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Biogeography of the Greater Antillean Mosses

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> *There is something fascinating about science. One gets such wholesome returns of conjecture out of such a trifling investment of fact.*
>
> *Mark Twain*
> *Life on the Mississippi*
> *Chapter XVII*

Abstract. The distinctions between dispersal and vicariance are discussed and shown how they relate to geological history. Postulated theories on the tectonic origins and history of the Greater Antilles are reviewed, as well as possible climatic events that would affect biogeography. Numerous zoological examples are presented to argue both dispersalist and vicariance viewpoints. It is proposed that the modern moss flora of the Greater Antilles is best explained primarily by dispersal events. Post-vicariant events, such as Pleistocene climate changes, would have extirpated the vast majority of mosses from the islands and even among those taxa that survived, disperal by the same taxa would have obscured their origins. It is assumed that many of the North American elements in the high elevations of Hispaniola are a result of invasions during the Pleistocene. The Andean elements are considered relatively recent dispersally derived taxa that have successfully colonized the Antilles because of ecologically compatible habitats.

Introduction

Biogeography as a subject has been of interest ever since naturalists noticed that plants and animals have discrete ranges. However, only in the past twenty years, with the widespread acceptance of continental drift, has biogeography regained interest because of the advent of vicariance theory. This theory has removed biogeography from purely armchair speculation to the realm of testable hypotheses. Although some vicariance biogeographers have tried to postulate that all distribution patterns are a result of vicariance events and dispersal is of little or no effect, in most cases both vicariance and dispersal are of use in explaining the origins of a given biota (McDowall 1978, Stace 1989).

Dispersal is the explanation for moss distributions that most bryologists have accepted. It is only natural in terms of the ease with which mosses disperse. However, even with organisms of such easy dispersal, vicariance is sometimes the better explanation for some distribution patterns. For example, *Echinodium* has what appears to be a perplexing distribution with taxa in Australasia and Macaronesia (Churchill 1986). However, fossil records from the Pliocene of

continental Europe give evidence of a wider, more continuous distribution in the past. Probably as a result of the Pleistocene glaciations and their associated climatic influences, the genus became extinct over much of its original range and was pushed to the fringes of its former range, where it still exists. This certainly seems a more elegant explanation of the current distribution of *Echinodium* than some odd dispersal between the Canary Islands and New Zealand.

Nevertheless, dispersal is a common and important agent in moss distribution. Simplistically, dispersal is where either an organism, some stage in its life cycle, or some part of it, crosses an area or barrier where the organism cannot survive, and establishes itself in an area discontinuous with the original population. Probably in its most common expression, dispersal is responsible for the range extension of taxa. It is also the most reasonable explanation for the biota of isolated oceanic islands. Dispersal works primarily at the level of the individual. Some organisms, among both plants and animals, are adapted to the possibility of long-range dispersal, while others are actually adapted for minimal dispersal because of the highly specialized habitats in which they live. Most mosses are adapted for ease of dispersal. This is not to imply that even most moss distribution patterns are attributable to dispersal, but rather that dispersal must always be considered a possibility. Indeed, some mosses, e.g., cleistocarpous taxa, seem not to fall into this class, but they are in the minority. Many mosses not only have resistant spores as dispersal agents, but have evolved highly efficient asexual diaspores (Miller & Ambrose 1976, Miller 1985). There is good evidence that not only are moss spores dispersed, but that they can and do survive the rigors of travel (van Zanten 1976, 1978). Why, then, might a bryologist evoke a scenario that does not directly involve dispersal?

Vicariance biogeography, almost of necessity, has developed with the understanding and acceptance of plate tectonics. Although vicariance, or as it has more traditionally been called, the historical factor, can be invoked with climatic changes or orogenic formation, it is often used in association with continental drift. In very basic form, vicariance begins with an organism that has a continuous range over a given area. The area is then changed or divided so that the organism is no longer contiguously distributed. The separated populations may then go on to evolve independently into different taxa. Consequently, in contrast to dispersal, vicariance works at or above the populational level. Undoubtedly, many of the African/South American distribution patterns in mosses (Buck & Griffin 1984, Reese 1985) are attributable to vicariance in which the continental separation of Africa and South America was the vicariant event.

