## Molecular Clocks, Flotsam, and Caribbean Islands

Guest Author

Box 11.2

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The islands of the Caribbean have provided a classic test of the two major mechanisms of historical biogeography: vicariance and dispersal. Formed in the Mid-Cretaceous (~100 mya), they have had a long and complex geologic history that included an early connection between North and South America (proto-Antilles) and a catastrophic asteroid impact (~66 mya). During the Cenozoic, some large islands (Greater Antilles) broke apart and fused, a stable carbonate platform (Bahamas Bank) kept up with sea-level changes, and a chain of volcanic islands (Lesser Antilles) migrated slowly from west to east. Soon after the theory of plate tectonics became accepted, it was recognized that the current biota of the islands may be the fragmented (vicariant) remnant of a once continuous proto-Antillean biota. For the last three decades, a debate has ensued over the importance of vicariance versus dispersal in the origin of the biota.

The answer has not come easily, nor has it been agreed upon by everyone. Nonetheless, most research suggests that the entire living biota of the Caribbean islands arrived by dispersal and not through the geologic breakup of an ancient landmass. Initially, it was thought that the key information to answer the question would come from the phylogenetic relationships of organisms. In part, this thinking emerged from the popularity—in the 1980s—of the field of cladistics (and vicariance biogeography) which emphasizes relationships of organisms over most other types of data. Undoubtedly, relationships are important, but the problem with this line of thinking is that the branching order of species might match the geologic breakup of land areas, but the timing could be very different. So it was soon realized that data on the times of divergence of organisms from their closest relatives on the mainland were critical data. The fossil record in this region is poor, but molecular clocks provided those data.

Molecular clocks (see Chapter 7, p. 215) need calibration against some external events, such as well-dated fossils, or geological events, such as the time of emergence of an island above sea level—for this is the earliest time at which it could be occupied by terrestrial organisms. For the Caribbean islands, it turned out that relationships were not important in answering the basic question of vicariance versus dispersal. This is because nearly all of the times of divergence measured by molecular clocks, for many different groups of terrestrial vertebrates, have been too young to have resulted from a Late Cretaceous vicariance event. Instead, the times were scattered throughout the Cenozoic, almost randomly, and in accord with a mechanism that relies on chance events such as dispersal. However, relationships were useful in determining the source area of dispersal. For most terrestrial vertebrates that cannot fly or otherwise disperse over water on their own powers, their closest relatives are in South America, while a majority of the birds, bats, and freshwater fishes in the Caribbean islands appear to have come from North and Central America.

Other diverse evidence, too, supports a dispersal origin for the Caribbean biota. Most important among them is the taxonomic composition of the endemic groups. There are some enormous adaptive radiations, often with species filling niches different from those in the same genus on the mainland. For example, some of the smallest and largest species of major groups (e.g., cycads, swallowtail butterflies, frogs, lizards, and snakes) occur on islands in the Caribbean. Yet at the same time, many major groups are absent, such as salamanders and caecilian amphibians, marsupials, rabbits, armadillos, and carnivorous placental mammals. The fossil record, including that of the 15–20 my old Dominican amber, which includes the remains of insects, frogs, lizards, and small mammals, shows a similar taxonomic composition. This is best interpreted as a strong filter effect, whereby a few colonists survive long-distance dispersal and then radiate into a diversity of unoccupied ecological niches. This same evidence also argues against an origin for the biota by way of a Mid-Cenozoic (~34 mya) land bridge from South America, which has also been suggested. Such a land bridge would not have acted as a strong filter and would have allowed many other groups to enter the archipelago that we do not in fact find there.

Ocean currents and geographic proximity best explain the source areas of the island colonists identified in molecular phylogenies. Water flows almost unidirectionally from east and southeast to west and northwest in the Caribbean—and this was true even prior to the uplift of the Isthmus of Panama. As a result, flotsam ejected carried down from the rivers in northern and northeastern South America will end up in the Caribbean, if it continues to float. For example, even though Cuba is much closer to North America than to South America, it is much easier for a lizard to arrive in Cuba by floating on vegetation from South America; this is reflected in the composition of the Cuban lizard fauna. But for organisms that can fly or swim, the geographically closer areas are the more likely sources, and the common air current direction in the Caribbean—northeast to southwest—might even assist dispersers flying from North America.

