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The Diversity and Significance of the Fossil Fauna from the Amber Deposits of the Dominican Republic

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Richly fossiliferous deposits are regarded as exceptional by palaeontologists if the enclosed biota either contains organisms which are rarely encountered in the rock record or the state of preservation itself is exquisite. The fossil faunas known from amber satisfy both of these criteria for exceptionality. The amber deposits of the Dominican Republic are unique in the Antillean region and are currently yielding new information regarding the ancient terrestrial fauna of the islands, while enabling rival theories of their biogeographic evolution to be tested.

Amber is the fossilised resin (gum) of trees such as conifers (Paul, 1980). Soft and fluid when first formed, resin soon hardens sufficiently to be capable of preservation in the rock record. While the palaeobotanical interest of amber deposits is obvious, the included fauna is of even greater interest to the palaeozoologist. When still soft, fresh resin forms a sticky trap capable of ensnaring terrestrial organisms, particularly small arthropods. Providing the animal is completely engulfed by the resin, it is usual for such a captive to be preserved as a component within the amber.

Terrestrial arthropods preserved in amber form a particularly significant part of that group's fossil record, which is otherwise poor. Most organisms that are common as fossils have hard bones or shells which persist after the decay of the soft tissues. Terrestrial arthropods, such as insects, arachnids and myriapods, lack such a hard, mineralised skeleton and are less likely to be fossilised. Indeed, many fossil insects are known only from rare compression (flattened) fossils, often from just disarticulated wings. Arthropods in amber are exceptional in showing three-dimensional preservation, which makes them of particular value to the palaeoentomologist. Although the soft tissues of such specimens are dehydrated, preservation of the external features is often exquisite, with minute and delicate anatomical features, such as hairs, being retained (Paul 1980). Such fragments of amber are thus invaluable, enabling detailed observations to be made on ancient, and usually extinct, species.

However, horizons yielding amber are rare. The only amber deposits known from the Antillean region occur in the Dominican Republic (Sanderson and Farr, 1960). The sedimentary sequences yielding amber in the D.R. also contain marine foraminiferans, indicating that there must have been some transport of the former, probably by river action, to enable this mixing of fossils from two contrasting environments.

Baroni-Urbani and Saunders (1980) reviewed the diverse terrestrial fauna of the D.R. amber. While the precise origin of the amber in the D.R. is obscure, available evidence suggests that it is derived from the leguminous tree *Hymenaea* (Baroni-Urbani and Saunders 1980), which occurs throughout Central America and the West Indies at the present day (Dr. P. Vogel, Personal Comm.). Thus, the enclosed fauna must largely represent those organisms which lived upon the surface of this taxon. Baroni-Urbani and Saunders (1980) noted fragments of pulmonate snails, woodlice, millipedes and a variety of arachnids, including scorpions, pseudoscorpions, mites and spiders, from the D.R. amber, but the greatest diversity is shown by the insects. The higher taxa recognised by Baroni-Urbani and Saunders are summarised in Table 1. An illustration that this diversity is continued at a lower taxonomic level is given by the ants, which are particularly abundant and diverse, including 37 genera and sub-genera (Wilson, 1985).

The deposits of the D.R. also contain the only complete vertebrate fossils that have so far been recognised from amber. Two lizards have been described; the first anoline recognised from amber, *Anolis domincanus* (Rieppel, 1980) and a member of the genus *Sphaerodactylus* (Bohme 1984). Poinar and Cannatella (1987) recently described a leptodactylid frog belonging to the genus *Eleutherodactylus* and, although it doesn't represent a complete specimen, Poinar (Anon. 1988) has recognised a tuft of mammal hair, probably derived from a rodent.

A fuller understanding of the fauna of the D.R. amber is important to enable testing of the two principal theories concerning the evolution of the Antillean terrestrial fauna (summarised in Briggs 1987). The most probable theory favours fortuitous rafting of terrestrial, flightless organisms, on objects such as floating logs, from continental regions to oceanic islands. The rival vicariance theory

Table 1.

SUPRAGENERIC DIVERSITY OF THE INSECT FAUNA IDENTIFIED FROM AMBER DEPOSITS OF THE DOMINICAN REPUBLIC, (after data in Baroni-Urbani and Saunders 1980).

