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Historical biogeography of Caribbean plants: introduction to current knowledge and possibilities from a phylogenetic perspective

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Knowledge of the evolution and biogeography of the Caribbean biota comes primarily from faunal studies, in spite of the tremendous richness of the Caribbean flora. The limited data to assess Caribbean phytogeography comes from fossils, floristic distributions, and phylogenetic studies. The geology in the Caribbean is extremely complex, but it is widely accepted that part of the Greater Antilles are old and precede the emergence of the Lesser Antilles and the Panamanian isthmus. Cuba and Hispaniola are each composed of a series of independent land blocks and Jamaica was mainly or entirely submerged during part of its history. Paleopalynological data, at present the only reliable source for reconstructing past plant communities, suggest warm-temperate to tropical conditions. Contemporary floristic data portray affinities with both Laurasian and Gondwanan derived plant groups. Shortcomings of traditional methodological approaches is a major criticism to studies assessing historical biogeography. Phylogenetics is an appropriate strategy to apply, because it: (1) elucidates the systematic relationships of taxa, (2) permits assessment of morphological and ecological evolution, and (3) illustrates the direction and sequence in which the distribution of a taxa originated. Study of Caribbean taxa with high levels of endemism allows tracing the correspondence between taxa and geographic areas, and thus, permits application of a phylogeny for assessments of geographic relatedness under both dispersal and vicariant scenarios. Caribbean plant groups in several angiosperm families have now been studied phylogenetically. Some biogeographic patterns are starting to emerge from these studies, but more studies are needed for generalizations to be drawn.

KEYWORDS: Antilles, biogeography, Caribbean, phylogeny, West Indies.

INTRODUCTION

For years, studies on the classification, evolution and geographic history of the Caribbean biota have ignited much interest, resulting in many studies addressing issues in a variety of contexts. Most of the works on biogeography of the region are predominantly on animal groups, and there is a marked deficiency in similar studies for plant groups. For instance, in the proceedings of a symposium (Morin, 1982) emphasizing the phytogeography of Central America, in which issues about the Caribbean islands were addressed, two of the most relevant contributions (Humphries, 1982; Savage, 1982) discussed only vertebrate groups. One of the authors (Humphries, 1982) acknowledged that the number of plant studies then available were very scarce, and because of the lack of phylogenies were unsuitable to apply in his cladistic methods.

A synthetic compilation on West Indian Biogeography (Woods, 1989) includes 32 works on paleontology, anthropology, ichthyology, entomology, ornithol-

ogy, herpetology, and conservation biology. In these proceedings, the editor emphasized that "...having reviewed much of the available data on West Indian biogeography, I have been struck by how few studies on plants and invertebrates there are in the overall body of data on West Indian biogeography compared with the information available on other groups" (Woods, 1989). Those "other groups" mentioned by Woods are primarily vertebrates, which at that time formed the predominant body of information for interpreting the biological history of the West Indies. In that symposium, only one of the 50 contributors (Adams, 1989) addressed ideas on the geographic origin and evolution of a plant group (*Juniperus*). A second contribution (Woods & Sergile, 2001) includes only one biogeographical study (Judd, 2001) of a Caribbean plant group (*Lyonia* sect. *Lyonia*). This disparity between knowledge on the evolution and biogeography of plants relative to animals is a prime indication that our ideas on the history of the Caribbean biota have been erected almost exclusively from faunal data.

Historically, zoological studies have dominated the scene of Caribbean evolution and biogeography. This is still the case today, where new contributions range over a diversity of vertebrate groups, including birds (e.g., Erard, 1991; Bermingham, 1994), mammals (e.g., Breuil & Masson, 1991), and especially reptiles (e.g., Savage, 1982; Hedges & al., 1991; Roughgarden, 1995; Hass, 1996; Seidel, 1996; Jackman & al., 1997), and amphibians (e.g., Bogart & Hedges, 1995; Hedges, 1999). Hedges (1996) reviewed the current knowledge on the historical biogeography of West Indian vertebrates. Zoogeographic studies of the region have diversified to include invertebrates (e.g., Liebherr, 1988; Schubart & al., 1998). Although these numerous zoogeographic contributions have made the Caribbean one of the most fertile regions for the study of biogeography, a comprehensive understanding of the evolution of the biota of the region can only be achieved by inclusion of other groups including plants.

Interest in applying phylogenetics to study the historical biogeography of Caribbean plants has increased in recent years, as evidenced by published works (e.g., Judd, 1981, 2001; Zona, 1990; Lavin & Luckow, 1993; Skee, 1993; Salzman & Judd, 1995; McDowell & Bremer, 1998) and a recent symposium (Fritsch & McDowell, 2003). In order to stimulate further interest among students and newcomers, we present in this work an outline on the present understanding of Caribbean phytogeography—with emphasis on the Greater Antilles. We provide general summaries on fossils, floristic data and with emphasis on case studies of Caribbean plant groups where a phylogenetic approach has been incorporated. We also discuss considerations for applying this approach to test hypotheses on evolutionary processes and biogeography in other plant groups of the region.

Several names are used to define different, but overlapping geographic regions mentioned in this review. Hence we define their use in this work for clarity. The terms “Greater Caribbean” or “Caribbean Basin” refer collectively to the islands and the neighboring continental regions along the Gulf of Mexico, Central America, and Northern South America. The main islands of the Caribbean belong to three different archipelagos: The Greater Antilles, the Lesser Antilles, and the Bahamas (Fig. 1). The Greater Antilles are composed of the four largest islands in the region: Cuba, Hispaniola, Jamaica, and Puerto Rico. The Lesser Antilles is separated from the Greater Antilles by the Anegada Passage, and comprise the arc of smaller islands extending from Sombbrero in the north, to Grenada. Collectively, the three archipelagos are referred to as the Caribbean Islands or the West Indies. This paper covers issues relevant to the entire Caribbean with emphasis on the island systems.

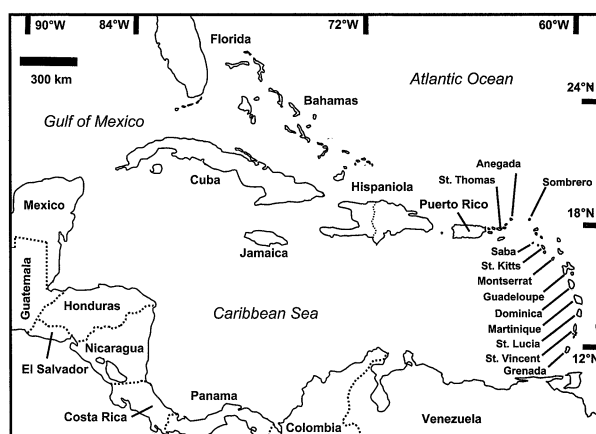


Fig. 1. Map of the Caribbean region.

PLANT DIVERSITY IN THE CARIBBEAN

The Caribbean is the oldest Neotropical region studied by western science. The first observations on plant diversity are documented in Columbus’ diary and other chroniclers of the 15th and 16th centuries, with plant descriptions predating Linneaus’ *Species Plantarum* of 1753. The long plant collecting history has resulted in numerous new taxa as well as published Floras, including among the most recent ones for Cuba (León, 1946; León & Alain, 1951–1957; Alain, 1963; Liogier, 1974), Hispaniola (Liogier, 1982–1996), Jamaica (Adams, 1972), Puerto Rico and the Virgin Islands (Acevedo-Rodriguez, 1996; Liogier & Martorell, 1982), the Cayman Islands (Proctor, 1984), the Bahamas (Correll & Correll, 1982), and the Lesser Antilles (Howard, 1974–1989). Ongoing botanical explorations keep refining present knowledge with the publication of florulas and checklists, the report of new records, and the description of new species.

Plant diversity is so remarkable in the Caribbean islands, that the region is considered a distinctive phytogeographic unit within the Neotropics (Gentry, 1982). The vascular plant flora of the region consists of approximately 12,000 species, including the southern tip of Florida (Myers & al., 2000, Table 1), in about 200 families. Over fifty percent of the vascular species are endemic to the region. These endemics represent about 2% of all vascular plants on Earth, placing the Caribbean as one of the leading hotspots in terms of species-level endemism (Myers & al., 2000). Endemicity is also present at the generic level in the Greater Antilles. Both generic and species-level endemism are particularly prominent in the two larger islands of Cuba and Hispaniola (Gentry, 1982). Cuba, the largest island in the Caribbean, has the richest flora and highest proportion of endemism (Table 2). About half of its approximately

Table 1. Diversity of vascular floras in selected large islands and archipelagos. Estimates are based on WWF & IUCN, 1994, 1995, 1997, and Myers & al., 2000.

Region	Land area (km ²)	Max. elevation (m)	Families	Genera	Endemic genera	Species	Endemic species	% Species endemism
Madagascar	594,150	2,876	160–181	>1289	260?	12,000	9,704	80.9
New Caledonia	18,600	1,628	191	863	110	3,332	2,551	76.5
Caribbean Is. (incl. S-Florida)	263,500	3,087	186	2500	c. 100	12,000	7,000	58.3
Borneo	738,864	4,101	–	–	61	~25,000	~7,000	~28
Philippines	300,800	2,954	–	–	23	8,931	3,500	39.1
Japan	376,520	3,776	229	–	17	5,565	>222	~4
Sumatra	427,610	3,805	–	–	13	>10,000	>1,200	~12

6,000 species of flowering plants and approximately 70 genera are unique to the island. Hispaniola, the second largest island, contains over 4,500 flowering plants, almost a third of which are endemic (T. Zanoni, pers. comm.) and about 30 endemic genera. Diversity in the smaller Jamaica and Puerto Rico is less, and endemism is primarily at the species level. The Jamaican flowering plants total over 2,500 species with about 30% endemism, whereas not more than 10% of Puerto Rico's approximately 2,000 native flowering plants are endemic.