Mosses, though, have problems not often encountered in vascular plants, obscure vicariance. It has been argued, and convincingly so, that good taxonomy can provide evidence for dispersal vs. vicariance (McDowall 1973). For example, vicariance has been postulated as the explanation for the distribution of some of the biotas of subantarctic islands. In some cases the organisms are poor dispersers (e.g., flightless birds) and the taxa on different islands are very distinct taxonomically. The distribution of these organisms can indeed be best explained as the result of vicariant events. In other cases, though, organisms are readily dispersed and when looking at them on distant islands there are no morphological differences. Since the postulated vicariant events took place millions of years ago, it is unreasonable to expect small populations not to have undergone speciation in that length of time and therefore dispersal seems a more logical explanation. This method

of distinguishing vicariance from dispersal is not so effective for mosses. In the vast majority of cases, mosses do not have small population sizes, but rather even in small colonies thousands of individuals may be involved. Speciation and genetic drift act much more slowly on large populations. Therefore, if large populations were separated by a vicariant event, morphological differences may be very slow in appearing between the two. Also, if even a single spore of an autoicous moss landed and survived in an area previously uncolonized by the taxon, it could potentially result in thousands of individuals in a single generation. The arrival of a single spore, though, is probably a rare event because if a dispersal event occurs once, there is an increased probability that it can happen again. So, as opposed to most terrestrial organisms with modest population sizes, mosses do not fit the common model, thus making biogeographic speculation even more tenuous than in other groups. Also, even if a vicariant event is responsible for geographic discontinuity, it is entirely reasonable for dispersal to continue between the two areas, and thereby retard or even prevent speciation. Therefore, even if the cause of distribution (dispersal or vicariance) in some other groups of organisms is fairly straightforward, it may not be so for mosses. This will become obvious later in this paper I present examples, mostly zoological, in connection with the Caribbean biotic history.

Caribbean Geological History

To invoke the use of vicariance, there must be a clear geological history or else vicariance becomes as untestable as dispersal. This is particularly true of an island situation such as in the Caribbean. Whether or not a hypothesis is falsifiable is of major importance to vicariance biogeographers. However, just because dispersal is not testable does not mean it is not true.

The geological history of the Caribbean is as complex as anywhere else in the world. Almost every possible geological phenomenon that can occur has occurred there. For this reason, there is no strong consensus on its history, but there are two main scenarios proposed, and these are all that I will present here. For a history of thought on Caribbean geology, see the review by Rull & Schubert (1989).

In a speculative reconstruction of western Pangaea in the Permo- Triassic (Pindell & Dewey 1982), Africa, South America and North America are all closely packed together; there is no South Atlantic Ocean, and the Caribbean region is occupied by the Yucatan Block. During the Jurassic as South America and Africa moved away from North America, the Yucatan Block moved closer to its present position in Mexico. Thus, the Caribbean opened up about the same time as the southern North Atlantic Ocean. At that time North America consisted of the current U.S./Canada mass and Nuclear Central America (Mexico, including the Yucatan but probably not Baja California, and the Chortis Block that corresponds more or less to modern Guatemala and Honduras). By the most established view (Malfait & Dinkelman 1972, Hedges 1982, Sykes et al. 1982, Durham 1985), sometime during the Cretaceous land originating in the eastern Pacific formed an island, or more likely an archipelago, in the current position of southern Central America, i.e., Costa Rica and Panama. This was the so-called proto-Antilles. As the Caribbean opened, the Pacific Plate intruded between North and South America, rafting the proto- Antilles from their position as a link between North and South America to their current positions. The proto-Antilles became most of what we consider the Greater Antilles, i.e., Jamaica, Cuba, Hispaniola and Puerto Rico. The Lesser Antilles are of volcanic origin and are not of interest here. In probably about the middle of the Miocene

(ca. 25 million years ago) the current positions of the Greater Antilles were reached, when the Caribbean Plate collided with the Bahamian Block. The Caribbean Plate became delimited by the formation of the Puerto Rican and Cayman trenches (Perfit & Heezen 1978). However, the situation is complicated by the fact that Hispaniola is apparently composed of three or four different land masses that eventually fused into the present-day island. Also there is good geological evidence (Arden 1975, Bowin 1975) that at least some of the islands, Jamaica and the southern peninsula of Haiti in particular, were submerged during part of the time they were rafting to their current positions. As water levels have risen and fallen through prehistoric times, it is difficult to know exactly how much, if any, land remained above water at any given time. Unfortunately, this question is not of great interest to geologists since a rock is a rock whether it is above or below water, but it is of major significance to the biogeographer. It does appear, though, that there was no time during the Cenozoic when all the islands of the Greater Antilles were submerged (Khudoley & Meyerhoff 1971). It is this model that most zoogeographers have incorporated into their vicariance models for the Caribbean.

However, a more recent reconstruction theory for the Caribbean (Anderson & Schmidt 1983) has Cuba, Hispaniola and Puerto Rico, as well as the Yucatan, appressed to the northern border of South America in the middle of the Mesozoic. Jamaica and the southern peninsula of Haiti are adjacent to or part of the Chortis Block. Apparently this fit is more in line with the geological formations in the Greater Antilles, Nuclear Central America and northern South America. In fact, these authors think that some sedimentary deposits in Cuba originated from the eroding Guyana Shield. The separation from South America took place about 158 to 145 million years ago, in the Jurassic, and the Yucatan remained attached to Cuba and Hispaniola. At the end of the Jurassic, though, in the middle Tithonian, most of Cuba was submerged. By the late Oxfordian ($\pm$ 140 million years ago), Cuba reached its present position. Also during the Jurassic the Chortis Block, with its eastern part composed of the Nicaraguan Rise and perhaps Jamaica and the southern peninsula of Haiti, rotated into its present position.

