THE ORIGIN OF WEST INDIAN AMPHIBIANS AND REPTILES

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Abstract.—The known West Indian herpetofauna is comprised of 175 species of amphibians (99% endemic) and 457 species of reptiles (93% endemic). Information on distributions, relationships, and times of origin, with emphasis on estimates of divergence time from albumin immunological data, are analyzed in an attempt to understand the origin of the herpetofauna. Seventy-seven independent lineages of West Indian amphibians and reptiles are identified and nearly all (95%) originated in the New World. Of those lineages for which a source area within the New World can be determined, most (79%) show a South American origin, with smaller contributions from Central America (15%) and North America (6%). One very old and diverse lineage, frogs of the genus *Eleutherodactylus*, originated by vicariance or dispersal in the late Cretaceous (70 mya). With one possible exception (the xantusiid lizard *Cricosaura typica*), all other lineages appear to have arrived by dispersal during the Cenozoic, and all but nine lineages in the last half of the Cenozoic (30–0 mya). Most West Indian lineages with multiple endemic species originated in the mid-Tertiary, whereas most lineages with a single endemic species arose in the late Tertiary. Quaternary dispersal is postulated to explain the origin of West Indian populations of mainland species.

The probable explanation for the predominately South American origin of the West Indian herpetofauna is the nearly unidirectional (towards the west-northwest) water current patterns in the Caribbean: water reaching the Greater Antilles originates near the Lesser Antilles and South America. Wide variation in the times of origin for the West Indian lineages does not support the recent suggestion of a mid-Cenozoic landbridge between South America and the Greater Antilles. Dispersal, in most cases, is believed to have occurred by the discharge of organisms attached to flotsam from the mouths of major rivers on the continents and carried by currents to the West Indies. Proto-Antillean vicariance remains a geological possibility, but recent paleocoastline data suggest that a dry land connection between the proto-Antilles and neighboring continents in the late Mesozoic may not have occurred. The widespread invoking of vicariance to explain nearly any distribution of West Indian organism without information on time of origin is seen as a popular trend but one that lacks support.

INTRODUCTION

AMPHIBIANS AND REPTILES MAKE UP ABOUT HALF (632 species) of the terrestrial vertebrates of the West Indies and exhibit the highest levels of endemism. For this reason, they have figured prominently in the literature on Caribbean biogeography. Most recently, attention has focussed on testing two theories for the origin of the West Indian biota. The vicariance model proposes that a proto-Antillean biota existed between North and South America in the late Cretaceous, and later moved eastward with the Caribbean plate during the Cenozoic (Rosen 1975, 1985). The alternative explanation is that overwater dispersal largely has been responsible for the origin of the current West Indian biota (e.g., Matthew 1918; Simpson 1956; Darlington 1957; Williams 1969; Pregill 1981b; Briggs 1984). Numerous combinations of these two mechanisms also have been suggested for various groups, although much of this has been speculation, and very few robust phylogenies or established times of origin have been presented.

The geologic history of the Caribbean is complex, but is becoming better understood (Perfit and Williams 1989; Pindell and Barrett 1990; Pitman et

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al. 1993). However, the proposal that a "proto-Antilles" existed between North and South America in the late Cretaceous (70–80 million years ago [mya]) has not changed substantially during the last two decades (e.g., Hedges 1982). Rosen's (1975) vicariance model requires a continuously emergent land mass, otherwise the proto-Antilles could not have provided a link between North and South America and transported terrestrial organisms eastward during the Cenozoic. If the proto-Antilles were not emergent, or if they became submerged at any time during their movement eastward, then the present West Indian biota must owe its origin to dispersal. Unfortunately, details on the emergence or submergence of land in the proto-Antilles are not known (Perfit and Williams 1989), although evidence exists for the complete or nearly complete submergence of Jamaica and the South Island of Hispaniola during the Oligocene (Horsfield 1973; Horsfield and Roobol 1974; reviewed in Buskirk 1985 and Hedges 1989a, 1989b).

Paleobotanical data suggest that well-developed plant communities, with high-altitude floras, were present in the Oligocene in at least part of the Greater Antilles (Graham and Jarzen 1969; Graham 1993). The oldest vertebrate fossil is a Jurassic pterosaur from Cuba, although the environment likely was shallow-water rather than terrestrial (Colbert 1969). Terrestrial vertebrate fossils from the Tertiary are rare and mostly are from mid-Cenozoic Dominican amber (Poinar 1992). These include frogs, anoline lizards, geckos, mammal hair (presumably rodent), and bird feathers (Rieppel 1980; Böhme 1984; Poinar et al. 1985; Poinar and Cannatella 1987; Poinar 1988, 1992). Fossils of *Anolis*, *Sphaerodactylus*, and *Eleutherodactylus* have been collected at the oldest mine (La Toca) and the age of those fossils has been estimated to be 30–40 my (Lambert et al. 1985; Poinar 1992). However, those older dates, using a somewhat unconventional method (nuclear magnetic resonance) for dating, are tied to a Lower Miocene (20–23 mya) date for Dominican
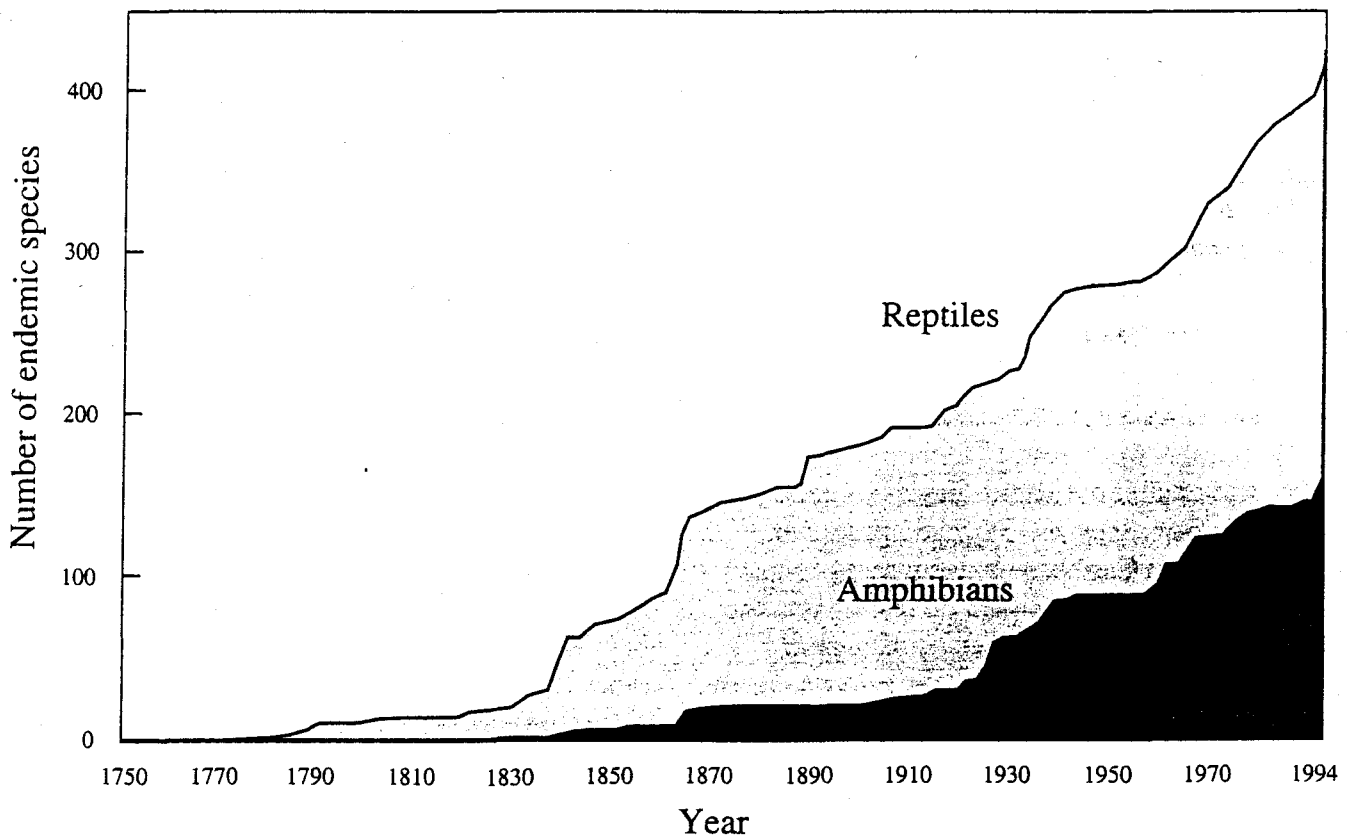

FIGURE 1. Discovery curves of West Indian amphibians and reptiles showing the number of known species at each time interval.

amber based on foraminiferal analysis, and thus a range of 20–40 mya for the La Toca fossils may be more realistic. Miocene fossils of a ground sloth (MacPhee and Ituralde-Vinent 1994) and cichlid fish (Cockerell 1923) also are known. Pleistocene fossils record a diverse vertebrate fauna, much of which disappeared at about the time of human colonization (Pregill and Olson 1981; Morgan and Woods 1986; Woods 1989; Morgan 1993).

Recently, these two hypotheses for the origin of the terrestrial vertebrate fauna — dispersal and vicariance — were tested using estimates of amino acid sequence divergence in the protein serum albumin in diverse groups of West Indian amphibians and reptiles: bufonid, hylid, eleutherodactyline, and

leptodactyline frogs; anoline, iguanine, sphaerodactyline, tropidurine, teiid, and anguid lizards; amphisbaenians; and alsophine and tropidophiid snakes (Hedges et al. 1992b). Albumin immunological distance (ID) is correlated with time of divergence in vertebrates (Maxson 1992) and this provided the means of estimating times of divergence between West Indian groups and their relatives on the mainland (with new data and those from the literature). All groups examined had lower estimates of divergence than would be predicted by proto-Antillean vicariance, suggesting an origin by overwater dispersal in the mid- to late Cenozoic. Further statistical analyses supported that conclusion (Hedges et al. 1994).

Several possible explanations exist for the finding of a recent origin for these major lineages of the West Indian amphibians and reptiles. The suggestion of an emergent proto-Antillean "isthmus" lacks support from geology and paleontology (Perfit and Williams 1989), in which case an opportunity for vicariance may not have occurred. Another possible explanation was suggested (Hedges et al. 1992b): the bolide (meteor or asteroid) impact at the Cretaceous/Tertiary boundary. The proto-Antillean islands were among the closest land areas to the Yucatán impact site (300 km crater; Sharpton et al. 1993) and they would have been devastated by the effects of this impact, including giant tsunamis (tidal waves). Evidence for the bolide impact is substantial (e.g., Hildebrand and Boynton 1990; Maurrasse and Sen 1991; Alvarez et al. 1992; Smit et al. 1992; Swisher et al. 1992; Kring and Boynton 1992; Sharpton et al. 1993), and it was this evidence that helped pinpoint the location of the impact structure. However, whether or not the local and global effects of the impact were sufficient to completely extinguish an ancient proto-Antillean biota that may have existed is speculative.

Analyses of phylogeny and distribution in other West Indian groups also have led to the suggestion of an origin by dispersal. Such groups include scorpions (Armas 1982; Armas and Marcano-Fondeur 1992), freshwater emydid turtles (Seidel 1988), rodents (Woods 1989), bats (Koopman 1989; Breuil and Masson 1991; although see Griffiths and

TABLE 1. Numbers of species of amphibians in the West Indies: total (T), native[1] (N), endemic[2] (E), introduced (I), and percent endemic[3] (%).

Taxon	T	N	E	I	%
Bufonidae					
Bufo [4]	13	12	12	1	100
Dendrobatidae					
Colostethus	1	1	1	0	100
Hylidae					
Hyla	3	1	1	2	100
Osteopilus [4,5]	9	9	9	0	100
Pseudacris	1	0	0	1	0
Scinax	1	0	0	1	0
Leptodactylidae					
Eleutherodactylus [4]	138	138	138	0	100
Leptodactylus	5	5	3	0	60
Microhylidae					
Gastrophryne	1	0	0	1	0
Ranidae					
Rana	3	0	0	3	0
Total	175	166	164	9	99

[1] Occurs naturally within the West Indies.
[2] Occurs naturally within the West Indies and nowhere else (except as introduced).
[3] Number of endemic species divided by number of native species.
[4] Includes some species currently being described.
[5] Includes *Calyptahyla* and some species previously placed in *Hyla* (see text).

Klingener 1988), and various Lesser Antillean plants and animals (Erard 1991; Lescure et al. 1991). For other groups, vicariance has been implicated. For example, the most basal lineage of xantusiid lizards survives as an eastern Cuba endemic (*Cricosaura*), possibly dating to the proto-Antilles (Hedges et al. 1991; Hedges and Bezy 1993, 1994). Also, the two major subgenera of West Indian *Eleutherodactylus* (*Euhyas* and *Eleutherodactylus*) are separated by a large ID, suggesting a late Cretaceous divergence (Hass and Hedges 1991).

Many groups of West Indian organisms have not yet been investigated, and therefore an origin by vicariance remains a possibility for those groups. Among mammals, the insectivores *Solenodon* and *Nesophontes* are believed to represent an ancient Antillean lineage (MacFadden 1980, 1981), and recently collected fossils establish ground sloths in Cuba in the Miocene (MacPhee and Iturralde-Vinent 1994). Antillean freshwater fishes (Burgess and Franz 1989) and butterflies (Miller and Miller 1989; Johnson 1991) are believed to have originated by both vicariance and dispersal, and Liebherr (1988*a*, 1988*b*) suggested an origin by vicariance for the carabid beetles. The giant endemic Cuban cycad (*Microcycas*) possibly represents an ancient lineage (Jones 1993).

