

Historical phytogeography of the Greater Antilles

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Alan Graham (Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A.; email: Alan.Graham@mobot.org). Historical phytogeography of the Greater Antilles. *Brittonia* 55: 357–383. 2003.—An understanding of the phyto-geographic history of a region depends upon an adequate fossil record to reveal migrational histories and the timing and direction(s) of introductions and extinctions, and to augment or circumvent undue reliance on molecular clocks. It further depends upon an accurate phylogeny of the taxa to establish real patterns of geographic affinities (phylogeography), and a relatively detailed geologic history to assess the relative roles of dispersal and vicariance in populating the islands. For the Greater Antilles new information is slowly emerging on the plant fossil record through study of new floras such as the Eocene Saramaguacán palynoflora from Cuba, and more is potentially available from the middle Oligocene San Sebastian megafossil flora of Puerto Rico that has not been revised since the early 1900s. Phylogeographic studies and area cladograms are still meager for plants, but data from various animal groups are providing a context for the general biotic history of the Antilles. Perhaps the area of greatest advance is being made in achieving an adequate plate tectonic model for the Caribbean region. There is now some convergence toward a mobilist model that depicts a Cretaceous volcanic island arc that extended from the Mexico/Chortis block in the north to Ecuador in the south, and gradually moved through the developing portal between North and South America to collide with the Bahamas Platform in the middle Eocene. Throughout this 70-million-year history there was an immensely complex pattern of collision/separation and submergence/emergence that provided opportunity both for vicariance and dispersal in the migration, evolution, and speciation of the flora of the Greater Antilles.

Key words: Phytogeography, phylogeography, Greater Antilles, Caribbean, fossil floras.

Progression in the understanding of complex biological systems frequently follows a sequence familiar to students of the history of science. There is an initial data-gathering phase, and in the case of historical phytogeography this means the study of individual micro- or megafossil floras. For the Cenozoic Era, 65 Ma (million years ago) to the present, there are 12 of these floras known for the Greater Antilles (Tables I, II; Figs. 1, 2).

The second phase involves various levels of synthesis. The initial level is achieved by combining results from the study of individual floras into a broader picture of vegetation and vegetation change. Floras of

similar age can be used to reconstruct regional vegetation at a given point in time, estimate paleoenvironments (climate and elevations), note geographic affinities between different regions, and propose modes and pathways of migration. For the Greater Antilles it is now possible to compare the middle Eocene Saramaguacán flora of Cuba and the Guys Hill (Chapelton) flora of Jamaica, and to further compare these with the middle Eocene Claiborne and Jackson floras of the southeastern United States (Frederiksen, 1980, 1981, 1988, 1994), the Burgos Basin flora of northeastern Mexico (Martínez-Hernández et al., 1980), the middle to late Eocene Gatuncillo flora of cen-

TABLE I
PRINCIPAL CENOZOIC FLORAS OF THE GREATER ANTILLES

Flora/formation	Age	Locality	Reference
MEGAFOSSIL FLORAS			
Chapapote-Sabanella Palmas	Quaternary	Santa Clara, Cuba	Berry, 1934
Yumari	Miocene	Matanzas, Cuba	Berry, 1939
San Sebastian	m. Oligocene	Lares, Puerto Rico	Hollick, 1928b
—	Tertiary	Dominican Republic	Berry, 1921
—	Tertiary	Haiti	Berry, 1923
MICROFOSSIL FLORAS			
—	Quaternary	Luquillo Mts., Puerto Rico	Ogle, 1970
—	Quaternary	Lake Miragoane, Haiti	Binford et al., 1987; Brenner & Binford, 1988; Higuera-Gundy, 1989
—	Pleistocene, Holocene	Cuba (Isla de la Juventud)	Ferrera et al., 1990–91
Artibonite	Mio-Pliocene	Haiti	Graham, 1990a,b
San Sebastian	m. Oligocene	Lares, Puerto Rico	Graham & Jarzen, 1969
Chapelton	m. Eocene	Jamaica	Graham, 1993
Saramaguacán	m. Eocene	Cuba	Graham et al., 2000

Geologic ages of older and unrevised floras are as listed in the original publication. (m. = middle).

tral Panama (Graham, 1985), and the Los Cuervos and Mirador floras of Colombia (González-Guzmán, 1967).

It is also possible to arrange floras of different ages in a sequence that reflects vegetational, biogeographical, and environmental trends through time. At present, this can be done for Panama where fossil floras are known from middle to late Eocene (Gatuncillo; Graham, 1985), early Miocene (Culebra, Cucaracha, La Boca; Graham, 1988a, 1988b, 1989), Mio-Pliocene (Gatun; Graham, 1991a, 1991b, 1991c) formations, and from the Quaternary (Bartlett and Barghoorn, 1973). This is not yet possible for the Greater Antilles because no one island has a sufficient number of fossil floras to trace changes in vegetation over time. It is possible to consider all of the paleofloras collectively and to seek regional trends from the combined assemblages. However, this introduces complications beyond those encountered in the study of sequential fossil floras at a single site or from within a unified physiographic province. First, the different floras must represent similar depositional environments; otherwise, it is impossible to distinguish differences due to environmental change from those due to ecology. For example, the San Sebastian

flora contains pollen of the mangroves *Pelliceria* Planch. & Triana and *Rhizophora* L. and the Guys Hill (Chapelton) flora contains pollen of *Pelliceria*, indicating that both floras were deposited under coastal brackish water conditions. In contrast, the Artibonite and Saramaguacán floras contain remnants of upland vegetation, lack mangroves, and were deposited in fresh-water swamp and lake-margin habitats beyond the influence of brackish water. Thus, differences between the Eocene Guys Hill (Chapelton) flora and the Mio-Pliocene Artibonite flora reflect the different habitats occupied by the two assemblages as well as environmental change over time. Another factor is that many of the land fragments constituting the islands of the Caribbean Basin have moved independently, at least to some extent, throughout Cenozoic time. The location of the fragments, and the estimated distances between them and to the continental landmasses at various points in time, differ among the various models of Caribbean tectonics. Until details of the geological history of the Caribbean Basin are better constrained, regional reconstructions of the vegetation based on the separate fossil floras are tentative.

Another level of synthesis is achieved

TABLE II
COMPOSITION OF CENOZOIC FLORAS FROM THE GREATER ANTILLES

Megafossils

CHAPAPOTE FLORA (QUATERNARY OF CUBA)

Juniperus L., *Pinus caribaea* Morelet, *Chrysobalanus icaco* L., *Conocarpus* L., *Mimusops emarginata* L., *Spondias lutea* L.

SABANILLA DE LAS PALMAS FLORA (QUATERNARY OF CUBA)

Chrysobalanus icaco, *Spondias lutea*

YUMARI FLORA (MIOCENE OF CUBA)

Gleichenia pectinataformia Berry, *Antholithes heimiaformis* Berry, *Bignonia zuliana* Berry, *Bumelia retusafolia* Berry, *Caesalpinia prebahamensis* Berry, *Caesalpinites incertus* Berry, *Calophyllum calabafornis* Berry, *Capparis prejaicensis* Berry, *Cassia yumariensis* Berry, *Celastrus simplex* Berry, *Dalbergia hesperia* Berry, *Dodonaea cubensis* Berry, *Drypetes laterifloraformia* Berry, *Eugenia ovatifolia* Berry, *Exostema precaribaeum* Berry, *Fagara miocenica* Berry, *Heliconia* sp., *Inga leonii* Berry, *I. miocenica* Berry, *Laguncularia racemosafolia* Berry, *Metopium prenuntium* Berry, *Mimusops leonii* Hollick, *M. miocenica* Berry, *Myrcia minor* Berry, *M. prerostrata* Berry, *Pisonia longifoliaformis* Berry, *Pithecolobium yumariensis* Berry, *Pseudolmedia spuriaformis* Berry, *Reynosia latifolioides* Berry, *Rheedia sylvagillacea* Berry, *Sapindus presaponaria* Berry, *Simaruba glaucaformis* Berry, *Sophora maranoides* Berry, *S. matanzana* Berry, *S. yumariensis* Berry, *Swietenia mahagoniformis* Berry, *Trichilia hirtaformis* Berry, *Zizyphus elliptica* Berry, *Z. minor* Berry

SAN SEBASTIAN FLORA (MIDDLE OLIGOCENE OF PUERTO RICO)

Acrodictidium pseudocanelo Hollick, *A. pseudosalicifolium* Hollick, *Aniba collazoensis* Hollick, *Anona cetera* Hollick, *A. pseudoglabra* Hollick, *Apocynophyllum pseudowillughbya* Hollick, *A. wilcoxense* Hollick?, *Aspidosperma collazoensis* Hollick, *Bactris pseudocuesco* Hollick, *Cassia?* *dubiosa* Hollick, *C. evidens* Hollick, *C. imitative* Hollick, *C. imparilis* Hollick, *C. ordinaria* Hollick, *C. puryearensis* Berry, *C. visibilia* Hollick, *Chondrites dictyotoides* Hollick, *Chrysophyllum comparabile* Hollick, *C. pseudargenteum* Hollick, *C. pseudargenteum oblongum* Hollick, *Combretum pseudojacquinii* Hollick, *Copaiva oligocenica* Hollick, *Cynometra rabellii* Hollick, *Dipholis pseudoleiantha* Hollick, *Echitonium?*, *Echites pseudostellaris* Hollick, *Eugenia comparabilis* Hollick, *E. pseudoaeruginea* Hollick, *Ficus hyphodroma* Hollick, *F. schimperii* Lesquereux, *F. vexativus* Hollick, *F. sp.*, *Guarea opinabilis* Hollick, *Guettarda intercalaris* Hollick, *Hancornia minor* Hollick, *H. pseudobubscens* Hollick, *Hemitelia brannerii* Hollick & Berry, *Hufelandia portoricensis* (Hollick) Hollick, *Icacorea prisca* Hollick, *I.?* sp., *Inga curta* Hollick, *I. pseudinsignis* Hollick, *I. pseudonobilis* Hollick, *I. pseudospuria* Hollick, *I.?* sp., *Iriarte collazoensis* Hollick, *Isoetes?* *incerta* Hollick, *Lonchocarpus praelatifolius* Hollick, *Malvocarpus clarum* Hollick, *Manicaria portoricensis* Hollick, *Melicocca immutata* Hollick, *M. sp.*, *Misanteca dubiosa* (Hollick) Hollick, *Musophyllum* sp., *Myrcia denutiativa* Hollick, *M. eugenioides* Hollick, *Myrsine pseudoferruginea* Hollick, *Oreodaphne mississippiensis* Berry, *Palmocarpus acrocomioides* Hollick, *P. cetera* Hollick, *P. exemplare* Hollick, *P. opinabile* Hollick, *P. rabelii* Hollick, *Palmacites alius* Hollick, *P. conformis* Hollick, *P. sparsistriatus* Hollick, *Palmophyllum* sp., *P. sp.?* (fragment of petiole), *Pithecellobium?* *imperfectum* Hollick, *P. pseudotrapezifolium* Hollick, *P. vexativum* Hollick, *Plumiera evidens* Hollick, *Psidium dissimile* Hollick, *P.?* sp., *Ramulus* gen. et sp.?, *Rhizophora?* *doctrinalis* Hollick, *Sapindus brittonii* Hollick, *S. gracilentus* Hollick, *S. obesus* Hollick, *S. pseudomarginatus* Hollick, *Sapota agnitionalis* Hollick, *Sideroxylon aequale* Hollick, *Sophora?* *suspecta* Hollick, *Trichilia evidens* Hollick, *T. pseudobarkerii* Hollick, *T. pseudohirta* Hollick, *T. spatulata* Hollick, *Zamia collazoensis* Hollick, *Z. noblei* Hollick, *Zizyphus pseudochloroxylon* Hollick