Unfortunately these two theories are not compatible and I have no way to knowledgably evaluate them. However, the geological data supporting the latter theory (Anderson & Schmidt 1983) does appear more sound. Certainly whichever one is correct, if either, will impact on Antillean vicariance theory very differently, especially since some zoogeographic speculation relies on North American elements being rafted into the Caribbean. Unfortunately, the biological data are inconclusive on the possibility of a land connection between North and South America during the Eocene, as postulated by Malfait & Dinkelman (1972). There is some evidence of a mammalian interchange from South America into North America in the Late Paleocene but it was apparently short-lived because there is no evidence of North American mammals invading South America (Gingerich 1985). Similarly, but somewhat earlier, in the Late Cretaceous, there was an interchange between the American herpetofaunas (Estes & Baez 1985). Again, though, it pales in comparison to that which occurred at the Pliocene-Pleistocene boundary when the current Isthmus of Panama linked the two continents. To even further complicate matters, a recent paper by Donnelly (1988) suggests the possibility that the Greater Antilles did not have as mobile a history as proposed by some geologists, and may have been formed more or less near their current positions. How then can a geological scenario be used in postulating

the biogeographic history of the Greater Antillean biota?

Biogeography of the Greater Antilles

Rosen was the first (1975), and strongest (1985), supporter of a vicariance explanation for the biotic history of the Caribbean. He argued that the biota of the proto-Antilles, which because of their geographical placement should be a combination of the floras and faunas of northwestern South America and southwestern North America, rafted to their current positions and their nearest ancestors should be found in the areas adjacent to the original placement. As evidence for this theory he found that cladograms of the geological movement of land corresponded to cladograms of selected organisms. The geographical features in which monophyletic groups of organisms are coincident are called distributional tracts. Unfortunately, there are no good papers on plant geography of the West Indies in which Rosen's ideas are considered. However, there are numerous papers concerning animals of every conceivable group, from freshwater fishes and amphibians to fossil mammals and insects, and these can be of use in evaluating the application of vicariance biogeography to the Greater Antilles. It should be made clear that undoubtedly vicariance is an important factor in understanding the world distribution of plants and animals, i.e., panbiogeography sensu Croizat (1958). Whether it is applicable to the Caribbean region, though, is still under debate.

One of stongest supporters for a vicariance explanation of the Greater Antillean biota is MacFadden (1980, 1981), who worked on the insectivore genera Nesophontes and Solenodon. The former genus consisted of about six species on Cuba, Hispaniola and Puerto Rico, all of which are now extinct; the latter genus has two marginally extant species, one each on Cuba and Hispaniola, and several extinct species, also from Cuba and Hispaniola. MacFadden argues convincingly that the distribution of these animals, whose ancestors were North American, is best explained by their rafting on the proto-Antilles.

Other proponents of Caribbean vicariance who actually presented original data include Ball (1971) who worked on planarians and Flint (1976) who provided evidence from caddisflies. Indeed, one might expect insects to be valuable biogeographic indicators. They are also similar to mosses in their small body size, large populations sizes and ease of dispersal in some species. Unfortunately this is not universally true, as for example in butterflies which seem not to have evolved as a group until after the major vicariance and tectonic events of the caribbean occurred (Scott 1972, Shields & Dvorak 1979). As in other groups of organisms, authors who work on different orders of insects have different ideas on biogeographical histories. For example, Eickwort (1988) considered dispersal over water to be the best explanation for West Indian sweat bees (Halictidae), whereas Hamilton (1988) reasserted Flint's (l978) contention that the caddisflies (Trichoptera) are vicariantly derived. Many entomologists, though, are not convinced that a single explanation is adequate to understand modern insect distributions. Liebherr (1988) considered dispersal and vicariance to have about equal importance in the distribution of carabid beetles of the genus Platynus, although Nichols (1988) considered dispersal as the sole explanation for the distribution of another group of carabid beetles. In an analysis of the West Indian Lygaeidae (Hemiptera), Slater (1988) considered the vast majority of the taxa to have been derived by dispersal with only a few primitive members to have had a vicariant origin.

