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An Upper Eocene Frog from the Dominican Republic and Its Implication for Caribbean Biogeography

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A frog of the leptodactylid genus *Eleutherodactylus* is reported from Eocene amber found in the Dominican Republic. It is the first described amphibian fossil in amber, and the oldest complete lissamphibian fossil from Mesoamerica (Central America and Mexico). Dating of the amber matrix indicates that by the end of the Eocene a diverse fauna was present in the Antilles, much earlier than has generally been proposed. The presence of this and other amber fossils from this same age suggests that Tertiary patterns of landmass movements were significant in determining the present distribution of species.

THE ORIGIN AND EVOLUTION OF THE highly endemic biota of the West Indies has been under debate in recent years. Two principal models, vicariance and dispersal, have been proposed to account for present faunal distributions. Under the vicariance model, the distribution of the present-day biota among the Caribbean islands is the result of a breakup of a contiguous "proto-Antillean archipelago" that was located between North and South America in the Mesozoic; the biological history of the Antilles is closely linked with its historical geology. An early formulation of this hypothesis held that ancestors of the Recent fauna were present in the "proto-Antilles" by the Late Cretaceous or early Tertiary (*1*). Current applications of the vicariance theory to Caribbean biogeography lead to testable predictions about the relations of biotas of the various islands on the basis of a reconstruction of landmass fragmentation and accretions throughout the past 65 million years (*2*).

In contrast, the more traditional dispersal model argues that the islands were colonized recently from the mainland (*3*). Although this model predates the general acceptance of plate tectonics (*4*), advocates of the dispersal model do not dispute the evidence for continental drift. Rather, the timing of the immigrations is thought to be post-Eocene and therefore relatively recent because the mainland fossil record for extant genera is not earlier than the Oligocene (*5*). Therefore, the fossil record suggests a mid-Tertiary date for the appearance of modern genera on the continents, and subsequent colonization of the Antilles. Additional evidence supports the dispersal viewpoint. The Antilles have been islands probably throughout most of the Cenozoic (*6*); this suggests that their inhabitants immigrated over water. Although the Pleistocene fossil record is quite extensive, there are almost no fossil terrestrial vertebrates older than the Pleistocene in the West Indies (*7*). The two exceptions are lizards of the genera *Anolis* and *Sphaerodactylus* in amber from the Dominican Republic. The *Anolis* was reported as Miocene (*8*), and the *Sphaerodactylus* as Oligocene (*9*), but new data have refined the date of these fossils.

A nearly complete fossil of the frog genus *Eleutherodactylus* was found in amber from the Dominican Republic, on the island of Hispaniola. The major source of Dominican amber is a leguminous tree, *Hymenaea*, which may have become established in the Caribbean from African relatives in the Tertiary (*10*). The specimen (*11*) was collected from the La Toca amber mine, located between Santiago and Puerto Plata in the Cordillera Septentrional. The mine is in the Altimira facies of the El Mamey Formation (upper Eocene), which is shale-sandstone interspersed with a conglomerate of well-rounded pebbles (*12*). In contrast, the presence of the marine foraminiferan *Miogypsina* in a matrix sample from another amber mine (Palo Alto) suggests a lower Miocene to upper Oligocene age (20 million to 23 million years) (*13*); analysis of foraminifera counts from the same mine also indicates a minimum age of lower Miocene (*14*). Thus, sedimentary and geological evidence indicate a range of upper Eocene to lower Miocene for various amber mines in the Dominican Republic.

Differences in the magnitude of absorption peaks of the exo-methylene group of amber from different mines in the Dominican Republic have been shown by nuclear magnetic resonance spectroscopy. From the 20-million- to 23-million-year-old figure obtained for Palo Alto amber as a calibration, a range of 15 million to 40 million years was determined for various specimens of Dominican amber, with that from the La Toca mine being the oldest, 35 million to 40 million years old (lower Oligocene to upper Eocene (*15*). This date agrees with the upper Eocene age assigned to the El Mamey Formation on the basis of the stratigraphic evidence mentioned above. Amber from different mines also varies in certain physical properties, such as color and hardness; the order of hardness and color scale of La Toca amber correlates well with chronological sequence established by analysis of nuclear magnetic resonance spectra (*15*). In summary, the evidence unequivocally indicates the presence of a fauna in the Antilles at a date much earlier than that postulated by the dispersal model.

A series of chemical and physical tests (*16*) performed on a small portion of the amber piece verify that it is authentic. In addition, the specimen has all of the visual characteristics of natural Dominican amber, as judged by the examination by G.O.P. of more than 15,000 pieces of amber with biological inclusions. The piece of yellow, transparent amber containing the frog weighs 36 g and is 5 cm by 5.5 cm (Fig. 1). The specimen measures 22.2 mm from the tip of the snout to the end of the urostyle (the approximate location of the vent). The right arm is broken at the distal end of the humerus and the left leg is broken at the tip of the tibiofibula. Events leading to the entombment of the frog were probably traumatic. Possibly the frog was captured by a predator (possibly a bird) and brought back to a nest in the cavity of a resin-producing tree. The frog came into contact with the resin before being eaten, and a portion of the predator's nest was also covered by the resin. The latter statement is suggested by the fact that in the piece of amber opposite the frog were three decomposing leg bones of another individual of *Eleutherodactylus* (Fig. 1). Numerous fly maggots and the remains of a large centipede were also preserved. Portions of the skin and the eyes of the frog are intact, although much of the skin has become transparent, rendering fine details of the skeleton visible (Figs. 2 and 3).