SEVERAL SITES (TERTIARY, DOMINICAN REPUBLIC)

Bucida sanchezensis Berry, *Bumelia reclinatafolia* Berry, *Calyptanthus domingensis* Berry, *Guettardia cookei* Berry, *Inga sanchezensis* Berry, *I. sp.*, *Melastomites domingensis* Berry, *M. sp.*, *Pisonia conditi* Berry, *Pithecolobium samanensis* Berry, *Poacites* sp., *Sapindus hispaniolana* Berry, *Sophora cookei* Berry

SEVERAL SITES (TERTIARY, HAITI)

Chara woodringi Berry, *Gymnogramma woodringi* Berry, *Bumelia cuneatafolia* Berry, *Chrysophyllum cahobasensis* Berry, *Guettarda cookei* Berry, *Mespilodaphne hispaniolana* Berry, *Mimusops praeparvifolia* Berry, *Pisonia conditi* Berry, *Simaruba haitensis* Berry

TABLE II
CONTINUED**Microfossils**

LUQUILLO MOUNTAINS (QUATERNARY [RECENT], PUERTO RICO)

Lycopodium L., *Selaginella* P. Beauv., Polypodiaceae-Cyatheaceae, *Alchornea* Sw., *Buchenavia* Eichler, *Casuarina* L., *Clusia* L. Compositae, *Cordia* L. *Cyrilla* Garden ex L., *Dacryodes* Vahl., *Didymopanax* Decne. & Planch., Ericaceae, *Eugenia* L., Gramineae, *Hedyosmum* Sw., *Ilex* L., Liliaceae, *Magnolia* L., *Micropholis* (Griseb.) Pierre, Palmae type, Rutaceae type, *Sloanea* L., *Tabebuia* Gómes ex DC.

Megafossils

CHAPAPOTE FLORA (QUATERNARY OF CUBA)

LAKE MIRAGOANE (QUATERNARY [RECENT], HAITI)

Pinus L., *Alchornea*, *Ambrosia* L. (and other composites), *Bursera* Jacq. ex L., *Caesalpinia* L., *Caladium* Vent., *Cecropia*, *Celtis*, Chenopodiaceae/Amaranthaceae, Cyperaceae, Euphorbiaceae, Gramineae, Melastomataceae, Meliaceae, Moraceae, Myrtaceae, *Nelumbo* Adans., *Nymphaea* L., *Phyllostylon* Capan. ex Benth., *Pilea* Lindl. (and other weeds), *Potamogeton* L., *Sapindus* L., Sapotaceae, Solanaceae, *Trema* Lour., *Typha* L.

ISLA DE LA JUVENTUD (PLEISTOCENE, HOLOCENE, CUBA)

Botryococcus Kütz., *Hystrichosphaera* Ramosa, "tipo trilete," *Selaginella*, *Acrostichum aureum* L., cf. *Anemia* Sw., *Blechnum* (*B. serrulatum* Rich.), *Lygodium* Sw., *Polypodium* L., *Pteris* L., *Pinus caribaea* Morelet, *P. tropicalis* Morelet, *Podocarpus angustifolius* Griseb., *Acoelorrhaphe wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc., *Acrocomia* Mart., *Allophylus* L., *Amaranthus* L./Chenopodiaceae, *Ambrosia*, Anacardiaceae, "tipo *Bombax* L.," *Borreria* G. Mey., Bromeliaceae, *Bucida* L./Conocarpus L., *Bunchosia* Kunth., *Bursera simaruba* (L.) Sarg., *Caladium jamaicense*?, *Caperonia plaustis* (L.) A. St.-Hil., *Casearia* Jacq., *Catostemma* Benth., *Cissus* L., *Colpothrinax wrightii* Griseb. & H. Wendl. ex Siebert & Voss, *Corchorus* L., *Cuphea* P. Browne, Cyperaceae, *Cyperus* L., *Cyrilla racemiflora* L., *Daphnopsis* Mart., *Eichornia crassipes* (Mart.) Solms, Ericaceae, *Evovulus* L., *Faramea occidentalis* (L.) A. Rich., *Ficus* L., *Gouania* Jacq., Gramineae, *Guettarda calyptrate* A. Rich., *Heliotropium* L., *Ilex*, *Ipomoea* L., *Jacaranda caerulea* (L.) J. St.-Hil., Labiatae, Malpighiaceae, Malvaceae, Melastomataceae, Meliaceae, *Metopium* P. Browne, Moraceae, *Myrica cerifera* L., Myrtaceae, *Nymphaea*, *Nymphoides* (*N. grayana* Kuntze), Onagraceae, Palmae, *Picrodendron macrocarpum* Britton, *Protium cubense*?, *Rauv[w]olfia* Gled., *Rhizophora mangle* L., *Sabal parviflora* Becc., Sapotaceae, *Spondias* L., *Typha domingensis* Pers., *Trema* Lour., *Tribulus* L., Umbelliferae (Apiaceae), *Utricularia* L., *Xylopia aromatica* (Lam.) Mart.

ARTIBONITE (MIO-PLIOCENE, HAITI)

Monolete fern spores, *Alsophila* R. Br., *Pteris* L., cf. *Antrophyum* Kaulf., trilete fern spores, *Pinus*, Palmae, *Hygrophila* R. Br., Chenopodiaceae-Amaranthaceae, Compositae, *Alchornea*, *Alfaroa*/*Oreomunnea*, *Oryctanthus* (Griseb.) Eichler, *Malpighiaceae*, *Allophylus* L.

SAN SEBASTIAN (MIDDLE OLIGOCENE, PUERTO RICO)

Cyathea Sm., *Hemitelia* R. Br. (*Cnemidaria* C. Presl.), *Jamesonia* Hook. & Grev. (*Eriosorus* Fée), *Lycopodium*, *Pteris*, *Selaginella*, *Podocarpus* L'Hér. ex Pers., *Abutilon* Mill., *Acacia*, *Aetanthus* (Eichler) Engl., *Alchornea*, *Bernoullia* Oliv., *Bombax*, *Brunellia* Ruiz & Pav., *Bursera*, *Casearia*, *Catostemma*, *Chrysophyllum* L., *Corynostylis* Mart. & Zucc., *Dendropanax* Decne. & Planch., *Engelhardia* Lesch. ex Blume (*Alfaroa*/*Oreomunnea*), *Eugenia*, *Fagus* L., *Faramea* Aubl., *Guarea* F. Allam. ex L., *Hautya* DC., *Ilex*, *Jacaranda* Juss., *Liquidambar* L., *Marcgravia* L., *Merremia* (Dennst.) ex Endl., *Myrcia* DC. ex Guill., *Norantea* Aubl., *Nyssa* L., *Oxalis* L., Palmae, *Pelliceria* Planch. & Triana, *Pleodendron* Tiegh., *Rauwolfia*, *Rhizophora* L., *Salix* L., *Tecoma* Juss., *Tetrorchidium* Poepp., *Tournefortia* L., *Zanthoxylum* L.

CHAPELTON (MIDDLE EOCENE, JAMAICA)

Deltoidospora [cf. *D. adriennis* (Potonié et Gelletich) N. O. Fred.; cf. *Acrostichum aureum* L.], *Psilatricolporites crassus* Hammen & Wijnstra (*Pelliceria*), *Retimonocolpites* Pierce (Palmae), *Bombacacidites* Couper (Bombaceae), *Cupaniedites* N. O. Fred. (Sapindaceae), *Corsinipollenites* E. Nakoman (Onagraceae), *Mauritiidites* van Hoeken-Klinkenberg (*Mauritia* L. f.)

TABLE II
CONTINUED

SARAMAGUACÁN (MIDDLE EOCENE, CUBA)

Laevigatosporites A. C. Ibrahim (smooth monolete fern spore), *Verrucatosporites usmensis* Hammen (verruca-te monolete fern spore), *Lygodiumsporites adriennis* (Potonié et Gelletich) N. O. Fred., trilete fern spore, *Undulatisporites concavus* Kedves, cf. *Pteris dentate* (Nagy) N. O. Fred., *Arecipites* Wodehouse (Palmae), *Liliacidites* Couper, *Retimonocolpites* Pierce, *Cupuliferoidaepollenites liblarensis* (Thompson) Potonié, *Fraxinoipollenites*, cf. *F. scoticus* (Simpson) N. O. Fred., *Echitricolpites* Hammen, *Retitricolpites* (Hammen) Hammen & Wijmstra, *Reticulataepollis* cf. *intergranulata* (Potonié) Krutzsch, *Retitricolporoides* Hammen, *Striatricolpites cataumbus* González Guzmán [cf. *Crudia* Schreb.], *Retitricolporites* (Hammen) Hammen & Wijmstra, *Myrtaceidites* cf. *parvus* Cookson & Pike (Myrtaceae), *Bombacacidites* cf. *tilioides* Krutzsch (Bombaceae), *Basopollis* Pflug/cf. *Choanopollenites* Stover (Normapolles group, cf. Juglandaceae?), *Retibrevitricolpites* González Guzmán, *Porocolpopollenites* Hammen [cf. *Symplocos* Jacq.], *Graminidites gramineoides* (Meyer) Krutzsch (= *Monoporites annuloides* Hammen; Gramineae), *Psilodiporites redundantis* González Guzmán (Moraceae), *Brosipollis* cf. *striata* N. O. Fred. [cf. *Bursera* Jacq. ex L.?], *Triporopollenites* Pflug & Thompson [cf. *Celtis* L.], *Lyningtonia* [cf. *L. rhetor* Erdtman (Nyctaginaceae)], *Pericopporites* Hammen, *Malvacipollis ischudyi* N. O. Fred. (Malvaceae?), *Retipollenites* cf. *confuses* González Guzmán

Identifications, spellings, and family assignments follow those of the original authors. Note that megafossils identified from the Caribbean region in the early 1900s included many that were fragmentary and poorly preserved. None have been revised and many identifications from adjacent floras by the same author(s) have proved incorrect (Dilcher, 1973). See Table I for age, locality, and references to the floras.

when data from fossil and extant plant communities are integrated with those from past and present animal assemblages into an overall model of biotic history. For the Greater Antilles this will require the study of additional fossil floras, monographs and biogeographic analyses of extant groups (e.g., *Juniperus* L.; Adams, 1989), and the completion of major floristic projects. Zoological contributions on past and present faunas are more numerous and presently include the syntheses by Liebherr (1988) on insects, Woods and Sergile (2001) mostly on various animal groups, and Iturralde-Vinent and MacPhee (1999) on fossil mammals.