Although the controversy continues to

rage, as evidenced by several recent symposia on the topic, the majority of zoogeographers involved in the argument seem to favor dispersal, at least for the majority of the Greater Antillean fauna. Probably the strongest opponent of Antillean vicariance is Pregill. He (1981) evaluated the work of Rosen (1975) and MacFadden (1980) and presented arguments that dispersal over water is the best explanation for the current biota of the Greater Antilles. He argued that there was insufficient geological evidence for the proto-Antilles and that current zoogeographic patterns were not consistent with a vicariant history. Although his geological arguments have been refuted (Hedges 1982), his other positions have not been adequately addressed.

Rosen's (1975) use of freshwater fishes as vicariance indicators at first glance would appear sound, since one would hardly expect them to be good dispersers across saltwater barriers. However, a more recent paper by Briggs (1984) disputes Rosen's position. Briggs' analysis of freshwater fishes reiterated Myers' (1938) original observations that there are no primary freshwater fishes (i.e., those fish which throughout their evolutionary history have had no tolerance to saltwater) in the Greater Antilles, but rather the fish fauna is entirely of secondary freshwater fishes (i.e., those that live in freshwater but have a salinity tolerance). Also, by mapping the distribution of these fishes in the Greater Antilles he demonstated that dispersal from the mainland through Cuba and from there to the other islands is the best explanation for current distributions. Briggs considered the lack of any native freshwater fishes at all in Puerto Rico to be evidence against a vicariance hypothesis since Puerto Rico is one of the islands proposed as continuously above the sea. More recently, though, Rauchenberger (1988) argued for a vicariant explanation for the freshwater fishes, but did not address Briggs' position. Work on Jamaica, though, which almost surely was submerged at some time in its history, has relied entirely on dispersal (Buskirk 1985), both from mainland Central America and the other Greater Antillean islands.

Even the interpretation of a single fossil can be controversial. The recent find of a frog of the genus Eleutherodactylus in amber from the Upper Eocene of the Dominican Republic (Poinar & Cannatella 1987, Poinar 1988) is just such an example. Poinar & Cannatella (1987) interpreted the fossil as evidence that a fauna existed in the Greater Antilles prior to postulated dispersal explanations and therefore its presence was evidence of an earlier vicariance event. Mayer & Lazell (1988) countered that the logic of Poinar & Cannatella was faulty and in fact the fossil, although not conclusively proving either a dispersal or vicariant viewpoint, provided a better argument for dispersal. Naturally, Poinar & Cannatella (1988) disagreed.

Some animal examples almost rival mosses in the problems of their biogeographic interpretation, particularly those with easy mobility over water, such as birds and bats. Bats have received special attention in part because of their fossil record, and in part because of their susceptibility to extermination from habitat destruction. Baker & Genoways (1978) have proposed a dispersal history for the modern Caribbean bat fauna based on the taxonomy of the group, the number of species on different islands, and their relationships. Most recently Phillips et al. (1989), through the use of mitochondrial DNA, have been able to estimate the number of arrivals on each island that each species has made. Like the biogeography of other taxa adapted for easy dispersal, that of bats may have been influenced by an early vicariant event but due to more modern extinction and subsequent dispersal, the effects of this event on the bats have been obscured. Consequently, the modern bat fauna is primarily the result

of dispersal over water.

Morgan & Woods (1986) have taken a somewhat middle ground. They have examined mammals in the Greater Antilles, with special emphasis on fossil mammals so as to understand the historical aspects of biogeography rather than just relying on current distribution. This is particularly critical for mammals in the West Indies because of the mass extinctions that have occurred there, both from natural and human causes. They find that the distribution of mammals is due primarily to dispersal but that in some few cases (e.g., MacFadden's, 1980, insectivores) vicariance may be the best explanation.

One of the perennial problems in the vicariance explanation is the lack of certain major animal groups in the Greater Antilles. As early as 1956 Simpson pointed out that there is no evidence, fossil or otherwise, that several large groups of mammals ever were in the Antilles. These include ungulates, marsupials and carnivores. These groups were represented on the continental Americas and if rafting did occur from near the continents, it should have carried an entire biota, not just selected members. Although these groups could have escaped fossilization, it seems unlikely when many smaller, more delicate mammals are represented in the fossil record. What could be the cause of massive extinction before the arrival of man? Could the extinction factors be the explanation for much of the seemingly negative evidence against vicariance?

Caribbean Climatic History

Extinction has received much attention in recent years (e.g., Pregill & Olson 1981, Martin 1984, Morgan & Woods 1986, MacPhee et al. 1989). Almost all the work has involved mammals because they are large, conspicuous animals that have disappeared in a relatively short geological time. Of particular interest here is the work by Pregill & Olson (1981). They have brought up two ideas, both of which are critical in understanding modern distribution patterns: sea level fluctuations and climatic changes through time. The first affects the amount of land available for terrestrial organisms, and the second determines whether the land is acceptable for the survival of an organism. In this section of my essay, it is irrelevant if the proto- Antillean hypothesis is accepted or not because many of the measurable changes have taken place while the islands are in their current positions, whatever their geologic histories.

