivulus*) are known from the West Indies. Their relationships are not well understood, and therefore the number of independent lineages is unknown, although at least two are indicated. The rivulids may have arrived by dispersal from South America (17). The order Atheriniformes is represented by a single endemic, monotypic genus of silverside, *Alepidomus*, occurring in western Cuba. It is believed to be of marine origin (17). A single, non-endemic, species of swamp eel (synbranchiform), *Ophisternon aenigmaticum*, occurs in Cuba. Its distribution in South and Central America suggests relatively recent (Quaternary) dispersal. The order Perciformes is represented by five endemic species of cichlids in the genus *Cichlasoma*. One of those species is the Miocene *C. woodringi* from Haiti (28); the remaining four are extant. The number of independent lineages is not known, but they are believed to have arisen by dispersal from South America (17). The oldest cichlid fossil is mid-Tertiary (Oligocene) and is from Somalia (137).

Amphibians

All West Indian amphibians are anurans (frogs and toads), and they represent 3.7% of all extant amphibian species. Of the four families and six genera, only one genus (*Osteopilus*) is endemic (Table 3). However, nearly all (99%) of the 166 native species are endemic, and most (138 species) are in the enormous Neotropical leptodactylid genus *Eleutherodactylus* (> 520 species). With few exceptions, each species is restricted to a single island and often to a small area within an island (< 100 km²; 75). Species diversity is concentrated in the Greater Antilles; there are no endemic species in the Bahamas, and only nine species are endemic to the Lesser Antilles. The nine independent lineages of West Indian amphibians are believed to represent one origin by late Cretaceous vicariance and eight independent Cenozoic dispersals from the mainland (74);

Table 3 Numbers of genera, and species of native West Indian amphibians (all, order Anura)^a

Family ^b	Genera			Species		
	Total	Endemic	% Endemic	Total	Endemic	% Endemic
Bufonidae	1	0	0	11	11	100
Dendrobatidae	1	0	0	1	1	100
Hylidae	2	1	50	10	10	100
Leptodactylidae	2	0	0	144	142	99
TOTAL	6	1	17	166	164	99

^aAfter Hedges (74).

^bThere are no endemic families.

the source area for seven lineages is South America, and the other two lineages are from Central or South America.

The West Indian bufonids (*Bufo peltocephalus* group) represent a monophyletic group (146) among Neotropical species of the cosmopolitan genus *Bufo*, with probable affinities to the *Bufo granulatus* group of South America (27). Albumin immunological distance (ID) data (78) suggested an early Cenozoic origin for this group, probably by dispersal from South America (74). The single dendrobatid from Martinique (89) belongs to a diverse genus distributed almost entirely in South America (including Trinidad and Tobago). This fact, its location in the southern Lesser Antilles, and consideration of albumin ID data among dendrobatids (124) together suggest that it arrived by dispersal from South America during the Cenozoic (74).

Several hypotheses for the origin of West Indian hylid frogs have been proposed. Albumin ID data (78) largely supported an earlier hypothesis (46) that suggested that the West Indian species (except for one) are monophyletic and represent an early Cenozoic origin by dispersal from South America (74) rather than six independent colonizations (183). Those data also indicated that a single species from Hispaniola, *Hyla heilprini*, represents a separate invasion (dispersal) from South America, but the timing of that event is not known.

The leptodactylid genus *Eleutherodactylus* is the largest genus of vertebrates, and resolving the origin of the 138 known West Indian species has been a formidable challenge. Infrageneric classification largely has been based on several key morphological and allozyme characters (73, 107, 108), and much of the internal phylogenetic structure of the genus remains to be determined. A combination of slow-evolving allozyme loci, albumin ID data, and some unconventional morphological characters defined a western Caribbean clade (subgenus *Euhyas*) of 82 mostly terrestrial species and an eastern Caribbean clade (subgenus *Eleutherodactylus*) of 50 mostly arboreal taxa, with a third group of six large species (subgenus *Pelorius*) confined to Hispaniola (66, 73). The time of separation between the subgenera *Euhyas* and *Eleutherodactylus* was estimated to be late Cretaceous (70 ± 6.8 mya), thus agreeing well with a proto-Antillean vicariance model (66, 73). However, additional phylogenetic data are needed to clarify the origin of the West Indian lineage or lineages (74). Aside from two species of South American origin in the southern Lesser Antilles (90), there is no evidence that any dispersal events took place from the mainland to the West Indies during the Cenozoic. However, a single dispersal back to the mainland (probably from Cuba in the mid-Cenozoic) likely occurred and led to the subgenus *Syrrhophus* in Central America and southern North America (66, 73). The 17 native Jamaican species, all *Euhyas*, are a monophyletic group that resulted from a single colonization (probably from