Two lineages of island vertebrates that show old (Cretaceous) times of divergence from their closest relatives on the mainland, using molecular clocks, have been debated as possible examples of proto-Antillean vicariance. These are the giant shrews (solenodons) of Cuba and Hispaniola and the night lizards (Xantusiidae) of Cuba. While an

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ancient origin cannot be ruled out, both groups are biogeographic relicts, for their mainland fossil record demonstrates a wider distribution in the past. This raises the possibility—not normally considered for other groups—that they diverged more recently from close relatives on the mainland that are now extinct and hence inaccessible to molecular clocks. Some geologists also are uncertain about whether there was any continuously emergent land in the Caribbean before the late Eocene (~37 mya), which would have been necessary for maintaining such lineages. Moreover, it is not clear how these organisms might have survived the end-Cretaceous asteroid impact, which occurred a short distance away. The origin of these two groups will likely continue to be debated.

Now we know that flotsam was critical for the origin of the Caribbean terrestrial biota, but surprisingly little is known about this mode of dispersal across ocean waters. How abundant are floating islands? How long do they stay afloat, and how far do they travel? What organisms do they typically carry? There are many anecdotal accounts of floating islands but almost no scientific studies. Analysis of satellite imagery, GPS tracking, and taxonomic surveys of floating islands might answer some of these questions. Whatever the details, we can be certain that long-distance dispersal by flotsam did occur and that fragile animals—such as small frogs—successfully colonized Caribbean islands millions of years ago after riding the ocean waves for weeks on a jumble of logs.

What is now the Caribbean region began as merely a gap between North America and South America (Fig. 11.13). In this gap, there was opposition between the expansion resulting from the mid-Atlantic spreading ridge to the east, and that resulting from the East Pacific spreading ridge to the west. Part of this expansion was taken up by an eastern trench, where old seafloor disappeared into the depths of the earth, and this would have been accompanied by volcanic activity and the appearance of a chain of volcanic islands. As the Americas moved westward, this whole system was left behind in a more eastern position, and today forms the Lesser Antillean island chain (see Fig. 11.12) and trench system. Here the Atlantic plate seafloor is still being consumed, and this marks the eastern boundary of the new, small Caribbean tectonic plate. (The Scotia Sea

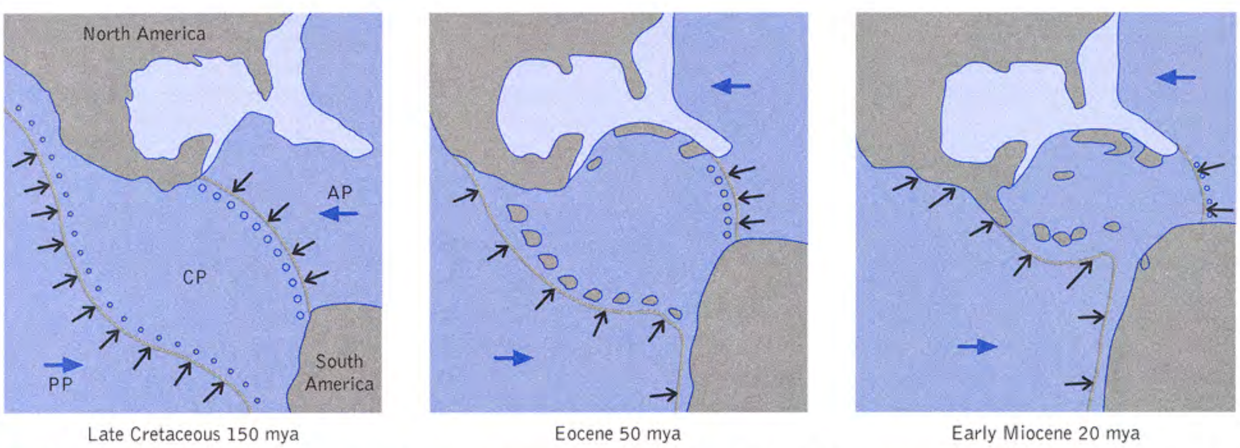


**Fig. 11.13** The formation of the West Indies. Dark gray tint indicates dry land, light blue tint indicates shallow water, dark blue tint indicates deep water. Filled arrows indicate plate motion: AP, Atlantic Plate, CP Caribbean Plate, PP Pacific Plate. Smaller arrows indicate where ocean crust is being consumed, leading to the appearance of volcanic islands. Modifed, after Huggett [57], with permission of Routledge Press.