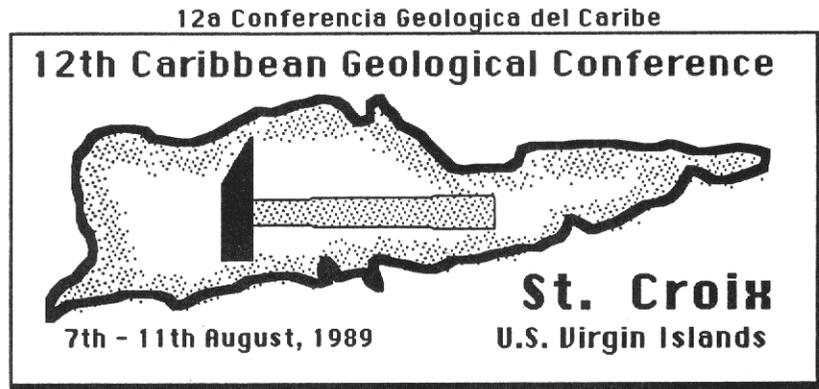


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## PRELIMINARY REPORT ON A LATE TERTIARY PLANT MICROFOSSIL ASSEMBLAGE FROM HAITI

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## ABSTRACT

Twenty-five fossil pollen and spore types have been recovered from the late Tertiary Artibonite flora of Haiti. These are monolete fern spore (36%), Alsophila (6%), Pteris types 1-3 (type 1 = 11%), cf. Antrophyum, trilete fern spore (types 1, 2), Pinus (16%), Palmae (types 1, 2), Hygrophila, Chenopodiaceae/Amaranthaceae, Compositae (types 1-4; 9%), Alchornea, Alfaroa/Oreomunnea, Oryctanthus, Malpighiaceae, Allophylus, and unknown types 1-3. The principal vegetation types suggested by the fossil flora are pine forest and cloud forest, with a fern marsh bordering the depositional basin. Communities of drier to arid aspect, savannas, and high altitude vegetation are not represented. The age of the flora is estimated as late Miocene to possibly middle Pliocene. Annual temperatures ranged between about 23-26° C at 400 m elevation, and 17-19° C at elevations of about 1,400 m. Annual rainfall is estimated at about 1,300 ml and was seasonal. The affinity of the flora is distinctly North American, consistent with plate tectonic models showing the proto-Greater Antilles located off southwestern Mexico during the early Tertiary and moving eastward at an average rate of 2-3 cm/yr. The development of South American affinities, other than by long-distance dispersal throughout the Cenozoic, was facilitated in later Tertiary times by eastward movement away from Mexico/proto-Central America and emergence of the Lesser Antilles in the Eo-Oligocene.

## INTRODUCTION

In the early 1900's the United States Geological Survey carried out field studies in Hispaniola under the direction of T. Wayland Vaughan. The Haitian phase of the project was supervised by W. P. Woodring, and in 1920 and 1921 he made collections of fossil plants from 13 localities which were sent to E. W. Berry for study. The specimens were few in number and generally fragmentary and poorly preserved, but from them Berry (1923) identified nine species (Table 1). Almost all of the better preserved specimens came from a locality designated W 185 F (station 7544). The location is given as "Department de l'Ouest, cut along road from Mirebalais to Las Cahobas, on north side of ravine at foot of mountain on north side of gap. W. P. Woodring, collector. January 8, 1921" (Berry, 1923, p. 2; Fig. 1). In 1981 permission was granted to remove small pieces from the outer matrix of the Haiti specimens, presently in the collections of the Smithsonian Institution, for pollen and spore analysis. A small assemblage of fair diversity and preservation was recovered. The flora is considered important, nonetheless, because it is the first paleopalynological study for Hispaniola, and provides the only paleobotanical information for the island since the publication of Berry (1923).

## MATERIALS AND METHODS

Small pieces from the outer matrix were broken off and scraped clean to remove contaminants and oxidized plant microfossils. The material was then broken in a mortar and pestle, transferred to 400 ml Nalgene beakers, and placed in HCl for one hour for removal of carbonates, overnight in HF for removal of silicates, and for one hour in HNO<sub>3</sub> for oxidation of organic debris. The samples were centrifuged for 4 minutes at 1,400 rpm in 150 ml Nalgene centrifuge tubes and washed four times with distilled water between each acid treatment. The material was then acetolyzed (nine parts of acetic anhydride to one part concentrated H<sub>2</sub>SO<sub>4</sub>) for three minutes in a water bath at ca. 85° C, preceded and followed by rinses in glacial acetic acid, and treated with 10% KOH at ca. 85° C for three minutes for final breakdown of organic debris. After the final centrifuging, the tubes were inverted and allowed to drain for four hours. Warm (melted) glycerine jelly was then added (about twice the amount of jelly for the amount of material in the centrifuge tube), stirred, two drops placed on a slide on a warming table, a cover slip added, and the slides allowed to cool to solidify the jelly. The slides were labeled (Haiti, Miocene, Berry specimen, Smithsonian, USGS 7544-station 185, and slide number), and sealed with CoverBond. The specimens were photographed with a Leitz Orthoplan microscope with automatic camera using Panatomic X film. Location of the specimens on the slides is by England Slide Finder coordinates (e.g., N-25). All materials are deposited in the palynology collections at Kent State University.