Cuba) in the Miocene (8, 66, 72). Most species in the southern portion ("South Island") of Hispaniola, which was a separate island until the late Miocene, also belong to the subgenus *Euhyas* and apparently had a similar history as the Jamaican species (73). After collision with the remainder of Hispaniola ("North Island"), there was a limited exchange of species between the two regions.

Four species of *Leptodactylus* represent four independent dispersals to the West Indies from South America (or possibly Central America in the case of *L. insularum*). Three of these represent relatively recent (Pliocene or Quaternary) arrivals, but the Puerto Rican endemic (*L. albilabris*) is estimated to have arrived 40 mya (74, 123).

Reptiles

With 449 species (93% endemic), this is the largest component of the West Indian vertebrate fauna (Table 4), representing 7.4% of all extant reptiles. There are no endemic orders or families, although 9 of the 50 genera are endemic. Two genera of lizards, *Anolis* (138 species) and *Sphaerodactylus* (80 species), account for about one half of the total species diversity. With the possible exception of one Cuban species (*Cricosaura typica*) that may represent an ancient vicariant relict, all 68 independent lineages of West Indian reptiles are believed to have arrived by overwater dispersal from the following source areas: North America (3 lineages), Central America (8 lineages), Central or South America (14 lineages), South America (35 lineages), Africa (4 lineages), and "New World" (4 lineages) (74).

The three species of crocodylians represent three separate dispersals in the late Tertiary or the Quaternary, apparently from Central and South America (74). The relationships of amphisbaenians still are poorly known, although albumin ID data (78) together with other data (e.g. 29) suggest the 14 West Indian species may comprise a single radiation (74). The origin of that lineage or lineages probably was from South America, and the dispersal was estimated to have occurred in the early Cenozoic (78).

West Indian anguid lizards belong to the Neotropical subfamily diploglossinae. Until recently, five genera were recognized, based on osteoderm structure (177); four of these were distributed on the islands. Although two of the genera (*Sauresia* and *Wetmorena*) were restricted to Hispaniola, they were considered to be derived from Hispaniolan *Celestus* (177). Recently, an earlier generic arrangement was resurrected and a classical proto-Antillean vicariance scenario postulated to explain the origin of the West Indian species (161). In it, the two Hispaniolan endemic genera were considered to be early derivatives of *Diploglossus*. However, albumin ID data (74, 78) support the closer relationship of those genera to Hispaniolan *Celestus*. Moreover, albumin ID data

Table 4 Numbers of genera and species of native West Indian reptiles^a

Order and family ^b	Genera			Species		
	Total	Endemic	% Endemic	Total	Endemic	% Endemic
Crocodylia						
Crocodylidae	1	0	0	3	1	33
Squamata						
Amphisbaenians						
Amphisbaenidae	1	0	0	14	14	100
Lizards						
Anguidae	2	0	0	22	22	100
Gymnophthalmidae	2	0	0	3	1	33
Iguanidae	5	2	40	172	169	98
Gekkonidae	7	0	0	97	89	92
Scincidae	1	0	0	2	1	50
Teiidae	4	0	0	24	20	83
Xantusiidae	1	1	100	1	1	100
Snakes						
Boidae	3	0	0	11	9	82
Colubridae	15	6	40	46	42	91
Elapidae	1	0	0	1	0	0
Leptotyphlopidae	1	0	0	8	6	75
Tropidophiidae	1	0	0	13	13	100
Typhlopidae	1	0	0	24	24	100
Viperidae	1	0	0	2	2	100
Testudines						
Emydidae	1	0	0	4	4	100
Kinosternidae	1	0	0	1	0	0
Testudinidae	1	0	0	1	0	0
TOTAL	50	9	18	449	418	93