The number of species of West Indian amphibians and reptiles has nearly doubled during the last four decades, largely through the efforts of Albert Schwartz, and the rate of species discovery has not yet declined (Figure 1). Currently 175 species of amphibians (Table 1) and 457 species of reptiles (Table 2) are known from the West Indies; these represent at least 77 independent lineages (see below). Hedges et al. (1992*b*) analyzed ID data for only a subset (13) of those lineages of West Indian amphibians and reptiles. Some minor lineages considered to be the result of recent dispersal were not included in that study, and new data for other lineages have become available since then. Therefore, that analysis is expanded here to include all lineages of West Indian amphibians and reptiles believed to have had independent origins, and, where possible, to (1) estimate the time of origin of each lineage, and (2) identify its mainland source area.

MATERIALS AND METHODS

This analysis draws from the literature pertaining to the origin of West Indian amphibians and reptiles. Albumin ID data were extracted from published and unpublished studies for the purpose of obtaining estimates of time of divergence. The protein serum albumin has excellent chronological properties (1 ID = approximately 0.6 million years; Maxson 1992), but several sources of error are involved in estimating divergence time from ID data (Hedges et al. 1992*b*, 1994). These include measurement error (± 2 ID; Maxson and Maxson 1979), differences in the reciprocal estimation of ID between two taxa (usually about 10%; Hass and Maxson 1993), unequal rates of change among lineages (Cadle 1988), error in estimating amino acid differences (apparently low; Hass and Maxson 1993), and error involved in calibrating IDs with divergence times estimated by fossils or geology. This last source of error, when estimated for the ID data presented in Hedges et al. (1992*b*), was found not to be substantial and did not affect the conclusions of that study (Hedges et al. 1994). Nonetheless, calibration error will be considered in this analysis (calculation of this error as in Hedges et al. 1994). Also, reciprocal IDs are not available for many species comparisons; this is likely to increase the error in divergence time estimates. However, one advantage of using an ID estimate of divergence time is that it is an estimate of the actual phylogenetic divergence event rather than a minimum or maximum age of that event determined by fossil-based estimates. For example, even if vertebrate fossils in Dominican amber were very accurately dated (now 20–40 mya), this would only establish a minimum time for the arrival of those lineages in the West Indies. The actual time of arrival (or divergence from mainland groups) could be much earlier, which apparently is the case for *Eleutherodactylus*.

The definition of the West Indies used here, and distributional data, are from Schwartz and Henderson (1988, 1991). Taxonomy follows Duellman (1993), King and Burke (1989), Schwartz and Henderson (1991), and Zug (1993), except where noted. All independent lineages of West In-

dian amphibians and reptiles are discussed. Lineages that clearly are the result of human introduction are mentioned but not treated in the analyses.

Relationships of species within a West Indian lineage, unless they have a bearing on the origin of that lineage, are not considered. For that reason,

TABLE 2. Numbers of species of reptiles in the West Indies: total (T), native (N), endemic (E), introduced (I), and percent endemic (%).

Taxon	T	N	E	I	%	Taxon	T	N	E	I	%
Squamata						Antillophis	2	2	2	0	100
Amphisbaenia						Arrhyton	12	12	12	0	100
Amphisbaenidae						Chironius	1	1	1	0	100
Amphisbaena [1]	14	14	14	0	100	Clelia	2	2	1	0	50
Sauria						Coniophanes	1	1	1	0	100
Anguidae						Darlingtonia	1	1	1	0	100
Ophisaurus	1	0	0	1	0	Diadophis	1	0	0	1	0
Celestus	19	19	19	0	100	Elaphe	1	0	0	1	0
Diploglossus	3	3	3	0	100	Hypsirhynchus	1	1	1	0	100
Gymnophthalmidae						Ialtris	3	3	3	0	100
Bachia	1	1	0	0	0	Liophis	5	5	4	0	80
Gymnophthalmus	2	2	1	0	50	Mastigodryas	1	1	1	0	100
Tretioscincus	1	1	0	0	0	Nerodia	1	1	0	0	0
Iguanidae						Pseudoboa	1	1	0	0	0
Anolis [1]	138	138	137	0	99	Tretanorhinus	1	1	1	0	100
Ctenosaura	1	1	0	0	0	Uromacer	3	3	3	0	100
Cyclura	8	8	8	0	100	Elapidae					
Iguana	2	2	1	0	50	Micrurus	1	1	0	0	0
Leiocephalus	23	23	23	0	100	Leptotyphlopidae					
Gekkonidae						Leptotyphlops	8	8	6	0	75
Aristelliger	7	7	6	0	86	Tropidophiidae					
Gekko	1	0	0	1	0	Tropidophis	13	13	13	0	100
Gonatodes	1	1	0	0	0	Typhlopidae					
Hemidactylus	5	4	1	1	25	Typhlops [1]	24	24	24	0	100
Phyllodactylus	2	2	2	0	100	Viperidae					
Sphaerodactylus [1]	80	80	78	0	100	Bothrops	2	2	2	0	100
Tarentola [1]	2	2	2	0	100	Testudines					
Thecadactylus	1	1	0	0	0	Emydidae					
Scincidae						Trachemys	5	4	4	1	100
Mabuya	2	2	1	0	50	Kinosternidae					
Teiidae						Kinosternon	1	1	0	0	0
Ameiva	20	20	19	0	95	Pelomedusidae					
Cnemidophorus	2	2	1	0	50	Pelusios	1	0	0	1	0
Kentropyx	1	1	0	0	0	Testudinidae					
Xantusiidae						Geochelone	1	1	0	0	0
Cricosaura	1	1	1	0	100	Crocodylia					
Serpentes						Alligatoridae					
Boidae						Caiman	1	0	0	1	0
Boa	1	1	0	0	0	Crocodylidae					
Corallus	1	1	0	0	0	Crocodylus	3	3	1	0	33
Epicrates	9	9	9	0	100						
Colubridae						Total	457	449	418	8	93
Alsophis	11	11	11	0	100						

[1] Includes some species currently being described.

many phylogenetic studies of West Indian amphibians and reptiles are not discussed here. For some groups, IDs are not available between the West Indian lineage and its closest relative on the mainland, and therefore several assumptions have been made concerning times of origin. If IDs are available between that group (e.g., a genus with representatives in the West Indies) and a more distantly related group (e.g., another genus), then it is assumed that the two groups are monophyletic and that the corresponding time estimate is an upper limit for the time of origin in the West Indies. For single species occurring both in the West Indies and on the mainland, a Quaternary (0–1.6 mya) divergence is assumed. Populations within species of amphibians and reptiles that have been examined using microcomplement fixation usually are separated by very low IDs (0–3) concordant with divergence in the Quaternary (e.g., Daugherty et al. 1982; Roberts and Maxson 1986; Hass 1991; Hass and Hedges 1991; Hass et al. 1992), although exceptions to this rule are known, especially in *Leptodactylus* (Maxson and Heyer 1988).

Because the continental source areas are much older than the West Indies and have a much greater diversity of amphibian and reptilian groups, it is assumed (except where noted) that the West Indian lineages originated from mainland source areas and not the reverse. For most lineages, this implicit assumption is supported by additional phylogenetic and distributional data. The primary source areas considered here are Africa and the New World; within the New World, they are North America, Central America, and South America. Neotropical groups occurring in the Lesser Antilles, especially the southern islands, are assumed to have been derived from geographically adjacent South America when no other information is available. South American groups that extend their range into Panamá are treated as South American because the Isthmus of Panama has been emergent only since the Pliocene (Savin and Douglas 1985) indicating recent dispersal northward for those groups.

Only proto-Antillean vicariance (e.g., Rosen 1975) is considered here; intra-Caribbean vicariance may have occurred but is not relevant to the origin of a West Indian group. Geologic models indicate that the proto-Antilles broke apart in the late Cretaceous 70–80 mya (Pindell and Barrett 1990) and therefore vicariance is assumed for groups that arose during that time. Dispersal is assumed for more recent times of origin (i.e., Cenozoic) and for the origin of Lesser Antillean taxa (based on the Eocene origin of that island arc; Pindell and Barrett 1990) when no ID data are available.

RESULTS

Amphibia: Anura
Bufonidae
Bufo marinus (species group) is native to Central and South America and has been introduced widely throughout the West Indies, although it is not established on Cuba (Schwartz and Henderson 1991).

(1) *Bufo peltocephalus* **group.**—This group of toads was recognized at the generic level by Pregill (1981a), who resurrected the genus *Peltophryne*. Although evidence for the monophyly of this group was given, no phylogenetic evidence was presented to substantiate its generic distinction from *Bufo*. Recently, an ID of 85 between *Peltophryne* and *B. marinus* (average of *P. guentheri* and *P. peltocephalus* each to *B. marinus*), was presented (Hedges et al. 1992b). Because IDs within the virtually global genus *Bufo* range up to 160, and the average ID between African and New World species groups of *Bufo* is 133 ± 14, the *peltocephalus* species group appears to be a radiation derived from within New World *Bufo* and does not warrant generic recognition. Cei (1972) suggested that the affinities of the *Bufo peltocephalus* group are with the *Bufo granulosus* group of South America. The ID data suggest an origin for the *peltocephalus* group in the early Cenozoic (51 ± 5.3 mya) or later by overwater dispersal, probably from South America.

Dendrobatidae
(2) *Colostethus chalcopis*.—This species is endemic to Martinique and its affinities within *Colostethus* are not clear (Kaiser et al. 1994a). Because *Colostethus* is almost entirely South American in

distribution, and species occur on Trinidad and To-bago (placed by some in a separate genus), *C. chalcopis* almost certainly arrived on Martinique by dispersal from South America. No IDs are available to estimate the time of that dispersal event, although distances among the genera *Colostethus*, *Dendrobates*, and *Phyllobates* (Maxson and Myers 1985) average about 100 (60 mya), suggesting that divergence within *Colostethus* probably occurred subsequently (i.e., during the Cenozoic). The geologic origin of the Lesser Antilles in the Eocene (Pindell and Barrett 1990) places an upper time limit on the origin of *C. chalcopis* (0–45 mya).

Hylidae

Four species have been introduced to the West Indies: *Pseudacris crucifer*, *Hyla cinerea*, *H. squirella*, and *Scinax rubra* (Schwartz and Henderson 1991).

(3) *Osteopilus.*—Ten native West Indian hylids are currently placed in three genera: *Calyptahyla* (1 species), *Hyla* (5 species), and *Osteopilus* (4 species, including an undescribed Jamaican species). Two of those genera (*Calyptahyla* and *Osteopilus*) are endemic to the West Indies. Hispaniola (4 species) and Jamaica (5 species) are the centers of hylid species diversity, with a single species native to Cuba and the Bahamas Bank. Dunn (1926) proposed that the Hispaniolan and Jamaican species represented independent island radiations but that the West Indian species were "allied," suggesting a single origin for the West Indian hylids. Trueb and Tyler (1974) examined morphological variation in these species and concluded that at least six independent invasions to the West Indies occurred, all from South America via the Lesser Antilles. Data from protein electrophoresis, microcomplement fixation, and DNA sequencing of the West Indian species (Hedges et al. 1992b; Hedges, Strafalace, and Maxson, in preparation) suggest that they represent a single monophyletic group (to take the generic name *Osteopilus*), with one exception (*Hyla heilprini*). An albumin ID of 80 (48 my) between *Osteopilus septentrionalis* and the mainland *Osteocephalus taurinus* (Hedges et al. 1992b) suggests an early Cenozoic origin by

dispersal for this major West Indian lineage. However, few mainland species have been examined and thus a more recent origin is possible. Large IDs (>100) between *Osteopilus septentrionalis* and Holarctic hylids (Maxson and Wilson 1975) indicate that the origin of the West Indian hylids is not from that group. Until more data become available, especially from Central American taxa, the suggestion by Trueb and Tyler (1974) of a South American origin seems most plausible.

(4) *Hyla heilprini.*—Trueb and Tyler (1974) suggested that the affinities of this species are with the predominantly South American *H. albomarginata* group. Aside from recognizing its distinctiveness among West Indian hylids, molecular data presently are unable to identify the time of entry of this lineage.

Leptodactylidae

(5) *Eleutherodactylus.*—This is the largest vertebrate genus (>520 species) and is distributed from Arizona and Texas south to Argentina and southeastern Brazil. Two major areas of particularly high species density are the Andes of South America, and the West Indies. All of the 138 West Indian species are endemic to that region and nearly all are restricted to single islands; all but seven species (= 95%) occur in the Greater Antilles (Hedges 1995).

Several studies have addressed higher level relationships in *Eleutherodactylus* (Lynch 1986; Savage 1987; Hedges 1989b; Joglar 1989; Hass and Hedges 1991). Five subgenera have been recognized based on evidence from morphological, allozyme, and ID data, three of which occur in the West Indies (Hedges 1989b). The subgenus *Euhyas* (82 species) is endemic to the western Caribbean (Cuba, Jamaica, Hispaniola), and *Pelorius* (6 species) is restricted to Hispaniola. The subgenus *Eleutherodactylus* (50 West Indian species) occurs throughout the West Indies and on the mainland (primarily South America). Albumin IDs indicated a close relationship between *Euhyas* and the Central American subgenus *Syrrhophus* (24 species), and between *Pelorius* and West Indian species of the subgenus *Eleutherodactylus* (Hass and Hedges

1991). More extensive sampling of mainland *Eleutherodactylus* and other leptodactylid genera with DNA sequence data has suggested that the subgenus *Eleutherodactylus* is not monophyletic, and that West Indian species of the genus *Eleutherodactylus* (all three subgenera) form a monophyletic group (Youngblood and Hedges, in preparation), although two species in the southern Lesser Antilles possibly have affinities with South American taxa (Kaiser et al. 1994*b*, 1994*c*). The ID data would indicate that *Syrrhophus* also is included in that monophyletic group. Thus, only a single origin is necessary to explain the presence of the genus *Eleutherodactylus* in the West Indies. Major lineages of *Eleutherodactylus* occur in both Central and South America, and the closest relative of the West Indian lineage has not yet been determined. However, the average ID between the two major lineages within the West Indies, 117 (70 mya; *Euhyas* vs. *Eleutherodactylus*; Hass and Hedges 1991), suggests a Mesozoic (Cretaceous) origin for the West Indian lineage, possibly by proto-Antillean vicariance. The calibration error associated with that divergence estimate 70 ± 6.8 mya (= 63.2–76.8 mya) indicates that an origin after the breakup of the proto-Antilles and after the bolide impact (65 mya) cannot be ruled out. Dispersal from Cuba (*Euhyas*) to Central America later in the mid-Cenozoic likely explains the origin of the subgenus *Syrrhophus* (Hedges 1989*b*).