Collembola (spring tails)	Trichoptera (caddis flies)	Rhysodidae
Thysaneura (silver fishes)	Lepidoptera (butterflies)	Staphylinidae
Machilidae	Diptera (flies)	Scydmaenidae
Ephemeroptera (mayflies)	Limoniidae	Elateridae
Odonata (dragon flies)	Psychodidae	Endomychidae
Zygoptera	Phlebotominae	Alleculidae
Embioptera (webspinners)	Bruchomyinae	Cerambycidae
Mantodea (mantids)	Culicidae	Curculionidae
Dermaptera (earwigs)	Ceratopogonidae	Platypodidae
Blattariae (cockroaches)	Chironomidae	Strepsiptera
Isoptera (termites)	Orthocladiinae	Hymenoptera (ants, bees,
Orthoptera (locusts, crickets)	Chironominae	wasps, etc.)
Tettigoniodea	Pachyneuridae	Ichneumonoidea
Grylloidea	Scatopsidae	(ichneumon flies)
Psocoptera (barklice)	Cecidomyiidae	Chalcidoidea
Psocidae	Mycetophylidae	Mymaridae
Lepidopsocidae	Sciaridae	Proctocrupoidea
Thysanoptera (thrips)	Tabanidae	Formicoidea
Psyllina	Bombyliidae	Formicidae (ants)
Aleyrodina	Empididae	Ponerinae
Auchenorrhyncha (plant lice)	Dolichopodidae	Myrmicinae
Fulgoriformes	Phoridae	Dolichoderinae
Sternorhyncha	Acalyptrata	Apoidea (bees)
Coccidae	Coleoptera (beetles)	Meliponini
Neuroptera (lace wings,	Carabidae	
ant lions)	Carabinae	
Chrysopidae	Harpalinae	

suggests that the terrestrial faunas of the Antillean islands are old, having arrived when the islands were carried close to continental areas by the movement of the Caribbean Plate.

The terrestrial fauna of the D.R. amber is unique in the Caribbean region. Other fossil faunas of terrestrial origin in the Antilles are late Quaternary in age (100,000 years old, or much less in most instances) and are dominated by terrestrial gastropods (for example, see Goodfriend and Mitterer, 1988) and/or vertebrate bones (rarely, if ever, articulated skeletons). Terrestrial arthropods, apart from occasional land crabs (for example, see Pregill *et al.* 1988), are undescribed. As the D.R. amber is undoubtedly pre-Quaternary (see below), its preservation, composition and age make it a potentially unique and powerful tool to test the rival theories of Antillean faunal evolution.

Unfortunately, there are problems with dating the D.R. fauna. Saunders (in Baroni-Urbani and Saunders, 1980) has dated the marine microfossil assemblages associated with amber at the Palo Alto mine in the D.R. as being early Miocene in age or possibly slightly older (about 20 to 23 million years ago; Poinar and Cannatella, 1987). In contrast, using advanced geochemical techniques, Poinar and Cannatella (1987) have estimated that the D.R. amber from various localities varies in age between 40 and 15 million years old, that is from Upper Eocene to Lower Miocene. Their frog came from the La Toca mine, which gave the oldest range of ages, between 35 and 40 million years old (Upper Eocene to Lower Oligocene); the same mine produced the lizards and rodent hair mentioned above (Poinar and Cannatella 1987).

Briggs (1987) demonstrated that the Antilles posses a disharmonic, unbalanced terrestrial fauna, comprising those groups which would be most likely to be dispersed across water (for example, the Antillean freshwater fish fauna only comprises groups that are secondarily adapted for that habitat). Pregill (1981) suggested that terrestrial vertebrates most probably began to disperse amongst the Antilles in the mid Tertiary. In contrast, Poinar and Cannatella (1987) and Poinar in Anon. (1988) have provided evidence of an older terrestrial fauna, dating back to at least the Upper Eocene. This provides support for a vicariance model; Anon. (1988) summarising Poinar considered that "instead of arriving comparatively recently on drifting debris, the animals may have come across on land bridges that once connected the islands to North or South America". There is no geological evidence for the former existence of land bridges *per se*. The concept of a land bridge essentially belongs to the period before the recognition of plate tectonics and continental drift. It was formerly suggested that land bridges were areas of sea floor which became dry land, enabling migration of organisms before the bridge once again sank. It is now realised that it is the land areas and sea floor that are in constant motion. Poinar's Eocene fauna more probably arose by rafting over short distances from a nearby continental land mass as the Antilles 'drifted' by.

Nevertheless, the late Eocene terrestrial fauna of the D. R. is not ultimate proof that the vicariance model was the true method whereby the Antillean islands became populated. The ancient fauna may itself have arrived by rafting and it has almost certainly been supplemented by this process during the intervening period. Further, large and flightless terrestrial organisms are absent from extant and fossil Antillean faunas. Other islands which formerly had undoubted continental connections, such as those of the Mediterranean, formerly supported faunas which included organisms which could not have arrived by rafting, including pygmy elephants and hippos (Davis 1985). None of the Antillean islands appears to have supported any animals that were too big to raft. For example, the largest endemic organisms known from the Jamaican fossil record are the large flightless ibis, *Xenicibus xympithecus* (Olson and Steadman, 1977), which probably evolved from a flying species which had migrated to the island, and the late Pleistocene monkey *Xenothrix mcgregori*, a member of a group well able to cling to a floating tree until it reached dry land.

Thirdly, it is probable that much of the Antillean region was not emergent until after the Eocene. If we once again consider Jamaica as our example, Eva and McFarlane (1985) have suggested that the island was probably entirely submerged from the late Middle Eocene until the end of the Lower Miocene. It is therefore unlikely that an ancient Jamaican terrestrial fauna was ancestral to that existing at the present day. We must therefore conclude that the vicariance model is not proven for the Antillean region.

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