A final level of synthesis is achieved when biotic histories are integrated with physical/climatic histories to produce a model of ecosystem evolution. The beginnings of this last phase are evident by the incorporation of geochemical and geophysical data into scenarios of vegetational history in and around the Caribbean Basin. One example is the consideration of Quaternary sea-surface temperatures based on the chemistry of coral walls, and extrapolation of the results to near-shore terrestrial environments. The Climate Long-Range Investigation and Mapping Program (CLI-

MAP, 1976, 1981, 1984) attempted to reconstruct the climates of the last glacial and interglacial interval from 18 kyr (thousand years ago) to the present. One conclusion was that while high-latitude climates were 12–14°C colder than at present at the glacial maximum, tropical marine temperatures remained relatively stable (0–2°C colder). This meant that biogeographical and evolutionary models for the low latitudes had to assume a relatively stable Quaternary climate. Then new evidence from studies on corals from Barbados allowed a different interpretation (Guilderson et al., 1994). The elements calcium and strontium are chemically similar and strontium can replace calcium in the walls of marine invertebrates. The rate of replacement is temperature sensitive (more strontium is taken up as the water cools) and calibration of the ratios provides a geothermometer for surface-water ocean temperatures. The results indicate that the temperatures of tropical waters during the cold intervals of the Quaternary were lower by 4–6°C than at present. Furthermore, studies of ocean cores and through the Greenland and Antarctic ice caps have shown that climates change much more rapidly than previously assumed. The older literature described four major glacial

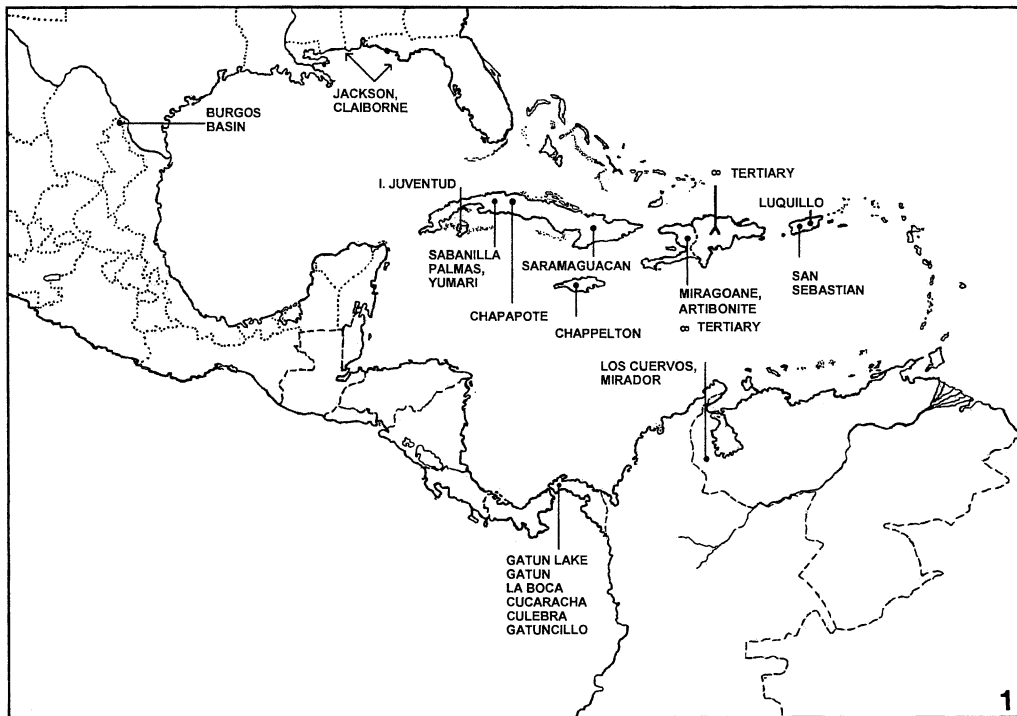


FIG. 1. Index map of the principal fossil floras of the Caribbean Basin and surrounding regions. ∞ = of undetermined Tertiary age.

advances separated by three interglacial stages, each with a period of about 175,000 years. New evidence indicates that there were 18–20 glacial advances within the past 800,000 years (see references in Graham, 1999, chapter 2). Collectively, these data suggest a much more dynamic tropical environment and a more rapid pace of biotic change than earlier thought. Measurements of the different amounts of atmospheric gases (principally CO_2) trapped in air bubbles and of the varying levels of dust in the cores (high during the dry and windy glacial intervals) suggest some possible mechanisms for these changes.

On a longer timescale, oxygen isotope ratios provide a marine temperature record for the past 100 m.y. (million years). This record is derived by measuring the relative amounts of ^{16}O and ^{18}O in shells of marine invertebrates obtained from deep-sea cores by the Deep Sea Drilling Project (DSDP) and its successor, the Ocean Drilling Program (ODP). More ^{18}O is taken up as the

water cools. By compensating for disproportionate amounts of the lighter ^{16}O trapped in ice during glacial intervals, an estimate of ocean temperature trends is revealed. Several of these cores are from in and around the Caribbean Basin; indeed, the first deep-sea drilling operation was on the Nicaraguan Rise and the first site of the DSDP was in the Venezuelan Basin (Bader et al., 1970). The overall trends from the marine realm have been found generally consistent with those derived from paleobotanical analyses of terrestrial floras (see Graham, 1999, pp. 86–92). The global benthic paleotemperature curve is shown in Figure 3 along with the principal fossil floras of the Greater Antilles and adjacent regions.

This type of ancillary information is independent of paleoclimatic reconstructions derived from paleontological data and it serves also as context information useful in evaluating conclusions about vegetation and faunal history. For example, the curve

AGE	S.E.U.S.	MEXICO	CUBA	JAMAICA	HAITI	DOMINICAN REPUBLIC	PUERTO RICO	PANAMA	COLOMBIA
QUATERNARY			CHAPAPOTE SABAN. PALMAS I. JUVENTUD		MIRAGOANE		LUQUILLO	GATUN LAKE	
PLIOCENE									
MIOCENE			YUMARI		ARTIBONITE MEGAFOSSILS TERTIARY	MEGAFOSSILS TERTIARY		GATUN LA BOCA CUCURACHA CULEBRA	
OLIGOCENE							SAN SEBASTIAN		
Eocene	JACKSON CLAIBORNE	BURGOS BASIN	SARAMA- GUACAN	CHAPELTON				GATUNCILLO	MIRADOR LOS CUERVOS
PALEOCENE									

2

FIG. 2. Age and approximate stratigraphic relationships between the principal fossil floras of the Caribbean Basin and surrounding regions.

shows that during the early Eocene, temperatures reached their maximum for all of the Cenozoic. This was about the time the middle Eocene Guys Hill (Chapelton) and Saramaguacán fossil floras were being deposited on Jamaica and Cuba, respectively, and at about the time the Claiborne, Jackson, Burgos Basin, Gatuncillo, Mirador, and Los Cuervos floras were accumulating in the surrounding regions. This evidence from isotopic paleotemperature analysis alone suggests widespread warm and moist climates, the likelihood of extensive tropical vegetation, and the absence of any significant climatic barrier to the migration of tropical elements through the Caribbean region. It also suggests that temperate environments and vegetation were limited. Beginning in about the middle Eocene (50 Ma), temperatures declined episodically to a new threshold until about 35 Ma, then fluctuated at or just above glacial/non-glacial conditions in the high latitudes until the end of the early Miocene (15 Ma). During this interval temperate conditions expanded, augmented locally by increasing elevations, and this facilitated the introduction of

temperate elements into the Antillean flora. This was the time (~30 Ma) that evaporites were being deposited near Punta Alegre in central Cuba and that coastal lignites were accumulating as part of the middle Oligocene San Sebastian Formation on Puerto Rico. Areces-Mallea (1987; see unpubl. report by Cousminer in 1957 cited therein) reported *Pinus* L. in the Antilles from the Cuban deposit, and temperate elements have been reported from the Oligocene San Sebastian flora (Graham and Jarzen, 1969). At the end of the early Miocene another lowering of global temperatures occurred that initially produced the early Arctic glaciations and then eventually culminated in the Pleistocene ice age. The Artibonite flora is of late Miocene to possibly early Pliocene age (7–5 Ma) and this small fossil spore and pollen assemblage also includes *Pinus*.

These six megafossil and six microfossil floras (Table I) constitute the principal data base for tracing the Cenozoic history of the Greater Antilles vegetation (Figs. 4–7). The data are more meager than these few floras imply, however, because none of the mega-