## RESULTS

The ferns are represented in the Artibonite microfossil flora by eight kinds of spores, including two unknowns (Table 1). Laevigatisporites (Fig. 2) is a smooth, reniform spore produced by many genera in at least three families- Blechnaceae, Polypodiaceae, and Pteridaceae. Laevigatisporites ranges from Paleozoic to Recent, and is of limited stratigraphic or paleoecologic value. Three kinds of Pteris spores are present, and the most common form is illustrated in Fig. 3. Pteris is a genus of ferns, with three species in Hispaniola having spores similar to the most abundant fossil specimens (Fig. 3), P. podophylla Sw., P. stridens J. G. Agardh, and P. tripartita Cav. (Mickel, pers. comm., 1989). Judd (1987) lists two additional species growing on Haiti, P. hispaniolica Maxon and P. longifolia L. Pteris stridens occurs at 1,400 to 2,300 m elevation in humid, broadleaf forests with Podocarpus, tree ferns, and Brunellia. Pteris podophylla grows at elevations of 500 to 1,500 m in very humid, broadleaf forests. Pteris tripartita occurs from sea level to about 800 m in humid, broadleaf forests with Prestoea (Palmae), but it is an Old World fern

Table 1. Composition of the megafossil and microfossil Artibonite flora, Republic of Haiti. Spellings and family assignments for megafossils follow original assignments in Berry (1923)

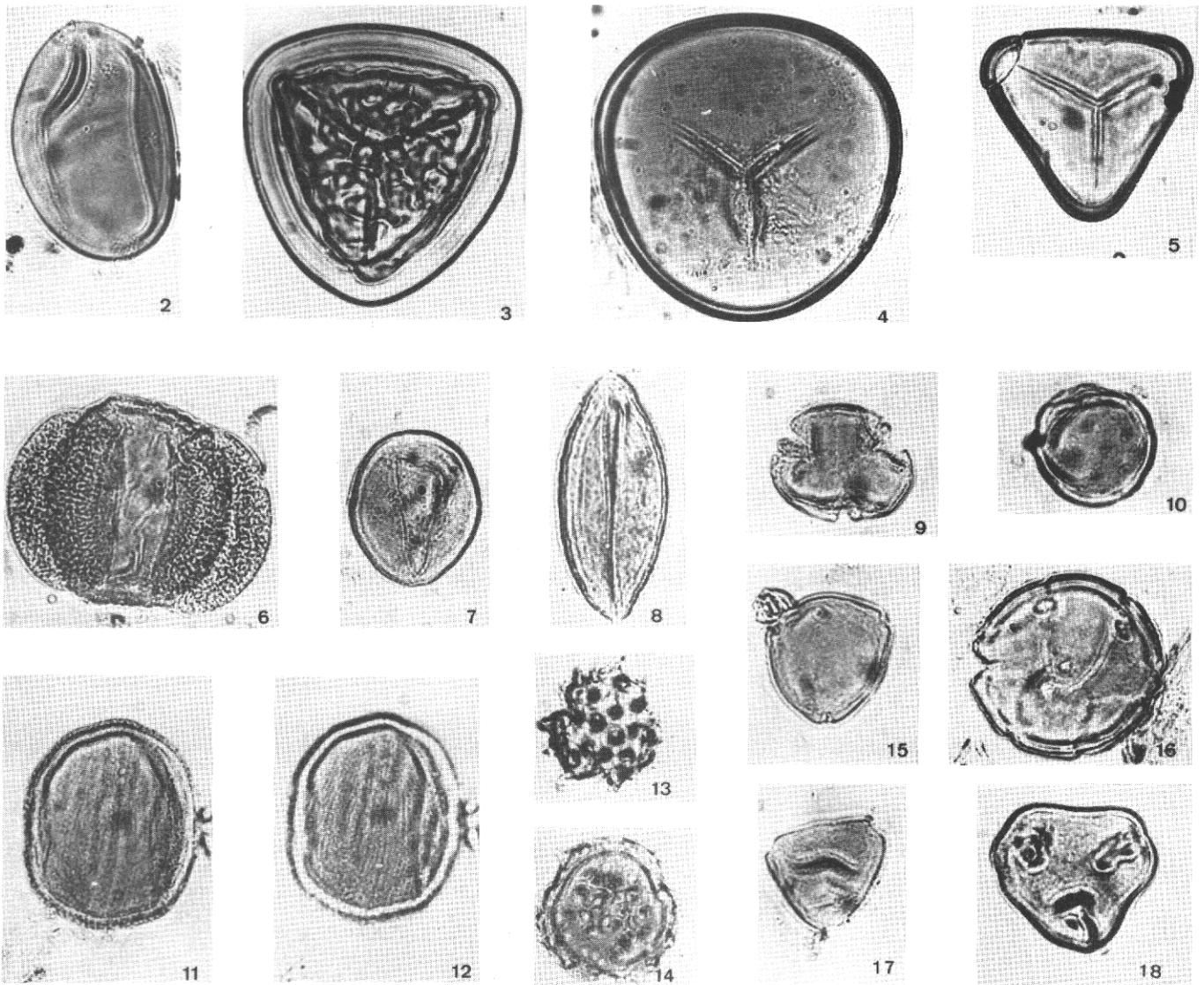
Megafossils		
Characeae	Nyctaginaceae	Sapotaceae
<u>Chara woodringi</u> Berry	<u>Pisonia conditi</u> Berry	<u>Bumelia cuneatafolia</u> Berry
		<u>Chrysophyllum cahobasensis</u> Berry
Polypodiaceae	Rubiaceae	<u>Mimusops praeparvifolia</u> Berry
<u>Gymnogramme woodringi</u> Berry	<u>Guettarda cookei</u> Berry	
Lauraceae	Simarubaceae	
<u>Mespilodaphne hispaniolana</u> Berry	<u>Simaruba haitensis</u> Berry	