(6) *Leptodactylus albilabris.*—Heyer (1978) synonymized *L. dominicensis* (Hispaniola) with *L. albilabris* (Puerto Rican Bank); Schwartz and Henderson (1991) continued recognition of these two apparently closely related taxa as distinct species. They are placed in the largely South American *fuscus* group (Heyer 1978), and *L. albilabris* has an ID of 66 (40 mya) to *L. labrosus* (Maxson and Heyer 1988), suggesting dispersal, probably from South America, during the mid-Tertiary.

(7) *Leptodactylus fallax.*—This Lesser Antillean species is placed in the largely South American *pentadactylus* group (Heyer 1979). It has very low IDs (5–11) to populations of a South American spe-

cies (*L. stenodema*) that may or may not be its closest relative (Maxson and Heyer 1988), suggesting very recent (3–7 mya) dispersal from South America.

(8) *Leptodactylus insularum.*—This species of the *ocellatus* group is distributed in Central and northern South America and occurs on Isla de San Andrés and Isla de Providencia. Presumably, those island populations originated by dispersal from Central or South America in the Quaternary.

(9) *Leptodactylus validus.*—This species of the *melanonotus* group occurs in the southern Lesser Antilles and on Trinidad and Tobago (Heyer 1970, 1994). No ID data are available, but Heyer (1970) suggested that *L. validus* (as *L.* "*wagneri*") arose by dispersal from South America in the Quaternary. A more detailed examination of geographic variation in *L. validus* supports the contention that the Lesser Antillean populations are conspecific with those from Trinidad and Tobago (Heyer 1994).

Microhylidae

A single species of this family, *Gastrophryne carolinensis*, has been introduced in the Bahamas Bank and in the Cayman Islands from North America (Schwartz and Henderson 1991).

Ranidae

One species in this family, *Rana catesbeiana*, has been introduced throughout the West Indies, and two others, *R. grylio* and *R. sphenocephala*, have been introduced in the Bahamas Bank; all are from North America (Schwartz and Henderson 1991).

Reptilia: Crocodylia

Alligatoridae

Caiman crocodilus has been introduced in Cuba and Puerto Rico; this species is native to Central and South America (Schwartz and Henderson 1991).

Crocodylidae

(10) *Crocodylus acutus.*—This species occurs in North, Central, and South America as well as Cuba, Hispaniola, Jamaica, and the Cayman Islands. Although most abundant in coastal areas, individuals

may swim a considerable distance offshore (Schwartz and Henderson 1991). An ID of 16 (10 mya) between *C. palustris* and *C. acutus* (Hass et al. 1992) establishes an upper time limit for divergences within *C. acutus*, although several species from the New World are believed to be even more closely related to *C. acutus* (Densmore and White 1991) and the origin of the West Indian populations may be much more recent (Quaternary).

(11) *Crocodylus intermedius.*—This species occurs in northern South America (including Trinidad and Tobago), primarily in large rivers. One record is known from Grenada (Schwartz and Henderson 1991), and is almost certainly the result of recent (Quaternary) dispersal from South America.

(12) *Crocodylus rhombifer.*—This species is endemic to Cuba (including Isla de Juventud), and occurred in the Cayman Islands until the last century (Morgan et al. 1993). It has an ID of 6 (4 mya) to the Old World species *C. palustris* (Hass et al. 1992), although it is believed to be most closely related to New World species (Densmore and White 1991). These animals most likely arrived by dispersal from Central or South America.

Reptilia: Squamata
Amphisbaenia
Amphisbaenidae

(13) *Amphisbaena.*—Low IDs among West Indian amphisbaenians and DNA sequence data suggest that the Cuban genus *Cadea* is part of the Antillean *Amphisbaena* radiation and should be synonymized within *Amphisbaena* (Hedges et al. 1992b; Hass, Frye, and Hedges, in preparation). Gans (1990) suggested a Mediterranean origin for New World amphisbaenids. However, relationships among African and New World *Amphisbaena* are poorly known, and thus two independent dispersals from Africa, one leading to the South American species and the other to the West Indian species, cannot be ruled out — but is less likely than a single dispersal from Africa to the New World (South America?). Aside from the Antillean taxa, *Amphisbaena* primarily is a South American genus (in the New World),

and therefore an ID of 91 (55 mya) between *A. schmidti* (Puerto Rico) and *A. alba* (South America) suggests an early Cenozoic dispersal from South America to the West Indies (Hedges et al. 1992b).

Sauria
Anguidae

Ophisaurus ventralis, a species native to the southeastern United States, was introduced in the Cayman Islands (Schwartz and Henderson 1991).

(14) *Celestus.*—Albumin ID data and DNA sequence data (Hedges et al. 1992b; Hass, Maxson, and Hedges, in preparation) indicate that the Hispaniolan endemic genera *Sauresia* and *Wetmorena* are part of a monophyletic radiation of Antillean *Celestus* and should be synonymized within that genus. Also included in *Celestus* are the three Hispaniolan species previously placed in *Diploglossus*. The remaining species of *Celestus* occur in Central America, and although no ID data are available for those species, an ID of 54 (32 mya) between a West Indian species (*haetianus*) and a mainland diploglossine genus (*Ophiodes*) establishes a maximum time (Hedges et al. 1992b), and the largest ID among Antillean *Celestus*, 16 (10 mya), establishes a minimum time for their origin. Therefore, the West Indian species of *Celestus* apparently arose by dispersal from Central America in the mid-Cenozoic (10–32 mya).

(15) *Diploglossus.*—Recent immunological and DNA sequence data (Hass, Maxson, and Hedges, in preparation), as noted above, have revealed that the Hispaniolan species of *Diploglossus* belong to *Celestus*, not *Diploglossus*. This finding leaves only three Antillean species with disjunct distributions: *D. delasagra* (Cuba), *D. pleei* (Puerto Rico), and *D. montisserrati* (Montserrat). Whether West Indian *Diploglossus* have affinities with Central or South American species (or both) in the genus is unclear. The absence of this genus on Hispaniola brings up the possibility that the Cuban species was derived from Central America and the Puerto Rican and Lesser Antillean species from South America. No IDs are available between mainland and West In-

dian species, although the ID between the Cuban and Puerto Rican species, 36 (22 mya), suggests a maximum time of origin, if those species were derived separately from mainland taxa (or, conversely, a minimum time if a single origin is indicated).

Gymnophthalmidae

(16) *Bachia heteropus*.—This species occurs on the Grenada Bank, and is placed in the same subspecies as populations on adjacent Tobago (Thomas 1965a; Schwartz and Henderson 1991). The species also occurs in Northern Venezuela, and therefore its origin in the West Indies almost certainly is the result of relatively recent dispersal (Quaternary) from South America.

(17) *Gymnophthalmus pleei*.—Based on morphology, this Lesser Antillean endemic appears to be most closely related to a species in northern South America, *G. lineatus* (Thomas 1965a), suggesting an origin by dispersal from that continent. The geologic origin of the Lesser Antilles in the Eocene (Pindell and Barrett 1990) places an upper time limit on the origin of *G. pleei* (0–45 mya).

(18) *Gymnophthalmus underwoodi*.—This unisexual species occurs in both the Lesser Antilles (Barbados, St. Vincent, and probably introduced on Guadeloupe) and northern South America (Thomas 1965a; Schwartz and Henderson 1991; Vanzolini and Carvalho 1991), suggesting a relatively recent (Quaternary) dispersal from South America.

(19) *Tretioscincus bifasciatus*.—This species occurs in northern South America and also on Isla de Providencia (Scott and Ayala 1984). The origin of that island population probably was by dispersal (or human introduction) from South America in the Quaternary.

Iguanidae

A vertebra of a large lizard found at an early Miocene site in Puerto Rico was tentatively identified as either a varanid, teiid, or iguanid (MacPhee and Wyss 1990). Until additional material is available allowing more accurate identification, the biogeo-

graphic significance of this fossil is uncertain. The reclassification of iguanian lizards proposed by Frost and Etheridge (1989) is not followed here because of the weak resolution of phylogeny obtained by morphological characters (e.g., Frost and Etheridge 1989: figures 8 and 16) and conflicting evidence from published molecular studies (see below).

(20) *Anolis*.—Lizards of this genus comprise a major fraction of the West Indian herpetofauna and studies on their relationships, biogeography, and origin are numerous. Initially, higher-level groupings within the West Indian species were based largely on karyotypes and osteology (Williams 1976), and since then albumin ID data (e.g., Wyles and Gorman 1980; Shochat and Dessauer 1981; Hass et al. 1993), allozyme data (Burnell and Hedges 1990), and DNA sequence data from the mitochondrial 16S rRNA gene (Hass et al. 1993) have helped to refine those relationships. Abundant evidence now exists for the presence of island radiations such as on Jamaica and Puerto Rico, which formed the basis of the ecomorph concept (Williams 1972, 1983), as well as for many of the series and species groups recognized by Williams (1976). However, the molecular data do not support the major alpha/ beta dichotomy based on characteristics of caudal vertebrae, the basal position (and recognition) of the Cuban endemic genus *Chamaeleolis*, or the recognition of the Hispaniolan endemic genus *Chamaelinorops*. For that reason, *Chamaeleolis* and *Chamaelinorops* were synonymized within *Anolis* by Hass et al. (1993). General concordance between albumin ID data and DNA sequence data and discordance with morphology suggests that the generic partitioning of *Anolis* based largely on morphology (Guyer and Savage 1986) was premature (as noted by Williams 1989b). The classifications of Williams (1976) and Burnell and Hedges (1990), where informal categories such as series and species groups are used, allow disagreements to occur without affecting non-systematist users of the formal classification.

Because relatively few mainland species were included in those molecular studies, it is not possible at this time to infer the number of independent

lineages of West Indian *Anolis* or their closest relatives on the mainland. The IDs among many West Indian species are relatively low, and it is possible, as suggested by Shochat and Dessauer (1981), that a major Antillean radiation exists within the West Indies. At the same time, both Central American affinities for some species and South American affinities for others are indicated by the ID data (summarized in Hass et al. 1993). Thus it would appear that West Indian *Anolis* comprise more than one independent lineage derived from different regions of the mainland.

Although the number of independent West Indian lineages of *Anolis* is not yet known, a maximum time of origin or origins can be estimated from the large amount of ID data now available for the species. Not counting the relatively recent (Pliocene) dispersal from Cuba to Florida leading to the origin of *A. carolinensis* (Buth et al. 1980), IDs between West Indian and mainland species range from 27–60 (Hass et al. 1993), suggesting a mid-Cenozoic (16–36 mya) origin for the West Indian lineages (from Central and/or South America). The oldest fossil West Indian *Anolis*, from Dominican amber (Rieppel 1980), also is mid-Cenozoic (20–40 mya) in age. Roughgarden (1995) recently proposed that the two major groups of anoles in the Lesser Antilles (*bimaculatus* series in the north and *roquet* series in the south) diverged due to plate tectonic separation of the proto-Lesser Antilles in the Mesozoic. He suggested that the islands to the north and south of the Martinique Passage (between Dominica and Martinique) have had separate geological histories. However, the available geological evidence does not support this hypothesis (see Hedges 1995 for a discussion), the distributions of other groups (e.g., *Eleutherodactylus*) show "break points" at different locations in the Lesser Antilles, and the molecular evidence argues strongly against such a vicariance model. Overwater dispersal best explains the distribution of anoles in the Lesser Antilles.

(21) *Ctenosaura similis*.—This Central American species also occurs on Isla de San Andrés and Isla de Providencia. Presumably, those island populations originated by dispersal from Central America in the Quaternary.

(22) *Cyclura*.—This endemic West Indian genus is a close relative of *Iguana*, and the ID between those two genera is 20 (mean of *I. iguana* vs. *C. cornuta* and *I. iguana* vs. *C. nubila*; Gorman et al. 1971) suggesting a Miocene (12 mya) origin by dispersal from the mainland (either Central or South America).

(23) *Iguana delicatissima*.—This Lesser Antillean endemic is a sister species to *I. iguana*. The ID of 7 separating the two species (Gorman et al. 1971) suggests Pliocene (4 mya) dispersal. The source area probably was South America based on geography.

(24–27) *Iguana iguana*.—At least four separate invasions (dispersals) from the mainland by this species probably occurred, resulting in the following distributions: (24) Swan Islands, (25) Isla de San Andrés and Isla de Providencia, (26) Cayman Islands, and (27) Puerto Rico through the Lesser Antilles. The source area for (24–26) probably was either Central America or South America, whereas the source area for (27) almost certainly was South America. Albumin immunological distances of 0 between Central and South American populations of *I. iguana* (Gorman et al. 1971), while not directly bearing on the West Indian populations, suggests that geographic variation within the species is not great. Presumably, the West Indian populations originated by dispersal in the Quaternary.