^aAfter Hedges (74).^bThere are no endemic families.

indicate a mid-Cenozoic origin, by dispersal, for the West Indian species (74, 78). Three species of gymnophthalmids represent independent colonizations of the West Indies from South America. Two of those (*Bachia heteropus* and *Gymnophthalmus underwoodi*) almost certainly dispersed in the Quaternary, whereas the time of arrival for the third lineage (*G. pleei*) is unknown, although it was most likely during the Cenozoic (74). Iguanid lizards have inhabited the West Indies at least since the early Miocene, but the exact number of colonizations is not known. There is broad agreement over the definition of species groups and series of anoline lizards, but the higher-level relationships have not been determined despite considerable study with morphological, chromosomal, and molecular data (e.g. 19, 68, 169, 187, 188, 198). An attempt at synthesis

of disparate sources of published data for anoline lizards (62) was unsuccessful (26, 63, 190).

Despite the current lack of consensus regarding anoline relationships, evidence for the timing of their arrival to the West Indies, from albumin ID data, supports an arrival by dispersal in the mid-Cenozoic (16–36 mya) from Central or South America (74). This timing is concordant with the fossil evidence noted above and contradicts speculation (62, 158) that their origin was the result of proto-Antillean vicariance. Future resolution of relationships will help determine the number of independent colonizations that occurred. Besides the anoline lizards, eight additional colonizations by iguanids to the West Indies can be identified, occurring in the Quaternary. Two exceptions are endemic genera that apparently arrived in the mid-Cenozoic from Central or South America (*Cyclura*) and North America (*Leiocephalus*), respectively (74).

The West Indian gekkonid lizards represent 11 independent colonizations, primarily from South America and Africa and mostly in the Quaternary (74). Of special note is the large genus *Sphaerodactylus* (80 species). Analysis of allozyme and albumin ID data led Hass (64) to postulate a South American origin for the West Indian species by dispersal in the mid-Cenozoic. This timing is in agreement with the presence of the genus in Dominican amber (9, 142). A recent DNA sequence analysis of relationships among *Sphaerodactylus* (65) identified several well-supported monophyletic groups in the West Indies and refined the classification of the genus but did not alter that hypothesis for the origin of the West Indian species. However, additional data are needed for all species, including those in the mainland *lineolatus* section (10 species), before the number or direction of dispersal events can be accurately determined. An origin for the mainland species by dispersal from the West Indies cannot yet be ruled out.

Only a single endemic scincid lizard is present in the West Indies. A possible relationship with a South American species in the same genus (*Mabuya*) suggests an origin by dispersal from that continent. At least eight independent lineages of teiid lizards are present, and most arose by dispersal from South America in the Quaternary. The relationships of the 20 endemic species of *Ameiva* (considered to be one lineage) are not yet established, but albumin ID data suggest a mid-Cenozoic origin by dispersal from Central or South America (74, 78).

The single endemic xantusiid lizard, *Cricosaura typica*, represents a biogeographic enigma because of its restricted distribution in an unexpected location: the Cabo Cruz region of eastern Cuba. Although analysis of some published morphological data supported a close relationship with *Lepidophyma* of Central America (32), several key morphological characters in that study

were found to be incorrectly scored, thus putting that conclusion into question (76). Instead, DNA sequence data provided statistical support for the basal position of *Cricosaura* within the family (76, 77), and this was further supported by chromosome evidence (67). The presence of Middle Paleocene xantusiid fossils from North America (50) suggests an early isolation, perhaps by proto-Antillean vicariance, for *Cricosaura*. However, a more recent dispersal to the West Indies, and subsequent extinction of the mainland source population, cannot be ruled out due to the relictual nature of xantusiid lizard distribution (6, 74, 77). No albumin ID data are available for these xantusiid lizards.

A single vertebra records the presence of boid snakes in the West Indies by the early Miocene (114). Of the four independent lineages now present, only one (*Epicrates*) contains endemic species (74). There is one mainland species in that genus, and the nine West Indian species are believed to form a monophyletic group (93, 182). Although proto-Antillean vicariance was postulated to explain the origin of the West Indian species (94), a low albumin ID between *Epicrates* and *Boa* (37), corresponding to a divergence time of about 22 mya, argues instead for a mid-Cenozoic origin by dispersal (74).