The relatively high plant diversity observed in the Caribbean is explained in part by proximity to the continental Neotropics to the south (South America), west (Mesoamerica), and north (Florida). In addition, the wide range of altitudes, the contrasting rainfall and temperature regimes, and the diverse geology have resulted in striking habitat mosaics even within the same island, permitting the occurrence of plants species with very different ecological requirements and tolerances. Many Antillean taxa are endemic to serpentine rocks. Such substrates in the Greater Antilles, particularly the ones in Cuba and Puerto Rico (Cedeño-Maldonado & Breckon, 1996), are regarded as among the most important of tropical America (Brooks, 1987). In Cuba, 13.5% of the endemic species (Berazain-Iturralde, 1976, 1981) and 34.3% of the endemic genera are confined to serpentine

(Brooks, 1987). Antiquity of portions of the Greater Antilles (of approximately 70 to 100 my, Donovan & Jackson, 1994) could also be a factor to explain endemism in the area.

Comparisons between the Caribbean and other areas. — Numerically, the approximately 12,000 vascular plants present in the Caribbean are comparable to other important centers of plant diversity, such as Madagascar and New Caledonia (Table 1). The Caribbean has roughly the same number of species known today for Madagascar, and has more than three times the number of species of New Caledonia. Furthermore, generic and species diversity in the region is also higher than in other oceanic archipelagos (Table 3), although the latter have considerably less land area when compared to the Caribbean. Species endemism in the region is higher than in Central America; ~50% versus ~20%, respectively (Gentry, 1982; Myers & al., 2000). It is also higher than in other islands (Table 1), such as the Philippines (39%), Borneo (30%), Sumatra (12%), Java (5%), and Japan (4%). The total number of endemics in the Caribbean islands is several times greater than in the Hawaiian Islands, although the latter hold a higher proportion of endemics per unit area (Table 3). Similarly, it comprises ten times the endemic species than in the Canary Islands, more than twenty times what

Table 2. Phanerogamic diversity and endemism in the Caribbean Islands. Estimates are based on WWF and IUCN (1994, 1995, 1997), Myers & al. (2000), and P. Acevedo (pers. comm.).

Archipelago	Land area (km ²)	Number of species	Number of endemic species (%)	Number of endemic genera
Greater Antilles				
Cuba	110,848	6,015	3,193 (53)	c.70
Hispaniola	76,190	~4,685	~1,400 (30)	c.30
Jamaica	10,830	2,746	852 (31)	7
Puerto Rico	9,308	2,128	215 (10)	1
Lesser Antilles*	6,466	~2,300	~290 (3)	0
Bahamas	10,010	1,068	117 (11)	0

* = Does not include the offshore islands north of South America.

is reported for the Galápagos, and over fifty times that of the Juan Fernández Islands. At the generic level, the Caribbean comprises about the same number of endemic genera found in Central America and roughly the same amount in New Caledonia (Table 1). Endemic genera in the region surpass the total found in Borneo (61), the Philippines (23), Japan (17), Sumatra (13), and Java (5). Furthermore, Caribbean-endemic genera triple the amount found in Hawaii, and are nine to ten times the amount for the Galápagos, the Juan Fernández, and Fiji (Table 3).

■ GEOLOGIC HISTORY OF THE CARIBBEAN

Although there are still diverse interpretations on key aspects of Caribbean geologic history, we present basic geologic information that will allow readers unfamiliar with this area to formulate an outline on the subject. A review including the historical development of geohistorical models for the Caribbean is out of the scope of the present work. For this purpose, we recommend Hedges (1996), Iturralde-Vinent and MacPhee (1999), and Graham (2003). The geologic history of the Caribbean is extremely complex, and basic issues, such as which areas were above sea level during the history of the islands (Hedges, 1996), remain unresolved.

The Greater Antilles and the younger Lesser Antilles are part of the Caribbean Plate, which originated from a portion of the East Pacific plate during the Jurassic-Cretaceous (Pindell, 1994). The North and South American separation from Laurasia and Gondwana, respectively, involved a westward movement towards the Pacific, which resulted in the intrusion of part of the East Pacific Plate in the area between both continents. This intrusion eventually fractured and formed the smaller Caribbean Plate. Some authors (e.g., Malfait & Dinkelman, 1972; Sykes & al., 1982; Pindell & Barrett, 1990) consider that portions of what would form the Greater Antilles, termed Proto-Greater Antilles, arose

during the Cretaceous as an arc of volcanic islands created from subduction of oceanic lithosphere located between North and South American continental plates (Ladd, 1976; Coney, 1982). Early in the Tertiary, compression of the westward-moving North and South American plates resulted in a relative eastward movement of the Caribbean plate and thus, drift of the Proto-Greater Antilles (Rosen, 1976, 1985). During that time, some portions of the Greater Antilles reached their present-day positions (Coney, 1982; Pindell & Dewey, 1982; Sykes & al., 1982) as the result of the collision of the northeastern boundary of the Caribbean plate with the Bahamas platform, which is fixed to the North American Plate. This collision caused subduction and volcanism in the Proto-Greater Antillean area, although orogeny from folding, faulting, and local uplift continued (Lewis & Draper, 1990). Subsequently, a major fault was formed to the south of Cuba, along with the small spreading center (the Cayman Trough) that could have influenced the eastward drift of Southwestern Hispaniola and Jamaica. Today, the Caribbean Plate is still moving eastwards with respect to North and South America, with volcanic activity along the eastern and western margins of the plates in the Lesser Antilles and Central America, respectively.

Historical relationships and composition of the land masses of the Greater Antilles is still very incomplete, but it is widely accepted that Cuba and Hispaniola are each formed by composite regions comprising no less than three land blocks (Pindell & Dewey, 1982; Sykes & al., 1982), each of which could have been unrelated to one another. The western and eastern portions of Cuba for instance, exhibit marked geological differences (Draper & Barros, 1994); the geology of the western portion is considered unique in the Antilles (Draper & Barros, 1994), probably due to its relationship with the North American Plate (Graham & al., 2000). On the other hand, Eastern Cuba, North-Central Hispaniola, and Puerto Rico were probably connected as a single magmatic arc during the Paleocene-Eocene (Draper & Barros, 1994) and until the Oligocene (Iturralde-Vinent, 1994) or Early Miocene (Sykes & al., 1982; Perfit &

Table 3. Diversity of vascular floras in selected island systems. Estimates are based on WWF and IUCN (1994, 1995, 1997), Marticorena & al. (1998), and Myers & al. (2000), excluding introduced taxa.

Region	Families	Genera	Endemic genera	Species	Endemic species
Caribbean Islands	186	2,500	c. 100	12,000	7,000
Fiji	210	1,013	12	1,628	812
Madeira-Salvagens	134	–	1	1,226	123
Hawaii	87	216	32	1,200	1000
Canary	–	–	20	1,200	500
Galápagos	90	292	7	541	224
Azores	–	–	1	300	81
Juan Fernández	57	107	12	211	127

Williams, 1989; Pindell & Barrett, 1990). Coalescence of eastern and western/central portions of Cuba may have occurred in the Late Tertiary or Early Quaternary (Draper & Barros, 1994; Iturralde-Vinent & MacPhee, 1999).

Hispaniola is composed of four different land blocks according to Sykes & al. (1982). During the Eocene the north and central portions of Hispaniola fused and had close relationships with eastern Cuba, a connection that remained until Early to Middle Miocene (Graham, 2003). This long land relationship is invoked by Graham (2003) as a plausible reason to explain the high number of Cuban-Hispaniola endemic plant genera. Both southwestern Hispaniola and Jamaica were considerably isolated from the rest of the Proto-Greater Antilles until the opening of the Cayman trench, and posterior seafloor spreading (Perfit & Heezen, 1978) moved them in a northeast direction, until southern Hispaniola collided with the rest of that island, probably early in the Miocene (Pindell & Barrett, 1990; Huebeck & Mann, 1991) or Pliocene (Sykes & al., 1982). During drift to its present-day position, most or all of Jamaica became submerged between Late Eocene to part of the Miocene, followed by uplift in the Late Miocene (Draper & Lewis, 1990; Robinson, 1994). Evidence of this mid-Tertiary inundation is the extensive karst topography and exposed limestone on much of the island. The most recent addition to Hispaniola comes via accretion of crustal terrane from the Bahaman Bank.

Puerto Rico and the Virgin Islands experienced considerable eustatic changes, although uplifts have apparently persisted in the Puerto Rican Bank since late Cretaceous (Lewis & Draper, 1990; Larue, 1994) or Middle-Late Eocene. The island reached its current position during Late Eocene to Early Oligocene, and separated from Hispaniola in Oligocene or Miocene (Graham, 2003). Later, during the Quaternary, sea level changes due to glacial-interglacial oscillations resulted in considerable modification of the outline and land extension in the Puerto Rican Bank. These changes are responsible for the separation of Puerto Rico from the Virgin Islands and Anegada.