(28) *Leiocephalus*.—A recent parsimony analysis of morphological characters in iguanian lizards placed this endemic West Indian genus of 23 species (Pregill 1992) in its own subfamily ("Leiocephalinae") and as the closest relative of the South American subfamily "Tropidurinae," both in the family "Tropiduridae" (Frost and Etheridge 1989). However, albumin IDs and DNA sequence data (Hedges et al. 1992*b*; Hass, Maxson, and Hedges, in preparation) indicate a closer relationship between *Leiocephalus* and the largely North American genera *Crotaphytus* and *Sceloporus*, placed in other families by Frost and Etheridge ("Crotaphytidae"

and "Phrynosomatidae," respectively). This suggests that the taxonomic rearrangement of Frost and Etheridge (1989) may have been premature. The mean ID between *L. schreibersii* and *Crotaphytus collaris*, 46 (28 mya), suggests a mid-Cenozoic origin by dispersal from North America.

Gekkonidae

One species of *Gekko* (*G. gecko*; Henderson et al. 1993) and one species of *Hemidactylus* (*H. turcicus*) were introduced in the West Indies from the Old World.

(29) **Antillean *Aristelliger*.**—Of the seven species in this genus, six are restricted to the West Indies and the single mainland species occurs in Central America (and nearby islands). Although *Aristelliger* has been considered to be a gekkonine (Kluge 1987), IDs between *Sphaerodactylus* and *Aristelliger* are lower (82.8 ± 3.3) than IDs between *Sphaerodactylus* and several other genera of gekkonines (107.8 ± 10.3: Hass 1991). *Aristelliger* possesses other sphaerodactyline-like traits, such as the absence of cloacal bones and sacs (Kluge 1982) and a single egg per clutch, suggesting that it may be incorrectly classified. Two species within *Aristelliger* (*barbouri* and *cochranae*) appear to be closely related (Hecht 1951, 1952; Bauer and Russell 1993). Otherwise, relationships among the species and to other gekkonids are unclear, therefore making the origin of the West Indian species difficult to infer. For example, the West Indian species may be monophyletic with a Central American origin, or, alternatively, the genus may have been isolated in the West Indies for a long time with the mainland species representing a relatively recent dispersal. In any case, the ID between *Sphaerodactylus* and *Aristelliger*, 83 (50 mya; Hass 1991), sets an upper time limit on the origin of *Aristelliger* and indicates that this event occurred no earlier than early Cenozoic and thus by dispersal. If West Indian species are found to be a monophyletic group with respect to the mainland species (*A. georgeensis*), then a more recent origin by dispersal from Central America would be the most likely scenario for the origin of the West Indian endemics.

(30) ***Aristelliger georgeensis*.**—This species is distributed in Central America and also occurs on Isla de Providencia, Isla de San Andrés, and Isla Santa Catalina. The origin of those island populations probably was by dispersal from Central America in the Quaternary.

(31) ***Gonatodes albogularis*.**—This species is distributed in Central and South America, and the West Indies (Cuba, Cayman Islands, Jamaica, Hispaniola). The Jamaican and Hispaniolan populations are recognized as an endemic subspecies (Schwartz and Henderson 1991), suggesting that at least those populations are not the result of human introductions. The origin of the West Indian populations of this species is most likely due to Quaternary dispersal from Central or South America.

(32) ***Hemidactylus haitianus*.**—Kluge (1969) argued that *H. brookii haitianus* originated by dispersal from the Old World, although human introduction from Africa was suggested by Vanzolini (1978). Powell et al. (this volume) consider this taxon to be a valid species. The origin of the West Indian populations probably occurred during the Quaternary.

(33) ***Hemidactylus mabouia*.**—The two possibilities for the origin of *H. brookii* also apply to this species: either natural dispersal or human introduction from the Old World in the Quaternary (Kluge 1969; Vanzolini 1978).

(34) ***Hemidactylus palaichthus*.**—This species of northern South America also is known from St. Lucia in the Lesser Antilles (Powell 1990; Murphy, this volume). Presumably, these geckos arrived by dispersal from South America at some time during the Quaternary.

(35) ***Phyllodactylus pulcher*.**—This species is endemic to Barbados. The genus occurs in both the Old and New World, including North, Central, and South America. However, this particular species (type species of the genus) has been associated with species from northern South America (Dixon 1962, 1964; Vanzolini 1968), which suggests an origin

from that continent. The geologic origin of the Lesser Antilles in the Eocene (Pindell and Barrett 1990) places an upper time limit on the origin of *P. pulcher* (0–45 mya).

(36) *Phyllodactylus wirshingi*.—This species is endemic to Hispaniola and Puerto Rico. Schwartz (1979) suggested that the Puerto Rican populations were derived from those on Hispaniola based on scale variation and distribution, although the reverse may have occurred (see below). The species also has been associated with species from the Dutch Leeward Islands and northern South America (Grant and Beatty 1944; Dixon 1962), suggesting an origin from South America.

(37) *Sphaerodactylus*.—Unlike the two other species-rich genera of West Indian amphibians and reptiles (*Eleutherodactylus* and *Anolis*), most of the species in this genus are West Indian (80 species), with the others occurring in Central and northern South America. Hass (1991) presented a phylogenetic analysis of immunological and protein electrophoretic data for most of the West Indian species, but only one mainland species (*S. molei*) was included. Harris and Kluge (1984) postulated that the mainland species (with only two exceptions) represent a monophyletic group (the *lineolatus* section of Hass 1991). If this suggestions is true, then the determination by Hass (1991) that *S. molei* is basal to the West Indian species suggests that the latter also may be monophyletic (the *sputator* section of Hass 1991). Unfortunately, no IDs are available between species in these two major divisions of *Sphaerodactylus*. However, the primarily South American distributions of other sphaerodactyline genera and the low ID (45; 27 mya) between *Sphaerodactylus* and *Lepidoblepharis* led Hass (1991) to postulate a South American origin for West Indian *Sphaerodactylus* by dispersal in the mid-Cenozoic. This is in agreement with the age, 20–40 mya, of the fossil *Sphaerodactylus* found in Dominican amber (Böhme 1984).

(38) *Tarentola*.—One species (*T. americana*) is endemic to Cuba and the Bahamas Bank and another

undescribed species is endemic to Cuba. All other species in the genus are from the Old World (primarily the Mediterranean region; southern Europe, northern Africa), and dispersal over water from Africa or southern Europe to the Antilles has been suggested (Schwartz 1968). Joger (1984) placed *T. americana* in its own subgenus (*Neotarentola*) within *Tarentola*. In a phylogenetic study of *Tarentola*, Joger (1985), using ID data for other species (none were available for *T. americana* itself), found that *Neotarentola* apparently diverged from the subgenus *Tarentola* about 30 mya, and this date was constrained by an earlier divergence (40 mya) leading to the two pairs of subgenera (Joger 1985: figure 3). According to those data, the origin of West Indian *Tarentola* was by dispersal from North Africa in the mid-Cenozoic (about 30 mya, but within the range 0–40 mya).

(39) *Thecadactylus rapicauda*.—This widely distributed Neotropical species is found in Central and South America and in the eastern Caribbean (Puerto Rican Bank through the Lesser Antilles). The origin of the West Indian populations, based on geography, would appear to be by dispersal from South America in the Quaternary.

Scincidae

(40) *Mabuya lineolata*.—The relationship of this Hispaniolan endemic to other congeners is not well known, although Dunn (1935) suggested that a possible affinity with a South American species (*M. guaporicola*) might exist. The time of origin for this species is unknown.

(41) *Mabuya bistriata*.—This species is distributed in northern South America (north to Panama), and ranges throughout most of the West Indies except for Cuba and the northern Bahamas Bank (Hoogmoed and Gruber 1983). This distribution suggests an origin for the West Indian populations by dispersals (multiple?) from South America in the Quaternary. Dunn and Saxe (1950) suggested that the population on Isla de Providencia may have been derived by human introduction from the southern Lesser Antilles.

Teiidae

(42) *Ameiva.*—This genus occurs in Central and South America and throughout the West Indies. Whether the West Indian species form a monophyletic group is not known, although ID data suggest that may be the case (Hedges et al. 1992*b*; Hass and Hedges, in preparation). The mean ID between two West Indian species (*A. exsul* and *A. chrysolaema*) and a predominantly mainland species (*A. ameiva*), 60 (36 mya; Hass and Hedges, in preparation) suggests an origin for the West Indian species in the mid-Cenozoic by dispersal from either Central or South America.

(43–45) *Ameiva ameiva.*—This species occurs from Panamá south through tropical South America. At least three separate dispersals from the mainland by this species probably occurred during the Quaternary, resulting in the following West Indian populations: (43) Swan Islands, (44) Isla de Providencia, both from northern South America (Dunn and Saxe 1950), and (45) the southern Lesser Antilles (St. Vincent and the Grenada Bank), from northern South America.

(46) *Cnemidophorus lemniscatus.*—This species is distributed in Central and tropical South America and also occurs on Isla de Providencia, Isla de San Andrés, and Isla Santa Catalina. The origin of those island populations probably was by dispersal from Central or South America in the Quaternary.

(47) *Cnemidophorus vanzoi.*—This species is endemic to the Maria Islands off St. Lucia. Although other species of the genus occur in North, Central, and South America, the location of *C. vanzoi* in the southern Lesser Antilles suggests an origin from South America (Baskin and Williams 1966). The geologic origin of the Lesser Antilles in the Eocene (Pindell and Barrett 1990) places an upper time limit on the origin of *C. vanzoi* (0–45 mya).

(48) *Kentropyx borckiana.*—This species occurs in northern South America, especially coastal areas (Hoogmoed 1973; Gallagher and Dixon 1992), and also is known from Barbados in the southern Lesser Antilles (Gallagher and Dixon 1992). Presumably, the species colonized Barbados by dispersal from the South American mainland at some time during the Quaternary.

Xantusiidae

(49) *Cricosaura typica.*—The lizard family Xantusiidae is distributed in a largely disjunct fashion in Central America, southwestern North America, and Cuba, and fossil evidence indicates that it previously occupied a wider distribution, at least in North America (Bezy 1972; Hedges et al. 1991). The single West Indian species, *Cricosaura typica*, is endemic to a small area in eastern Cuba and its origin has been discussed in several phylogenetic studies. Crother et al. (1986) analyzed some published morphological data and concluded that the closest relative of *Cricosaura* is the Central American genus *Lepidophyma*. However, Hedges and Bezy (1993) demonstrated that several key morphological characters in that analysis were incorrectly scored, putting into question that conclusion. DNA sequence data from portions of three mitochondrial genes provide statistical support for *Cricosaura* as the basal lineage within the family (Hedges et al. 1991; Hedges and Bezy 1993, 1994), and this was further supported by chromosome evidence (Hass and Hedges 1992). Indirect evidence from Middle Paleocene (60 mya) xantusiid fossils from North America (Estes 1976) suggests that the lineage leading to *Cricosaura* may have diverged before that time, possibly due to proto-Antillean vicariance (Hedges et al. 1991). However, other explanations are possible. The *Cricosaura* lineage may have dispersed to Cuba in the early Cenozoic after the proto-Antilles broke apart and after the bolid impact at 65 mya; or, alternately, this lineage may have arisen on the mainland and persisted throughout most of the Cenozoic (with dispersal to Cuba occurring at some point during that time), subsequently becoming extinct in all areas except for the small region in eastern Cuba. Although the latter hypothesis is admittedly a considerably more complicated scenario than vicariance, it remains a distinct possibility due to the relictual nature of xantusiid lizard distribution.

Serpentes

Boidae

(50–51) *Boa constrictor*.—Three subspecies of *B. constrictor* occur in the West Indies and two are endemic (one each on Dominica and St. Lucia). Otherwise, the species is distributed in Central and South America to about 36°S Latitude. Based on geography and subspecific allocation, two independent origins (in the Quaternary) by dispersal are indicated for the West Indian populations: (50) from Central America, leading to the populations on Isla de San Andrés, Isla de Providencia, and Isla Santa Catalina; and (51) from South America, leading to the populations in the southern Lesser Antilles.

(52) *Corallus hortulanus*.—This is a widely distributed species in Central and South America, and it occurs on St. Vincent and the Grenada Bank in the southern Lesser Antilles. A phylogenetic analysis of mitochondrial DNA sequence data from seven widely separated localities indicated that the West Indian populations were derived from the southern (South America) subspecies and not the northern (Central America and northwestern South America) subspecies (Henderson and Hedges 1995). Presumably, dispersal occurred in the Quaternary.

(53) *Epicrates*.—Nine of the ten species in this genus are endemic to the West Indies and they are thought to form a monophyletic group (Kluge 1989). No IDs are available among species of *Epicrates*, but an ID of 37 (22 mya) between *Boa constrictor* and *Epicrates cenchria* (Dessauer et al. 1987) sets an upper time limit for evolution within the genus and hence the origin (by dispersal) of West Indian *Epicrates*. This date also is in agreement with an Early Miocene date for the oldest fossil boid in the West Indies, from Puerto Rico (MacPhee and Wyss 1990). This argues against the vicariance model for the origin of West Indian *Epicrates* (Kluge 1988: figure 10) and favors a dispersal model (e.g., Tolson 1987). The mainland species believed to represent the basal lineage within the genus, *E. cenchria*, is widely distributed in Central and South America, and thus the New World source area for the West Indian lineage is not obvious.

Colubridae

Two species, *Diadophis punctatus* and *Elaphe guttata*, have been introduced in the Cayman Islands from North America (Schwartz and Henderson 1991).