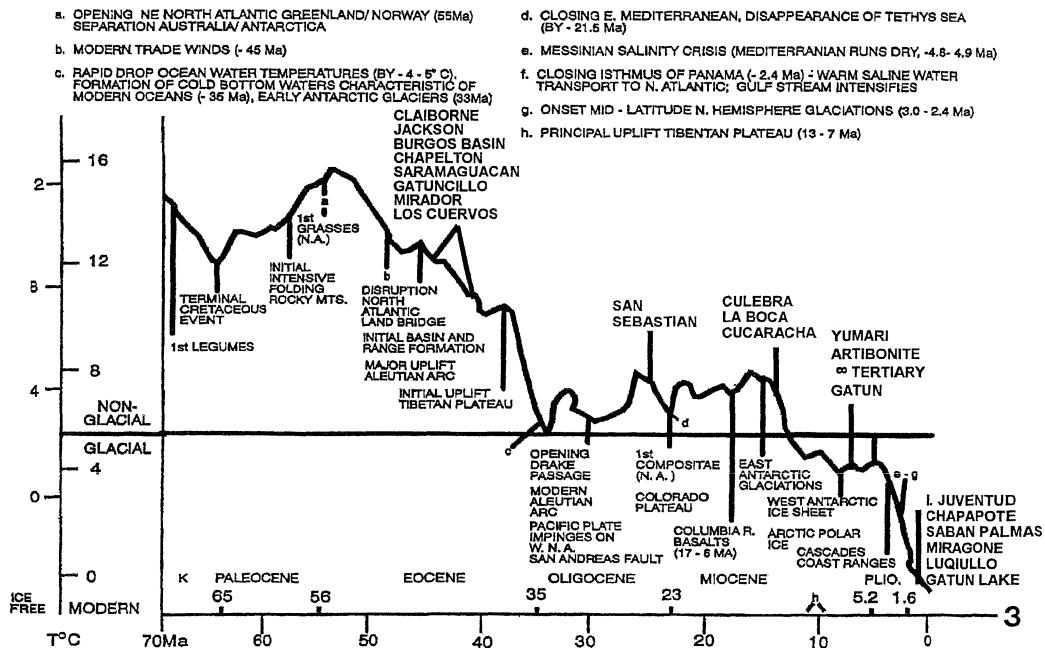
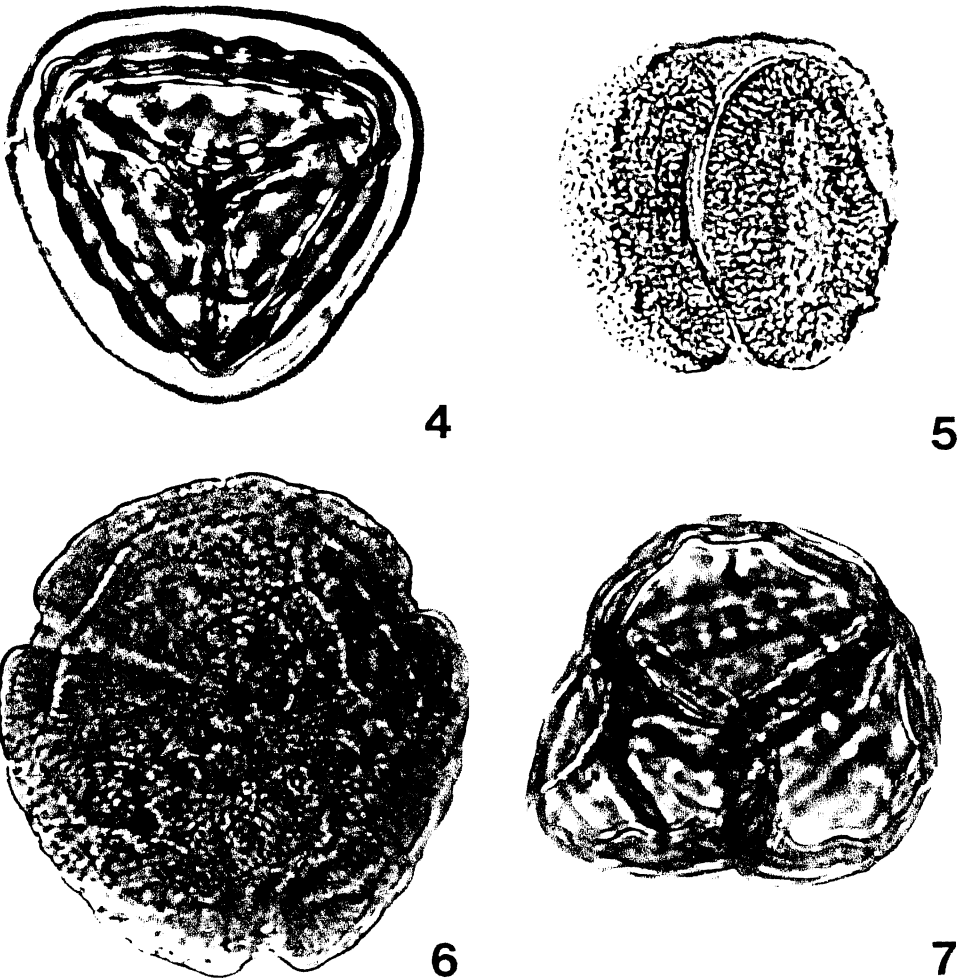


Fig. 3. Global paleotemperature curve based on oxygen isotopes (e.g., Miller et al., 1987), plotted with major geologic and biologic events and the principal floras of the Caribbean Basin and surrounding regions.

fossil floras have been revised since the early 1900s; none have been analyzed using leaf margin analysis (LMA) or the Climate-Leaf Analysis Multivariate Program (CLAMP; Wolfe, 1993) and its associated statistical tests; the floras are of different sizes making direct comparisons and statistical analyses difficult; some of the Tertiary floras are small (e.g., the Chapapote flora includes only four genera, and the Sabanilla de Las Palmas flora has only two species) and the Quaternary microfossil assemblages from Haiti and Puerto Rico are both relatively small and very recent in age; factors that influence the deposition of plant microfossils and megafossils are different (see Graham, 1999, pp. 117–121, 122–123); and the San Sebastian flora was published more than 30 years ago and requires revision (e.g., *Bombax* L. is now treated as an African genus; and *Eugenia* L. pollen cannot be distinguished from other Myrtaceae at the level of light microscopy; Graham, 1980)¹. The San

Sebastian megafossil flora would be a good candidate for LMA and CLAMP studies because it contains more than the minimum number of species necessary for valid statistical analyses (~30); the preservation is good; the age is well established (middle Oligocene); it is within the age range that would allow reconstructions based on both LMA and the NLR (nearest living relative) method; and seeds, spores, and pollen are present in the same deposits. As noted previously, even though there are limited paleobotanical data available for the Greater Antilles, an increasing amount of ancillary information is accumulating from faunal studies; strontium/calcium ratios preserved in corals; and oxygen isotope and other studies on cores from Greenland, Antarctica, and the ocean basins including the Caribbean Sea. Also important is the fact that advances are being made toward an improved model of land-sea relationships in the Caribbean Basin (e.g., Donnelly, 1985, 1988, 1990; Iturralde-Vinent & MacPhee, 1996; Pindell, 1994; Pindell & Barrett, 1990) and this is providing the essential physical basis for tracing the origin of biogeographic patterns in the region.

¹ Fossil Myrtaceae pollen identified to genus has been reported from very young deposits (e.g., late Holocene) where it was reasonable to assume that the fossils/subfossils were produced by plants still represented in the local vegetation (e.g., Burney, 1987).



FIGS. 4–7. Fossil spores and pollen from the Tertiary of the Greater Antilles. 4. *Pteris* (50 μm ; Artibonite, Haiti). 5. *Pinus* (40 μm ; Artibonite, Haiti). 6. *Pelliceria* (55 μm ; San Sebastian, Puerto Rico). 7. Ericaceae (42 μm ; San Sebastian, Puerto Rico). See Table 1 for ages and references.

Geologic History

There is no single model that as yet fully explains the details of the tectonic evolution of the Caribbean Basin (Fig. 8), and especially the submergent/emergent history of the component land fragments (see review in Graham, 2003a, 2003b). In the Forward to the *Decade of North American Geology*, Case and Dengo (1990, p. x) noted that, “Students and others unfamiliar with the region should remember that virtually every chapter would have had a different set of interpretative conclusions if a different set of authors had been selected. It has been

said that a new model for the tectonic evolution of the region has been formulated by each new worker in the region.” Donnelly (1989, p. 110) further noted that few of the biological-geological summaries published to that time “reflect the flavor of the controversy that dominates [as of the late 1980s] almost all aspects of the historical geological synthesis.” Nonetheless, considerable advances have been made on the broader picture in the last decade.

The models that have been proposed may be grouped into two broad categories. One emphasizes results from studies along the

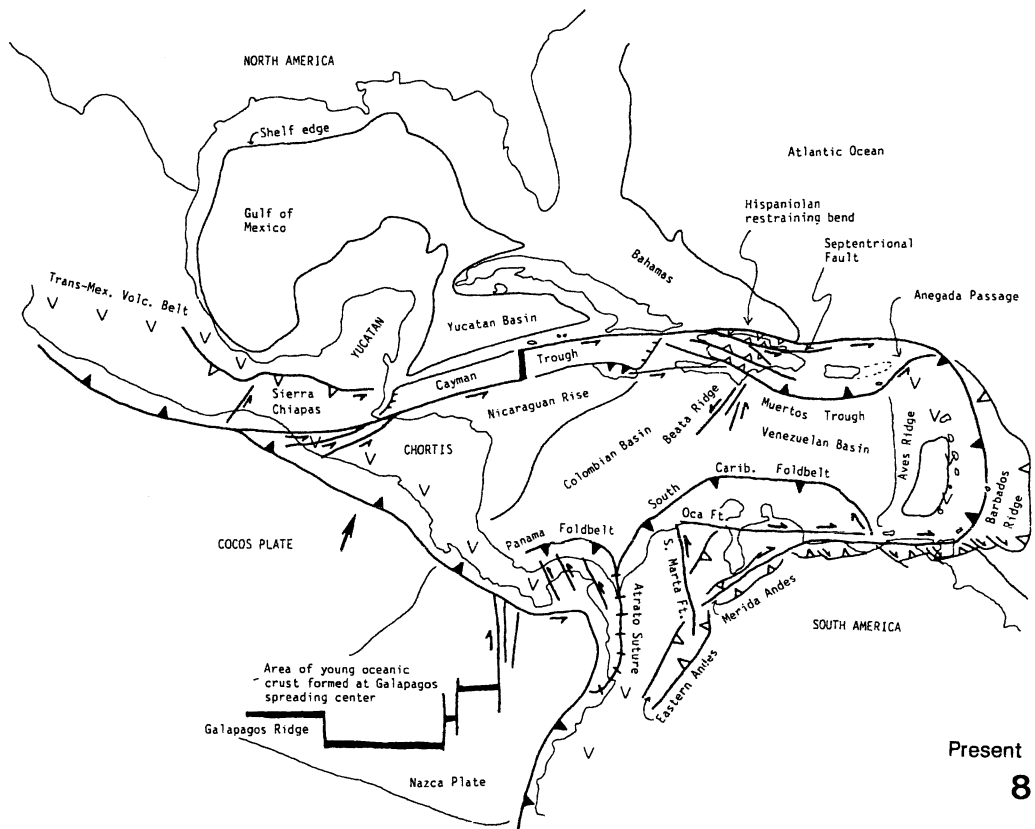


FIG. 8. Index map of the present geography and principal geological features of the Caribbean Basin and vicinity. (From Pindell & Barrett, 1990, used with permission; see also Iturralde-Vinent & MacPhee, 1999, fig. 1; Scotese & Sager, 1989.)

Motagua-Polochic fault system across northern Guatemala (Anderson et al., 1985; Burkart, 1978, 1983; Donnelly et al., 1990). Donnelly et al. (1990, pp. 54–55) noted with reference to the Guatemala faults that most recent authors “have all argued persuasively for about 130 km total offset. Anderson et al. (1985) challenged these estimates; they prefer a total offset of only “several kilometers.” Most workers [on this on-land segment of the North America-Caribbean plate boundary] favor the Burkart interpretation, and none favors a larger offset. Several lines of evidence point to 130 km of offset on the Polochic fault system and perhaps no more than a few tens of kilometers on the Motagua system.” By this “minimalist” view, the Caribbean plate and islands of the Antilles originated near their present positions and have been trans-

ported relatively short distances. However, a difficulty in assessing this model is that if the movement was more extensive (see below), there would not be any on-land markers to measure it by because the greater offset (e.g., 1000–1200 km) would be several times greater than all the exposed land area across Guatemala along the Motagua-Polochic fault zone (Pindell, pers. comm., 2001).