Pleistocene glaciation affected not only north temperate areas, but had a severe impact on tropical areas as well. Although climatic changes are often considered in connection with Pleistocene glaciation, , sea level changes are rarely discussed. However, the sea level probably dropped as much as 120 m (Gascoyne et al. 1979) as a result of the water tied up in the ice. What is even more surprising, though, is that toward the end of the last interglacial period, ca. 65,000 years ago, the sea level was probably about 8-10 m above the present level (Alt & Brooks 1965). When sea levels were much lower, the amount of available land in the West Indies was considerably greater than at present. The Bahamas went from minor islands to one of the largest islands in the region. Cuba was much closer to both Florida and Mexico. Hispaniola and Puerto Rico probably had a land connection. In terms of biogeography, this increased land mass in the Caribbean and its increased proximity to continental areas is of major significance. During this time period dispersal would have been much easier because the distance to be traveled would be significantly less. This possibility of increased dispersal would obscure original vicariance elements, but probably not eliminate them, unless more evolved organisms from the mainland could outcompete them. Although this is indeed

a possibility for animals, it is very unlikely for plants and a virtual impossibility for mosses.

Higher sea levels, though, would have even a more drastic impact on the biota. Organisms adapted for lowland situations might conceivably be extremely pressured as their habitats gradually disappeared. Perhaps comparable habitats would be created in areas with elevations above the new sea levels similar to the original levels, but somewhere habitats would be eliminated or severely compressed. Again, animals would be the hardest hit because of the greater need of land by each individual. Surely with the decreased area available, certain habitats would no longer be available, or available only in diminished size, and this would push some organisms to extinction, including mosses. For example, bats that require caves for their survival would be negatively affected by increased water levels since most caves are at low elevations. However, at least for mosses, it is not the size of the habitat that seems critical, but the quality of it. For example, the montane areas in some the Lesser Antilles are quite small, but nevertheless support a rich flora. Presumably the bryoflora is its current size not because the habitat could not support a larger one, but because the small area makes a smaller target for the arrival of newcomers. If, as postulated Pleistocene events suggest, the Greater Antilles were even larger than present before rising sea levels decreased their area, colonization would not be a problem because the organisms were already there and only needed—over numerous generations—to move.

Climatic changes, though, surely had more of an impact on the Caribbean biota than just changing sea levels did. Most organisms are adapted to survival in specific habitats. Admittedly there are some generalists, especially among animals, that move easily between extreme habitats, but plants are rarely among them. Without question, north temperate glaciation caused major changes in tropical climates (Hammen 1974). Most neotropical areas, from Mexico to southern Brazil, became significantly drier during the Pleistocene (for a review see Prance 1982), and lowland wet forests were greatly restricted. Organisms of small stature, like mosses, are even more affected than larger ones. Therefore, even if an organism were in the Greater Antilles as a result of a vicariance event but was adapted to a hydric or even mesic habitat, it probably would have been exterminated as a result of Pleistocene climatic conditions.

Although eliminating some organisms, Pleistocene sea levels and climate could have allowed other organisms to invade the Greater Antilles. During the Wisconsinan and previous glaciations, there was an extensive development of xeric habitats (Donnelly 1988). These ranged in a broad belt from the American Southwest across the Gulf Coast to Florida. Similarly, much of the Greater Antilles were covered by savannas and scrub forests (Pregill & Olson 1981). These same habitats dominated most of Central America and the lowlands of northern South America (Prance 1982). Of significance also is that Cuba was much closer to the Yucatan Penisula and to Florida because of the lower sea levels, and thus plants adapted to arid conditions were offered an opportunity to expand their ranges into new areas. Probably some of the northern plants driven south by glaciation but which were adapted to xeric habitats, be they in xeric climates or dry microhabitats within a moist climate (e.g., exposed rocks), were able to colonize tropical latitudes previously unavailable to them because of climatic conditions. Most of these probably moved north with the melting of the glaciers, but some may have persisted in tropical areas where the climate was ameliorated by either microhabitat or elevation. This, then, was

an opportunity for continental elements to invade the insular land masses of the Caribbean. Thus, when determining the provenance of a particular element in the biota of an area, one needs not only to consider geological factors but ecological ones as well (Endler 1982). What application, then, do the possibilities of a rafting proto-Antilles and climatic changes through history have for an understanding of the modern moss flora of the Greater Antilles?

Postulated Sources and History of the Greater Antillean Mosses

Because of the ease of dispersal of most mosses, the low to middle elevational moss flora of the Greater Antilles is unexceptional. A similar flora ranges from the lowlands of northern South America, throughout most of central America, and to a more limited extent across the Gulf Coastal Plain of the United States from eastern Texas to southernmost Florida. There are a few exceptions, but they are just that, exceptions. For example, *Mittenothamnium salleanum* (Besch.) Card. is known only from Mexico, Belize and a few collections from Cuba. However, the species seems to be restricted to limestone habitats along streams and it may this habitat specialization that is the cause of the relatively narrow distribution.

