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Evolution

Caribbean biogeography: Molecular evidence for dispersal in West Indian terrestrial vertebrates

(vicariance/plate tectonics/albumin/systematics)

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ABSTRACT **The geological association of the Greater Antilles with North and South America in the late Cretaceous led to the hypothesis that the present Antillean biota reflects those ancient land connections. Molecular data from diverse West Indian amphibians and reptiles and their mainland relatives support a more recent derivation of the Antillean vertebrate fauna by overwater dispersal. The catastrophic bolide impact in the Caribbean region at the close of the Cretaceous provides a proximate cause for the absence of an ancient West Indian biota.**

Plate tectonic reconstructions for the Caribbean region (1–3) agree that the Greater Antilles were formed between North and South America in the early Cretaceous [130–110 million years ago (Myr)] and remained in close proximity to those continents until the islands began migrating with the Caribbean Plate in the late Cretaceous (80 Myr). It has been proposed that some or most of the present West Indian biota reflect this ancient connection of the proto-Antillean Island arc, in contrast to an origin by overwater dispersal (4, 5). Testing these alternative hypotheses has proven difficult because of the virtual absence of late Cretaceous or early Tertiary terrestrial fossils in the West Indies (6–11). We present data on albumin evolution in several diverse vertebrate groups that do not show an ancient origin for the fauna but instead support overwater dispersal as the primary mechanism of colonization in the West Indies. We suggest that the bolide impact at the Cretaceous–Tertiary boundary at 64 Myr (12, 13) and its catastrophic effects explain the virtual absence of ancient lineages in the present fauna.

MATERIALS AND METHODS

Collection localities for taxa used in antiserum production and as antigen sources are listed in the *Appendix*. Animals were sacrificed by cryothermy (14) or anesthetized using tricaine methanesulfonate. In the field, blood samples were mixed with an equal volume of the tissue preservative phenoxyethanol prepared as PPS (15), and in the laboratory, plasma and erythrocytes were separated and stored at −20°C. Some samples used as antigens were obtained from muscle samples placed in PPS to elute albumin. Albumin for use in antiserum production was obtained from the plasma samples using single-step polyacrylamide gel electrophoresis. Antiserum production followed standard procedures (16), with between one and three rabbits used, depending upon the amount of albumin available. Antisera were made to 15 species (see *Appendix*) representing the majority of West Indian terrestrial vertebrate groups, excluding birds and bats which show relatively low rates of endemism. Additional immunological data were extracted from the literature.

Microcomplement fixation experiments were performed following established protocols (16). The data are reported as immunological distance (ID) units, where one unit is equivalent to approximately one amino acid difference between the albumins compared (17, 18). This data set consists of both reciprocal and one-way estimates of ID. Although reciprocal comparisons give a more robust estimation of the number of amino acid substitutions between taxa, one-way distances still serve as a useful indicator of the degree of sequence divergence between albumins.

An independent calibration of the albumin immunological clock for each taxon is not possible due to lack of fossil information or independent geologic events for the majority of groups examined here. A "standard" calibration (1 ID unit = 0.6 million years of divergence) has been derived for a number of vertebrate groups based upon both fossil and geological information (19, 20), including a group of West Indian frogs (21). The consistency of this calibration of the albumin clock over diverse lineages justifies its use in this type of study.

By using this rate of albumin evolution, expected ID values can be obtained by referencing the geologic history of the Caribbean. The separation of the proto-Antilles from the mainland occurred in the late Cretaceous (1–3) and any evolutionary divergence resulting from that event should be 70–80 million years old, corresponding to an ID range of 117–133. Jamaica also was isolated from the remainder of the Greater Antilles at this time so the expected ID between Jamaican and other taxa is 117–133. The only likely contact between Cuba and another major land mass during the Cenozoic was with northern Hispaniola in the early and mid-Tertiary, although the various geologic models are not in agreement with the timing or even the existence of such a connection (1–3, 22). If there were a physical land connection between these two islands, it probably would have been broken in the Oligocene or early Miocene (20–30 Myr) as Hispaniola moved eastward on the Caribbean Plate while Cuba remained essentially stationary on the Atlantic Plate (1–3); this separation corresponds to an expected ID range of 33–50. Puerto Rico apparently separated from southeastern Hispaniola at about the same time (1–3). Southwestern Hispaniola was isolated from northern Hispaniola during the early and mid-Tertiary (23). This does not affect the comparisons in this study (except for one group of frogs; ref. 24) and thus we treat Hispaniola as one island.