Microfossils		
Monolete fern spore	Pinaceae	Juglandaceae
	<u>Pinus</u>	<u>Alfaroa/Oreomunnea</u>
Cyatheaceae	Palmae (types 1, 2)	Loranthaceae
<u>Alsophila</u>		<u>Oryctanthus</u>
Pteridaceae	Acanthaceae	Malpighiaceae
<u>Pteris</u> (types 1-3)	<u>Hygrophila</u>	
Vittariaceae	Cheno/am	Sapindaceae
<u>Antrophyum</u>		<u>Allophylus</u>
Trilete fern spore (types 1, 2)	Compositae (types 1-4)	Unknowns (types 1-3)
	Euphorbiaceae	
	<u>Alchornea</u>	



Figure 1. Index map of place names cited in text. The fossil locality is about mid-way on a road connecting Mirebalais and Las Cahobas. The dot on the inset map shows the location of Port-au-Prince.



Figures 2-18. Fossil pollen and spores from the upper Tertiary (upper Miocene to middle Pliocene) Artibonite group, Republic of Haiti. (2). Monolete fern spore (*Laevigatisporites*), slide 1, England Slide Finder coordinates N-25, size: 60 x 38  $\mu\text{m}$ . (3). *Pteris* (*Polypodiaceoisporites*; Pteridaceae), slide 3, ESF M-26, size: 65  $\mu\text{m}$ . (4). cf. *Antrophyum* (*Triletes*; Vittariaceae), slide 8, ESF J-50, size: 81  $\mu\text{m}$ . (5). *Alsophila* (Cyatheaceae), slide 8, ESF N-35, size: 48  $\mu\text{m}$ . (6). *Pinus* (Pinaceae), slide 9, ESF V-45, size: 68 x 50  $\mu\text{m}$ . (7). Palmae, slide 8, ESF K-46, size: 38 x 32  $\mu\text{m}$ . (8). Palmae, slide 1, ESF G-47, size: 58 x 26  $\mu\text{m}$ . (9). *Alchornea* (*Psilatricolporites operculatus*; Euphorbiaceae), slide 10, ESF N-36, size: 32  $\mu\text{m}$ . (10). Chenopodiaceae/-Amaranthaceae (*Psilaperiporites*), slide 3, ESF G-52, size: 24  $\mu\text{m}$ . (11). *Hygrophila* (Acanthaceae; no previous reports in the Gulf/Caribbean microfossil record), slide 7, ESF F-52, size: 52 x 42  $\mu\text{m}$ , equatorial view. (12). *Hygrophila*, surface view showing numerous pseudocolpi giving striate appearance to exine sculpture. (13). Compositae (*Echitricolporites*), slide 5, ESF U-28, becoming common as a microfossil in the Gulf/Caribbean area only in the early Miocene, and in association with Chenopods (*Psilaperiporites*) more typically in the late Miocene, size: 30  $\mu\text{m}$ . (14). Compositae, slide 9, ESF U-47, size: 38  $\mu\text{m}$ . (15). *Alfaroa/Oreomunnea* (Momiapites; Juglandaceae), slide 9, ESF P-38, size: 30  $\mu\text{m}$ ; the only microfossil in the Artibonite flora whose modern analog does not occur in the modern vegetation of Haiti (present range: cloud forests of Mexico and Central America, northern Colombia). (16). Malpighiaceae, slide 8, ESF J-34, size: 50  $\mu\text{m}$ ; note distinctive arcing colpi connecting pores. (17). *Allophylus* (Sapindaceae), slide 1, ESF G-24, size: 26  $\mu\text{m}$ . (18). *Oryctanthus* (Loranthaceae), slide 5, ESF R-48, size: 32  $\mu\text{m}$ ; note distinct apertures set off the equatorial plane (heterocolpate).