Colubrid snakes colonized the West Indies at least 11 times, mostly from South America and mostly in the late Cenozoic (74). Of special note is the large assemblage (33 species) of alsophines, including six endemic genera. Three dispersals from the mainland were proposed to explain their origin, based on a morphological analysis (115). However, albumin ID data are more suggestive of a single, monophyletic group (22, 78). Those same data, and others (23), also indicate a mid-Cenozoic origin by dispersal from South America (74). The recent suggestion (31) that the North American genus *Farancia* is "internested" among West Indian alsophines is not supported by the strict consensus tree of that same study, and it is contradicted by albumin ID data (24), indicating that *Farancia* is not closely related to alsophines.

A single (nonendemic) species of elapid snake is recorded from Isla de Providencia off the coast of Nicaragua. Its origin likely was by dispersal from Central America in the Quaternary (74). Four independent colonizations of the West Indies by leptotyphlopoid snakes are believed to have occurred (74). Relationships of species in this family are poorly known and in need of study, but the five endemic species of the *bilineata* group are believed to represent a single colonization and radiation (181). A single Bahamian species, *L. columbi*, may represent a separate colonization, perhaps from South America in the late Tertiary or Quaternary (74). The snake family Tropicophiidae is Neotropical, and the genus *Tropidophis* is primarily West Indian. An origin by dispersal from South America in the early to mid-Tertiary is indicated by albumin ID data (74, 78). Most West Indian typhlopoid snakes are believed to form a monophyletic

group (20 species) with African affinities, whereas the remaining four species are believed to represent a single group with New World affinities (180). However, albumin ID data suggest a closer relationship between those two lineages and an origin by dispersal in the Cenozoic (74, 78). Two species of viperid snakes are endemic to islands in the southern Lesser Antilles. Consideration of their distribution, affinities (100), and albumin ID data among related species (25) suggests that they arrived by dispersal from South America in the late Tertiary or Quaternary (74).

The Antillean genus of emydid turtles (*Trachemys*) has a single non-West Indian species, *T. scripta* (165). There are no albumin ID data, but consideration of the fossil record, distribution, and relationships suggests a single dispersal from Middle or North America in the mid- to late Cenozoic, with a reverse dispersal leading to *T. scripta* on the mainland (74, 165, 165a). The single, non-endemic kinosternid turtle species occurring on islands adjacent to Central America probably arrived by dispersal in the Quaternary. It is unknown whether the Miocene pelomedusid turtles inhabited freshwater or saltwater, and little is known of their origin (74, 112a, 114). The single extant testudinid turtle is not endemic; it likely arrived by dispersal in the Quaternary. Fossils of giant species in this family are known from the West Indies, but their time of origin and source area are not known.

Birds

There are 15 orders and 49 families of native West Indian birds representing about 4.4% of the world's bird fauna, although endemism is relatively low (Table 5). One family (Todidae) out of 49 (2%), 38 of the 204 genera (19%) and 150 of the 425 species (35%) are endemic to the West Indies. There never has been a comprehensive treatment of the historical biogeography of West Indian birds, although some general patterns have been discussed (10, 97, 134). Also, the phylogenetic relationships of many West Indian endemic groups remain poorly known, limiting biogeographic inferences (92, 125, 166) or tests of ecological models (51, 152, 153, 179).

Notwithstanding the limitations of the avian database, it has been postulated that the origin of the entire West Indian avifauna was by dispersal, largely from North America (10, 134), except for the avifauna of the southern Lesser Antilles, which appears to be mostly South American in derivation (49). The single endemic family, the Todidae, is believed to be the oldest lineage in the West Indies, having arrived from North America in the Oligocene; this theory is based on mainland fossils (134), but also some known from France. Each of the 275 non-endemic species represents at least one separate dispersal from the mainland, most likely in the Quaternary. However, that number is almost certainly an underestimate based on the finding of complex and multiple

colonization patterns in some well-studied species (92, 166). The remaining 150 endemic species represent fewer than that number of colonizations, but the actual number of independent lineages presently is unknown.