On the other hand, the moss flora of the higher elevations in the Greater Antilles is indeed remarkable and shows interesting disjunctions. Although some of these were described as new, endemic taxa, my work on the flora has demonstrated that virtually all these can be assigned to continental taxa, primarily Andean and, to a lesser extent, North American. For comparison of the floras I have used the most recent (in many cases only) and comprehensive list or flora for each island—Cuba (Leon 1933), Jamaica (Crum & Bartram 1958), Hispaniola (Buck & Steere 1983), Puerto Rico (Crum & Steere 1957)—modified by my own recent collections and those of others I have examined.

Probably because of its distance from the mainland, its relatively small size, and its lack of extensive highlands, Puerto Rico is not a phytogeographically interesting island. This is not to imply that there are not interesting mosses there, but rather there seems to be no pattern to their distribution. For example, *Anacamptodon cubensis* (Sull.) Mitt. was recently found there (Buck & Sastre-De Jesús in press), and it otherwise is known only from Cuba and northern South America, but this is not a distribution pattern followed by other Puerto Rican mosses. Likewise, there are a few endemic mosses known from the island, but they are usually restricted to unusual habitats, such as serpentine outcrops (Pursell 1985).

Jamaica likewise does not have a bryogeographically significant flora. This surely is due to its submersion during its geologic history. Again, though, Jamaica has some very interesting mosses, and some that have interesting disjunctions. For example, *Hookeriopsis websteri* Crum & Bartr., recently transferred to *Brymela* (Buck 1987), has turned up in Panama (Allen 4943, MO, NY), and on the surface its distribution would appear to be a result of vicariance following the Malfait & Dinkelman (1972) model. However, since Jamaica was submerged after its proximity to Central America, one can only assume that the current distribution is due to recent dispersal. A similar example *Taxiphyllum ligulaefolium* (Bartr.) Buck, comb. nov. (*Glossadelphus ligulaefolius* Bartr., Bryologist 49: 123. 1946), known from Mexico and Guatemala, and which was described from Jamaica as *Taxiphyllum gallorum* Buck. The best explanation of its distribution seems to be a habitat specificity, in this case shaded, limestone in humid forests, that is not common in Middle America.

Cuba, because of its large area and complex geological history, has a relatively rich moss flora. Numerous apparent disjunct species are present, and these are disjunct from both the north and south. Again, though, the fact that the same species, not the most closely related ones as in higher plants and animals, occurs in these disjunct areas makes speculation on their biogeographic history tenuous. Were they endemic species then one could reasonably hypothesize on their origin and assume that dispersal in recent times was not an option. Unfortunately, this is rarely the case. One good candidate for a vicariantly dispersed species, though, is *Eucamptodontopsis pilifera* (Mitt.) Broth., especially if the Anderson & Schmidt (1983) scenario is correct. This species is known from an old mountain chain in Cuba, the Sierra de Moa, and from the Guayana Highland of northern South America. It also is known from Martinique and Guadeloupe, but these occurrences are best explained by recent dispersal because the islands are of recent volcanic origin. Since Cuba may have been appressed to northern South America and even some of its sedimentary rocks may have arisen from erosion products of the Guyana Shield, the distribution of *Eucamptodontopsis pilifera* is most elegantly explained as a result of a vicariance event. Unfortunately such clear examples are few at best. Possibly the distribution of *Mittenothamnium salleanum* (discussed above) may be the result of an ancient vicariant event separating a fused Yucatan and Cuba, but dispersal during the Pleistocene when Cuba and Mexico were much closer and had similar climates is a more probable explanation. Admittedly, though, with such meager evidence, this speculation is possibly just pure fantasy.

I think some mosses in Cuba are undoubtedly a result of recent dispersals. For example, *Schwetschkeopis fabronia* (Schwaegr.) Broth., a species whose primary distribution in eastern Asia and eastern North America is almost surely due to a vicariant event, has been found in Cuba. Because of the species' history in its primary range, it most probably arrived in Cuba by long-distance dispersal.

Some examples of mosses that appear to have anomalous distributions may in fact be due to poor taxonomy. For example, the supposed Cuban endemic genus *Pseudotrachypus*, with its single species *P. pinnatus* P.-Varde & Ther., is assigned to the primarily Old World Trachypodaceae (van Zanten 1959). It is the only member of the family in the New World except for a couple of varieties of the widespread *Trachypus bicolor* Reinw. & Hornsch. However, it turns out that the Cuban 'endemic' is in fact only the local name for the more widespread, New World *Papillaria martinicensis* Broth. in Urban. Certainly some additional taxa that appear to have bizarre distributions may be explained when their taxonomy has been clarified.