The other view is based primarily on observations along the off-shore Cayman Trough and fault systems around the margins of the Caribbean plate (Figs. 8–10). It envisions movement of the proto-Antilles 1000–1200 km from the eastern Pacific through a portal between North and South America (Hess & Maxwell, 1953; Freeland & Dietz, 1971; Malfait & Dinkelman, 1972; Wadge & Burke, 1983; Burke et al., 1984;

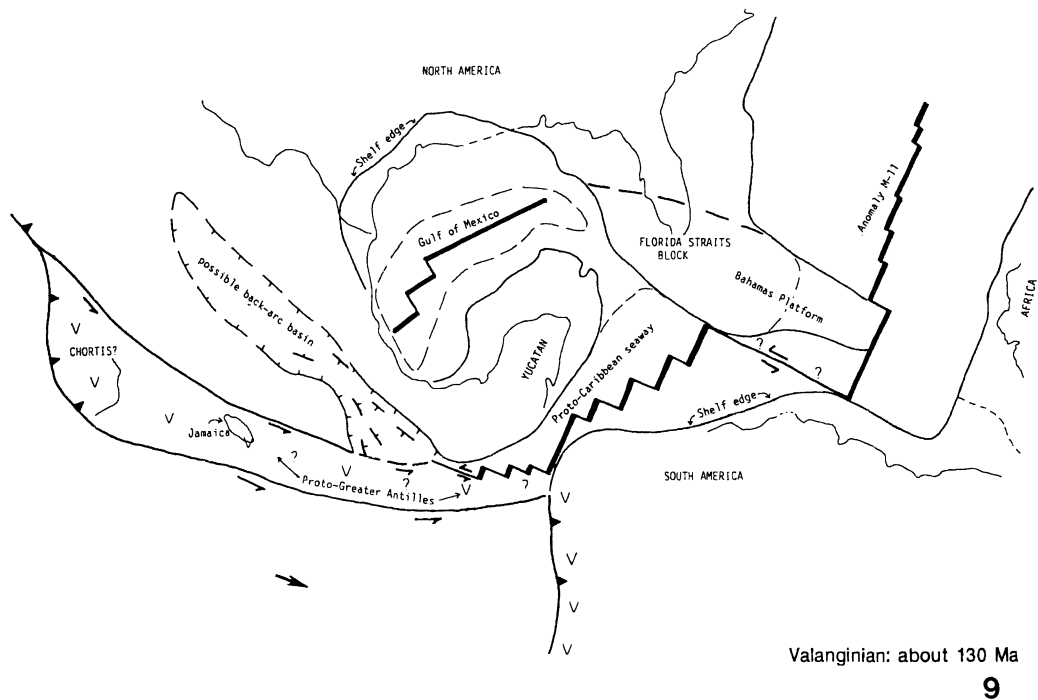


FIG. 9. The Valanginian stage (~130 Ma) in the tectonic evolution of the Caribbean Basin and vicinity. (From Pindell & Barrett, 1990, used with permission.)

Pindell & Barrett, 1990; Pindell, 1994; Iturralde-Vinent & MacPhee, 1999 and references therein). The issue is not fully settled (Mann, 1999, p. 16–18), and even among proponents of the more extensive-transport model there is not full agreement as shown by the 13 versions summarized by Pindell and Barrett (1990). Even so, there is recent convergence toward the model of Pindell and Barrett (1990; Pindell, 1994; Mann, pers. comm., 2000), and the options are either to select one for which supporting data are developing and use this as a working hypothesis, or to remain without any predictive tectonic model for Caribbean biogeography.

The plate tectonic history proposed by Pindell and Barrett (1990; Pindell, 1994) shows that during the Valanginian (Early Cretaceous, ~130 m.y.; Fig. 9) the Caribbean plate, including an island arc representing the proto-Greater Antilles, was developing in the eastern Pacific Ocean adjacent to the separating North and South American continents. According to Pindell

and Barrett (1990), Cuba, the Cayman Ridge, Hispaniola, Puerto Rico, and the Virgin Islands have similar Cretaceous-Paleogene histories, suggesting they belonged to the same arc system. At this time the proto-Greater Antilles were mostly submerged, although there is an unpublished report of land plants (*Gleichenites* Göpp., *Zamites* Brongn., *Phoenicopsis* Herr, *Yuccites* Mart., *Podozamites* (Brongn.) C. Braun, and others) from Neocomian (Early Cretaceous, ~145–130 Ma), deposits in Hispaniola (Smiley unpubl., cited in Kesler et al., 1991; Iturralde-Vinent & MacPhee, 1999, p. 19). However, these beds are overlain by marine deposits of Albian age (~112–97 Ma), and there is no compelling geologic evidence that North and South America were connected or near-connected by continuous land or extensive emergent islands in the Late Cretaceous.

The Caribbean plate moved through this portal between the continents as a result of both absolute eastward movement and relative motion as North America and South

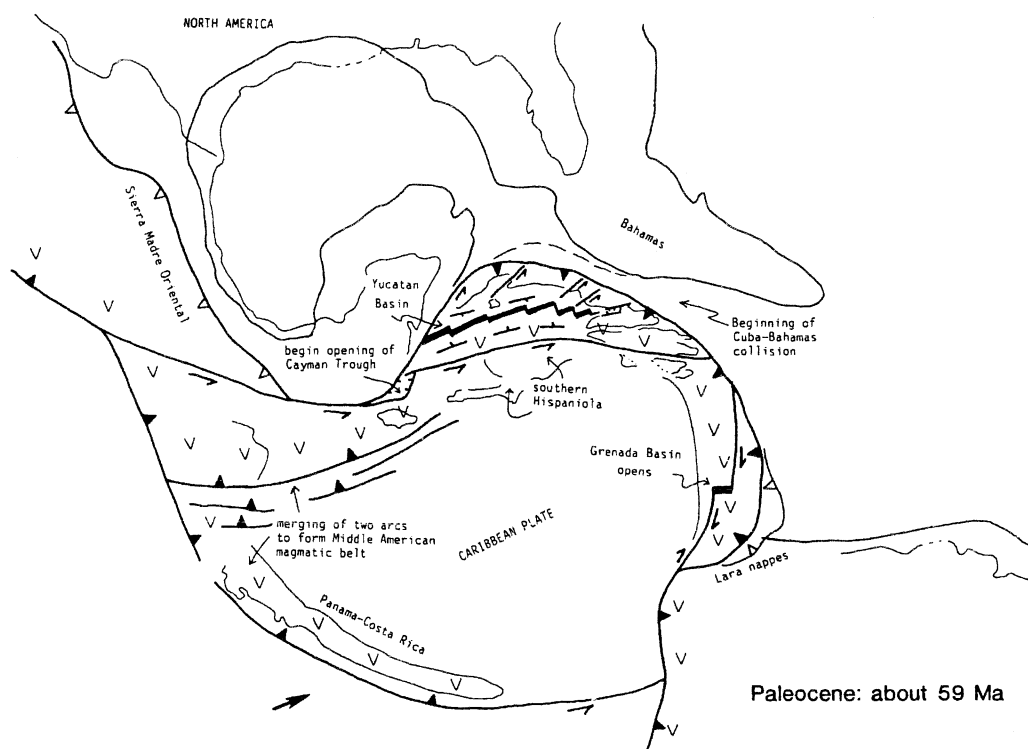


FIG. 10. The Paleocene stage (~59 Ma) in the tectonic evolution of the Caribbean Basin and vicinity. (From Pindell & Barrett, 1990, used with permission.)

America moved westward. In an older report (DeMets, 1990; cited in Meschede, 1998, and Gordon et al., 1997), the Caribbean plate was described as moving eastward at 1.3 cm/yr relative to South America and 1.1 cm/yr relative to North America. New evidence suggests eastward movements of 2.0 and 2.1 cm/yr, respectively. These values are most consistent with the extensive motions proposed in the Pindell and Barrett model (Pindell, 1994; Pindell & Barrett, 1990).

The frontal (east-facing) margin of the Caribbean plate began colliding obliquely (transpression) with the stable Jurassic-Cretaceous Bahamas Platform (the southeastern margin of the North American plate) between the late Paleocene and earliest Eocene (~56 m.y.) with fragments of western Cuba arriving first and followed progressively to the east by other islands of the Greater Antilles (Gordon et al., 1997). During this interval there may have been periods of emergence and submergence, but the

principal period of sustained emergence probably began with compression of the island arc against the Bahamas Platform in the middle Eocene (~49 Ma). According to Iturralde-Vinent and MacPhee (1999), "the existing Greater Antillean islands, *as islands*, are no older than Middle Eocene. Earlier islands may have existed, but it is not likely that they remained as such (i.e., as subaerial entities) due to repeated transgression, subsidence, and (not incidentally) the K/T bolide impact and associated megatsunamis. Accordingly, we infer that the on-island lineages forming the existing . . . Antillean fauna [and flora] must all be younger than the Middle Eocene." The relevancy of the bolide impact on the north coast of the Yucatán Peninsula at Chicxulub to the early biogeographic history of the Antilles and the time of origin of the existing biota is a cogent observation because, considering the horrific effects proposed for distant parts of the world (see Graham, 1999, pp. 65–68, 159–161), the devastation

in the immediate vicinity must have been extreme if not complete.

Running from the southwest to the northeast across Cuba is the Pinar Fault zone that separates the western and central part from the eastern part. North and west of the Pinar Fault zones the rocks appear to be part of the ancient Cretaceous arc. The Cauto fault zone (Cauto Basin) separates eastern from central Cuba, and may represent a suture line where eastern Cuba (with northern Hispaniola + Puerto Rico) was added to central/western Cuba in the early to middle Eocene. Another interpretation is that eastern Cuba was already part of the developing island by the Paleocene (Pindell & Barrett, 1990, plate 12E; Fig. 10). When proto-Cuba began colliding with the Bahamas Platform, the western and central parts were slowed first because of the curvature of the platform, while the eastern part continued to move eastward along the Cauto fault zone with drift of the Caribbean plate. In the Middle to Late Miocene western Cuba "achieved dryland contact with central Cuba after the disappearance of the Havana-Matanzas Channel" (Iturralde-Vinent & MacPhee, 1999, p. 35). Cuba has had an immensely complex geologic history, however, and it is likely composed additionally of "fragments assembled in the early Cenozoic that included everything from fragments of the Chortis Block [northern Guatemala to northern Costa Rica] to the Bahamas platform, including the newly formed ocean crust of the Yucatan Basin" (Donnelly, pers. comm., 2000). Western Hispaniola separated from Cuba in the early to middle Miocene (20–25 Ma), and southern Hispaniola was added on to the main island of Hispaniola in about the middle Miocene (~15 Ma; Fig. 10) with the contact represented by the Cul-de-Sac/Enriquillo Basin. Continued compression of Hispaniola against the Bahamas Platform produced the modern basins and ranges of that island by the Miocene (Gordon et al., 1997, p. 10,078). The Virgin Islands formed in the late Eocene, and the Lesser Antilles formed and were probably uplifted in the middle Eocene in the north and in the Oligocene to early Miocene toward the south. Puerto Rico was at or near its present

position in the late Eocene to early Oligocene (21–23 Ma) and separated from Hispaniola later in the Oligocene/early Miocene. Jamaica probably originated as a land fragment in the Chortis Block/Nicaraguan Rise region of Central America (Iturralde-Vinent, in press). It was transported eastward, and the presence of vertebrate fossils (ungulate mammal, iguanid lizard) indicates that it was emergent at the end of the late middle Eocene (MacPhee, pers. comm., 2000). However, for the interval between the middle Eocene through the late Miocene (49–10 Ma) sedimentary rocks on Jamaica are virtually all marine; i.e., there are few or no rocks of terrestrial origin (Lewis and Draper, 1990), indicating that the island was submerged. It re-emerged in the late Miocene (~10 Ma) and there is no conclusive geological evidence that after that time Jamaica was connected to any other land mass. Thus, the modern biota of Jamaica is of comparatively recent origin dating back only to the late Miocene (Buskirk, 1985). With this event the general configuration of the modern Greater Antilles was established.