Mammals

There are 5 orders and 16 families of native West Indian mammals representing about 3.1% of the world's mammal fauna (Table 6). Four families, 38 of the 65 genera (58%), and 116 of the 145 species (80%) are endemic to the West Indies. Although all West Indian vertebrate groups have suffered at least some human-caused extinctions, mammals have, by far, suffered the most. Almost 90% of the known species of nonvolant West Indian mammals went extinct during the last 20,000 years (129). Climatic changes related to the Pleistocene glaciations are believed to have caused some extinctions (149), while Amerindians and Europeans both have been implicated in other extinctions (129). Phylogenetic relationships are still not well established, but at least 51 independent lineages can be identified: 9 for nonvolant species and 42 for bats (129). Of those, the nonvolant mammals show a strong South American influence (7 lineages) with only one lineage showing affinities to Central America and one to Central or North America. Bats, on the other hand, show a greater influence from the

Table 5 Numbers of families, genera, and species of native West Indian birds^a

Order	Families ^b	Genera			Species		
		Total	Endemic	% Endemic	Total	Endemic	% Endemic
Craciformes	1	1	0	0	1	0	0
Galliformes	1	1	0	0	1	0	0
Anseriformes	2	6	0	0	20	1	5
Piciformes	1	7	2	29	12	9	75
Trogoniformes	1	1	1	100	2	2	100
Coraciiformes	2	2	1	50	7	5	71
Cuculiformes	2	4	2	50	10	6	60
Psittaciformes	1	3	0	0	13	11	85
Apodiformes	1	4	0	0	7	2	29
Trochiliformes	1	10	5	50	17	14	82
Strigiformes	4	10	2	20	16	6	38
Columbiformes	1	6	1	17	17	10	59
Gruiformes	3	3	1	33	13	1	8
Ciconiiformes	18	59	0	0	104	3	3
Passeriformes	10	87	23	26	185	80	43
TOTAL	49	204	38	19	425	150	35

^aAfter Bond (11); with subsequent taxonomic changes and classification of Sibley and Ahlquist (170) and Sibley and Munroe (171).

^bThe Todidae (Coraciiformes) is the only endemic family.

Table 6 Numbers of genera and species of native West Indian mammals^a

Order and family	Genera			Species			
	Total	Endemic	% Endemic	Total	Endemic	% Endemic	% Extinct
Edentata							
Megalonychidae	11	11	100	18	18	100	100
Insectivora							
Solenodontidae ^b	1	1	100	4	4	100	25
Nesophontidae ^b	1	1	100	8	8	100	100
Chiroptera							
Emballonuridae	1	0	0	1	0	0	0
Noctilionidae	1	0	0	1	0	0	0
Mormoopidae	2	0	0	8	6	75	25
Phyllostomidae	18	8	44	27	16	59	11
Natalidae	1	0	0	4	2	50	0
Vespertilionidae	5	0	0	9	4	44	0
Molossidae	4	0	0	8	1	13	0
Primates							
Cebidae	4	2	50	4	4	100	100
Callitrichidae	1	1	100	2	2	100	100
Rodentia							
Echimyidae	4	4	100	7	7	100	100
Capromyidae ^b	8	8	100	34	34	100	61
Heptaxodontidae ^b	4	4	100	5	5	100	100
Muridae	2	1	50	8	8	100	100
TOTAL	68	41	60	148	119	80	54

^aAfter Baker and Genoways (4), Jones (88), Koopman (95), MacPhee and Iturralde-Vinent (112a), Wilson and Reeder (192), and Woods (195).

^bEndemic family.

west: 18 lineages from Central America, 14 from South America, and 2 from North America.