RESULTS

All albumin IDs between West Indian and mainland (Central and South America) taxa are considerably less than the IDs predicted by the geologic history outlined above (Table 1 and Fig. 1). Most comparisons indicate evolutionary divergence in the mid-Cenozoic (Eocene to Miocene), not in the late

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Abbreviations: Myr, million years ago; ID, immunological distance.
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Table 1. Albumin IDs among vertebrate taxa in the Caribbean region

Group	ID Expected	ID Observed	Taxa examined*	Reference
			West Indies ↔ Mainland (70–80 Myr)	
Bufonid frogs	117–133	85	***Peltaphryne peltacephalus/Peltaphryne guentheri*** vs. ***Bufo marinus***	This paper
Hylid frogs	117–133	80	***Osteopilus septentrionalis*** vs. ***Osteocephalus taurinus***	This paper
Eleutherodactyline frogs†	117–133	62	***Eleutherodactylus gossei/E. nubicola/E. planirostris*** vs. *E. marnockii*	21
Leptodactyline frogs	117–133	66	*Leptodactylus albilabris* vs. ***Leptodactylus labrosus***	25
Anoline lizards	117–133	28	*Anolis garmani/Anolis evermanni* vs. ***Anolis gadovi***	26
Anguid lizards	117–133	54	***Wetmorena haetiana*** vs. *Ophiodes striatus*	This paper
Iguanine lizards	117–133	20	*Cyclura cornuta/Cyclura nubila* vs. ***Iguana iguana***	15
Sphaerodactyline lizards	117–133	45	***Sphaerodactylus asterulus*** vs. *Lepidoblepharis xanthostigma*	27
Teiid lizards	117–133	79	***Ameiva exsul*** vs. *Ameiva ameiva*	This paper
Tropidurine lizards	117–133	40	***Leiocephalus schreibersi*** vs. *Crotaphytus collaris*	This paper
Amphisbaenians	117–133	91	***Amphisbaena schmidti*** vs. *Amphisbaena alba*	This paper
Alsophine snakes	117–133	43	***Alsophis cantherigerus*** vs. *Philodryas viridissimus*	28
Tropidophiid snakes	117–133	70	***Tropidophis haetianus*** vs. *Tropidophis paucisquamous*	This paper
			Cuba ↔ Jamaica (70–80 Myr)	
Hylid frogs	117–133	42	***Osteopilus septentrionalis*** vs. ***Osteopilus brunneus***	This paper
Eleutherodactyline frogs	117–133	41	***Eleutherodactylus planirostris*** vs. ***E. gossei/E. nubicola***	21
Anoline lizards	117–133	33	*Anolis equestris* vs. ***Anolis valencienni***	29
Sphaerodactyline lizards	117–133	23	*Sphaerodactylus ruibali/S. oliveri* vs. ***S. argus***	27
Alsophine snakes	117–133	6	***Arrhyton landoi*** vs. *Arrhyton callilaemum*	This paper
Tropidophiid snake	117–133	9	***Tropidophis haetianus*** vs. *Tropidophis feicki*	This paper
			Jamaica ↔ Hispaniola (70–80 Myr)	
Hylid frogs	117–133	26	***Osteopilus brunneus*** vs. ***Osteopilus dominicensis***	This paper
Eleutherodactyline frogs	117–133	38	***Eleutherodactylus gossei/E. nubicola*** vs. *E. pictissimus*	21
Anoline lizards	117–133	24	***Anolis valencienni*** vs. *Anolis distichus*	29
Anguid lizards	117–133	10	*Celestus crusculus/Celestus barbouri* vs. ***Wetmorena haetiana***	This paper
Sphaerodactyline lizards-1	117–133	18	***Sphaerodactylus argus*** vs. ***S. asterulus***	27
Sphaerodactyline lizards-2	117–133	8	*Sphaerodactylus richardsoni/S. parkeri* vs. ***S. asterulus***	27
			Cuba ↔ Hispaniola (20–30 Myr)	
Bufonid frogs	33–50	36	***Peltaphryne peltacephalus*** vs. ***Peltaphryne guentheri***	This paper
Hylid frogs	33–50	37	***Osteopilus septentrionalis*** vs. ***Osteopilus dominicensis***	This paper
Eleutherodactyline frogs	117–133‡	37	***Eleutherodactylus planirostris*** vs. *E. pictissimus*	21
Sphaerodactyline lizards	33–50	10	*Sphaerodactylus oliveri* vs. ***S. asterulus***	27
Tropidurine lizards	33–50	14	*Leiocephalus cubensis* vs. ***Leiocephalus schreibersi***	This paper
Alsophine snakes-1	33–50	23	***Alsophis cantherigerus*** vs. *Hypsirhynchus ferox*	28
Alsophine snakes-2	33–50	11	***Arrhyton landoi*** vs. *Darlingtonia haetiana*	This paper
			Hispaniola ↔ Puerto Rico (20–30 Myr)	
Bufonid frogs	33–50	16	***Peltaphryne guentheri*** vs. *Peltaphryne lemur*	This paper
Anoline lizards	33–50	21	*Anolis distichus* vs. ***Anolis evermanni***	29
Sphaerodactyline lizards	33–50	20	***Sphaerodactylus asterulus/S. copei*** vs. *S. klauberi/S. roosevelti*	27
Teiid lizards	33–50	46	*Ameiva taeniura* vs. ***Ameiva exsul***	This paper
Amphisbaenians	33–50	16	*Amphisbaena manni* vs. ***Amphisbaena schmidti***	This paper
Typhlopid snakes	33–50	18	*Typhlops capitulata* vs. ***Typhlops platycephalus***	This paper