By this scenario, emergent land between South America and North America involving the Antilles dates primarily from the middle to late Eocene; the land has been discontinuous in the form of islands, and intermittent from submergence/emergence events throughout the Cenozoic (viz., for the past 65 Ma). Development of the Isthmian land connection began in the middle Eocene; this is reflected in restriction of deep-water circulation between the Caribbean Sea and the Pacific Ocean as indicated by the history of silicate deposition (Donnelly, 1989). Land surfaces available for the interchange of terrestrial plants and animals developed between ~4.2 and 3.5 Ma, though there was still deep-water circulation through the Darien region of Panama; by 1.9 Ma continuous land and the exchange of terrestrial mammals between North and South America had occurred.

Vegetational History

In discussing the past vegetation and environments of the Greater Antilles, limited

use is made of the megafossil record because of the uncertainty of many identifications in this older literature. A revision of these floras would be a significant contribution to a better understanding of the vegetation. It is further noted that to trace the past record of extant vegetation it is necessary to establish the biological affinities of the fossils at least to the level of genus. This is possible with the plant microfossils (spores and pollen) mostly back to about the late to middle Eocene. Before that time, an increasing number of specimens differ in morphology from those of modern forms and they presumably represent extinct or biologically different taxa. For this reason a morphologically based nomenclature must be used for most pre-middle Eocene specimens (e.g., *Striatricolpites* Hammen), and ancillary information from independent sources becomes increasingly important.

The earliest reports of fossil plants from the Antilles (including the Lesser Antilles) are primarily of historical interest because the age and location of the sites are frequently unknown, many of the localities are no longer accessible, the preservation is often poor, and the identifications are questionable. They include Anonymous (1818; Antigua, wood), Felix (1883; "West Indies," wood), Galtés, 1887; (Puerto Principe, megafossil plant remains), and Stenzel (1897; Antigua, wood). Fossil algae and other microorganisms are described by Ayala-Castanares (1959; Haiti), Beckmann and Beckmann (1966; Cuba), Germeraad (1978c; Jamaica), Howe (1919; Lesser Antilles), Lemoine (1917; Martinique), Margolis and Rex (1971; Bahamas), and Rácz (1971; Jamaica). Fossil fungi are described by Germeraad (1979a, 1997b; Jamaica), Hibbett et al. (1997; Dominican Republic), Poinar and Singer (1990; Dominican Republic, amber), and Stubblefield et al. (1985; Dominican Republic, amber; see also Sanderson & Farr, 1960). There are also unpublished reports, abstracts, reviews, and descriptions of individual taxa including Brasier (1975), Den Hartog (1970), and Eva (1980) on sea grasses; Germeraad (1978a, 1978b; Jamaica), Graham (1972, 1974, 1977, 1978), Habib (1968; Puerto Rico), Hollick (1924, 1926a, 1926b,

1928a), Kaul (1943; Antigua, wood), Kumar (1981; Miocene, Trinidad), Leon (1929; Cuba), Loubiere (1940; Antilles, monocot wood), Maury (1930), Traverse and Ginsburg (1966; Bahamas), and Weinstein (1969; Puerto Rico). The present summary is based on terrestrial vascular plants from the principal plant microfossil floras of the Greater Antilles (Figs. 1, 2, 4–7; see Graham, 1973, 1979, 1982, 1986 for additional references).

CUBA

The material from Cuba comes from a well core drilled in Camagüey Province, eastern Cuba, and was provided by Alberto Areces-Mallea (pers. comm., 1993; Graham et al., 2000; see also Areces-Mallea, 1985, 1988, 1989). The sediments are part of the Saramaguacán Formation and are middle Eocene in age (~45 m.y.). By the geologic scenario presented earlier, this was the interval when western/central Cuba was colliding with the Bahamas Platform, and was probably the time of principal emergence for these parts of the Greater Antilles. In total, 46 plant microfossils were recovered and because of limitations imposed by the age of the flora previously discussed, an artificial system of nomenclature is used. Nonetheless, there are two aspects of the paleoenvironments of Cuba that can be addressed from study of the Saramaguacán material. One is a general characterization of the middle Eocene climate that prevailed in Cuba and presumably on other islands of the region. The most abundant palynomorph is *Arecipites* Wodehouse, a member of the Palmae. This palynomorph constitutes 50.5% of the assemblage, which is augmented by fern spores and possibly *Bursera* Jacq. ex L., *Celtis* L., *Crudia* Schreb. (a genus primarily of tropical lowlands), Bombacaceae, Malvaceae, Moraceae, Myrtaceae, and Nyctaginaceae. The composition of the flora suggests a tropical climate but within that broad range a more precise characterization is precluded by the low resolution of the identifications. However, when the flora is considered in the context of the global paleotemperature curve (Fig. 3), it is evident that temperatures were near

TABLE III
GEOGRAPHIC OCCURRENCES OF THE MOST ABUNDANT PALYNOMORPHS IN THE MIDDLE EOCENE SARAMAGUACÁN
FLORA, CUBA

Taxon	%	NA	SA	W	E?
<i>Arecipites</i>	50.5			x	
<i>Bobmacacidites</i> cf. <i>tillioides</i>	9	x			
<i>Retitricolpites</i> type 2	8				x
<i>R.</i> type 4	7				x
<i>R.</i> type 3	4.5				x
<i>Malvacipollis tschudyi</i>	6	x			
<i>Triporopollenites</i> type 2	5.5			x	
<i>Echitricolpites</i>	3.5				x
<i>Drosopollis</i> cf. <i>striata</i>	1.5	x			
<i>Retitricolporoides</i> type 2	1.5			x	
<i>Lymingtonia</i> cf. <i>rhetor</i>	1	x			
<i>Retimonocolpites</i> type 5	1				x
<i>R.</i> type 1	0.5		x		
<i>Retitricolporites</i> type 1	0.5			x	
Total percentage	100				
Other taxa		12	0	14	6
Total taxa		16	1	18	11

Percentages are based on a count of 200 specimens. The distribution of taxa not encountered in the tabulation is summarized at the bottom of the table. (NA = North America; SA = South America; W = widespread; E? = endemic?).

their maximum for the Cenozoic. Atmospheric physics generally associates warm temperature with high moisture and increased precipitation because of greater evaporation from the ocean surface. Barring extensive orographic deflection of moisture-laden winds by extensive mountain systems, continentality (precluded by the insular nature of the Antilles), a major shift in the position of the descending arm of the Hadley atmospheric convection cell or the subtropical jet stream, or redirection of the northeast trade winds, the collective evidence suggests that overall warm, moist tropical climates prevailed in the region. This does not mean that local drier habitats did not exist as a result of slope, exposure, or edaphic factors. Also, ash from extensive volcanism sets the successional clock back to barren ground and provides a temporal, shifting mosaic of restricted, open, drier sites possibly reflected by the presence of grasses and perhaps *Celtis*(?) pollen in the Saramaguacán flora (see Graham, 1999, pp. 56–60, 256–257 and references therein for the effects of volcanism on plant and animal, especially ungulate, communities in the western United States).

Another aspect of Cuba's biotic and geologic history that can be addressed by data

from the Saramaguacán flora is the geographic affinities of the Eocene vegetation. This is of interest because of the unsettled tectonic history of the region. In the early literature the Greater Antilles were often depicted wherever it was convenient for solving a particular biogeographic problem for an individual taxon regardless of the problems this may have created in explaining the distributions of other groups, or the geophysical improbabilities of the placements. For example, Corral (1939) showed Cuba and the other islands of the Greater Antilles located along the north coast of South America as recently as the Miocene (see Borhidi, 1996, p. 257) and Vandel (1973) used this paleogeography to explain similarities in vertebrate faunas between Cuba and South America. Although there are a number of models available, none place the Greater Antilles immediately adjacent to northern South America during the last 65 m.y.

In Table III the most abundant palynomorphs from the Saramaguacán assemblage are listed along with their occurrences in other paleofloras surrounding the Caribbean Basin. The taxa shown are representative of the affinities of the total flora and a complete listing is given in Table II and in Gra-

ham et al. (2000). Of the total 46 palynomorphs recovered, 18 are widespread, 16 are similar to ones known elsewhere from land belonging to the North American plate (the southeastern United States, the Burgos Basin of northeastern Mexico) or the Caribbean plate (Jamaica, Panama), 11 are unique to the Saramaguacán flora (possibly reflecting paleoendemism), and only one (*Retimonocolpites* Pierce, type 1) is found elsewhere (only in South America). In the middle Eocene (45 Ma) the interchange of plants of the Greater Antilles lacking means of long-distance dispersal was primarily with vegetation of adjacent North and Central America.

Areces-Mallea (1990) has reported *Basopolis* Pflug from the Saramaguacán Formation. *Basopolis* belongs to the Normapolles group of fossil pollen forms that are characterized in part by the complex structure of the apertures. Their affinities are unknown but they may represent extinct members of the Juglandales. The distribution of the Normapolles group is stratigraphically from the Cretaceous to the early Oligocene and geographically from eastern North America eastward to Europe. It defines the Normapolles province and is a further indication of the primarily North American affinities of the Paleogene vegetation of Cuba. Such affinities argue against any extensive land connection between the Greater Antilles and South America during the early Cenozoic.

JAMAICA

A small assemblage of plant microfossils is known from the late middle Eocene Guys Hill (Chapelton) Formation of Jamaica (Graham, 1993, then cited as a member of the Chapelton Formation; Tables I, II). The fossils represent vegetation that grew on the island during the Eocene but was subsequently eliminated by inundation. The composition of the Guys Hill flora is consistent with the tropical nature of the Caribbean climate during the Paleogene as suggested by the Saramaguacán flora and the paleotemperature curve. The presence of pollen of the mangrove *Psilatricolporites crassus* Hammen & Wijmstra (*Pelliceria* Planch. &

Triana), however, indicates a coastal brackish water depositional environment different from the fresh water marsh and swamp setting for the Saramaguacán flora. Nonetheless, *Deltoidospora* Miner (cf. *Acrostichum* L.), *Arecipites* Wodehouse (Palmae), and *Bombacacidites* Couper (Bombacaceae) occur in both floras reflecting a general similarity in the Eocene tropical vegetation throughout the Caribbean region.