Colubrinae

(54) *Chironius vincenti*.—This colubrine species is endemic to St. Vincent. Although other species of the genus occur in Central and South America, the location of *C. vincenti* in the southern Lesser Antilles suggests an origin from South America. An ID of 40 (24 mya) between *Trimorphodon biscutatus* and *C. exoletus* (Cadle 1984c) places an upper time limit on divergence within *Chironius*; and IDs among congeneric species of colubrid snakes rarely exceed 25 (15 mya) and typically range between 5–15 (3–9 mya) (Cadle 1984a, 1984b, 1984c). This suggests an origin by dispersal from South America in the late Cenozoic (within 0–24 mya, but most likely 0–10 mya).

(55) *Mastigodryas bruesi*.—This colubrine species is endemic to St. Vincent and the Grenada Bank. Although other species of the genus occur in Central and South America, the location of *M. bruesi* in the southern Lesser Antilles suggests an origin from South America. An ID of 28 (17 mya) between *Trimorphodon biscutatus* and *M. melanolomus* (Cadle 1984c) places an upper time limit on divergence within *Mastigodryas*, and considering the IDs typically encountered among congeneric species of colubrid snakes (5–15), *M. bruesi* likely arose by dispersal from South America in the late Cenozoic (within 0–17 mya, but most likely 0–10 mya).

Natricinae

(56) *Nerodia clarkii*.—This North American natricine species inhabits salt marshes and mangrove swamps in the southeastern United States and occurs in similar habitats along the northern coast of Cuba. The Cuban populations are assigned to the same subspecies as those in the Florida Keys. Low IDs (2-3) between species of *Nerodia* and *Thamnophis* (Dowling et al. 1983) suggest that speciation in those genera has been relatively recent and indicates that the origin of Cuban *N. clarkii* almost

certainly was by dispersal from nearby Florida in the Quaternary.

Xenodontinae

(57) *Clelia clelia.*—This widely distributed xenodontine species is found in Central and South America, and on Grenada (Underwood 1993). Presumably, this snake reached Grenada by dispersal from South America during the Quaternary.

(58) *Clelia errabunda.*—This species is endemic to St. Lucia and is believed to be most closely related to a clade of three mainland species (*C. clelia, C. equatoriana,* and *C. scytalina*) the present ranges of which are in Central and South America (Underwood 1993). No IDs are available between this species and other species within the genus, although an ID of 8 (5 mya) between *C. scytalina* and *Pseudoboa coronata* places an upper limit on divergences within *Clelia* (Cadle 1984a) and suggests that the origin of *C. errabunda* was in the Pliocene or Pleistocene (within 5 mya) by dispersal from nearby South America.

(59) *Liophis cursor* **group.**—Four species of the xenodontine genus *Liophis* are endemic to islands of the Lesser Antilles, and appear to form a monophyletic group that is most closely related to the South American (and Grenada) species *L. melanotus* (Maglio 1970). No IDs are available for comparisons among species of *Liophis*, although a mean ID of 30 (18 mya) between *Xenodon severus* and three species of *Liophis* (Cadle 1984a) places an upper limit on divergences within *Liophis* and suggests that the origin of this West Indian group was in the late Cenozoic (within 0–18 mya, but most likely 0–10 mya) by dispersal from South America.

(60) *Liophis melanotus.*—This xenodontine species is widely distributed in South America, including Trinidad and Tobago (Dixon 1989), and a record exists for nearby Grenada, although its validity has been questioned (Henderson 1992; Murphy, this volume). The origin of the Grenada population apparently was by dispersal from South America in the Quaternary.

(61) *Pseudoboa neuwiedi.*—This primarily South American xenodontine species has been recorded from Grenada in the southern Lesser Antilles, and the validity of this record also has been questioned (Henderson 1992; Murphy, this volume). Presumably, it arrived by dispersal from South America at some time during the Quaternary.

(62) *Coniophanes andresensis.*—This species is endemic to Isla de San Andrés. Low IDs between *Coniophanes fissidens* and species in closely related genera (*Pliocercus, Rhadinea*), 8–15 (5–9 mya) (Cadle 1984b), suggest that divergences within *Coniophanes* probably are not greater. These data, and the association of *Coniophanes* with the Central American xenodontine clade (Cadle 1984b) indicate that the origin of this island endemic was by dispersal from Central America in the late Cenozoic (0–9 mya).

(63) *Tretanorhinus variabilis.*—This species is endemic to Cuba and the Cayman Islands. Cadle (1984b) identified the genus *Tretanorhinus* as a member of the "Central American xenodontines" (the "Dipsadidae" of Pinou and Dowling 1994). The distribution of the West Indian species in the western Caribbean along with the distribution of the remaining members of the genus in Central America (extending slightly into northwestern South America) indicates that the source area for *T. variabilis* was Central America. Again considering the IDs typically encountered among congeneric species of colubrid snakes (5–15), this West Indian species likely arose by dispersal from Central America in the late Cenozoic. That individuals have been found in saltwater estuaries (Barbour and Amaral 1924) suggests that waif dispersal is not unlikely.

(64) **Alsophines.**—Six of the remaining seven genera are endemic to the Greater Antilles: *Antillophis, Arrhyton, Darlingtonia, Hypsirhynchus, Ialtris,* and *Uromacer. Alsophis* also occurs in the Lesser Antilles, Galapagos Islands, and western Ecuador. Primarily on the basis of osteological and hemipenial morphology, Maglio (1970) proposed three dispersals from the mainland to account for the origin of

these West Indian xenodontines. However, IDs among species in this assemblage are low (0–27, but most <20 [12 mya]; Cadle 1984*a*; Hedges et al. 1992*b*; Hass and Hedges, in preparation) and are suggestive of a single West Indian radiation. Extensive ID comparisons of Neotropical xenodontines indicated that species in this West Indian group are most closely related to the South American xenodontines (Cadle 1984*a*, 1985). The ID between *Alsophis cantherigerus* and *Philodryas viridissimus* (Cadle 1984*a*), 43 (26 mya), suggests a mid-Cenozoic (12–26 mya) origin for this West Indian assemblage of snakes by dispersal from South America.

Elapidae

(65) *Micrurus nigrocinctus*.—A single specimen of this species was collected on Isla de Providencia ("Old Providence," the original name for the island) by the "Albatross Expedition in 1884" and deposited in the National Museum of Natural History, but it has since been lost (Dunn and Saxe 1950). Schwartz and Henderson (1988, 1991) did not recognize this species as part of the West Indian herpetofauna. However, the species is widespread in Central America, and occurs on Great Corn Island off the coast of Nicaragua, and therefore little reason exists to doubt the validity of the record for Isla de Providencia, regardless of whether or not a population still is extant on the island. Presumably, this species reached Isla de Providencia by dispersal from Central America.

Leptotyphlopidae

(66) *Leptotyphlops bilineata* group.—The five species placed in this group are believed to represent a single West Indian radiation (Thomas et al. 1985). The time of origin for the *L. bilineata* group is unknown. However, differences in hemipenial structure between Old and New World species of *Leptotyphlops* (Branch 1986) indicate some geographic cohesiveness, and thus a New World origin for the *bilineata* group appears to be the most likely explanation.

(67) *Leptotyphlops columbi*.—This Bahamian endemic (San Salvador Island) represents something

of a biogeographic anomaly in that it apparently is not closely related to other West Indian species (Thomas et al. 1985), and no *Leptotyphlops* presently occur in the nearby southeastern United States. Klauber (1939) suggested an association with *L. albifrons*, although Thomas (1965*b*) did not consider it close to that species. The *albifrons* group is primarily South American (Peters and Orejas-Miranda 1970), although one species (*L. goudotii*) extends its range up into Central America. Because the Bahamas Platform was completely submerged at times in the Pliocene or Pleistocene, the origin of *L. columbi* likely was by dispersal in the late Tertiary or in the Quaternary (0–5 mya), probably from South America.

(68) *Leptotyphlops goudotii*.—This species is distributed in Central and northern South America and also occurs in the Swan Islands, Isla de Providencia, and Isla de San Andrés. The origin of those island populations probably was by dispersal from Central or South America in the Quaternary.

(69) *Leptotyphlops albifrons*.—An old record exists for this South American species (as *L. tenella*) on Antigua (Thomas 1965*b*; Hoogmoed and Gruber 1983). Apparently, it arrived by dispersal from South America in the Quaternary.

Tropidophiidae

(70) *Tropidophis*.—Except for three South American species, this is primarily a West Indian genus. Albumin ID data among species in the genus indicate that the West Indian species form a monophyletic group with an ID of 70 (42 mya) between *T. haetianus* (West Indies) and the mainland species *T. paucisquamis* (Hedges et al. 1992*b*; Hass and Hedges, in preparation). These data suggest an origin by dispersal from South America for West Indian *Tropidophis*.

Typhlopidae

(71) *Typhlops*.—This pan-tropical genus is distributed throughout the West Indies as well as Central and South America. Most New World species are West Indian, and Thomas (1989) concluded that

most West Indian species form a monophyletic group ("major Antillean radiation") whose closest relative is in Africa (*T. caecatus*). The remaining four West Indian species also were considered to form a monophyletic group with affinities to other New World species (Thomas 1989). However, IDs between *T. platycephalus* (Puerto Rico) and other West Indian species (1–44 = 1–26 mya), with lower IDs to *T. biminiensis* than to some species in the "major Antillean radiation," do not support that dichotomy and indicate that West Indian species form a relatively closely related assemblage (Hedges et al. 1992*b*; Hass and Hedges, in preparation). No IDs are available to other New World *Typhlops*, but an ID of 96 (58 mya) between *T. platycephalus* and *T. luzonensis* (Philippines; Hass and Hedges, in preparation) suggests a Cenozoic origin (26–58 mya) for the West Indian species.

Viperidae

(72) *Bothrops*.—Two species of this Neotropical genus are endemic to islands in the southern Lesser Antilles. No ID data are available for these species, but IDs between *Bothrops atrox* and other species of *Bothrops* range from 0–21 (0–13 mya) and the reciprocal ID between *B. atrox* and *Crotalus enyo* is 23 (14 mya), placing an upper time limit on divergence within *Bothrops* (Dessauer et al. 1987; Cadle 1992). However, the two West Indian species are most closely related to *B. atrox* (Lazell 1964) or are part of the "polytypic *B. atrox* complex" itself (Gosner 1987). Therefore, the lowest ID between *B. atrox* and another species in the genus, *B. asper* (ID = 7, 4 mya; Cadle 1992), may be a more realistic upper limit on the time of origin for the Antillean species. These data and the distribution of the two species suggest an origin by dispersal from South America in the late Tertiary or Quaternary (0–4 mya).

Reptilia: Testudines
Emydidae

One species of this family, *Trachemys scripta*, has been introduced on Guadeloupe.

(73) *Trachemys*.—According to Seidel (1988), this genus includes only a single non-West Indian species, *T. scripta*, although some mainland subspecies of *T. scripta* recently have been elevated to species status (e.g., Seidel 1989; Ernst 1992). A morphological and biochemical analysis of relationships within the genus found that *T. scripta* is polyphyletic, with the North American populations representing a basal lineage within the genus and the Central and South American populations most closely related to *T. decussata* of Cuba (Seidel 1988). He suggested that this may indicate a single invasion of the West Indies from North America (temperate *T. scripta*), radiation within the Greater Antilles, and then dispersal from Cuba to Central America (leading to neotropical *T. scripta*), although he did not rule out an origin for the Antillean radiation by vicariance. Moll and Legler (1971) speculated that *T. scripta* arrived on the Neotropical mainland only recently (Pleistocene) based on life history data, which would support part of that scenario. *Trachemys* can survive in seawater for at least a week (Dunson and Seidel 1986), indicating that over-water dispersal is not unlikely. Pre-Quaternary fossil *Trachemys* are known only from North America and only as far back as the Miocene (Seidel 1988). No evidence exists that *Trachemys* arrived in the West Indies any earlier than the mid-Tertiary, and thus the origin of West Indian *Trachemys* probably was by dispersal from North America in the mid- to late Cenozoic (0–25 mya).

Kinosternidae

(74) *Kinosternon scorpioides*.—This is a widely distributed Central and South American species that occurs also on Isla de Cañas and Isla de San Andrés. The origin of those island populations presumably was by dispersal from Central or South America in the Quaternary.

Pelomedusidae

An African species of this family, *Pelusios subniger*, was introduced on Guadeloupe (Schwartz and Henderson 1991).

(75) **Pelomedusids**.—Oligocene fossils of this family are known from Puerto Rico (Wood 1972; Williams 1989*a*; MacPhee and Wyss 1990), although

whether they were saltwater or freshwater turtles is not known with certainty. Presently, the family is restricted to Africa and South America, but it had a much wider distribution in the late Mesozoic and early Cenozoic (Romer 1966) and therefore the source area for this lineage is unknown, but is likely to have been in the New World.

Testudinidae

(76) *Geochelone carbonaria*.—This widely distributed Neotropical species also occurs in the eastern Caribbean (Virgin Islands through the Lesser Antilles). The species' absence from the Greater Antilles suggests that it arrived in the West Indies by dispersal from South America in the Quaternary. However, literature reports of specimens from the Greater Antilles exist, and the possibility of human introduction to the West Indies has not been ruled out (Censky 1988).

(77) *Geochelone* sp.—Although now extinct, giant tortoises occurred throughout the West Indies at least into the Quaternary (Auffenberg 1967). The time of origin and source area for this lineage or lineages is unknown, but was presumably in the New World.