*Taxa in boldface are represented by antisera; all others are antigens only; IDs between two antisera or among more than two taxa are means.
†All taxa examined are members of the subgenus *Euhyas* (21, 24).
‡This earlier date is based on the isolation of southern and northern Hispaniola during the Cenozoic (22).

Cretaceous. The wide variation in observed values for the comparisons further suggests that a single event was not responsible for the divergences. The difference between observed and expected values is especially pronounced for Jamaica, which has been isolated from other land masses throughout the Cenozoic (1–3). The low IDs between the Jamaican vertebrate fauna and groups on different islands (Fig. 1) clearly implicate overwater dispersal as the mechanism, and the timing (Miocene or later) is in agreement with geologic evidence that Jamaica was mostly or entirely submerged from the mid-Eocene (40 Myr) to the late Oligocene (25 Myr) (30–32). Furthermore, 80% of the IDs measured between Cuban and Hispaniolan taxa, and between taxa from Hispaniola and Puerto Rico, post-date the separation of those islands, indicating that dispersal has occurred between the islands during the last 20 million years.

The estimation of divergence time of two lineages using the albumin clock can have several sources of error. The reciprocal estimation of ID between two taxa has an average deviation of about 10% (33) and would not cause a consistent underestimation of distance across many taxonomic groups. Unequal rates of change among lineages can cause an under- or over-estimation of divergence time. The rate of albumin evolution, determined by relative rate tests, has been found to be variable (but not directional) among lineages in certain groups. Recent concerns about variation in the rate of albumin evolution are based primarily upon interpretation of precipitin analyses of rodent albumins (34). Even for those data, no lineage was even close to a doubling or halving of the rate of albumin evolution, with an average deviation of less than 10%. The most detailed study in a group of reptiles found an average rate change of 10–15% in the rate of albumin evolution in several snake lineages (35). Deviations of this magnitude would not affect the interpretation of the data presented in this paper.