All West Indian (and other) ground sloths are extinct, although some apparently were contemporaneous with Amerindians as recently as 3715 years ago (129). The West Indian species all belonged to the family Megalonychidae, which was distributed in North and South America and first appears in the fossil record in the Lower Oligocene of Puerto Rico (112a). Relationships among the species of megalonychids are not well known, although recent studies (112, 112a, 195) have supported an earlier suggestion (117) that the West Indian species likely arose by a single dispersal from South America in the mid-Tertiary. A continuously exposed Oligocene land bridge (Aves Ridge) was proposed to explain that dispersal event (112). However, geologic evidence favors only a small chain of islands, if up to 1000 m of subsidence is

taken into account (83). Also, if a dryland connection occurred, it must be explained why groups that were present in South America at that time (e.g. marsupials, notoungulates, and astrapotherians among mammals; and many groups of amphibians and reptiles) did not come across and are not represented in the later fossil record or among extant fauna. Moreover, the fossil discovery of a marine ground sloth (35) indicates that saltwater dispersal probably would not have been a problem for these animals. Thus, the origin of West Indian ground sloths probably was the result of a single overwater dispersal from South America in the mid-Tertiary, possibly using the Aves island arc as "stepping stones."

Both families of West Indian insectivores, Solenodontidae and Nesophontidae, are endemic. Although none of the eight known species of nesophontids is extant, most became extinct in post-Columbian times (129). The surviving solenodontids are reduced in numbers and approaching extinction (196). Reconstructing the biogeographic origin of insectivores in the West Indies has proven to be difficult because of the present lack of consensus regarding relationships of the families of insectivores (21, 113), although the two West Indian families often are considered closest relatives (109) and the result of a single colonization event (129). A late Mesozoic origin by Proto-Antillean vicariance has been suggested (109, 110) and is compatible with the age (late Cretaceous) of insectivore fossils from North America (178). However, it also has been noted that the presence of insectivores on Ile Tortue (separated from Hispaniola by deep water) and in the Cayman Islands is evidence that they were capable of dispersing over salt water (195). No molecular data are available that would permit time estimations for the origin of these two families in the West Indies. However, some amber-encased bones believed to be of an insectivore recently were reported from the Dominican Republic (111a), which would establish their presence in the West Indies by 20–30 mya.

Seven families of bats are known from the West Indies (Table 6). There are no endemic families, and only 8 of the 32 genera (25%) and 29 of the 58 species (58%) are endemic. The number of species on each island is partly correlated with island area (59), but it also is related to distance from mainland source areas (4). Bahamian species are derived entirely from the West Indian fauna (almost all from Cuba) rather than from Florida (127), and those in the southern Lesser Antilles (e.g. Grenada) are derived from South America. It has been emphasized in the past that much of the West Indian bat fauna was derived from Central America (e.g. 95, 195). This is true for the non-endemic Jamaican and Cuban species (4, 95) but the Lesser Antillean bat fauna is largely derived from South America (15). The total number of known colonizations ($N = 42$) for all West Indian bats, including those from Grenada, reflects the different origins

for the Greater versus Lesser Antillean bat faunas: 18 from Central America, 14 from South America, 2 from North America, and 8 of undetermined source (88, 95, 129, 192). However, the origin of the lineages leading to the endemic Antillean genera has yet to be determined (4, 59).

The low level of endemism in West Indian bats is almost certainly the result of their enhanced dispersal abilities compared with nonvolant vertebrates: "most bats hardly need a raft" (4). Late Pliocene or Quaternary dispersal can be assumed for all non-endemic species (4). The time of origin for the remainder of the bat fauna is difficult to determine, because no pre-Quaternary West Indian fossils exist, and the bat fossil record, in general, is poor (178). No pre-Quaternary fossils exist anywhere for noctilionids, mormoopids, or natalids, whereas the earliest phyllostomid is Middle Miocene, and vespertilionids and molossids first appear in the mid-Eocene (178). Although drawing inferences concerning divergence times from the fossil record is subject to sampling biases (116), there is no evidence (e.g. an endemic family) of ancient lineages of bats in the West Indies that may have arisen by late Cretaceous vicariance. Thus, the best explanation for the origin of the endemic West Indian bat fauna is by dispersal during the middle or late Cenozoic.