The Lesser Antilles are considered as a classic island arc of volcanic islands emerging from above a subduction zone (Wadge, 1994). They originated independently from the Greater Antilles, due to the subduction of the Atlantic plate under the Eastern Caribbean Plate. The volcanic activity that formed the Lesser Antilles started at the end of volcanism in the Greater Antilles and persists today.

In an attempt to bring together geological knowledge and geographic scenarios of biological importance, a recent contribution by Iturralde-Vinent and MacPhee (1999) presents a detailed paleogeographical and paleoceanic reconstruction for the Caribbean Basin. They

consider that the Greater Antillean land blocks that existed previous to the Eocene very likely did not remain continuously as subaerial land masses due to geologic activity and to catastrophic events resulting from the K/T bolide impact (Hildebrand & Boynton, 1990). Thus, such areas must have limited or no relevance for the biogeographic assessment of the current Greater Antillean biota. Based on geological constitution, geographical position, and physical paleogeography, Iturralde-Vinent & MacPhee (1999) infer that the current Greater Antilles—or at least portions of them—are no older than Middle Eocene. Later, during the Eocene-Oligocene transition, the northern Greater Antilles and Northwestern South America were connected by a landspan that involved the Aves Ridge (“GAARlandia”, the Greater Antilles + the Aves Ridge). The Eocene-Oligocene transition was a period of general uplift in this landspan, followed by high sea levels (and presumably less connections between island areas) during Late Oligocene. During Early to Middle Miocene, tectonic activity promoted further subdivisions of Greater Antillean land blocks, an event of potential biogeographic relevance.

FOSSILS AND PALEOVEGETATION

Availability of fossil evidence. — Plant fossil data from the Caribbean are scanty; several factors make the reconstruction of paleoenvironments a very difficult task (Graham, 1989a). In a review of the status of Tertiary paleobotanical studies in Northern Latin America (comprised of Mexico, Central America, and the Antilles), Graham (1993) reported 59 studies specific to paleobotany and paleopalynology in the Antilles, but only 16 of them include lists of identified plant fossils. Of these, several works are marred by imprecise identification of the megafossils and are inconsistent with other more recent evidence derived from fossil mammalian and marine invertebrate fauna, ^{18}O isotope studies, and plate tectonics (Graham, 1988). Graham (1993) recommended their exclusion from any paleoenvironmental interpretation until the material is restudied or until new megafossils are available. Palynological data are at present the most reliable basis for reconstructing Tertiary communities in the Caribbean and Northern Latin America (Graham, 1988, 1993, Graham & al., 2000).

The Antillean paleocommunities. — In general, Graham argues that most of the currently-known Tertiary plant fossils of the Antilles are warm-temperate to tropical with affinities to North America (including Mexico) (Graham, 1990a, 1990b, Graham & al., 2000). The Mid-Eocene Chapleton deposit of Jamaica (Graham, 1993) and the approximately contemporary Sarama-

guacán flora of east-central Cuba (Graham & al., 2000) are the oldest plant microfossil sites described for the region (Graham, 1993). The age of the Jamaican deposit is supported by independent stratigraphic and paleontological evidence (Robinson, 1988). The nature of the sediment deposition, the presence of dinoflagellates mixed with the pollen and spores, and the presence of the pollen of *Pelliciera*, and cf. *Acrosticum* suggests that the depositional environment at Chapelton was a warm-temperate (tropical) coastal one (Graham, 1993). The sediments and fossil remains in the Saramaguacán flora indicate that it was a freshwater swamp or marsh community with warm-temperate to tropical elements. Graham & al. (2000) recognized 46 palynomorphs, including 16 with North American affinity, 11 endemics (unique to that palynoflora), and only one of South American origin. The rest were widespread taxa. Comparisons with other contemporary fossil floras from the Antilles (e.g., Chapelton) and Central America are not feasible due to the small size of those floras. However, this flora and ones from NE Mexico and Panama are more similar than any of them are to any contemporary South American fossil floras. This is consistent with the hypothesis that West and Central Cuba are of North American continental plate origin (Graham & al., 2000).

The Mid-Oligocene San Sebastián deposits in Puerto Rico (45 million years old) comprise a diversity of habitats including coastal, brackish-water swamps, upland tropical and subtropical forests, and an arboreal cool-temperate forest (Graham & Jarzen, 1969). The majority (75%) of the identified microflora consisted of genera that presently grow in Puerto Rico or the Antilles, suggesting that the climate in the region was not dramatically different from that of today and that evolution of some of these taxa might have occurred “in situ”. However, several northern cool-temperate genera that are not extant in Puerto Rico were found: *Engelhardia*, *Fagus*, *Liquidambar*, and *Nyssa*. Based on similarity of the fossils and the present tropical vegetation, and assuming that the Oligocene climate was comparable to that of today, it can be inferred that a greater physiographic relief must have existed in Puerto Rico to provide suitable conditions for the temperate genera and the tropical communities at the same time (Graham & Jarzen, 1969). In addition, the authors interpret pathways of migration in the region. They found that all 14 genera from the San Sebastián flora that are not in the Antilles today are presently distributed throughout Mexico, Central America, and South America, an indication that, although San Sebastián contains elements present today in the temperate Eastern United States, it has stronger floristic affinities with Mexico, Central America, and Northern South America.

Work on the Late Miocene-Middle Pliocene

Artibonite pollen from Haiti (Graham, 1990a, b) is the first Tertiary paleopalynological study of Hispaniola. The most common microfossils at Artibonite are fern spores of at least three families, but also included *Pinus* and palms, among others. Two genera represented in the deposits, *Alfaroa* and *Oreomunnea*, do not occur today in Haiti, but are elements of the cloud forests of Mexico and Central America. Graham (1990a) estimates that highest elevations during the Late Miocene-Middle Pliocene in Artibonite could have been about 1,400 m (the highest point today, Morne de la Selle, is 2,900 m). Furthermore, pollen of Asteraceae, Chenopodiaceae, and Amaranthaceae suggest local openings in the vegetation, but there is no evidence of dry forests. The latter, as well as savannas, are thought to have developed later in the Pliocene and during the Quaternary (Leyden, 1984).

Insights from Tertiary Paleocommunities in Central America and Southern Mexico. — The Greater Antilles is part of a paleogeographic province that also includes southern Mexico and Central America (Graham, 1993). Consequently, and given the lack of fossil sites in the Antilles, our interpretation of the vegetational history of the islands during most of the Tertiary could be facilitated by analyzing available evidence from the Gulf-Caribbean deposits of Mexico and Central America. The vegetational history of these deposits is congruent with other independent studies of paleotemperature patterns and paleofauna (Graham, 1988).

In general, regional cooling since the Miocene along with Quaternary climate fluctuations have been the main factors shaping the plant communities in southern Mexico, which has always had a continuous land connection to the North. Prior to the Miocene temperature drop, warm tropical conditions predominated in southern Mexico, as suggested by the elements present in the deposits (Graham, 1999a). On the other hand, regional climatic cooling has apparently played a lesser role in defining the principal plant communities of Central America (Graham, 1996). The vegetation of proto-Central America remained predominantly tropical throughout the Eocene-Miocene until the Pliocene, and very similar to that of today’s low-lying regions (Graham, 1989b, 1990b, 1996). None of the earlier Central American paleofloras suggest elevations that support high altitude and páramo vegetation, and thus there was not a continuous habitat that would have allowed interchange of temperate elements between North and South America (Graham, 1990b, 2003; Burnham & Graham, 1999). Also, the surrounding ocean waters of the low-relief, insular proto-Central America, could have buffered the effects of global cooling (Graham, 1989a). The increased diversity of the habitats and elevations of present-day Central America resulted primarily from recent volcanism and uplift associated

with plate movements and Quaternary climate fluctuations (Graham, 1996, 2003; Burnham & Graham, 1999). One of the most remarkable events in the Central American Pliocene was the connection of North and South America, about 3 to 3.5 million years ago (Graham, 1996). It is believed that dry forest originated as the result of this land connection and the recently formed higher mountain ranges, factors that deflected the northeast winds and produced marked differences in the rainfall regime seen today between the wetter Atlantic slope and the dryer Pacific slope (Graham, 1989c, 1990b; Graham & Dilcher, 1995). Following formation of the isthmus of Panama, plant migration proceeded in both directions affecting the floras of northern South America and Central America. Fossil studies (reviewed in Burnham & Graham, 1999; Graham, 1999b, 2003) indicate that North American elements primarily invaded high elevation temperate zones in South America, whereas as much as 75% of the rainforest canopy trees in southern Mexico may be of South American origin (Wendt, 1993).