In this study, a third source of error may be present. The species used here may not be representative of the most

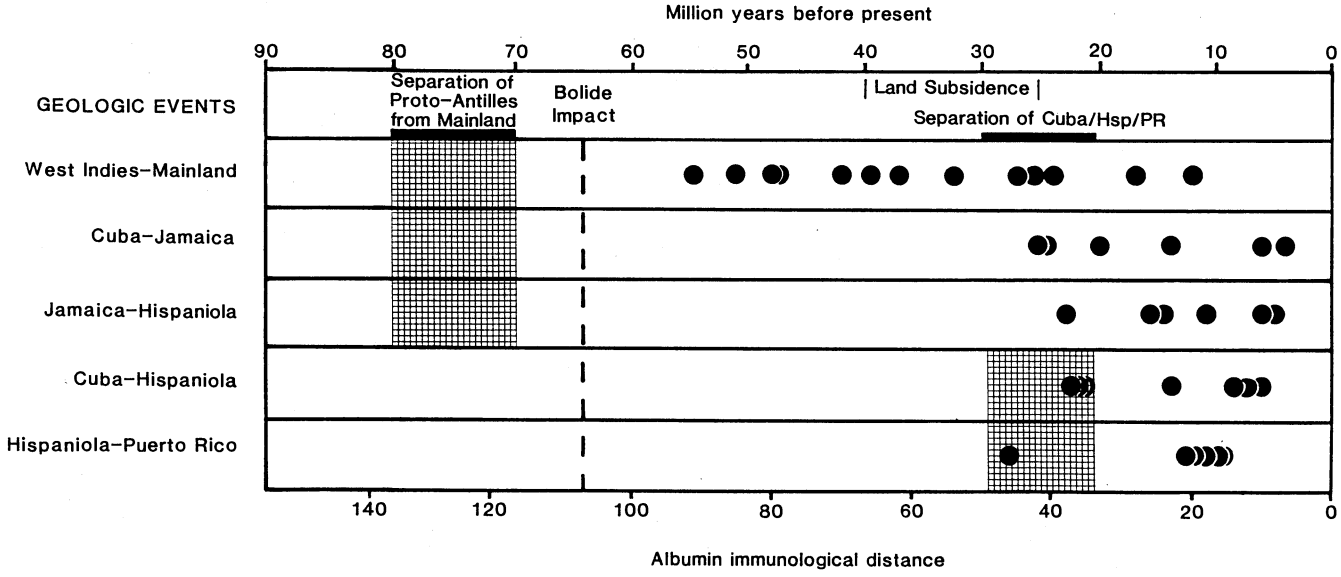

FIG. 1. Albumin IDs between groups of terrestrial vertebrates in the Caribbean region (data from Table 1). Geologic time is indicated on the upper scale; ID is on the lower scale. Shading denotes the approximate range of IDs predicted by vicariance for each comparison. HSP, Hispaniola; PR, Puerto Rico.

recent divergence event between the lineages examined (i.e., a member of the mainland taxon closest to the island taxon examined inadvertently was not used); this type of error always will result in an overestimation of the time of lineage divergence for the taxa from different land masses. If this systematic error could be corrected, some distances reported could only be lower, further suggesting dispersal as the primary mechanism for vertebrate colonization of the West Indies.