A total of 77 independent lineages of West Indian amphibians and reptiles can be defined (Table 3). Slightly more than half (42/77 = 55%) have species endemic to the West Indies. At least some information pertaining to the time of origin is available for nearly all lineages (73/77 = 95%), and of those, all but one (99%) are in the Cenozoic (65–0 mya) and all but nine in the last half (30–0 mya) of the Cenozoic. Nearly all (73/77 = 95%) lineages appear to have originated in the New World. Of those, a continental source cannot be determined for four (4/73 = 5%), and a distinction between Central America and South America cannot be made for 16 (16/73 = 22%). Of the remaining 53 lineages where a source area within the New World can be identified, most (42/53 = 79%) show a South American origin, eight (8/53 = 15%) indicate a source in Central America, and three (3/53 = 6%) originated in North America. Of the 42 lineages that include endemic West Indian species (Table 4), the propor-

tions change little: 39 (93%) are New World; of those, the continental source cannot be determined for three (3/39 = 8%) and eight (8/39 = 21%) are from either Central or South America; of the rest, most (22/28 = 79%) are from South America, four (4/28 = 14%) are from Central America, and two (2/28 = 7%) are from North America. Of the four lineages for which no data on the time of origin are available (*Hyla heilprini*, *Phyllodactylus wirshingi*, *Mabuya lineolata*, and the *Leptotyphlops bilineata* group), all have congeneric species on mainland Central or South America) and none have highly divergent morphologies that would suggest a long period of isolation. Therefore, all four of those lineages likely also arose in the Cenozoic by dispersal.

DISCUSSION

Overwater Dispersal

The major finding of this analysis is that all but one or two of the 77 independent lineages of amphibians and reptiles present in the West Indies apparently originated by dispersal in the Cenozoic, and the majority of those came from South America. A notable exception is the frog genus *Eleutherodactylus*, which would appear to have originated in the Cretaceous by vicariance (but see below). That one of the most species-rich lineages of terrestrial vertebrates in the West Indies also is one of the oldest, is not surprising, but it presents an unexpected twist in the vicariance-dispersal debate of the last two decades. Whereas dispersal clearly dominates in explaining the origin of nearly all lineages of amphibians and reptiles, vicariance may have been an important mechanism in explaining the origin of nearly one-quarter of the species.

Williams (1989a) identified the "central problem in Caribbean biogeography" as the depauperate nature of the Antillean fauna, by which he was referring to higher taxa rather than species diversity. The absence of many groups typical of mainland herpetofaunas has been used as primary evidence to support a dispersal origin for the West Indian fauna. Among amphibians, these include all salamanders and caecilians; and centrolenid, microhylid, pelobatid, pipid, ranid, and rhyno-

TABLE 3. The origin of native West Indian amphibians and reptiles. Each lineage listed is independent in the West Indies and has affinities to a mainland group; those lineages with one or more species endemic to the West Indies are listed in bold. Times of origin indicated in bold are based on albumin ID data calibrated to the vertebrate fossil record (1 ID = 0.6 million years); calibration error estimates are indicated for comparisons believed to indicate approximate time of origin; ranges are given for other estimates; origin in the Quaternary (0–2 mya) is assumed for all West Indian populations of species also occurring on the mainland. Abbreviations: Swan Islands (SI), Isla de San Andrés (ISA), Isla de Providencia (IP), Cayman Islands (CI), Puerto Rico (PR), Lesser Antilles (LA), Isla Santa Catalina (ISC).

Lineage	Number of species	Source area	Time of origin (mya)	Mechanism
(1) *Bufo peltocephalus* group	12	South America	**51 ± 5.3**	Dispersal
(2) *Colostethus chalcopis*	1	South America	0–45	Dispersal
(3) *Osteopilus*	9	South America?	**48 ± 5.0**	Dispersal
(4) *Hyla heilprini*	1	South America	?	Dispersal
(5) *Eleutherodactylus*	138	Central/South America	**70 ± 6.8**	Vicariance
(6) *Leptodactylus albilabris*	1	South America	**40 ± 4.5**	Dispersal
(7) *Leptodactylus fallax*	1	South America	3–7	Dispersal
(8) *Leptodactylus insularum*	1	Central/South America	0–2	Dispersal
(9) *Leptodactylus validus*	1	South America	0–2	Dispersal
(10) *Crocodylus acutus*	1	New World	0–2	Dispersal
(11) *Crocodylus intermedius*	1	South America	0–2	Dispersal
(12) *Crocodylus rhombifer*	1	Central/South America	**4 ± 4.0**	Dispersal
(13) *Amphisbaena*	12	South America	**55 ± 5.6**	Dispersal
(14) *Celestus*	19	Central America	**10–32**	Dispersal
(15) *Diploglossus*	3	Central/South America	**22 ± 4.5**	Dispersal
(16) *Bachia heteropus*	1	South America	0–2	Dispersal
(17) *Gymnophthalmus pleei*	1	South America	0–45	Dispersal
(18) *Gymnophthalmus underwoodi*	1	South America	0–2	Dispersal
(19) *Tretioscincus bifasciatus*	1	South America	0–2	Dispersal
(20) *Anolis*	138	Central/South America	**16–36**	Dispersal
(21) *Ctenosaura similis*	1	Central America	0–2	Dispersal
(22) *Cyclura*	8	Central/South America	**12 ± 5.4**	Dispersal
(23) *Iguana delicatissima*	1	South America	**4 ± 4.0**	Dispersal
(24) *Iguana iguana* (SI)	1 (part)	Central/South America	0–2	Dispersal
(25) *Iguana iguana* (ISA/IP)	1 (part)	Central/South America	0–2	Dispersal
(26) *Iguana iguana* (CI)	1 (part)	Central/South America	0–2	Dispersal
(27) *Iguana iguana* (PR/LA)	1 (part)	South America	0–2	Dispersal
(28) *Leiocephalus*	22	North America	**24 ± 4.4**	Dispersal
(29) Antillean *Aristelliger*	6	Central/South America	**0–50**	Dispersal
(30) *Aristelliger georgeensis*	1	Central America	0–2	Dispersal
(31) *Gonatodes albogularis*	1	Central/South America	0–2	Dispersal
(32) *Hemidactylus haitianus*	1	Africa	0–2	Dispersal
(32) *Hemidactylus mabouia*	1	Africa	0–2	Dispersal
(34) *Hemidactylus palaichthus*	1	South America	0–2	Dispersal
(35) *Phyllodactylus pulcher*	1	South America	0–45	Dispersal
(36) *Phyllodactylus wirshingi*	1	South America	?	Dispersal
(37) *Sphaerodactylus*	78	South America	**27 ± 4.4**	Dispersal
(38) *Tarentola*	2	Africa	30 (0–40)	Dispersal
(39) *Thecadactylus rapicauda*	1	South America	0–2	Dispersal
(40) *Mabuya lineolata*	1	South America	?	Dispersal
(41) *Mabuya bistriata*	1	South America	0–2	Dispersal
(42) Antillean *Ameiva*	19	Central/South America	**36 ± 4.4**	Dispersal
(43) *Ameiva ameiva* (SI)	1 (part)	South America	0–2	Dispersal
(44) *Ameiva ameiva* (IP)	1 (part)	South America	0–2	Dispersal

TABLE 3 (continued).

Lineage	Number of species	Source area	Time of origin (mya)	Mechanism
(45) *Ameiva ameiva* (LA)	1 (part)	South America	0–2	Dispersal
(46) *Cnemidophorus lemniscatus*	1	Central/South America	0–2	Dispersal
(47) *Cnemidophorus vanzoi*	1	South America	0–45	Dispersal
(48) *Kentropyx borckiana*	1	South America	0–2	Dispersal
(49) *Cricosaura typica*	1	Central America	>60	Vicariance
(50) *Boa constrictor* (ISA/IP/ISC)	1 (part)	Central America	0–2	Dispersal
(51) *Boa constrictor* (LA)	1 (part)	South America	0–2	Dispersal
(52) *Corallus hortulanus*	1	South America	0–2	Dispersal
(53) *Epicrates*	9	Central/South America	**0–22**	Dispersal
(54) *Chironius vincenti*	1	South America	**0–10? (0–24)**	Dispersal
(55) *Mastigodryas bruesi*	1	South America	**0–10? (0–17)**	Dispersal
(56) *Nerodia clarki*	1	North America	0–2	Dispersal
(57) *Clelia clelia*	1	South America	0–2	Dispersal
(58) *Clelia errabunda*	1	South America	**0–5**	Dispersal
(59) *Liophis cursor* group	1	South America	**0–10? (0–18)**	Dispersal
(60) *Liophis melanotus*	1	South America	0–2	Dispersal
(61) *Pseudoboa neuwiedi*	1	South America	0–2	Dispersal
(62) *Coniophanes andresensis*	1	Central America	**0–9**	Dispersal
(63) *Tretanorhinus variabilis*	1	Central America	**0–10?**	Dispersal
(64) **Alsophines**	33	South America	**12–26**	Dispersal
(65) *Micrurus nigrocinctus*	1	Central America	0–2	Dispersal
(66) *Leptotyphlops bilineata* group	5	New World	?	Dispersal
(67) *Leptotyphlops columbi*	1	South America?	0–5	Dispersal
(68) *Leptotyphlops goudotii*	1	Central/South America	0–2	Dispersal
(69) *Leptotyphlops albifrons*	1	South America	0–2	Dispersal
(70) *Tropidophis*	13	South America	**42 ± 4.6**	Dispersal
(71) *Typhlops*	24	Africa?	**26–58**	Dispersal
(72) *Bothrops*	2	South America	**0–4**	Dispersal
(73) *Trachemys*	4	North America	0–25	Dispersal
(74) *Kinosternon scorpioides*	1	Central/South America	0–2	Dispersal
(75) **Pelomedusids**	1	New World	30?	Dispersal
(76) *Geochelone carbonaria*	1	South America?	0–2	Dispersal
(77) *Geochelone* **sp.**	?	New World	0–2?	Dispersal

phrynid frogs, as well as most genera of hylid frogs. Among the "missing" reptiles are most turtles; helodermatid lizards, gerrhonotine and anguine lizards, and most genera of Neotropical iguanid and teiid lizards; anomalepid snakes, elapid snakes (aside from a recent dispersal; lineage 65), and most genera of Neotropical colubrid snakes. Certainly, not all major mainland taxa would be expected to occur in the West Indies, but for large, ecologically diverse islands, at least some are notable absences. Such absences may occur for two reasons: (1) the islands originally were without a fauna, with the present fauna having arisen gradually through dispersal; and (2) the original fauna of the West Indies

was a cross section of the mainland fauna (through vicariance) but since has become impoverished due to extinctions. The fossil record of the West Indies, while admittedly poor, has indicated that a slightly more diverse fauna existed before human colonization (Pregill and Olson 1981; Morgan and Woods 1986), but it has not demonstrated that the West Indies ever carried a "cross section" of the mainland fauna (Williams 1989*a*). This analysis provides independent evidence for the interpretation that such a depauperate herpetofauna is the result of dispersal during the Cenozoic.

Recently, a variation on the Cenozoic dispersal model (MacPhee and Iturralde-Vinent 1994) at-

tempted to explain the presence of a Miocene ground sloth fossil in Cuba. They postulated that a land bridge existed between northern South America and the Greater Antilles in the mid-Cenozoic. The underlying geological basis for such a land bridge, the Aves Ridge, has long been recognized and often has been referred to as an "island-arc" (e.g., Malfait and Dinkelman 1972; Pindell and Barrett 1990), although most of the area presently is under deep water (>1000 m). MacPhee and Ituralde-Vinent (1994) speculated that the sharp drop in sealevel during the Oligocene (30 mya), was enough to "create continuous land, or groups of very closely spaced islands from western Cuba through to northern South America." A rising sea level in the late Oligocene (27 mya) and later subsidence of the Aves Ridge caused this opportunity for landbridge dispersal to be very short in geologic time (3 million years).

Whether or not the Aves Ridge, or the proto-Antilles, was a continuous landmass or just a chain of islands (island arc) is not known, although the latter normally is assumed (Donnelly 1989; Perfit and Williams 1989). From a biogeographic standpoint, a direct land connection should have allowed a "cross section" of the mainland fauna to enter (e.g., the Panamanian Isthmus during the last 3 million years) and that is not evident in the fossil or extant faunas, as noted above. In addition, a closer look at the times of origin for the endemic West Indian lineages (Figure 2) does not indicate a cluster or peak in the Oligocene, as would be predicted by such a mid-Cenozoic (30–27 mya) land bridge. Instead, the wide variation in times of origin, with several major lineages appearing earlier and later in the Cenozoic, is in better agreement with an overwater dispersal model.

The times of origin for lineages of West Indian amphibians and reptiles (Table 3; Figure 2) can be arranged, albeit somewhat arbitrarily, into four groups: (I) ancient lineages (e.g., *Eleutherodactylus* and possibly *Cricosaura*), that may have arisen by proto-Antillean vicariance in the late Mesozoic; (II)

TABLE 4. Source areas for lineages of amphibians and reptiles with species endemic to the West Indies.

South America	Central/South America	Central America	North America
Bufo peltocephalus group	*Eleutherodactylus*	*Celestus*	*Leiocephalus*
Colostethus chalcopis	*Crocodylus rhombifer*	*Cricosaura typica*	*Trachemys*
Osteopilus	*Diploglossus*	*Coniophanes andresensis*	
Hyla heilprini	*Aristelliger*	*Tretanorhinus variabilis*	
Leptodactylus albilabris	*Anolis*		
Leptodactylus fallax	*Cyclura*		
Amphisbaena	*Ameiva*		
Gymnophthalmus pleei	*Epicrates*		
Iguana delicatissima			
Phyllodactylus pulcher			
Phyllodactylus wirshingi			
Sphaerodactylus			
Mabuya lineolata			

Africa	"New World"
Hemidactylus haitianus	*Leptotyphlops bilineata* group
Tarentola	Pelomedusids
Typhlops	*Geochelone* sp.