Hispaniola is the Greater Antillean island with the most interesting flora. Not only does it have a complement of widespread mosses that are found in the circum-Caribbean region, but it has a distinctive continental element first noticed by Crum & Steere (1958) and later expounded on by Steere (1985). The continental mosses have their primary ranges both in the Northern and Southern Hemispheres. The immediate reason for such a rich flora is the presence of a large expanse of land above 2000 meters, with peaks reaching over 3000 meters. If one were to uncritically examine these disjunct elements, one could ascribe their origin to past vicariance events. Although a few of them may indeed be due to such causes, I think the vast majority can be assigned to categories of more recent events.

In general I think that many of the Hispaniolan continental elements

assignable to primarily North American taxa are a result of Pleistocene events. Recent evidence (Donnelly 1988) even suggests that areas of Hispaniola may have been glaciated at that time. During this time, as elaborated above, a belt of savanna and dry scrub forest stretched across the southern part of the United States, through Central America, and into South America. Similarly, most of the Greater Antilles were covered by such vegetation. During this time transoceanic distances between Hispaniola and the continents were much less because of lower water levels. It is during this time that I speculate many of the northern elements arrived in Hispaniola. This view is reinforced by the fact that many of these northern elements grow in fairly xeric habitats. Included here are some mosses only recently discovered in Hispaniola (Buck 1989). I would place among the Pleistocene invaders *Acaulon muticum* (Hedw.) C. Muell., *Bryoerythrophyllum recurvirostre* (Hedw.) Chen, *Bryoxiphium norvegicum* (Brid.) Mitt. (although not a specifically xerophytic moss, it grows in very sheltered habitats), *Campylium stellatum* (Hedw.) C. Jens., *Dicranum flagellare* Hedw., *Encalypta ciliata* Hedw., *Eurhynchium pulchellum* (Hedw.) Jenn., *Forsstroemia trichomitria* (Hedw.) Lindb., *Hedwigia ciliata* (Hedw.) P.-Beauv., *Herpetineuron toccoae* (Sull. & Lesq.) Card., *Hygroamblystegium varians* (Hedw.) Lindb., *Leucodon julaceus* (Hedw.) Sull., *Orthotrichum anomalum* Hedw., *Pleurochaete squarrosa* (Brid.) Lindb., *Ptychomitrium lepidomitrium* (C. Muell.) Schimp., *Pylaisiadelpha tenuirostris* (Sull.) Buck, *Schistidium apocarpum* (Hedw.) B.S.G., *Thelia hirtella* (Hedw.) Sull., and *Tortella tortuosa* (Hedw.) Limpr. Two endemic taxa that may be included in this category are *Pleuridium holdridgei* Crum & Steere and *Limbella bartlettii* (Crum & Steere) Buck. The *Pleuridium* in particular may best be explained by Pleistocene climatic differences because the species mostly occurs in areas that are dry part of the year and because the genus is both common in and has many species in North America. The capsules are cleistocarpous and therefore do not allow ready dispersal of their spores. Therefore in post-Pleistocene times when distances from the mainland were greater, the chances of long-range dispersal were less and the insular populations may have had time to speciate without the reintroduction of the parental stock. This process may have been accelerated by the short generation time of an ephemeral moss. *Limbella*, on the other hand is harder to explain. Ochyra (1986) placed the species in a new genus, *Sciaromiella*, along with a fossil species from the Soviet Pliocene. I cannot imagine such a placement. I think that in an aquatic genus such as *Limbella* it is a pleasant departure from the norm to have a distinctive species, but that is no reason to accord it generic status. To speculate on an origin for this Haitian endemic is difficult. *Limbella* is known from both North and South America, but it is not common in either. However, it seems more probable that the Antillean plant differentiated from the plant that is common in parts of the southeastern United States and which may have been distributed further south in earlier times than from a plant that is now common from the southern Andes to southernmost South America.

Although Hispaniola has an interesting, often xerically adapted North American element, it is the Andean South American element that makes the flora so exciting. It would be tempting to speculate that this large component of the flora could be derived by a vicariant event, if only the geological history were more cooperative. However, it appears that the Andes themselves were uplifted in the Late Pliocene (Hammen 1974), long after Hispaniola reached its present position. Also, even if the Andes had been present when the proto-Antilles were adjacent to South America, the highlands of