DISCUSSION

The vertebrate groups examined have very high levels of endemism in the West Indies (>95%) and thus would be most likely to reveal a vicariant pattern. The finding that these groups apparently originated by dispersal suggests that other groups not examined here, many with lower levels of endemism, may also have colonized the islands by dispersal. Possible exceptions are the endemic Antillean insectivores (36) and fresh-water fishes (37); nonmolecular data suggest both groups may have had a long history in the West Indies. The only West Indian vertebrate groups whose pattern of distribution, relationships, and level of molecular divergence are compatible with an ancient origin are a Cuban xantusiid lizard, *Cricosaura typica*, and the frog genus *Eleutherodactylus*. An antiserum was not available to examine albumin evolution within the Xantusiidae. However, DNA sequence data indicate a large degree of divergence between the Cuban species and the mainland taxa (38). In *Eleutherodactylus*, the major split between the subgenera *Euhyas* and *Eleutherodactylus* (*auriculatus* section) may have occurred when the proto-Antilles separated, with *Euhyas* isolated on Cuba and *Eleutherodactylus* on the north island of Hispaniola (24, 39). The average ID between these taxa, 117, corresponds to the timing of the break-up of the proto-Antilles (21). That comparison was not included here because both taxa are West Indian and are not each others closest relatives. The comparisons reported here indicate that the genus *Eleutherodactylus* has dispersed among the islands and between the West Indies and the mainland subsequent to any vicariant event that may have occurred (Table 1).

One plausible explanation for the virtual absence of ancient lineages among present West Indian vertebrates is the bolide impact at the Cretaceous–Tertiary boundary (12, 13). The western Caribbean recently has been identified as the probable area of impact (40); this event has been dated to 64 Myr (41). The tsunami resulting from that collision had an estimated height of 2 km and may have been as high as 4–5 km near the impact site (42). When it reached Cuba, it probably was >500 m high (40) and there is evidence that it scoured the southern coast of North America at a height of 50–100 m (43). A wave of such proportions almost certainly would have decimated much of the biota existing on the islands at that time. Especially susceptible would have been groups that presently occupy lowland areas, such as leptodactyline frogs, amphisbaenians, typhlopid snakes, and teiid lizards. Of the two West Indian groups suggested to be of ancient origin, the eleutherodactyline frogs are the most diverse in upland areas and they presently occupy the highest points of land in the Antilles. It is possible that ancient members of this group survived the catastrophic tsunami because of their occurrence in upland areas. Unfortunately, there is little distributional information available for the other possible ancient lineage, *Cricosaura typica*, which occurs to at least 450 m.

Additional ecological effects of the bolide impact, including a possible increase in the acidity of precipitation (44), also would have affected the biota. Because the islands already had separated from the mainland when the impact occurred at 64 Myr (1–3), subsequent colonization in the Tertiary only could have occurred by overwater dispersal. As indicated in Fig. 1, all ID values postdate the bolide impact.

Another important factor believed to have played a major biogeographic role was the mid-Tertiary subsidence of land throughout the West Indies. Besides the essentially complete submergence of Jamaica, much of Cuba, Hispaniola, and Puerto Rico also were covered by sea water for 10–15 million years (22). Although this drastic reduction in land area probably resulted in many extinctions, an ancient biota could have survived in areas of Cuba and Hispaniola known to have been above sea level at that time (45, 46). The physiography of the ancient Antillean Islands is not well known; the present upland areas are nearly all of late Tertiary origin (1–3) and cannot be used as a guide to infer past landscapes. Thus, by itself, the mid-Tertiary subsidence cannot explain the virtual absence of ancient lineages in the vertebrate fauna.

Dispersal is known to have occurred on some West Indian islands. The Bahamas are on a limestone platform that has been stationary since the Mesozoic, while the present Lesser

Antilles apparently have been an island arc only since the Eocene (1–3); both island groups have a biota reflecting an evolutionary history guided by overwater dispersal to islands with no previous land connections.