(continued in South America column)

Cnemidophorus vanzoi
Chironius vincenti
Mastigodryas bruesi
Clelia errabunda
Liophis cursor group
Alsophines
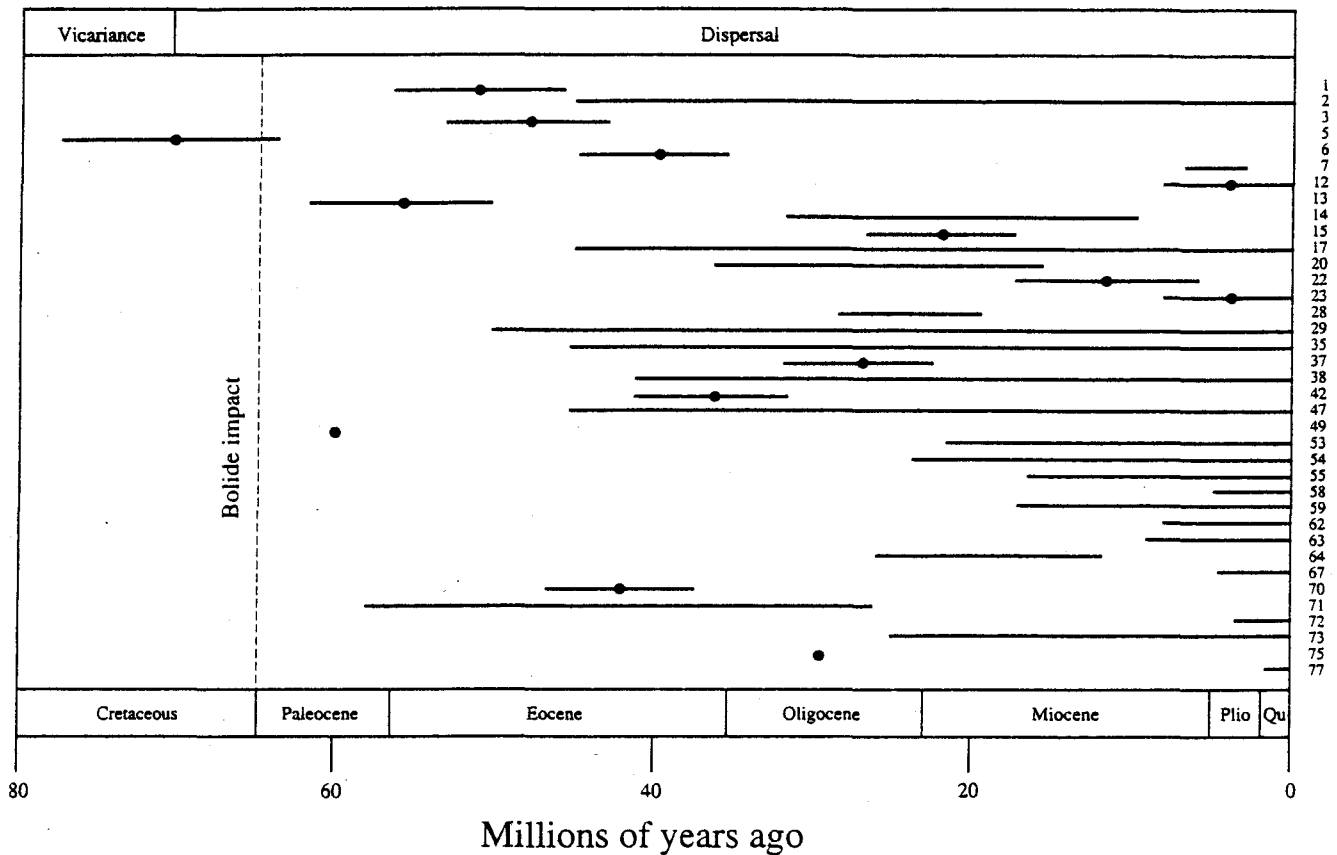*Leptotyphlops columbi*
Tropidophis
Bothrops

FIGURE 2. Times of origin for the 37 independent lineages of endemic West Indian amphibians and reptiles. The data are from Table 3, with lineage number indicated on right; the 40 non-endemic lineages, all with origin in the Quaternary (0–2 mya), are not shown.

mid-Tertiary colonizers, including most of the large radiations (e.g., *Bufo peltocephalus* group, *Osteopilus*, *Leptodactylus albilabris*, *Amphisbaena*, *Anolis*, *Leiocephalus*, *Sphaerodactylus*, *Ameiva*, *Epicrates*, alsophines, *Tropidophis*, and *Typhlops*; (III) Late Tertiary colonizers, which include mostly single endemic species or small groups of species (e.g., *Leptodactylus fallax*, *Crocodylus rhombifer*, *Cyclura*, *Iguana delicatissima*, *Chironius vincenti*, *Mastigodryas bruesi*, *Liophis cursor* group, *Coniophanes andresensis*, *Tretanorhinus variabilis*, *Bothrops*, and *Trachemys*; and (IV) Quaternary colonizers, which include species present on both the mainland and in the West Indies (all other lineages of known time of origin). The large number of group IV lineages almost certainly is an artifact due to fewer extinctions expected for recent lineages. Also, conspecific populations were assigned to this stage au-

tomatically as an initial assumption. Later studies possibly will show some island populations to be considerably more divergent than indicated. The distinction between these four groups facilitates discussion but is artifactual; they are on a time continuum and no reason exists to believe that they represent discrete stages in the evolution of the fauna such as is postulated for the taxon cycle (e.g., Wilson 1961; Ricklefs and Cox 1972).

Water Currents

If no direct land connections existed between the West Indies and the mainland during the Cenozoic, then why do most lineages of amphibians and reptiles show a South American origin? One of the most important considerations in overwater dispersal is the direction of the water currents that carry flotsam from the mouths of large rivers. The current
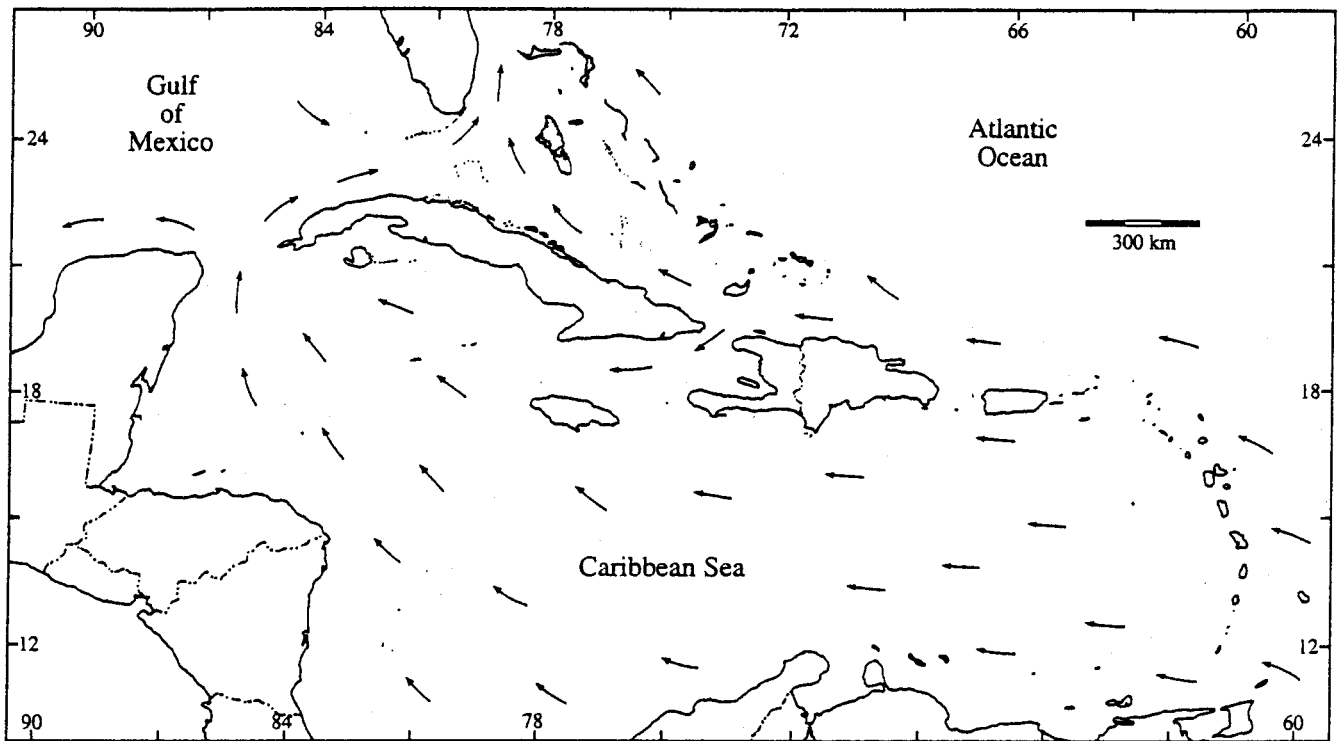
FIGURE 3. The West Indies, showing major water current patterns.

patterns in the West Indies are not random, but flow in a strong westerly and northwesterly pattern (Figure 3), as has been noted earlier (i.e., Guppy 1917; Williams 1969). Because the Caribbean always has been north of the equator during geologic history (Smith et al. 1994), the Coriolis Force would have produced the same clockwise current flow in the past, even while a water connection to the Pacific Ocean was in existence. Such a current pattern agrees with the finding of a strong South American influence in the West Indian herpetofauna in this analysis. The ability of flotsam to carry organisms great distances is well known and already has been discussed for the Caribbean biota (Guppy 1917; King 1962; Heatwole and Levins 1972).

If overwater dispersal has been a significant factor in the origin of the herpetofauna, then two biogeographic "anomalies" are predicted based on this pattern of current flow: (1) that some organisms inhabiting islands in the Western Caribbean will have a greater affinity with South America rather than adjacent Central America; and (2) that some groups inhabiting the southern Lesser Antilles will show a greater affinity with populations from the southeast

in the Guianas rather than nearby mainland South America (Figure 4). Both of these patterns are seen in the herpetofauna. For example, Ameiva ameiva and possibly Tretioscincus bifasciatus for (1), and Gymnophthalmus underwoodi, Kentropyx borckiana, and Corallus hortulanus for (2).

Another interesting distribution pattern is seen in Tarentola americana (and the undescribed Cuban sibling species), which colonized the West Indies in the mid-Cenozoic from the Old World. The closest relatives of those species, members of the subgenus Tarentola, inhabit islands off the west coast of Africa, including the Cape Verde and Canary Islands (Joger 1984). The distance from those islands to Cuba is 5,300 km (3,800 km to the Lesser Antilles), but this distance would have been about one-third shorter (3,500 km) in the mid-Cenozoic when South America and Africa were closer (Pitman et al. 1993). The Atlantic water current used by Christopher Columbus (North Equatorial Current) was likely the same that brought Tarentola to the New World in the mid-Cenozoic (Figure 5). A similar dispersal route was suggested by Kluge (1969) for Hemidactylus haitianus and H. mabouia,

although Vanzolini (1978) argued that human introduction is a more likely explanation (see also Bauer 1993).

Systematic Bias

Recently, a trend has been evident in the literature on Caribbean biogeography to ascribe a vicariance origin for almost any lineage, without knowledge of time of origin (e.g., Crother et al. 1986; Guyer and Savage 1986; Kluge 1989). In some cases, geologic models are modified to fit the phylogenetic or distributional data for a particular group (e.g., Guyer and Savage 1986: 557). For example, a close relationship between Cuba and Jamaica was suggested for a few taxonomic groups, and because this was at odds with the geologic models, the author suggested that "further geological research is necessary" (Kluge 1989: 323). Although possibly true, a more parsimonious explanation is that overwater dispersal is the reason for any particular close biological relationship between Jamaica and Cuba, especially given the complete or nearly complete mid-Cenozoic submergence of Jamaica. Others have suggested that ". . . dispersal should be a last resort for explaining modern distributions and used only after all vicariance possibilities have been considered" (Grimaldi 1988).

The roots of this apparent tendency to reject dispersal in all but the most obvious cases are in the widespread misconceptions throughout the systematic literature that dispersal is "unscientific" and untestable (e.g., Nelson and Platnick 1981: 50; Kluge 1991: 49), and that congruence between phylogenies, and between phylogenies and area relationships, indicates vicariance (Rosen 1978; Humphries 1992). Concordance between phylogenies can just as easily be explained by concordant dispersal (Cadle 1984c; Tolson 1987; Page and Lydeard 1994; Hedges et al. 1994), as illustrated by the result of this analysis (concordant dispersals from South America). And concordance between phylogenies and most area relationships also can be explained by dispersal, because organisms are more likely to disperse between geographically closer areas (those areas that usually are geologically more closely related) than between more distant areas

(Hedges et al. 1994). Both dispersal and vicariance can be tested with information on time of origin (Hedges et al. 1992b, 1994), as has been done in this analysis.