Two families of primates are known from the Tertiary and Quaternary fossil record of the West Indies, but there are no extant species (112a, 195). The Hispaniolan cebid is thought to have affinities with South American species in the genus *Cebus* (196). One of the two Cuban cebids, *Ateles fusciceps*, probably was introduced in historical times (112a, 129). The species *Xenothrix mcgregori* occurred on Jamaica and is believed to have had South American affinities; it has been placed both in the Callitrichidae (53, 191) and its own monotypic family Xenotrichidae (111, 128). The remaining West Indian primate material is insufficient to clearly infer taxonomic position or affinities (52, 128, 129, 195).

The oldest cebid and callitrichid fossils are Lower Miocene and Middle Miocene, respectively (112a, 178). If the divergence between Old World and New World monkeys occurred about 55 mya, considering sampling biases (116), then the split between the cebids and callitrichids must have occurred more recently (55–20 mya); this would provide an upper bound on the time of origin for lineages within either family. Considering these constraints, the origin of West Indian primates is best explained by at least two independent overwater dispersals from South America during the middle or late Cenozoic.

Of the four families of native rodents known to have existed in the West Indies, only one (Capromyidae) is extant (194). The greatest generic and species diversity is seen in the three hystricognath families: Echymyidae, Capromyidae, and Heptaxodontidae. Echymyids show their greatest generic diversity on

Puerto Rico, but they also are known from Hispaniola and Cuba. Capromyids are not known from Puerto Rico but occurred on Hispaniola (where they show their greatest generic diversity), Cuba, the Cayman Islands, Jamaica, and the Bahamas. The giant hutias (heptaxodontids), some as large as 200 kg (7), are known from the northern Lesser Antilles, Puerto Rico, Hispaniola, and Jamaica.

Based on phylogenetic relationships and distribution, it has been proposed that all West Indian hystricognath rodents form a monophyletic group and owe their origin to a single overwater dispersal from South America in the late Oligocene or early Miocene (194). The initial disperser was believed to be a heteropsomyine echymyid, which colonized and diversified on Puerto Rico, later dispersing to Hispaniola and Cuba. A lineage of that initial Antillean radiation on Hispaniola, in turn, is thought to have led to the radiation of capromyids. Finally, the heptaxodontids are believed to have arisen from a capromyid ancestor on Hispaniola (194). If that hypothesis is correct, then perhaps the West Indian echymyids (Heteropsomyinae) and heptaxodontids should be placed in the Capromyidae. A different scenario involving more than one dispersal of hystricognaths to the West Indies also has been proposed (136).

West Indian sciurognaths are represented by two genera and eight species of murids, all extinct. Except for a single species from Jamaica, they are known only from the Lesser Antilles (194). The several species of *Oryzomys* are thought to represent two dispersals to the West Indies in the late Pliocene or Pleistocene: one from Central America leading to the Jamaican species *O. antillarum*, and the other from South America leading to the Lesser Antillean species. The several species of *Megalomys* are believed to represent one dispersal from South America in the late Pliocene or Pleistocene (194).

GENERAL PATTERNS

Knowledge of the diversity and phylogeny of West Indian vertebrates remains incomplete, but sufficient data are available now to draw some conclusions regarding the origin of the fauna. The general pattern that emerges is an origin by dispersal during the Cenozoic for an overwhelming majority (99%) of the independent lineages. In addition, the source area for a large fraction (66%) of the nonvolant vertebrate fauna is South America rather than the closer mainland areas of North America (16%) and Central America (11%) (Table 7). If fish are removed, this pattern is even more pronounced. Such a dispersal pattern can be explained by the nearly unidirectional current flow from the southeast to the northwest (18, 61), bringing flotsam from the mouths of South American rivers (e.g. Amazon, Orinoco) to the islands of the West Indies.

In contrast, the primary source areas for the freshwater fish and volant groups are North and Central America, suggesting that this difference lies in the mode

of dispersal: passive (flotsam) versus active (swimming and flying). Passive dispersers must rely on the surface currents to transport them, whereas active dispersers such as fish, bats, and birds have more control over their direction and speed of movement. Although air currents reaching the West Indies are mostly from the northeast, which might explain an origin from peninsular Florida for the volant fauna, this would not explain the large number of bat and bird lineages derived from Central America, or the Antillean derivation of the Bahamian bird and bat faunas. A more likely explanation for the origin of the fish and volant faunas involves a simple distance effect, with dispersal over shorter distances being favored. During Pleistocene sea-level lows, Cuba was nearly in contact with the exposed Great Bahama Bank, and Jamaica was much closer to Central America via the exposed Nicaraguan Rise, facilitating active dispersal. The other Bahamian vertebrate groups also show a derivation from the Antilles rather than from North America, which may be the result of both short distance and northward flowing water currents. However, the relatively low levels of endemism in the Bahamas probably reflect an origin following the Pleistocene high sea levels, when most or all of the Bank was submerged.