■ PHYTOGEOGRAPHIC PATTERNS SUGGESTED BY FLORISTIC DATA

Early notions of floristic affinities of Caribbean plants can be attributed to the authors of the first detailed floras for the region, whose comments revolved primarily around the island each one was studying (e.g., Urban, 1923; Eggers, 1879; Alain, 1958). Initial observations led to distinguish distributions in the Caribbean flora as being primarily Greater Antillean or Lesser Antillean. The Greater Antillean flora was considered to be older and to have North, South, and especially Central American affinities (Asprey & Robbins, 1953; Alain, 1958). Within the Greater Antilles, affinities between Hispaniola and Cuba were considered stronger than those of Hispaniola with Jamaica (Woodson, 1940). Affinities were also observed between Puerto Rico and Hispaniola. Most of the relationships in the region were explained by land bridges between Honduras and the Greater Antilles (Schuchert, 1935; Asprey & Robbins, 1953), and by Cuban land connections with Yucatan and Florida (Alain, 1958). Dispersal by sea and wind currents, and by birds and bats, was suggested to explain more recent migrations (Alain, 1958), or those for which land bridges did not fit interpretation of current distributions (Beard, 1949; Asprey & Robbins, 1953). The unique distributions and the unexplained absence of certain taxa in Jamaica led to the development of a combined argument involving the existence of an old land bridge with Central America and more recent dispersal events after the re-emergence of the island (Asprey &

Robbins, 1953). In contrast, dispersal, and not land bridges, was the undisputed interpretation for the origin of the vegetation of the Lesser Antilles. The advent of plate tectonics (Hess, 1962; Tuzo-Wilson, 1965; Morgan, 1968; Cox, 1973; Bird & Isacks, 1980) was a major revolution that led to the rejection of land bridges (Williams, 1989), and to the establishment of a different vicariant scenario.

In a study describing the vegetation of the Antilles, Howard (1973) provides a summary of generic affinities between that region and continental America by tabulating distribution data in several combinations of islands and continental regions. Based on the total number of genera sharing a similar range, he defined five main patterns or "units". The first, the Pan-Caribbean unit, are those genera occurring across the Greater and the Lesser Antilles, Mexico, Central America, and Northern South America. The second, the Western Continental unit, comprises genera in Central America, Northern South America, and the Greater Antilles. That is, genera that are absent from Lesser Antilles. This second unit is further subdivided by whether the genera are exclusive to the Greater Antilles and Central America or to the Greater Antilles and South America. The second unit also separates genera whose distribution exclude Jamaica or Puerto Rico. The third, or Southern Continental unit, includes genera distributed in Central America, Northern South America, and the Lesser Antilles, but missing from the Greater Antilles. The fourth, or Antillean unit, groups genera restricted to or better developed in the Greater Antilles. The fifth, or Greater Antillean unit, is formed of genera endemic to one or more islands in the Greater Antilles, which could be considered a subset of unit four, the Antillean unit. Geographic affinities in this work are descriptive in nature, and although some of the units are reminiscent of León Croizat's idea of mapping independent ranges that coincide to define "tracks" (Croizat, 1952, 1958), no interpretation of such units is given (Howard, 1973). Furthermore, the work also addresses the presence of long distance disjuncts in the Antilles based on the works by Good (1964), but besides stating that this region shares genera with Africa, Madagascar, and Asia, there is no inference to explain how these disjuncts arose.

Phytogeographical patterns of the Caribbean were revisited as part of a larger scale assessment of Neotropical floristic diversity, using distributional data on available regional floras, published monographs, herbarium specimens, and fossils (Gentry, 1982). Gentry also considered the following geological and climatic forces as relevant to his interpretations: the emergence of the Proto-Greater Antilles between North and South America (Late Cretaceous-Early Tertiary), the more recent Central American isthmian connection (Pliocene),

the uplift of the Northern Andes (Pliocene-Pleistocene), and the Quaternary climatic fluctuations (Pleistocene) (Gentry, 1982).

The Neotropical flora presents two major dichotomies. The first distinguishes Laurasian-derived from Gondwanan-derived taxa (Gentry, 1982). In most of the Neotropics, Laurasian-derived taxa, if present, are primarily montane, higher altitude plant groups of herbs and sometimes canopy trees mixed within the Gondwanan elements. Some examples in the Caribbean include Magnoliaceae, Pinaceae, Aquifoliaceae, Cyrillaceae, Rosaceae, and Ranunculaceae. They are not very species-rich, a fact interpreted by Gentry as evidence of their recent (Late Tertiary-Quaternary) arrival. On the other hand, Gentry points out that in the Caribbean islands some old Laurasian-derived groups have thrived and diversified well in lowland dry areas including members of Aristolochiaceae, Vitaceae, Rhamnaceae, Boraginaceae, and Buxaceae. In general, taxa of Laurasian derivation are better represented in the Caribbean than in other parts of the Neotropics and thus the Laurasian-Gondwanan dichotomy is more pronounced in the islands than in other Neotropical regions (Gentry, 1982). Some of the northern taxa of the dry lowlands may be considered reminiscent of the endemic tropical Laurasian families and could have been some of the stocks that during the Late Cretaceous-Early Tertiary reached the Proto-Greater Antilles, an idea inferred by other authors (e.g., Graham, 1990b; Lavin, 1993).

Gentry's second dichotomy is the subdivision of the Gondwanan group into Neotropical Amazonian-centered and extra-Amazonian ("Andean-Centered") subgroups. The Amazonian-centered subgroups include most of the Neotropical lowland canopy trees and lianas, and generally have few species per genus. On the other hand, taxa predominantly epiphytic or shrubby have their distribution centers in low and mid-elevations of the Andes. Many exhibit explosive radiation, including Bromeliaceae, Gesneriaceae, Piperaceae, Orchidaceae, Melastomataceae, Acanthaceae, Myrsinaceae, Rubiaceae, and Solanaceae (Gentry, 1982). Both Gondwanan groups are common forest components of the Caribbean islands.

STUDIES APPLYING PHYLOGENETICS TO BIOGEOGRAPHICAL INTERPRETATIONS OF CARIBBEAN PLANTS

In recent years, a growing number of plant systematists and biogeographers have applied phylogenetic information to test hypotheses of evolutionary relationship and historical biogeography. Analytical approaches to biogeography are varied, depending upon the ques-

tions involved (Page & Lydeard, 1994; Morrone & Crisci, 1995). We believe, however, that phylogenetic analysis provides the most objective approach to assess the historical biogeography of a given taxon. A phylogeny provides a direction and a sequence to the reconstruction of geographic distributions whether dispersal, vicariance or a mix is inferred.

Few studies on Caribbean plant groups have incorporated phylogenetic reconstructions. Consequently, even answers to basic questions on evolutionary relationships, systematic placement, morphological or ecological evolution are lacking for most taxa in the region. Here we present outlines of studies on Caribbean plants in which a phylogenetic approach, most using molecular data, has been incorporated into biogeographic assessments. Various methods of tree construction and biogeographic inference were used. It is not our intent to reanalyze these data, but rather to look for common patterns.

***Lyonia* (Ericaceae).** — One of the pioneering studies applying phylogenetics to the biogeography of Caribbean plants was that for the genus *Lyonia* section *Lyonia* (Judd, 1981, 1995, 2001). The genus, with members in Eastern Asia and Eastern North America, comprises a monophyletic group (Judd, 2001) of approximately 25 species in the Greater Antilles. Many of the Greater Antillean *Lyonia* are narrow endemics that occur in a variety of environments, including low-elevation thickets, savannas, and moist montane and cloud forests. Within-island isolation is in many cases due to edaphic conditions, as well as by altitudinal differences (Judd, 2001). The major centers of diversity of *Lyonia* in the Antilles are the Cordillera Central, and the Massif de la Selle-Sierra de Bahoruco, both in Hispaniola, and the mountains of Eastern Cuba (Judd, 1981).

Phylogenetic reconstructions using morphological characters were analyzed by with a Wagner-Groundplan-Divergence Analysis (Judd, 1981) and later reassessed using heuristic and branch-and-bound algorithms (Judd, 1995, 2001). A strict consensus tree based on this latter reassessment (Fig. 2) illustrates that all Antillean members of *Lyonia* sect. *Lyonia* (except the Jamaican *L. jamaicensis*, see below) belong in two major clades. The "Hispaniolan clade", is formed by taxa occurring in Hispaniola, Puerto Rico, and St. Thomas (Virgin Islands). The second clade or "Cuban clade" includes all the Cuban taxa, as well as *Lyonia octandra*, from Jamaica. Within the Cuban clade all but one of the taxa from Cuba group together. In this phylogenetic reconstruction, the lineage of the Jamaican taxon *L. jamaicensis* comes out unresolved and outside of the Hispaniolan and Cuban clade.

An area cladogram resulting from a Brooks Parsimony Analysis for the Antillean *Lyonia* (Judd, 2001) was in agreement with geographic relationships

suggested by the species phylogeny. This was not surprising, because species of *Lyonia* growing on each island (especially in the case of Cuba and Hispaniola) came out in the phylogeny as closely related to species from the same island. In the area cladogram, taxa from the Cordillera Central and Massif de la Selle (Hispaniola) formed a clade with a taxon distributed in Puerto Rico and the Virgin Islands, and taxa of the northern Oriente region (Cuba) form a clade with other Cuban taxa and one Jamaican species. The derived taxa in both islands exhibit adaptations to extreme habitats (Judd, 2001).