Hispaniola were not developed at that time. Similarly, the Andes-like habitats now present in Hispaniola would surely have been much drier in the Pleistocene and those mosses adapted to moist montane environments would not have survived there during that time. Therefore, the only reasonable explanation for the Andean element in the Antillean bryoflora is relatively recent long-distance dispersal. That is, an ecological rather than historical explanation (Endler 1982) seems preferable in this circumstance: once a moist, montane environment became available in Hispaniola, it was colonized by those mosses adapted to such a habitat that were able to make the journey there. This would also explain why the Andean element in not larger in an area that should be able to support it. Additional evidence supporting dispersal rather than vicariance is that several of the dioicous species in Hispaniola are only known by a single sex. This is easily explained by chance, long- distance dispersal. However, large populations separated by a vicariance event probably would have had both sexes. This same dispersal scenario explains the presence of the few, but distinctive Northern Hemisphere elements that are adapted to wetland conditions. These mosses, such as *Aulacomnium palustre* (Hedw.) Schwaegr. and *Calliergon trifarium* (Web. & Mohr) Kindb., are probably recent arrivals from the North whose spores happened to land in a favorable habitat. The Andean element, though, is much more extensive and indicates a more common, and effective, dispersal track. Since most major storms move from south to north in the Caribbean, it is not unexpected that southern elements are more common in the West Indies than northern ones. A fair number of Andean elements in the Caribbean also occur in the highlands of southeastern Brazil. One possible explanation for this is that at one time the floras of southeastern Brazil and the Andes were continguous but due to some climatically related vicariance event became separated. A few taxa, though, such as *Wijkia flagellifera* (Broth.) Crum, occur in southern Brazil and the Greater Antilles, but not in the Andes. It is possible that for some reason the taxa did not reach the Andes, or perhaps they did but became extinct there. In some cases, perhaps like that of *Wijkia*, the Andean populations differentiated into independent species, leaving an apparent anomalous disjunct between Brazil and the Antilles. The Andean element includes *Anacolia laevisphaera* (Tayl.) Flowers, *Andreaea brevipes* Spruce, *Aptychella proligera* (Broth.) Herz., *Bartramia angustifolia* Mitt., *Brachymenium fabronioides* (C. Muell.) Par., *Calyptrochaeta haitensis* (Crum & Steere) Crosby, *Chrysoblastella chilensis* (Mont.) Reim., *Didymodon laevigata* (Mitt.) Zander, *Eustichia longirostris* (Brid.) Brid., *Lepyrodon tomentosus* (Hook.) Mitt., *Mesonodon flavescens* (Hook.) Buck, *Neckera scabridens* C. Muell., *Plagiothecium conostegium* Herz., *P. lucidum* (Hook.f. & Wils.) Par., *Porotrichodendron superbum* (Tayl.) Broth., *Racomitrium crispulum* (Hook.f. & Wils.) Hook.f. & Wils., *Rhacocarpus purpurascens* (Brid.) Par., *Rhizogonium lindigii* (Hampe) Mitt., and *Thuidium pseudo-protensum* (C. Muell.) Mitt.

Conclusions

The Greater Antilles have a rich and diverse moss flora, reflecting a complicated geological and climatic history. However, the extreme length of time that has passed since the presumed vicariance event, during which time both dispersal and extinction have been active, has obscured the biogeographic history of the Greater Antilles (Mayer & Lazell 1988). It is even more obscured for mosses because of their ease of and adaptation for dispersal. Nevertheless, some generalized patterns seem to emerge. From the meager data supplied by mosses the hypothesis of

the geological history of Anderson & Schmidt (1983), where the proto-Antilles were appressed against northern South America, seems better than that supplied by Malfait & Dinkelman (1972), in which the proto-Antilles occupied the area of current southern Central America. The number of possibly vicariantly derived taxa, though, is very small indeed. Rather, because mosses are so intricately tied to their habitats and microenvironments, events in the Greater Antilles long after most tectonic events occurred seem to have had more influence on the modern floristic composition. It is postulated here that most of the northern elements of the flora are a result of Pleistocene climatic-related events in which savanna habitats dominated not only the Antilles, but also southern North America and most of the land between the two tropic lines. During this time many northern elements, particularly those with somewhat xeric adaptations, invaded the Antilles when water levels were lower (as much as 120 m lower) and land masses were closer together. When current climatic conditions began these northern elements were able to survive in high elevation habitats. One might reasonably expect many of the same taxa to have been stranded in similarly appropriate sites in Central America. The distinctive Andean element, however, can only have been derived by relatively modern dispersal since at the time of the postulated proto-Antillean vicariance event, the Andes themselves had not evolved, and a moist, montane environment was not present in the islands. Vicariance probably in geological times past had more of an impact on the bryoflora. However, many of the early colonizers of the Antilles, whatever their origin, surely became extinct with changing climates and geological events. Perhaps some of these vicariantly derived taxa are still present, but dispersal from continental areas by these same taxa has obscured any possibility of knowing how the original populations on the Antilles arrived. Although vicariance has indeed played a major role in the biogeography of all organisms, it seems as if the biota of the West Indies has primarily been influenced by dispersal, with vicariance having only a minor part. This is particularly true for mosses.

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