Evidence for this general pattern comes from a diversity of sources. The unusual taxonomic composition of the West Indian vertebrate fauna, with reduced higher-taxon diversity, always has favored overwater dispersal, and the growing Tertiary fossil record has yet to alter that conclusion. Evidence that this "unbalanced" fauna is not an artifact of an incomplete fossil record is found in the morphologies and ecologies of lineages that have radiated in the West

Table 7 The origin of West Indian vertebrates^a

	Fish	Amphibians	Reptiles	Birds ^b	Mammals		Total
					Bats	Other	
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

^aShown are the numbers of independent lineages.

^bThe exact number of lineages is not known for birds; there are at least 300 and probably more than 500 independent colonizations (see text). The predominate source area for West Indian birds is North America, but the specific number of lineages from each source area is not known.

^cSome of these lineages may have arrived from Central America (see text).

Indies. For example, the ground sloths and hystricognath rodents underwent unusually large radiations, filling niches normally occupied by primates, squirrels, porcupines, and ungulates (129, 195). And the absence of carnivores is believed to be responsible for the evolution of giant raptorial birds, now extinct, in the West Indies (134). Additional examples are found among the amphibians and reptiles. The primary source area for nonvolant colonists, South America, agrees with long-established current patterns, and the widely scattered Cenozoic dates of origin estimated by molecular data (74, 78) are concordant with a random mechanism such as overwater dispersal.

The large number of claims in the literature of an origin by vicariance is remarkable considering that geologists have not been able to establish a clear pattern of area relationships for the proto-Antilles (42), and that congruence of multiple phylogenies also can be attributed to concordant dispersal (79). In fact, the general pattern proposed here, dispersal on currents coming from South America, is such an example of concordant dispersal.

Some ancient lineages of West Indian vertebrates nonetheless may be present, and several candidates are the Cuban gar, frogs of the genus *Eleutherodactylus* (73), the xantusiid lizard *Cricosaura* (77), and the insectivores (109). The proto-Antillean land mass required by the vicariance theory cannot be eliminated on geological grounds, and indirect evidence suggests that some land areas in the Greater Antilles have been above water throughout the Cenozoic. For these reasons, vicariance may explain the origin of some lineages of vertebrates. However, catastrophic local effects of the K-T bolide impact, especially the giant tsunamis, must have resulted in widespread extinctions on any Antillean islands that were emergent at the time. For this reason, dispersal in the early Tertiary, immediately following the impact, also may explain the presence of ancient lineages in the West Indies.

The idea of the Lesser Antilles being a classic dispersal filter is well supported by the different distances that South American groups have extended up the chain (102, 103). For example, the faunal break for eleutherodactyline frogs occurs between St. Lucia and St. Vincent (90), whereas the break for anoline lizards is between Dominica and Martinique (55). Geologic evidence (see above) and the position of faunal breaks for different groups do not support the recent suggestion that the northern and southern Lesser Antilles were separated by a fault between Dominica and Martinique with major biogeographic consequences (158).

Future molecular phylogenetic studies of West Indian vertebrates should help to refine time estimates for the origin of independent lineages and more accurately determine source areas. Also, as the geological evolution of the Caribbean region becomes better known, it should be possible to examine the

influence of intra-Caribbean tectonic events on organismal evolution. At least one such event, the fusion that resulted in the present-day island of Hispaniola, appears to have had an impact on some of the fauna (73). Additional fossils, especially from the Tertiary, will give a better estimate of the taxonomic composition of the early vertebrate fauna and its bearing on biogeographic models. Although the recent trend in historical biogeography has been to focus on only one element of information, phylogeny, the integrative approach provides a better explanation of the geographic distribution of organisms through time.

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