HAITI

Berry (1923) reported megafossil plants from several localities of undetermined Tertiary age (∞ in Fig. 1, and a Mio-Pliocene spore and pollen assemblage of 25 taxa is known from near Mirebalais (Graham, 1990b; Tables I, II). In another study, a core 72 cm long was drilled through sediments of Lake Miragoane on the north side of the southern peninsula and analyzed for spores and pollen (Binford et al., 1987; Brenner & Binford, 1988; Higuera-Gundy, 1989). The lower part (58–30 cm) records pre-Columbian dry mesic forest at 1000–500 B.P. The upper part (500 B.P. to the present) reveals two periods of deforestation represented by a decrease in forest types and an increase in the pollen of weeds. One of these is between 30 and 10 cm (A.D. 1500–1800) at the time of Spanish (A.D. 1500–1700) and French (A.D. 1700–1800) occupations. During the interval represented by the 6–8 cm sediments there is an increase in tree pollen, suggesting brief reestablishment of the forest. This corresponds to the time when Haiti gained independence from France (1804) and small subsistence farms replaced large plantations. The pollen spectrum from the 6–0 cm zone (the past century) records increased human activity and forest decline.

DOMINICAN REPUBLIC

Plant megafossils of Tertiary age from the Dominican Republic include those studied by Berry (1921) and the fungi mentioned earlier from the amber deposits. The age of the amber is late early Miocene to early middle Miocene (15–20 Ma; fide Iturralde-Vinent & MacPhee, 1996). In addition, Gómez P. (1982) described the fern

Grammitis succinea L. D. Gómez P. from the amber. Huber and Langenheim (1986) reported *Hymenaea* L. with affinities to the African species *H. verrucosa* Gaertn. (the source of the amber), along with the leafy liverworts *Bazzania* S. F. Gray, *Frullania* Raddi, and *Drepanolejeunia* (Spruce) Schiffner; the moss *Octoblepharum* Hedw.; and a mimosoid flower. The flower has been identified as *Acacia* Mill. and described as *A. eocaribbeanensis* Dilcher, Herendeen and Hueber (Dilcher et al., 1992).

PUERTO RICO

By the middle Oligocene (~29 Ma) Puerto Rico had collided with the Bahamas Platform and the San Sebastian Formation was deposited on the eroded surface of the fold belt (Mann, pers. comm., 2000). There had been a significant lowering of global mean annual temperature (MAT; Fig. 3) from the early Eocene global maximum (Huber et al., 2000; Schmitz et al., 2000). Glaciers appeared on Antarctica by the middle to late Eocene, cooling temperatures reduced evaporation from ocean surfaces with concomitant expansion of seasonally dry climates and drier forest types, and continued uplift from tectonic forces produced more temperate upland habitats in the Greater Antilles. This climatic and topographic diversity allowed for a greater variety of vegetation to exist on the island. The communities included mangroves (*Pelliceria*, *Rhizophora*), low and middle elevation tropical vegetation (*Cnemidaria* C. Presl., *Bombacaceae*), vegetation of drier open habitats (*Acacia*, *Bursera*), and upland temperate plants (*Podocarpus* L'Hér. ex Pers., *Aflaroa* Standl., *Oreomunnea* Oerst.). Study of the San Sebastian flora also allows one refinement in the geologic reconstruction of Puerto Rico. Lewis and Draper (1990) note that subsidence took place in two phases between the middle Eocene and middle Oligocene, then between the middle Oligocene and Pliocene: "Most of Puerto Rico was probably submerged during the whole of this time" (p. 120). However, allowance must be made for an extensive terrestrial paleoflora in the middle Oligocene of ~165 morphological types of spores and

pollen representing lowland to highland vegetation (see also Iturralde-Vinent & MacPhee, 1999).

Revision of the San Sebastian flora, and taxonomic/biogeographic studies incorporating new molecular techniques on extant analogs (phylogeography), will be necessary to adequately establish the geographic origins of the flora. However, using the methodologies of the day, Raven and Axelrod (1974) suggest that a number of genera in the San Sebastian flora are of South American origin. These may have arrived by chance long-distance dispersal, used a fragmented Central American/Yucatán/Cuban route, followed a pathway through the Lesser Antilles (emergent by the middle to late Eocene), resulted from fragmentation of a more extensive land mass (vicariance), or possibly migrated along a recently proposed route involving the now submerged Aves Ridge (see later section). The genera listed by Raven and Axelrod (1974) are *Podocarpus*, *Acacia*, *Aethanhus* (Eichler) Engl., *Bombax* L., *Brunellia* Ruiz & Pav., *Casearia* Jacq., *Catostemma* Benth., *Chrysophyllum* L., *Corynostylis* Mart. & Zucc., *Eugenia*, *Famea* Aubl., *Guarea* F. Allam. ex L., *Jacaranda* Juss., *Marcgravia* L., *Norantea* Aubl., *Pelliceria*, *Pleodendron* Tiegh., *Rauwolfia* Gled., *Tecoma* Juss., and *Tetrorchidium* Poepp.

Wendt (1993), in an analysis of the origin of rain forest canopy trees in Mexico, gives examples of plants likely of South American origin that migrated into Mesoamerica directly from South America (as opposed to following an African-Laurasian route from the north). He divided these into those of probable recent (Neogene) arrival and those already present in North America by the Paleogene, based on fossil records and modern distribution/diversity patterns. In the following lists I have used the symbol (f) to indicate that the taxon is known from the fossil record of the Greater Antilles (Table II), and (m) to indicate that it occurs in the modern vegetation of the Greater Antilles. Included in the category of relatively recent arrivals in Mesoamerica are *Dialium guianense* (Aubl.) Sandwith, *Terminalia amazonia* (J. F. Gmel.) Exell (m, genus), *Symphonia globulifera* L. f. (m), and species of

Cecropia Loebl. (m), *Couepia* Loebl., *Pseudolmedia* Trécul (m), *Vatairea* Aubl., *Virola* Aubl., *Vochysia* Aubl., *Coussapoa* Aubl., *Eschweilera* Mart. ex DC., *Hernandia* L. (m), *Licania* Aubl., and *Pera* Mutis. Thus, none of those estimated to have arrived in Mesoamerica only in the Neogene are known from Eocene floras of the Greater Antilles. More ancient arrivals were *Catostemma* (f), *Crudia* (f, m), *Eugenia* (f?, m), *Glycydendron* Ducke, *Inga* Mill. (m), and *Licania* Aubl. (m); three of these are known from the Paleogene of the Greater Antilles. There does appear to have been a greater representation of South American genera in Puerto Rico in the middle Oligocene than in Cuba in the middle Eocene. In addition to being consistent with Wendt's overall estimates of arrivals in the region, this observation further suggest that, during the Eocene, the interchange of plants lacking capacities for long distance dispersal was primarily within the Antilles, Central America, and adjacent North America, and increasingly with northern South America by the Oligocene. This is obviously due in part to the time interval (11 m.y.) available for additional gradual migration and abrupt chance dispersal; probably a net increase in land surfaces (target areas); and greater topographic, climatic, and habitat diversity to accommodate new arrivals. In contrast, the distance between the Greater Antilles and South America was increasing, and near-continuous land surfaces through the Panama region would not develop until between ~4.2 (end of deep to mid-depth water circulation between the Caribbean Sea and the Pacific Ocean) and 1.9 Ma (terrestrial mammal interchange across the Isthmus; Burnham & Graham, 1999; Coates, 1997; Graham, 1992; Jackson et al., 1996; Stehli & Webb, 1985). The importance of these two sets of contrasting events for migration depends on the dispersal potential of each taxon. Nonetheless, it is clear that the increased biotic interchange between the Greater Antilles and South America, suggested by the middle Eocene Guys Hill (Chapelton) flora to the middle Oligocene San Sebastian flora, would be facilitated by a greater extent of land surfaces. A proposal for this recently has been presented based

on fossil land mammals from Cuba and Puerto Rico.

Iturralde-Vinent and MacPhee (1999) interpreted geological and terrestrial vertebrate faunal evidence to suggest a land connection between the Greater Antilles and northwestern South America for a brief interval at the Eocene-Oligocene transition (35–32 Ma). This was during a period of increasing land surfaces called the Pyrenean uplift, a global event, that further corresponds to a general fall in sea level marking early continental glaciations on Antarctica. Stratigraphic sections from the Greater Antilles are read to indicate a minimum of marine sediments and widespread terrestrial deposits at this time (but see Lewis & Draper, 1990). Iturralde-Vinent and MacPhee (1999) believe that for a period of ~3 m.y. or less there was a greater extent of land than perhaps in all of the Cenozoic up to modern times. The Aves Ridge was exposed and formed a landspan ("A subaerial connection between a continent and one or more offshore islands," p. 3). They conclude that "the landspan model is consistent with most aspects of Antillean land-mammal biogeography as currently known; whether it is consistent with the biogeography of other groups remains to be seen." However, much deep-sea drilling indicates that the Caribbean Sea was deep water at this time (Donnelly, pers. comm., 2001), and the meager paleobotanical evidence is equivocal. Undoubtedly vigorous assessment of the model will be forthcoming from geologists and from taxonomic specialists in the various plant and animal groups.

Dispersal "Versus" Or Dispersal "And" Vicariance

There is a considerable literature on the means by which organisms have become distributed throughout the lands of the Caribbean Basin. The early view was that all migration was by dispersal (movement of organisms) based on the prevailing assumption that the position of the continents and ocean basins was permanent. With the acceptance of plate tectonics it became apparent that organisms also could be distributed through vicariance (fragmentation and

movement of land; Cox, 1998; Crother & Guyer, 1996; Hedges, 1996; Hedges et al., 1994; Kluge, 1988; Nelson & Platnick, 1980, 1981; Nelson & Rosen, 1981; Page & Lydeard, 1994; Platnick & Nelson, 1978; Pregill, 1981; Ronquist, 1997; Rosen, 1976, 1985; Wiley, 1988). The study of these two modes of distribution became broadly categorized as dispersal biogeography and vicariance biogeography although Morrone and Crisci (1995) propose a more detailed subdivision into dispersalism, phylogenetic biogeography, panbiogeography, cladistic biogeography, and parsimony analysis of endemism. Implied in both dispersal and vicariance is that segments of a population may become geographically and reproductively isolated resulting in the subsequent production of novel genotypes and phenotypes; viz., they constitute mechanisms for evolution and speciation. The acknowledgment of genetic isolation has forged a new coalition among the fields of molecular systematics, cladistics, and biogeography. Among the emerging results of this coalition are an improving taxonomy through the recognition of monophyletic groups; more biologically valid patterns of distribution, disjunction, and endemism; and the formulation of area cladograms as a means of detecting the site of ancestral populations and the direction of their subsequent migration and differentiation. Also, the unsettled issue of molecular clocks is being used to estimate the time of divergence (Hedges et al., 1992, 1994; Page & Lydeard, 1994). If successful, this will allow a comparison between the time of divergence and the time of land separation to assess whether the two events are causally related. It has been suggested that area cladograms might prove of further importance if concordant dispersal patterns suggest connections between islands previously undetected from geologic evidence (Page & Lydeard, 1994). Although this is theoretically possible, in my opinion the principal basis for reconstructing the physical history of the Caribbean Basin will continue to be geophysics and related geological disciplines (e.g., Gordon et al., 1997; Pindell & Barrett, 1990; Pindell, 1994); biogeographic models will

mostly have to accommodate the results obtained by the other disciplines.