Results of this study were also evaluated, in light of Rosen's (1976, 1985) vicariant model to explain the origin of the biota of the Greater Antilles and the geologic history of the Antilles (Judd, 2001). A close relationship is seen between Eastern Cuba, North-Central Hispaniola and Puerto Rico, as well as between Western Cuba and Southwestern Hispaniola. Results of this study are in agreement with the close relationship between Eastern Cuba, North-Central Hispaniola, and Puerto Rico. Thus, this suggests the possibility of a vicariant scenario in some lineages of *Lyonia*. However, Western Cuba comes out as closely related to Eastern Cuba and Southwestern

Hispaniola as closer to Central Hispaniola. An interpretation of this disagreement with Rosen's vicariant model is that *Lyonia* was originally restricted to Eastern Cuba and North-Central Hispaniola, and that these areas provided the source of more recent lineages in Western Cuba and Southwestern Hispaniola, respectively (Judd, 2001). This could have occurred as the result of within-island dispersal events. One argument to provide support for the antiquity of Eastern Cuba and Southwestern Hispaniola is that *Lyonia* is most diverse in those areas. The Jamaican species are also considered to be the result of dispersal. That most species of *Lyonia* occur in limited ranges and species in the same island are closely related indicates that successful long-distance dispersal (at least between islands) is not very common. The eastward (i.e., Cuba to Virgin Islands) decrease in *Lyonia* diversity (the "Western continental distribution pattern" described by Howard in 1973) and the absence of the genus in the Lesser Antilles suggests that taxa arrived in the islands from Mexico/Eastern North America (Judd, 2001).

***Sabal* (Arecaceae: Coriophioideae).** — A monograph of *Sabal* includes a phylogenetic analysis based on morphology, leaf anatomy, and flavonoid phytochemistry (Zona, 1990). This work recognizes 15 species dis-

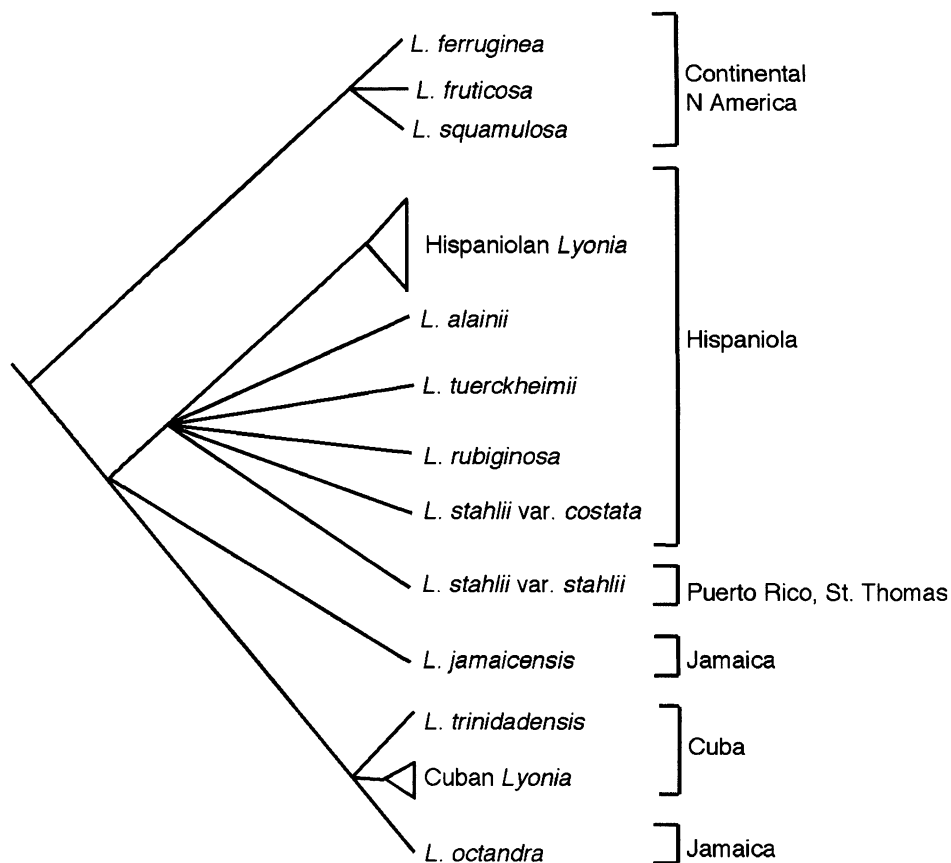


Fig. 2. Strict consensus tree of selected species of *Lyonia* sect. *Lyonia* based on morphological characters (adapted from Judd, 1995, 2001).

tributed throughout the southern United States (four species, three endemic), Mexico and northern Central America (six species, five endemic), Cuba (three species, none endemic), Jamaica (one species, none endemic), Hispaniola (two species, one endemic), Puerto Rico (one species, none endemic), and Bermuda (one species, endemic). One species (*Sabal mauritiiformis*) shows a notably patchy distribution, occurring in Guatemala, Belize, southeastern Costa Rica, eastern Panama, and scattered along northern South America.

The cladistic analysis of Zona (1990) identified five major lineages (Fig. 3). Using the Mexican palms *Washingtonia filifera* and *Brahea dulcis* as outgroups, the resulting tree shows the most basal clades with species endemic to (or mainly with) a U.S. distribution. The western Mexican species form a clade that is sister to the southern Mexican species and the Antillean-endemic species, which in turn form clades that are sister to each other. One species each from the SE US and Mexican clades also occurs in Cuba. The presence of tannins within the bundle sheath surrounding the vascular

bundles is a synapomorphic trait for the Antillean-endemic clade (Zona, 1990).

Based on the patterns of phylogenetic relationships and distributional data, Zona hypothesized origin of *Sabal* in North America, with the Antillean-endemic species being derived from Mexican lineages rather than from those in the Southern United States. The presence of a species of *Sabal* in Bermuda and the apparent origins of Greater Antillean taxa from three areas outside the Antilles, together with evidence of zoochory (Zona & Henderson, 1989) and hydrochory (in at least some species in the genus), points towards over-water dispersal as a plausible mechanism to explain the distributions of this palm genus in the Caribbean (Zona, 1990). The phylogeny of Asmussen & al. (2000) indicates that a clade of five genera (*Chelyocarpus*, *Coccothrinax*, *Crysophila*, *Thrinax*, and *Trithrinax*) are sister to *Sabal*, with *Washingtonia* and *Brahea* more distantly related. The inferred ancestry of this sister clade is South American. It is uncertain whether this would alter the inference of a North American origin for extant *Sabal*



Fig. 3. Phylogeny of *Sabal* and related genera (adapted from Zona, 1990, and Asmussen & al., 2000).

species, but it is unlikely to alter the inference of a Mexican origin for Antillean species.

Mecranium (Melastomataceae). — A monographic study on the Antillean-endemic genus *Mecranium* included a very detailed assessment of morphology, as well as anatomical, phenological, and cytological data (Skean, 1993). *Mecranium* is most species-rich in Hispaniola, with 16 species, 14 of which are endemic. The southwestern portion of Hispaniola (the “south island” of Skean) contains most of the diversity in this genus. Of the 13 species occurring there, 10 are endemic to that portion of the island, and seven of those are unique to the Massif de la Hotte of Haiti (Skean, 1993). Northern Hispaniola contains only five species, two of which are endemic to the region. The other species in the genus are in Cuba (five species, three endemic), Jamaica (three endemic species), and Puerto Rico (one endemic species).

Using cladistic analysis, Skean divided the genus into two sections: sect. *Sagreoides* with two Hispaniolan endemic species, and sect. *Mecranium* with the remaining species (Fig. 4). The presence of a calyptra is a synapomorphy for the large section *Mecranium*. The latter clade presents a basal trichotomy. One of the lineages consists of a single Cuban species. A second lineage consists of a trichotomy that includes two southwestern Hispaniola and one Jamaican species. The third clade contains Cuban and Hispaniolan species, plus a polytomy with taxa from the four islands (the *Mecranium multiflorum* complex, Skean, 1993). Despite these three polytomies, the phylogeny demonstrates that none of the species occupying islands form monophyletic groups, except the trivial case of the sole species in Puerto Rico.

Skean proposes that the current distribution of *Mecranium* has resulted from tectonic events, dispersal by birds, and climatic changes. The striking level of endemism in southwestern Hispaniola suggests that isolation there must have been of much greater extent than the 20 km-wide Cul de Sac-Enriquillo plain that today separates this region from Northern Hispaniola. This is consistent with the geological hypothesis of the independent, insular nature of southwestern Hispaniola. Because Hispaniola is the center of diversity for *Mecranium* (Skean, 1993), the author suggested that the ancestral stock that gave rise to the genus might have first occurred and radiated in insular southwestern Hispaniola, followed by dispersal to northern portions of Hispaniola, Puerto Rico, Cuba, and finally Jamaica. This hypothesis is consistent with the phylogeny, but the sequential order of some of these island colonizations cannot be assessed with the present cladogram due to lack of resolution, especially in the *M. multiflorum* complex, which comprises 11 species, representing all four islands (Skean, 1993). The fact that most members of

Mecranium grow in higher elevations, mainly above 800 m (Skean, 1993), and that many species have very restricted ranges—in some cases confined to a single mountain range—led Skean to infer that Pleistocene cooling might have played a role in shaping the current distribution of the genus. The sister group to *Mecranium* is not clear (W. Judd, pers. comm.); thus no continental origin of the ancestral stock that gave rise to *Mecranium* can be inferred.

Poitea (Fabaceae). — Lavin (1993) assessed the biogeography and systematics of the Antillean-endemic genus *Poitea*, a member of the North-American-centered tribe Robinieae, using phylogenetic reconstruction based on morphological and chloroplast DNA restriction site data. This was expanded to the entire Robinieae using cpDNA and ITS sequences (Lavin & al., 2003). *Poitea* with 12 species is confined to Cuba (two endemic species), Hispaniola (seven species, six endemic), Puerto Rico (three species, two endemic) and the Lesser Antillean island of Dominica (one endemic species). The genus does not occur in Jamaica. Current circumscription of the genus includes the formerly recognized genera *Sabinea*, *Sauvallella*, *Corynella*, *Notodon*, and *Bembicidium* (Polhill & Souza, 1981; Lavin, 1993). *Hebestigma*, with two species endemic to Cuba, was also included in the study of Lavin & al. (2003).

