

Central America–proto-Antilles before the splitting off of the latter, the upper Eocene is also consistent with the dispersal view—the age of a taxon alone does not tell how it got to where it is. It is also not clear that such an age is old enough for a taxon to have taken part in the postulated splitting off of the proto-Antilles from Central America, although it may be sufficient to provide evidence for intra-Antillean vicariance (4, 5).

Extinction and occasional dispersal may cause an insular fauna initiated by vicariance to come to resemble that of a truly oceanic island (6). Thus an insular fauna may present much clearer evidence of its origins immediately after the vicariance event that produced it, than it does millions of years later, when extinction and dispersal may have obscured its origin (7). Fossil evidence of the composition of the Greater Antillean fauna in the early Cenozoic, just after the postulated vicariance event, can therefore be of critical importance in choosing among proposed reconstructions. According to the vicariance view, we would expect to find an upper Eocene fauna much like that of contemporaneous continental Central America, including taxa never known to occur on oceanic islands (8), while the over-water dispersal view would lead us to expect a fauna of insular character. That the known vertebrates from amber are *Anolis* (9), *Sphaerodactylus* (10), and *Eleutherodactylus*, which together make up more than 60% of the current West Indian herpetofauna (11) and which are all known to be capable of over-water dispersal from their occurrence on islands that were completely submerged during Pleistocene interglacials (12), supports the dispersal view. If, as knowledge of the Tertiary faunas of the Greater Antilles accumulates, the character of the fauna remains as indicated by these genera, the dispersal view will receive further support; discovery of bolitoglossine salamanders or centrolenid frogs would provide impressive evidence for vicariance reconstructions. However, the amber vertebrate record is as yet too fragmentary, consisting of only a handful of specimens, to provide strong support for any view.

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3. G. Pregill, *Syst. Zool.* 30, 147 (1981).
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6. J. M. Diamond, *Proc. 16th Int. Ornithol. Congr.* 616 (1976).
7. Recent continental islands, such as Trinidad in the West Indies, have undergone vicariance due to Holocene sea level rise, and their faunas are clearly little-modified fragments of the adjacent continental faunas [P. J. Darlington, *Zoogeography* (Wiley, New York, 1957)]. If Trinidad were to remain long isolated from South America, extinction, immigration, and autochthonous evolution might so change its fauna as to make its vicariant origin unclear.
8. The strongest biological (as distinct from geological) evidence for the vicariance view is the partial confirmation of just such an expectation: E. O. Wilson's report [*Science* 229, 265 (1984)] of a diverse ant fauna from the Dominican amber of a more continental character than the present Hispaniolan fauna.
9. O. Rieppel, *Nature (London)* 286, 486 (1980).
10. W. Böhm, *Salamandra* 20, 212 (1984).
11. Of 455 West Indian reptiles and amphibians, 114 are *Anolis*, 114 are *Eleutherodactylus*, and 65 are *Sphaerodactylus* [A. Schwartz and R. Thomas, *Carnegie Mus. Nat. Hist. Spec. Publ.* 1, 1 (1975); L. D. Ober, *Carnegie Mus. Nat. Hist. Spec. Publ.* 5, 1 (1978)]. By comparison, Honduras on the Central American mainland has less than 14% of its herpetofauna in these genera (29/208) [L. D. Wilson, *Herpetol. Rev.* 14, 125 (1985)].
12. E. E. Williams [*Q. Rev. Biol.* 44, 345 (1969)] demonstrated this for *Anolis*; *Sphaerodactylus* and *Eleutherodactylus* occur as well on most of the islands discussed by Williams.

Response: Models for the origin of the Caribbean biota continue to be controversial. However, we did not juxtapose vicariance and dispersal models as exclusive explanations, but rather suggested that vicariance models offer possibilities for critical tests of specific hypotheses. We agree with Mayer and Lazell that the age of the amber frog “does not tell how it got to where it is.” However, the age does constrain the date of the earliest occurrence of dispersal (1). We suggested (and Mayer and Lazell seem to concur) that the Eocene age of the fossil is sufficient to provide evidence for (or against) intra-Antillean vicariance; elucidation of the relationships of the amber *Eleutherodactylus* to species on the north and south islands would test vicariance models of the breakup of the once contiguous land masses of Cuba, Puerto Rico, and northern Hispaniola and accretion of northern and southern parts of Hispaniola 5 to 9 million years ago (2). In contrast, no amount of contrary data is likely to damage dispersal theory, which consists of positioning ad hoc explanations for distributional patterns, rather than hypotheses amenable to refutation.

We agree that the composition of an island fauna just after a vicariant event may provide a better indication of its origin than does the extant fauna; this is part of the value of the amber fossils. However, the expectation of “an upper Eocene fauna much like that of contemporaneous conti-

mental Central America” is not relevant, because similarity with the Central American fauna was never an issue in our argument. The discovery of centrolenid frogs or bolitoglossine salamanders in amber would suggest vicariance, but their absence among a handful of vertebrate fossils certainly does not preclude vicariance.

We also agree that the presence of *Anolis*, *Eleutherodactylus*, and *Sphaerodactylus* on islands that were partially or completely submerged during Pleistocene interglacials suggests dispersal. However, certain patterns exist in spite of potential for dispersal. The beta anoles, a monophyletic group (3), occur in the Antilles only on Jamaica, Cuba, and the Bahamas; none occur in Hispaniola, Puerto Rico, or the Lesser Antilles. A monophyletic group of alpha anoles, to which the amber species *Anolis dominicanus* is related (4), occurs primarily on Cuba and Hispaniola; none are found on Jamaica or in Central or South America. These distributions suggest that factors other than over-water dispersal regulate the distribution of these lizards.

Supportive evidence for a vicariant origin of part of the Hispaniolan fauna is provided by amber fossils of invertebrates with seemingly poor dispersal abilities, including scorpions, tailless whip scorpions, Diplura, Collembola, and representatives of the insect orders Phasmatodea, Mantodea, Dermaptera, Zoraptera, Trichoptera, and Ephemeroptera. None of the above are represented as endemic forms on the Hawaiian Islands, one of the best studied groups of truly oceanic islands, where dispersal alone accounted for the assemblage of life (5).

Last, with the recent report of mammalian hair in Dominican amber, there is now fossil evidence for most of the major groups of terrestrial vertebrates (6) in northern Hispaniola in the Tertiary.

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5. E. C. Zimmerman and D. E. Hardy, *Insects of Hawaii* (Univ. of Hawaii Press, Honolulu, HI, 1948), vol. 1.
6. G. Poinar, *Experientia* 44, 89 (1988); records to date (including unpublished finds known to the senior author) include six *Sphaerodactylus*, four *Anolis*, seven frogs, three bird feathers, and six amber pieces with mammalian hair. Thus, Lissamphibia, Squamata, Aves, and Mammalia are represented; Crocodylia and Testudines are not known.