One factor usually overlooked in the vicariance-dispersal debate has been the extent of emergent land in North and South America that presumably connected the proto-Antilles to the mainland in the late Cretaceous (Rosen 1975). New paleocoastline data, however, indicate that much of southern North America and northern South America were below sea level in the late Cretaceous, 90–70 mya (Smith et al. 1994), a problem alluded to earlier by Perfit and Williams (1989: 67). Those data, based on geology and global sea level changes, indicate that even if the proto-Antilles were emergent, they may not have formed a direct land connection to the neighboring continental areas. If the possibility of proto-Antillean vicariance is made less likely by paleocoastline data, then is another explanation possible for the late Cretaceous time of origin for
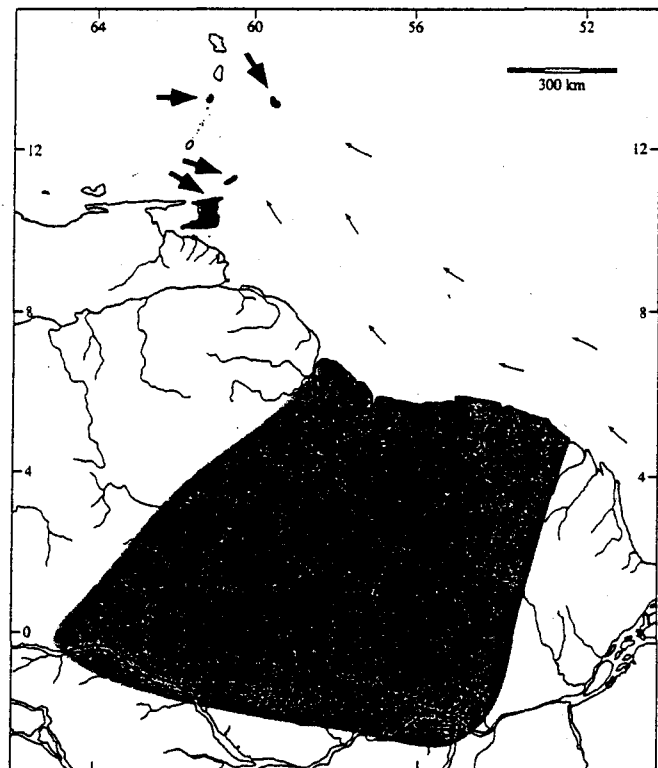

FIGURE 4. Distribution of *Gymnophthalmus underwoodi* in South America (including Trinidad and Tobago) and the Lesser Antilles (Barbados and St. Vincent). The direction of major current patterns is indicated (small arrows).
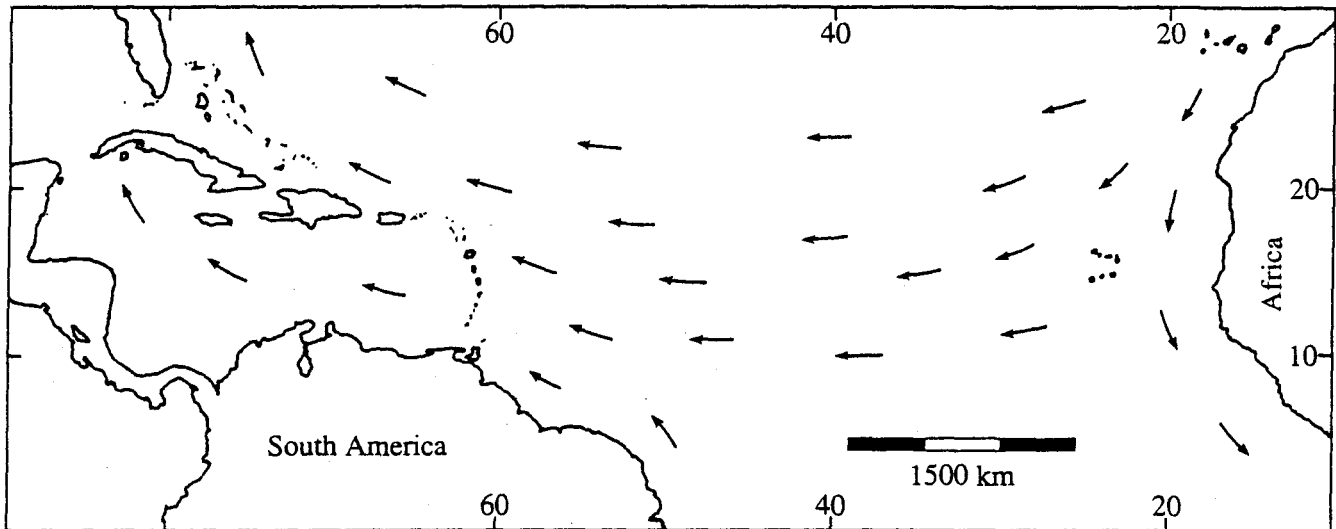
FIGURE 5. The North Equatorial Current flowing from Africa to South America and the West Indies, representing the southern portion of the clockwise pattern of surface currents in the North Atlantic Ocean due to the Coriolis Force. This is the probable mechanism and route for the origin of West Indian geckos of the genus *Tarentola* (and possibly two species of *Hemidactylus*; see text).

Eleutherodactylus (and possibly *Cricosaura*)? Ancient lineages may have arrived in the proto-Antilles by overwater dispersal rather than by vicariance, even in the late Cretaceous. Whereas the current trend in the literature is to accept proto-Antillean vicariance as the "null hypothesis," careful scrutiny of the geologic evidence indicates that such confidence is misplaced.

Predictions

Because most of the information on time of origin in this analysis is based on the chronological properties of serum albumin, the potential error in time estimates must always be considered. Also, the relationships (and number of lineages) of some of the West Indian groups – such as the species-rich genus *Anolis* – have yet to be resolved. In essence, this analysis represents an hypothesis to be tested by additional data. Those data likely will be DNA sequences, although the Tertiary fossil record for the West Indies still has considerable potential for making important contributions (Williams 1989a).

For the groups with endemic species on multiple islands in the West Indies, some predictions can be made now that water currents are seen as a probable major factor in the origin of the herpetofauna. Relationships within the West Indies

(among islands) also should reflect the prevailing east to west-northwest current flow (Figure 3). In other words, it should be very difficult for an organism to colonize Puerto Rico from Hispaniola (by flotsam) but very easy to do the reverse. Likewise, getting to Hispaniola from either Cuba or Jamaica should be very difficult, but going from Hispaniola to Cuba or Jamaica should be much easier. Colonization of the Lesser Antilles from the Greater Antilles should be much harder than colonization of the Lesser Antilles from South America, as was noted by Baskin and Williams (1966). The direction of water currents allows the Bahamas Platform to be colonized by the Lesser Antilles, Puerto Rico, Hispaniola, and Cuba, but not likely from Jamaica.

Frogs of the genus *Eleutherodactylus* exhibit a pattern of distribution in the West Indies that fits these predictions to some degree. The two major subgenera (*Euhyas* and *Eleutherodactylus*) each have been isolated in the West Indies since the late Mesozoic. However, the western Caribbean group *Euhyas* has not successfully colonized any islands east of Isla Mona (between Hispaniola and Puerto Rico), whereas the primarily eastern subgenus *Eleutherodactylus* occurs throughout the Greater and Lesser Antilles except for Jamaica. In Cuba, the "arboreal" subgenus *Eleutherodactylus* (10 species)

clearly is the invader to an island with a large and diverse assemblage of *Euhyas* (Hedges et al. 1992*a*). Likewise, the two species occurring in the southernmost islands of the Lesser Antilles (Grenada and St. Vincent) were derived from lineages in South America (Kaiser et al. 1994*b*).

Hispaniola and Puerto Rico share several species, or have closely related species pairs, that may be the result of relatively recent dispersal from Puerto Rico to Hispaniola (e.g., *Leptodactylus albilabris/L. dominicensis*, *Phyllodactylus wirshingi*, and *Trachemys stejnegeri*). Other cases of inter-island relationships may be ascribed to dispersal, but more phylogenetic studies are needed before firm conclusions can be drawn. In general, the prevailing current directions in the West Indies predict that if an "invader" species or lineage can be identified on an island, it most likely arrived from land areas to the east or southeast. For some older groups, intra-Caribbean vicariance also may help to explain distribution patterns (Hedges 1989*b*), although the geologic relationships of the islands still are not well known (Pindell and Barrett 1990).

These predictions pertain to organisms transported on flotsam by water currents. Airborne transport is more complicated, because the prevailing winds from the northeast favor only North America as a source, but nearly all hurricanes follow a path similar to the water currents. Thus, the source area for jetsam (e.g., seeds, many insects, flying vertebrates) depends on which of these two forces (prevailing winds or tropical storms) is more important.

CONCLUSION

The origin of the diverse West Indian herpetofauna appears to be entirely, or almost entirely, the result of overwater dispersal during the Cenozoic. This agrees with a similar analysis conducted on a subset of the herpetofauna (Hedges et al. 1992*b*). Two possible exceptions are the frog genus *Eleutherodactylus* and the lizard *Cricosaura typica*, which may have arrived in the West Indies in the late Mesozoic, possibly by proto-Antillean vicariance. The largely South American composition of the herpetofauna probably is due to prevailing water

current flow from that continent. Because the West Indies have remained north of the Equator since they originated in the Mesozoic, the direction of the currents, due to the Coriolis Force, is inferred to have been the same in the past. The Amazon Basin has the highest levels of terrestrial biodiversity in the World, and most of the region is drained by rivers (e.g., Amazon and Orinoco) that empty into ocean currents that in turn flow through the West Indies. The result is that the West Indies have been in an ideal location for the immigration of a diverse tropical herpetofauna throughout the Cenozoic.

ACKNOWLEDGMENTS

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Resumen.—La herpetofauna antillana comprende unas 175 especies de anfibios (99% endémico) y 457 especies de reptiles (93% endémico). Se analiza información sobre la distribución, relaciones y época de origen, con énfasis en estimados de epocas de divergencia a partir de datos moleculares, en un intento por entender el origen de la herpetofauna. Son identificados sententa y siete linajes independientes de anfibios y reptiles y casi todos (95%) fueron originados en el Nuevo Mundo. En aquellos linajes donde se puede identificar un area fuente dentro del Nuevo Mundo, la mayoria (79%) muestra un origen sudamericano, con contribuciones mas pequeñas desde centroamerica (15%) y norteamerica (6%). Un linaje muy viejo y diverso, las ranas del genero *Eleutherodactylus*, fue originado por vicarianza o dispersión en el Cretaceo Tardío (70 mya). Con una posible excepción (el lagarto xantúsiido *Cricosaura typica*), todos los otros linajes parecen haber arrivado por dispersión durante el Cenozoico y todos, exceptuando nueve linajes, en la ultima mitad del Cenozoico (30–0 mya). La mayoría de los linajes antillanos con múltiples especies endémicas fueron originados en el Terciario Medio mientras que la mayoria de los linajes con una sola especie endémica se originaron en el Terciario Tardío. Se postula la dispersión durante El Cuarternario para explicar el origen de las poblaciones antillanas de especies continentales.

La explicación probable del origen predominantemente sudamericano de la herpetofauna antillana, es el patrón casi unidireccional (hacia el oeste-noroeste) de las corrientes marinas en el Caribe: el agua que alcanza las Antillas Mayores se origina cerca de las Antillas Menores y Sur America. La amplia variación en las epocas de origen de los linajes antillianos no sustenta la reciente sugerencia de un puente de tierra durante el Cenozoico Medio entre Sud America y las Antillas Mayores. Se cree que, en la mayoria de los casos, debe haber ocurrido la dispersion por la descarga de organismos viajando en balsas desde las desembocaduras de los ríos mas grandes en el continente y arrastrados por las corrientes hacia las Antillas. La vicarianza de las Proto Antillas queda como una posibilidad geológica, pero datos recientes de las paleolinea de costas sugieren que puede que no halla ocurrido una coneccion de tierra seca entre las Proto Antillas y las tierras continentales vecinas en el Mesozoico Tardío. La extendida invocación de la vicarianza para explicar casi cualquier distribución de organismos en las Antillas sin información acerca de la epoca de origen es visto como una tendencia popular pero carente de sustentación.

Résumé.—La faune herpétologique connue des Antilles comporte 175 espèces d'amphibiens (98% endémiques) et 457 espèces de reptiles (93% endémiques). Les données sur la répartition, les rapports entre espèces, l'origine (notamment à l'aide d'évaluations du temps de divergence au moyen de données immunologiques sur l'albumine) ont été analysées pour essayer de comprendre l'origine de la faune herpétologique. Soixante-dix-sept lignées indépendantes d'amphibiens et de reptiles des Antilles ont été identifiées et presque toutes (95%) proviennent du Nouveau Monde. Lorsque l'origine même de ces lignées au Nouveau Monde peut être déterminée, il s'avère que la plupart (81%) origine d'Amérique du Sud et que les autres, à savoir 15% et 6%, proviennent respectivement d'Amérique Centrale et d'Amérique du Nord. Une lignée très ancienne et diversifiée de grenouilles du genre *Eleutherodactylus* doit son origine à la vicariance ou à la dispersion de la fin du Crétacé (70 millions d'années). À une seule exception près (le Xanthusidé *Cricosaura typica*), toutes les autre lignées sont arrivées par dispersion pendant le Cénozoïque et toutes sauf neuf, à la fin du Cénozoïque (30–0 millions d'années). La plupart des lignées des Antilles comportent plusieurs espèces endémiques dont l'origine remonte au milieu de l'ère tertiaire alors que la plupart des lignées à une seule espèce endémique datent de la fin de l'ère tertiaire. La dispersion du quaternaire est émise comme hypothèse pour expliquer l'origine des populations antillaises d'espèces que l'on retrouve sur le continent.

L'origine majeure d'Amérique du Sud de la faune herpétologique des Antilles est probablement due au sens quasi unidirectionnel (ouest/nord-ouest) des courants marins dans la mer des Caraïbes: l'eau qui baigne les grandes Antilles provient des petites Antilles et d'Amérique du Sud. Les grandes variations au titre de l'origine des lignées antillaises ne permettent pas de confirmer l'hypothèse récente d'un pont continental entre l'Amérique du Sud et les grandes Antilles, vers la moitié du Cénozoïque. La dispersion, dans la plupart des cas, semble s'être produit par l'évacuation d'organismes attachés aux épaves dans les embouchures des principales rivières continentales, transportés ensuite par les courants vers les Antilles. La vicariance proto-antillaise reste une possibilité géologique mais des données paléo-côtières récentes donnent à penser qu'il n'y a pas eu de pont en terre ferme entre les proto-Antilles et les continents voisins à la fin du Mésozoïque. L'invocation de la thèse de la vicariance pour expliquer pratiquement toutes les distributions d'organismes antillais sans données sur leur origine temporelle semble être aussi répandue qu'infondée.