The cladistic analysis reflects two main lineages or subgroups within *Poitea*: (1) the *Poitea galeoides* alliance, comprised of species with reddish tubular corollas and imparipinnate leaves, and (2) the *Poitea florida* alliance, with papilionaceous flowers and paripinnate leaves (Lavin, 1993; Fig. 5). The *Poitea galeoides* alliance is distributed in Western Cuba, and southwestern to north-central Hispaniola, whereas the *Poitea florida* alliance is found in eastern Cuba, north-central Hispaniola, the Puerto Rican bank, and Dominica. The biogeographic assessment of *Poitea* by Lavin (1993) is based on the ideas of geohistory of the Greater Antilles outlined by Rosen (1976, 1985), Pindell & Barrett (1990), and Perfit & Williams (1989). Lavin initially suggested that if a vicariant model is applied to interpret the current distribution of *Poitea*, the group must have originated in the Early Tertiary (Lavin, 1993). Close relationships between members of the *Poitea galeoides* alliance from western Cuba and Hispaniola (primarily in the southwestern peninsula of Hispaniola) is consistent with diversification during the Early Eocene when western Cuba and southwestern Hispaniola were closer to each other and to northern Central America. Later in the Tertiary, during the accretion of southwestern Hispaniola to the rest of the island, members of this alliance expanded its range to central Hispaniola. For members of the *Poitea florida* alliance, Lavin found that the Eastern Cuban and the north-central Hispaniolan species are sis-

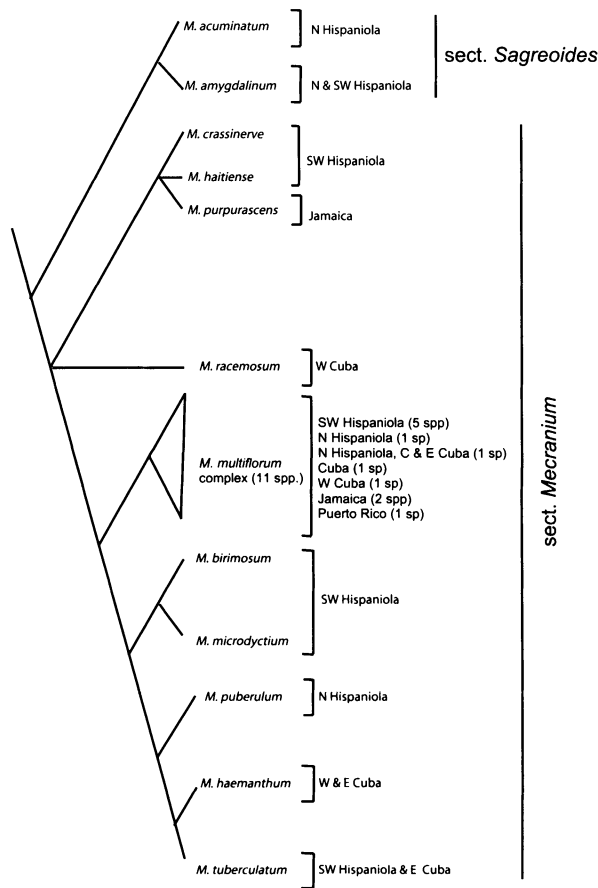


Fig. 4. Phylogeny of *Mecranium* (adapted from Skean, 1993).

ter to each other, and this clade is sister to three species centered in Puerto Rico. This pattern of relationship is consistent with the hypothesis of a close land connection between eastern Cuba, Central Hispaniola, and Puerto Rico during the Early Tertiary (Rosen, 1985; Perfit & Williams, 1989; Pindell & Barrett, 1990). However, based on the molecular clock in Lavin & al. (2003), the dates for this diversification appear to be much more recent than the vicariant model would predict. They estimated minimum divergence times of 16 mya for *Poitea* and its sister *Gliricidia* and ca. 9.3 mya for extant *Poitea* species. The vicariant model, therefore, seems highly unlikely.

Gliricidia, the sister to *Poitea*, is distributed in Mexico and northern South America. Sister to the *Poitea/Gliricidia* clade is a group of nine genera comprising the remainder of tribe Robinieae. The first branch in this clade comprises *Lennea* (Central America) and *Hebestigma*; the next branch is *Olneya* (SW North America). The remaining six genera are widely distributed in North, Central, and South America. A simple par-

simony optimization of ancestral distributions suggests a probable origin for Robinieae in Central America or Mexico. This further suggests two colonizations of the Antilles (*Hebestigma* and *Poitea*), most likely in Cuba, with subsequent eastward colonization in *Poitea* (but not *Hebestigma*) including two lineages reaching Hispaniola and diversifying there, one of these spawning two migrants to Puerto Rico, and another dispersing to Dominica.

Bactris (Arecaceae). — Salzman & Judd (1995) investigated the ingroup relationships of the Antillean species of *Bactris*, which were previously found to be a monophyletic group embedded in a larger clade containing northern South American species (Sanders, 1991). *Bactris*, one of the largest Neotropical palm genera (over 60 species according to Henderson & al., 1995), has only three species endemic to the Greater Antilles, one each in eastern Cuba, Hispaniola, and Jamaica.

The cladistic analysis of morphological and anatomical characters by Salzman and Judd confirmed monophyly of the Antillean *Bactris*, placing the Hispaniolan *B. plumeriana* as sister to the Jamaican *B. jamaicensis*, and both as sister to the Cuban species *B. cubensis* (Fig. 6). Salzman and Judd invoke both vicariance and dispersal explanations to reconstruct the historical development of the Antillean clade, basing their ideas on the obtained phylogeny, current distributions of species within the islands, and the present models of geological evolution in the Caribbean. In their interpretation, the stock to which *Bactris* belongs occurred in western Gondwana (Uhl & Dransfield, 1987) and could have reached the Proto-Greater Antilles during late Cretaceous-Early Tertiary. Under this scenario, the eastward drift of the Proto-Greater Antilles represented the vicariant event responsible for the split between the Antillean and the northern South American lineages (Salzman & Judd, 1995). The original Antillean stock could have been on the Eastern Cuba-Central Hispaniolan block, which eventually split. Subsequently, the Hispaniolan populations could have reached Southwestern Hispaniola and then the younger Jamaica via water dispersal.

Exostema (Rubiaceae). — Phylogenetic reconstruction and biogeographic interpretations on the basis of ITS and *rbcL* sequence data (Fig. 7) were carried out for *Exostema*, a neotropical genus of 25 species of trees and shrubs with a high level of endemism in the Greater Antilles (McDowell & Bremer, 1998; McDowell & al., 2003). The initial biogeographic conclusions based on morphology and ITS sequences, but with limited outgroup sampling (McDowell & Bremer, 1998), were overturned with the addition of *rbcL* sequences and more extensive outgroup sampling (McDowell & al., 2003). *Exostema* comprises four predominantly Antillean clades (one clade includes a derived Central American species)

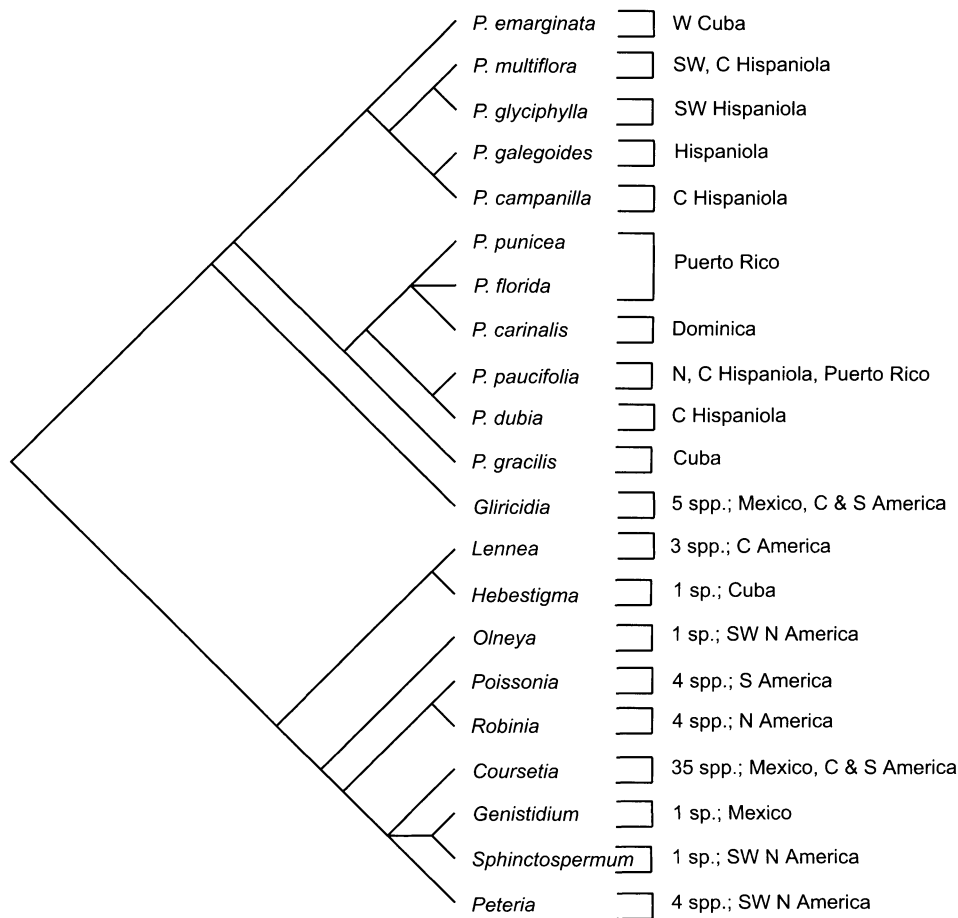


Fig. 5. Phylogeny of *Poitea* and related genera of Robinieae (adapted from Lavin & al., 2003).