Two indirect lines of evidence have been used to support dispersal in West Indian terrestrial vertebrates. (*i*) The taxonomic composition of the fauna, with many mainland groups absent, suggests a filter effect caused by dispersal (11). A weakness in this argument is that extinctions during the Tertiary may have radically altered the taxonomic composition of the endemic biota. (*ii*) The fossil record of vertebrate groups recorded in mainland strata suggests that those groups with members found today in the West Indies could not have participated in the late Cretaceous vicariant event because they had not yet evolved (47). A weakness in this argument is that the Dominican amber fossils of vertebrates now have been dated to Upper Eocene (9, 48), which is older than predicted by mainland fossil evidence (although still 30–35 million years younger than the hypothesized late Cretaceous proto-Antilles). Our molecular data, involving direct comparisons of extant West Indian and mainland groups, now provide a comprehensive body of evidence implicating dispersal as the primary mechanism for the origin of the West Indian biota.

APPENDIX

Localities and numbers for taxa used the following key: LM, Linda R. Maxson frozen tissue collection; SBH, S. Blair Hedges frozen tissue collection; MVZ, Museum of Vertebrate Zoology, University of California at Berkeley.

Ameiva ameiva (LM 1933) from Peru, Cuzco Amazonico; *Ameiva exsul* (SBH 172204) from Puerto Rico, 12-km radius of Arecibo; *Ameiva taeniura* (SBH 104391) from Haiti, Sud'Est, 9.5 km E (east of) Jacmel; *Amphisbaena alba* (LM 1988) from Peru, Cuzco Amazonico; *Amphisbaena manni* (SBH 102373) from Dominican Republic, Hato Mayor, 4.5 km N, 5.8 km W Sabana de La Mar; *Amphisbaena schmidti* (SBH 172169, 172173) from Puerto Rico, 12.3 km SSE Arecibo; *Arrhyton callilaemum* (SBH 172463) from Jamaica, St. Mary, 2.9 km N Port Maria; *Arrhyton landoi* (SBH 161893-95, 161985) from Cuba, Guantanamo Bay United States Naval Station, east side of base; *Bufo marinus* (LM 206) from Costa Rica; *Celestus barbouri* (SBH 161120) from Jamaica, Trelawny, vicinity of Quick Step; *Celestus crusculus* (SBH 101572) from Jamaica, Hanover, 3.2 km SE Content; *Crotaphytus collaris* (LM 2534) from United States, Texas, Hays County, vicinity of Devil's Backbone; *Darlingtonia haetiana* (SBH 103806-10) from Haiti, Grande'Anse, 2–3 km S Castillon; *Leiocephalus cubensis* (SBH 172409) from Cuba, Matanzas, Soplillar; *Leiocephalus schreibersi* (SBH 102721, 102879-80, 102889) from Dominican Republic, Independencia, Tierra Nueva; *Ophiodes striatus* (MVZ 191047) from Brazil, Estado Sao Paulo; *Osteocephalus taurinus* (LM 1866) from Peru, Cuzco Amazonico; *Osteopilus brunneus* (LM 1190) from Jamaica, Trelawny, vicinity of Quick Step; *Osteopilus dominicensis* (SBH 101244) from Dominican Republic, Barahona, 15.8 km S Cabral; *Osteopilus septentrionalis* (LM 1768) from United States, Florida; *Peltaphryne guentheri* (LM 1191-92) from Dominican Republic, Independencia, 12.2 km W Cabral; *Peltaphryne lemur* (SBH 190648-50) from Puerto Rico (no specific locality); *Peltaphryne peltacephalus* (SBH 161934) from Cuba, Guantanamo Bay United States Naval Station; *Tropidophis feicki* (SBH 172745) from Cuba, Pinar del Rio, Soroa; *Tropidophis haetianus* (SBH 103592) from Jamaica, Trelawny, vicinity of Quick Step; *Tropidophis paucisquamous* (LM 908) from Brazil, Sao Paulo, Boraceia; *Typhlops capitulata* (SBH 103826) from Haiti, l'Ouest, Soliette; *Typhlops platycephalus* (SBH 172176-79) from Puerto Rico, 12.3 km SSE Arecibo; *Wetmorena haetiana* (SBH 102564-566) from Dominican Republic, Barahona, 15.3 km S, 6.7 km E Cabral.

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