Low-voltage radiographs of the specimen indicate that the frog was an adult, as evidenced by the degree of ossification of the skeleton. Details of the osteology (shape of the vomer and its dentition, features of the vertebral column, pectoral and pelvic gir-

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Fig. 1. Specimen of Dominican amber containing the *Eleutherodactylus* fossil and three limb elements of a second individual of *Eleutherodactylus*.

dles) permit confident assignment to the genus *Eleutherodactylus* (family Leptodactylidae), the most speciose genus of vertebrates, with approximately 400 species distributed in Mexico, Central America, South America, and the West Indies (*17*). More than 100 species are found only in the West Indies, where the degree of endemism on islands of the Greater Antilles is very high.

On Hispaniola there is a North Island group of 16 endemic species of *Eleutherodactylus*, and a South Island group of 28 endemic species; 5 other species are common to both regions. Until rather recently, this pattern was thought to be the result of isolation of the northern and southern parts of the island by a paleostrait that is represented today by the Cul de Sac–Valle de Neiba plain (*18*). However, evidence indicates that Hispaniola is a composite landmass of two formerly widely separated paleoislands, corresponding to the North and South Island regions, which collided about 5 million to 9 million years ago (*19*). The Hispaniolan fauna, therefore, may be of composite origin.

A synthesis of geological models (*6*) indicates that landmasses of Cuba, Puerto Rico, and northern Hispaniola were contiguous in the Eocene, approximately 40 million years ago, and later separated. Also, southern Hispaniola was closely juxtaposed to Jamaica and the Yucatan region of Mexico, rather than to northern Hispaniola. The fact that the amber frog is a fossil of known minimum age that predates the accretion of the North and South Island elements permits a test of vicariance models. If the fossil proves to be more closely related to the South Island *Eleutherodactylus* than to those of the North Island, it would suggest that the paleogeographic models for vicariance are incorrect.

Because the age of the amber frog predates the union of the North and South Islands, the vicariance model would predict that the fossil *Eleutherodactylus* will be most closely related to species on the North Island region, and Puerto Rico and Cuba, rather than to species on the South Island or Jamaica. Such a hypothesis is derived from the paleogeographic models for the composite origins of Hispaniola. A similar situation exists with another amber fossil from the La Toca mine, the iguanid lizard *Anolis dominicanus*. The species was referred to a monophyletic subset of anoles (*8, 20*), a group that exhibits high levels of endemism in the Antilles (*21*). Members of this monophyletic group (*Anolis*, sensu stricto) are distributed primarily on Cuba and Hispaniola; none is found in Jamaica or in Central or South America. At a broad level the biogeography and relationships of the fossil *Anolis* corroborate the predictions of the vicariance model (*22*).

Aside from the fact that this fossil frog is the third described intact vertebrate in amber, its discovery is significant because in conjunction with many invertebrate fossils (Insecta, Diplopoda, Arachnida) (*14*), it documents that a relatively diverse fauna was present on northern Hispaniola 35 million to 40 million years ago, prior to dates postulated by dispersal models. The occurrence of an *Anolis, Sphaerodactylus*, and an *Eleutherodactylus* in this fauna, at the time when Cuba, Puerto Rico, and northern Hispaniola were joined, suggests that dispersal hypotheses need not be invoked a priori. Moreover, it supports the vicariance view that the biohistory and geohistory of the Caribbean are causally related. There is no doubt that Pleistocene effects were important in determining present biogeographic patterns (*23*); however, the millions of years of Tertiary history of the West Indies and the potential contribution of the amber fauna to the historical biogeography of the Caribbean cannot be overlooked.

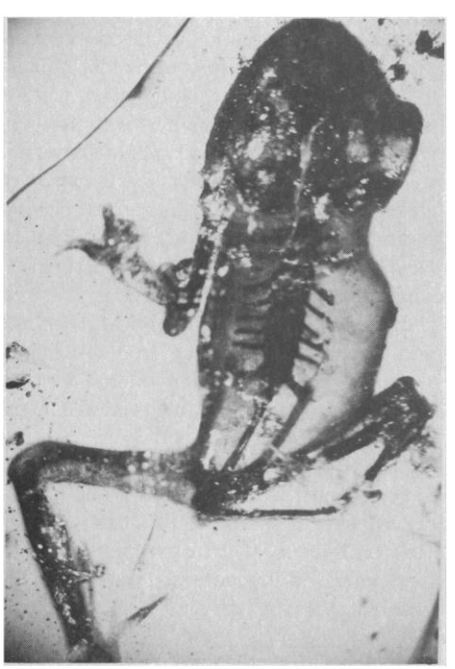

Fig. 2. Dorsolateral view of the fossil *Eleutherodactylus* in Dominican amber.

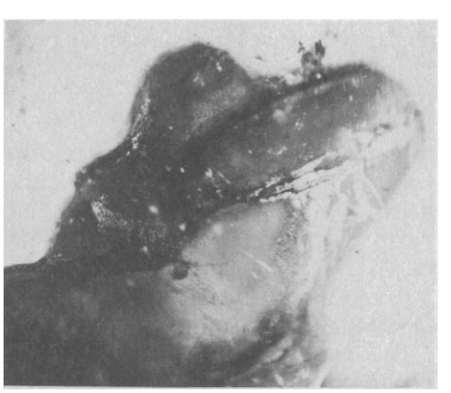

Fig. 3. Lateral view of head of the fossil *Eleutherodactylus* showing striking degree of preservation of the skin and eye.

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