and one South American clade, which also includes the genus *Coutarea*. None of the Antillean clades represent taxa of a single island; each includes at least one species endemic to Cuba and to Hispaniola. Nested within *Exostema* is a clade comprised of *Chiococca* (Antilles, Florida, and tropical America) and *Erithalis* (Antilles, Bahamas, and Florida; see below). The three sequential outgroups to the clade of *Exostema* (*Cubanola*, *Isidorea*, and *Catesbaea*, in order of increasing distance) and its three derivative genera are all Antillean in distribution. Thus, this entire clade diversified in the Caribbean basin and has at least three descendant lineages in Central and South America (Fig. 7).

***Erithalis* (Rubiaceae).** — A study on the phylogenetics, systematics, and biogeography of the genus *Erithalis* (Rubiaceae) was carried out by Negrón-Ortiz & Watson (2002, 2003) using chloroplast DNA sequences (*trnF-trnL*), as well as nuclear sequences (ITS and ETS). *Erithalis* is a small group of about eight to ten species of trees and shrubs distributed in the West Indies, Mexico, Honduras, Venezuela, and Brazil. Some species have a Pan-Caribbean distribution, whereas others are narrow

endemics. In this analysis, taxa with broad distributional ranges were sampled from different geographic areas.

Parsimony analysis of the combined dataset supports monophyly of *Erithalis*. The obtained phylogeny consists of two major clades (Fig. 8). One clade groups several lineages of *E. fruticosa* (from Cuba, Jamaica, Puerto Rico, and Florida) as sister to the Jamaican *E. harisii*. The other clade groups five other species with the Jamaican *E. quadrangularis* and one lineage of *E. odorifera* (from the Bahamas) coming out as early lineage splits; the rest of the lineages form two subclades. One of the subclades forms a polytomy consisting of lineages from the Bahamas, Cuba, and Hispaniola. Accessions identified as *E. fruticosa* from Florida and the Bahamas were also part of this clade, but were suspected to be of hybrid origin and not included in subsequent studies (Negrón-Ortiz & Watson, 2002, 2003). The other subclade comprises several lineages of *E. odorifera* from Puerto Rico and the Lesser Antilles (Dominica and St. Vincent). *Erithalis* is sister to *Chiococca* (Antilles, Central, and South America) and together are nested within the paraphyletic genus *Exostema* (see above), thus

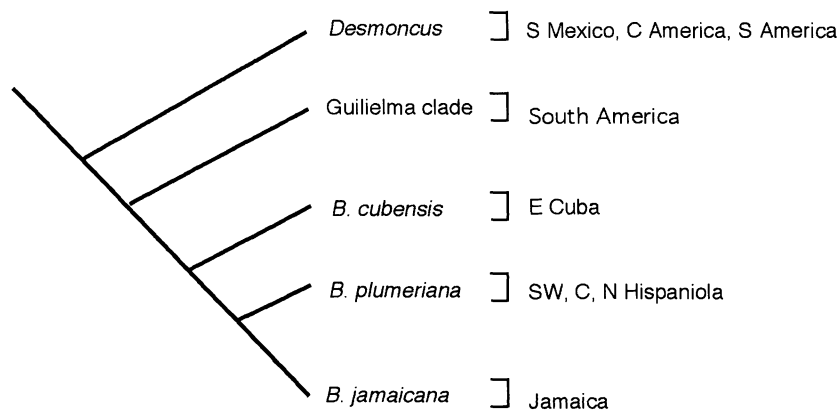


Fig. 6. Phylogeny of *Bactris* (adapted from Salzman & Judd, 1995).

suggesting an in situ origin of *Erithalis* in the Antilles.

In this study, branch lengths are short and most clades have weak bootstrap support. Extremely low sequence divergence indicates recent diversification. Taken together with the widespread occurrence of several species (*E. fruticosa*, *E. odorifera*, *E. salmeoides*) suggests dispersal as the primary historical factor in present distributions.

Goetzeoideae (Solanaceae). — A study by Santiago & Olmstead (2003) investigated the evolutionary relationships of the Antillean genera *Goetzea*, *Espadaea*, *Henoonia*, *Coeloneurum*, and the South American genera *Duckeodendron* and *Metternichia*. *Goetzea* consists of two species, one each in Hispaniola and Puerto Rico. *Coeloneurum* is a monotypic genus of Hispaniola. *Espadaea* and *Henoonia* are each monotypic genera endemic to Cuba. No member of this plant group is present in Jamaica. *Duckeodendron* and *Metternichia* are monotypic genera endemic to Brazil. The systematic placement of all of these taxa, except *Metternichia*, have been a long-standing question. The Antillean genera were suggested (Hunziker, 1979) to form the only plant family (Goetzeaceae) endemic to the Greater Antilles and *Duckeodendron* was believed to represent the only plant family endemic to the Amazon basin (Kuhlmann, 1930, 1947).

Phylogenetic reconstruction using nuclear and chloroplast DNA sequence data (Fay & al., 1998; Santiago & Olmstead, 2003) strongly supported monophyly of these genera and placed them in Solanaceae (Fig. 9). Within the clade, the Antillean genera are most closely related to each other, and the Brazilian genera are the basal lineages. These taxa represent an early diverging lineage within Solanaceae (Fay & al., 1998), providing evidence for the establishment of a new subfamily in Solanaceae, Goetzeoideae (Olmstead & al., 1999). Based on the phylogeny and current geological knowledge, a plausible explanation of the history of the group in the

Antilles involves colonization from South America to Hispaniola or Cuba. The Puerto Rican lineage then arose from Hispaniola. Phylogenetic reconstruction in Goetzeoideae indicates evolution towards xeric environments (in *Coeloneurum* and *Henoonia*), and a shift in the pollination syndrome from moth pollination (in the South American *Metternichia* and *Duckeodendron*) to bird pollination (in the Antillean taxa).

Additional studies. — Several additional studies have addressed phylogeny and biogeography of Antillean plant groups. *Pictetia* (Fabaceae) is a genus of eight species with one endemic to Puerto Rico, one endemic to Hispaniola, one occurring on both Cuba and Hispaniola and the other five endemic to Cuba. A phylogeny based on ITS and morphological data found the genus to be monophyletic and sister to a clade occurring predominantly in Africa and Madagascar and the inclusive clade is sister to *Diphysa*, which is restricted to Central America (Beyra M. & Lavin, 1999). This distribution of related groups and the relatively high sequence divergence among species in *Pictetia*, suggests a long history in the Antilles with probable origin from what is now Central America. Present distributions are consistent with an early diversification on a land mass consisting of the present-day Puerto Rico, north-central Hispaniola, and eastern Cuba, with a basal polytomy in the phylogeny between the three islands. Subsequent radiation has been restricted to Cuba and an apparent dispersal event in *P. sulcata* between Cuba and Hispaniola.

Ginoria, including *Haitia* (Lythraceae), is a clade of 16 species, 14 of which are restricted to either Hispaniola or Cuba, one in Puerto Rico and the Virgin Islands, and one in Mexico. A phylogenetic analysis based on morphology found that the Hispaniolan plus Cuban species form a clade, with the Mexican and east Caribbean species unresolved at the base (Graham, 2002, 2003). Neither of the groups of species occurring on Cuba or Hispaniola form monophyletic groups. Sister to *Ginoria*



Fig. 7. Phylogeny of *Exostema* (adapted from McDowell & Bremer, 1998; McDowell & al., 2003).

is a small clade of two species inhabiting coastal environments in northern South America and the island of Mauritius in the Indian Ocean. Outgroups to this inclusive clade are Afro-Asian in distribution, thus, the geographic ancestry of this group is uncertain.

Four species of *Styrax* sect. *Valvatae* (Styracaceae) occur in the Antilles, one endemic to Puerto Rico, one endemic to Hispaniola, one on both Cuba and Hispaniola, and one in the Lesser Antilles and northern South America. A phylogenetic study of sect. *Valvatae* found that three separate origins in the Antilles are required to explain present distributions, with two originating in South America and one from Mexico (Fritsch, 2003). Another case study similar to *Styrax*, in which there were multiple introductions to the Antilles,

involves *Cuphea* (Lythraceae). A phylogenetic study based on morphology and ITS sequence data found at least five, and more likely as many as eight (including one human introduction), separate origins of Antillean lineages (Graham, 2003). Colonization from eastern South American ancestors occurred at least three times and from Central American ancestors at least twice (including the recent introduction); the remaining introductions are of uncertain origin, because the clades to which they belong contain species in each area and sampling is not complete. There has been limited subsequent speciation in the Antilles, with only seven species being endemic.