Another important aspect of vicariance is that by identifying an alternative means of distribution, dispersal explanations must be examined critically rather than casually offered as the means by which any organism gets anywhere. To this end, systematists have been encouraged to produce more phylogenetic studies of endemic taxa (Nelson & Platnick, 1980, p. 342), present the results in the form of species cladograms, examine the species cladograms from different groups for repeated patterns of geographic relationships, and summarize the results as area cladograms. In comparison with certain animal groups like *Anolis* Daudin (lizards) and *Eleutherodactylus* Cochran & Goin (frogs), few plant taxa have been investigated from this standpoint and the Antilles would be an ideal setting for such studies. Endemism is a notable feature of the vegetation. For example, Borhidi (1996, p. 216) estimates the number of endemic plants on Cuba at 3178 or 49.9% of the total flora (53% of the native flora), and Howard (1973) lists 40 plant genera found only on Cuba. Also, the region is tectonically active with continents and land fragments having separated and collided throughout the late Cretaceous and Cenozoic.

Identifying the roles of vicariance and dispersal in the distribution of individual taxa in such a dynamic setting will require cooperative efforts and continued refinements in the vicariance method. However, early discussions of vicariance biogeography were often presented in a mode that required a choice be made as to which was more important; i.e., dispersal "versus" vicariance biogeography. "Croizat et al. (1974: 278) stated that: 'Vicariance is, therefore, of primary importance in historical biogeography, and dispersal is a secondary phenomenon of biotic distribution'" (Hedges et al., 1994); "The best first-order explanation for an observed disjunct distribution between sister groups is that it represents a fragmentation of a widespread ancestral species, rather than a dispersal phenomenon from a more restricted "center of origin" (Wiley, 1988); dispersal events

have been grouped together as “haphazard processes” resulting from “organisms moving restlessly about” (Rosen, 1976); and dispersal biogeography has been characterized as “a science of the improbable, the rare, the mysterious, and the miraculous” (Nelson, 1978). The synergy necessary to expand participation and improve the methodology is delayed by such pronouncements and the seemingly inevitable need to canonize new approaches. With reference to dispersal over water, dispersal across land connections, and vicariance, Iturralde-Vinent and MacPhee (1999) note that “it seems inescapable that all three were involved in the formation of the Antilles land-mammal fauna. . . .”

For plant studies several problems need further attention to encourage broader participation, gradually improve the theoretical basis of the approach, and provide further convincing evidence of its success. One such problem for vicariance biogeography is the inconvenience of the fossil record. If vicariance is to account for the distribution of a given group of organisms, the organisms must have been present in the region prior to the fragmentation of the land. The fossil record indicates that the appearance, evolution, and migration of organisms, as well as vicariance events, are not consistently coordinated with regional tectonic events (Donnelly, 1990, pp. 607–608); hence, it is tempting to try to minimize the importance of the fossil record if, for some reason, vicariance must be elevated to “primary importance” in historical biogeography. This can be done by observing that fossils give only a minimum rather than a maximum age for a taxon (Rosen, 1985) and by then applying this truism to the fossil record generally. In this manner the fossil record is made irrelevant, and any inconsistencies between geohistory and biohistory are explained away. However, in some instances fossils of a group are abundant, and their record is sufficiently consistent throughout the Caribbean region that it can be taken to reflect an accurate history. For example, pollen of *Rhizophora* is consistently absent from northern Latin America in sediments older than the late Eocene (e.g., Guys Hill, Saramaguacán, Burgos Ba-

sin, Los Cuervos, Mirador), but it is widely present in deposits of late Eocene (Gatuncillo) and younger age (San Sebastian; Graham, 1995). Similarly, in the Gulf/Caribbean region mid- to high-spine pollen of the Compositae first appear in the Oligocene and become abundant in the Miocene, while more ornate types are found only in Miocene and younger sediments (Graham, 1996). These and other palynomorphs have such a regionally to globally consistent range that they find practical use in the petroleum industry for zonation and stratigraphic correlation. In contrast, the pollen of *Psilatricolporites crassus* Hammen & Wilmstra (*Pelliceria*) is known from the oldest pollen-bearing Tertiary formations in the Caribbean region (middle Eocene) and, therefore, its initial appearance is unknown. The fossil record is uneven but there are instances where it can be used to indicate with a high degree of probability the time of appearance of a taxon in relation to a tectonic event. If both the fossil record and molecular clocks are summarily dismissed, some inconveniences to the vicariance methodology are removed along with a bit of its credibility.

Another point that needs to be assessed further is the possibility of multiple origins for some concordant distribution patterns. If the ancestral forms of several different taxa are found on one land mass and the derived forms consistently found on another, vicariance may likely be the explanation because dispersal would probably produce a more random distribution. This assumption becomes even more convincing when dispersal is objectively considered as a possibility. In the Antilles the directional flow of winds (from the northeast) and ocean currents (mostly toward the north), pathways of bird migration, and hurricane tracks theoretically can produce similar patterns among unrelated groups. As noted by Page and Lydeard (1994), “concordant dispersal patterns also can explain congruence between phylogenetic relationships and geologic history.”

An issue of theoretical concern is raised by Ronquist (1997): “In the classic vicariance scenario, a widespread ancestor speciates by responding to successive subdi-

visions of its distribution range. This scenario implies that ancestral species were generally more widespread than their descendants. We can escape this paradox by allowing successive dispersal events that counter the decrease in distribution range caused by vicariance." This creates a very fine line between vicariance and dispersal as a credible means of achieving isolation in the first place.

Another area that constantly needs to be reviewed with reference to vicariance events is the immensely complex geologic history of the Caribbean region. Rosen (1976) followed the model of Malfait and Dinkelman (1972), and later (Rosen, 1985) those of Pindell and Dewey (1982), Sykes et al. (1982), and Wadge and Burke (1983). The relevancy of this unsettled geohistory to vicariance and the biohistory of the Caribbean region is manifest. The early versions of the mobilist model (e.g., Malfait & Dinkelman, 1972) were used in the early studies on vicariance (e.g., Rosen, 1976) to show an arc of continuous or nearly continuous land through the present Isthmian region connecting or nearly connecting North and South America. Subsequently this land mass detached, fragmented, and reached an eastern position to constitute the Greater Antilles. The Isthmian region later became continuous land through the compressive uplift and coalescence of another volcanic island arc. This would be an ideal history for vicariance events because a land segment was first connected or nearly so to two continents, then separated, then fragmented into islands. The movement of proto-Cuba from the eastern Pacific to the southern margin of the Bahamas Platform in the Eocene, and the subsequent separation of Hispaniola (+Puerto Rico), are examples of this history. However, in the most recent models the Antilles are depicted as originating as islands, mostly submerged until the Eocene (or re-submerged, as with Jamaica), and not as a near-single unit directly connected to continental land masses. This would argue for a greater role for dispersal in the movement of organisms in the Greater Antilles throughout their history (see e.g., Malone et al., 2000 with reference to the rock iguana *Cyclura* Harlan). Iturrall-

de-Vinent and MacPhee (1999, p. 3) note that "Typically, the historical biogeography of the Greater Antilles is discussed in terms of whether the fauna was largely shaped by strict dispersal or strict continent-island vicariance. Continent-island vicariance sensu Rosen appears to be excludable for any time period since the mid-Jurassic. Even if vicariance occurred at that time, its relevance for understanding the origin of the modern Antillean biota is minimal." They further note (p. 39) that in the early vicariance model (Rosen, 1976, 1985) the islands of the original Cretaceous arc are identified too closely (e.g., "the same," "transported original archipelago") with the present islands. The radiation of chameleons out of Madagascar, also by dispersal and involving oceanic islands (Raxworthy et al., 2002), is instructive in that what was once interpreted as an excellent example of vicariance is now interpreted as an excellent example of dispersal.

These observations symbolize two factors that continue to complicate an understanding of the origin(s) of biogeographic patterns in the region; namely, collision/separation of land fragments and the timing of these events, and the poorly known emergent-submergent history of these fragments. Just as cladistics does not handle hybridization well, vicariance biogeography does not handle well the collision of lands that bring together once isolated populations. The complex submergent-emergent history of the Caribbean islands is illustrated by that of Jamaica. As noted previously, there are few sediments of terrestrial origin known from the middle Eocene to the late Miocene (42–10 Ma) in Jamaica. The middle Eocene vegetation represented by plant microfossils from the Guy's Hill Formation was mostly destroyed by inundation. The biota had to be replenished by dispersal because there is no geological evidence that Jamaica was ever connected to other lands after the middle Miocene. The problem includes more than just Jamaica because as Donnelly (1989) notes, "A large part of the problem is that geologists do not address some of the questions that biologists need for their analyses. To a geologist it is relatively unimportant if an island arc is broad-

ly emergent or mainly submergent, whereas the biologist is vitally interested in that information.” The lack of these data, along with the unsettled details of the tectonic history, make it difficult to document geologic events with the certainty and precision required for vicariance biogeography.

A case in point is the plant genus *Haitia* Urb. (Lythraceae) that is endemic to Hispaniola and is likely derived from *Ginoria* Jacq. (S. Graham, pers. comm., 2000). There are several species in Cuba and two in Haiti. Hispaniola separated from Cuba in the early to middle Miocene and this is consistent with derivation of *Haitia* from *Ginoria* through vicariance. However, there is no evidence from the fossil record that either *Ginoria* or *Haitia* were present on either Cuba or Hispaniola at the time of separation, and the seeds of both are minute and easily dispersed by a variety of vectors (Cuba is presently separated from Hispaniola by the Windward Passage 72 km wide). Either dispersal (probably) or vicariance (possibly) can account for the isolation and subsequent differentiation of *Haitia*. Such situations probably apply to the majority of plants in the Greater Antilles, and although both modes of distribution presently remain viable options, the emerging geologic history of the Caribbean region is consistent with dispersal as a prominent means of migration, isolation, and speciation among plants of the Antilles.

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