Major biogeographic patterns from the previous phylogenies include the following:

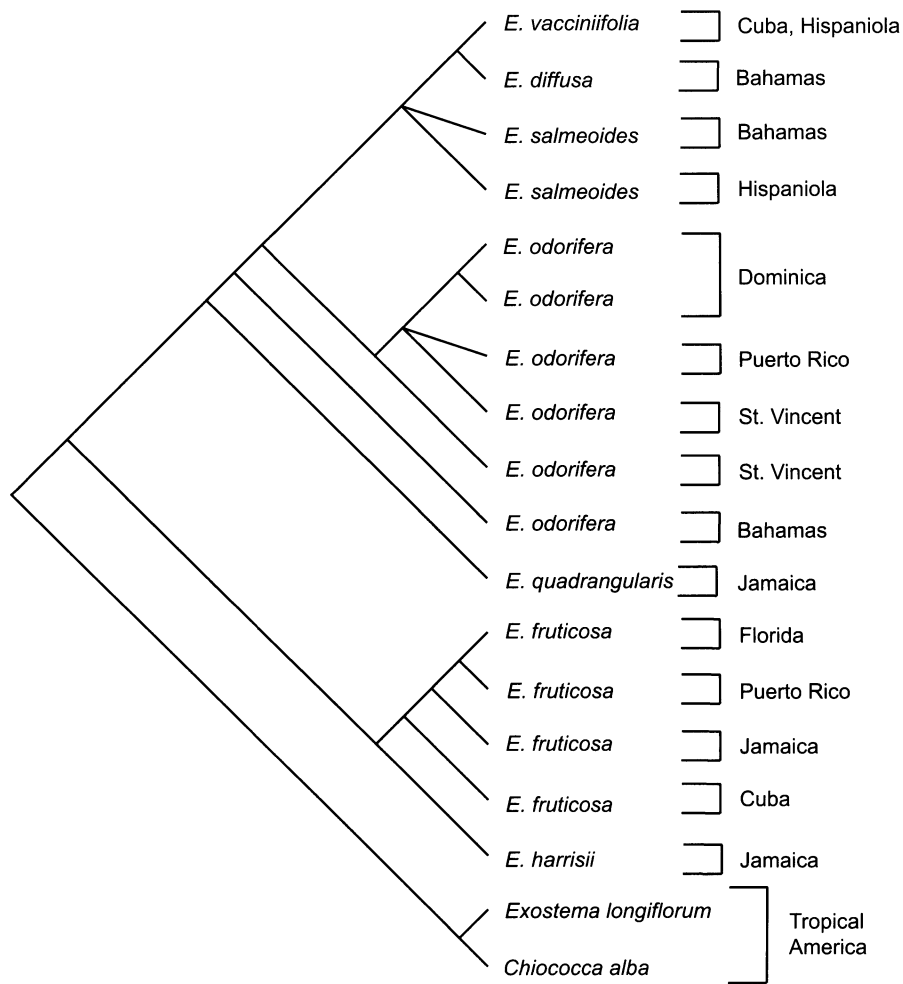


Fig. 8. Phylogeny of *Erithalis* (adapted from Negrón-Ortiz & Watson, 2003).

1. North American and South American origins of Caribbean plant groups. — Phylogenies for *Lyonia*, *Poitea*, *Hebestigma*, *Pictetia*, and *Sabal* indicate closer relationship to stocks from North America, mainly Mexican lineages. This contrasts with *Bactris* and Goetzeoideae, which are derived from South America. *Styrax* and *Cuphea* each have one or more lineages in the Antilles derived from each continent.

2. Groups of in situ origin. — *Exostema* and *Erithalis* both belong to the same lineage of Rubiaceae that apparently occupied the Antilles before the origin of either genus. Each has members (*Exostema*) or a closely related group (*Erithalis*) with continental distributions, leading to erroneous earlier hypotheses.

3. Groups of unknown origin. — *Mecranium* and *Ginoria* (including *Haitia*) both have geographically distant and/or diverse continental relatives and, thus, are of unknown continental origin.

4. Plant groups recolonizing continental land masses. — This is illustrated best in *Exostema*, where three colonizations of Central and South America

are inferred. *Erithalis* exemplifies another pattern, with two lineages that have colonized Florida from Antillean ancestors.

5. In Cuba and Hispaniola, species within an island do not form monophyletic groups. — Species on one island often have their closest relatives on another island (*Exostema*, Goetzeoideae, *Mecranium*, and *Poitea*). The presence of a diverse assemblage of unrelated lineages has been suggested as evidence for the composite nature of these islands (Lavin, 1993), but it also could indicate relatively frequent inter-island colonization events. A contrasting pattern is found in *Lyonia*, where all the Cuban species are in the same lineage, and another lineage comprises all the Hispaniolan species (plus Puerto Rico and the Virgin Islands, see below). *Pictetia* is similar, with a clade of Cuban species, one of which also occurs on Hispaniola. In *Ginoria* (including *Haitia*) the primary radiation was on Cuba with two or three colonizations of Hispaniola. Evaluation of diaspore dispersal will be of importance to understand these differences (Judd, 2001).

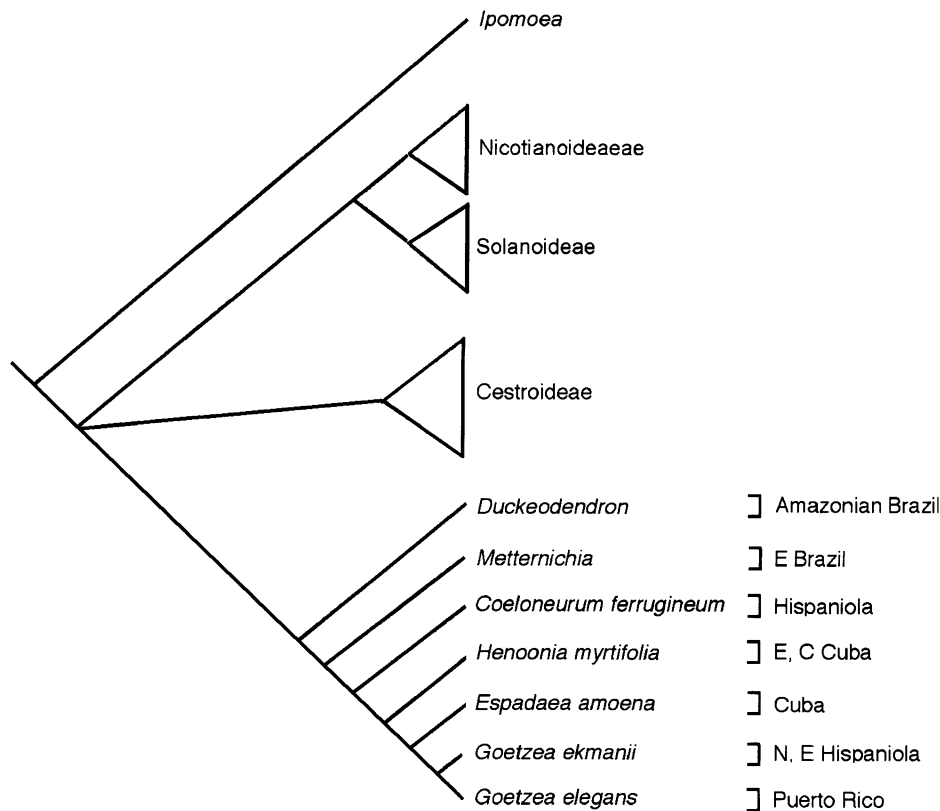


Fig. 9. Phylogeny of Goetzeoideae (from Santiago-Valentín & Olmstead, 2003).

6. Relationship of Jamaica taxa with Cuba and Hispaniola. — *Lyonia octandra* (Jamaica) is closely related to the Cuban lineages of the genus. Relationships of Jamaican *Lyonia jamaicensis* is still unclear. A lineage in *Sabal* is shared between Jamaica and Cuba, as is an unresolved lineage of four species of *Exostema* with two species each on Cuba and Hispaniola. Affinities between Jamaica and southwestern Hispaniola are found in a clade in *Mecranium*. A similar relationship has been suggested for *Bactris* (Salzman & Judd, 1995), but the phylogeny is equivocal.

7. Relationship of Puerto Rican taxa with Hispaniola. — Phylogenies of four independent plant groups support the close relationship of Puerto Rico and Hispaniola: *Sabal*, *Lyonia*, *Poitea*, and *Goetzea*.

8. Greater Antillean-centered groups with representatives in the Virgin Islands or the Lesser Antilles, which are closely related to, and most likely derived from Puerto Rico. — This is observed in *Erithalis* (a relationship of Puerto Rico with St. Vincent and Dominica), *Lyonia* (Puerto Rico and St. Thomas), and *Poitea* (Puerto Rico and Dominica).

9. Relationship between eastern Cuba, north-central Hispaniola, and Puerto Rico. — Lineages that, to different extents, suggest a relationship

between these land areas include *Lyonia*, *Poitea* and *Goetzeoideae*. These taxa are absent or not very well represented in Jamaica. Judd (2001) infers that members of *Lyonia* may be the result of vicariant events between Cuba, north-central Hispaniola, and Puerto Rico, but the pattern is obscured by subsequent dispersal events of recent lineages.

10. Relationships between western Cuba and southwestern Hispaniola. — This pattern is found only in the *Poitea galeoides* alliance.

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