naturalized in the American tropics. *Pteris hispaniolica* and *P. longifolia* are both found in moist habitats, typically associated with the pine forest at elevations between 1,000 to 2,150 m. *Pteris* is known in the stratigraphic literature as *Polypodiaceoispores* (e.g., Lorente, 1986, p. 154), and in our other Caribbean studies it ranges from middle(?) to upper Eocene (Gatuncillo Formation, Panama; Graham, 1985) to Recent. Spores of cf. *Antrophyum* (Fig. 4) are large (ca. 80  $\mu$ m), smooth, and with a trilete mark that is small in relation to the size of the spore. About 10 species occur in the neotropics, usually in moist or wet forests, often in deep shade, in rain or cloud forests (Tryon & Tryon, 1982). *Antrophyum feei* Schaffner is listed for Haiti (Judd, 1987, p. 78) as occasional in the cloud forest at ca. 2,210 m elevation. In the stratigraphic literature *Antrophyum* would probably be classified as *Triletes*, and in our studies it ranges from middle(?) to upper Eocene to Recent. Spores similar to those of the tree fern *Alsophila* (Fig. 5) are common in the fossil flora. The spores are trilete, smooth, and frequently bear a row of minute pits bordering the triradiate scar. The genus is represented in the neotropics by about 13 species, typically growing in cloud forests, wet montane forests, or elfin forests, commonly as an understory plant (Tryon & Tryon, 1982, p. 184). Judd (1987) lists three species for the Morne La Visite and Pic Macaya National Parks in Haiti, growing in the moist pine and cloud forests at elevations between about 950 to 2,200 m.

The gymnosperms are represented in the fossil flora by abundant pollen of *Pinus* (Fig. 6). Pine forests are one of the principal communities in the modern vegetation of Haiti, consisting of the single species *P. occidentalis* Sw. It occurs either as a dominant, forming pine forests, or as an overstory tree in the cloud forest, typically at elevations between 1,000 to 2,340 m, although in the Cordillera Central of the Dominican Republic it occurs locally at elevations as low as 500 m (Judd, pers. comm., 1989). Another conifer with winged pollen, *Podocarpus aristulatus* Parl., grows on Haiti but was not present in the fossil flora.

Thirteen types of angiosperm pollen were recovered, including two kinds of palm (Figs. 7, 8), which cannot be identified to genus. *Coccothrinax* and *Prestoea* are among cloud forest palms presently growing on Haiti. The specimens are more similar to the scabrate pollen of *Prestoea* than to the finely reticulate pollen of *Coccothrinax* examined in our reference collection. The finely striate pollen of *Mygrophila* (Figs. 11, 12) is of interest because the genus has never been reported in the megafossil record, or as a microfossil from the New World. *Mygrophila* pollen is known from the Miocene of Senegal (Médus, 1975; see Muller, 1981, p. 97; 1984, p. 430). It grows in marshes, along the margins of ponds and lakes, and in waterways, often partly submerged and sometimes floating, from sea level to about 1,500 m (Durkee, 1978). The common Caribbean species is *H. costata* Nees (*H. guianensis* Nees). The spherical, periporate pollen of the families Chenopodiaceae and Amaranthaceae usually cannot be distinguished, and the microfossils are commonly designated as Cheno/am (Fig. 10; *Psilaperiporites*; upper Oligocene to Recent for northern Venezuela; Lorente, 1987, p. 179). In our studies from northern Latin America it ranges from lower Miocene (Culebra Formation, Panama, Graham, 1988) to Recent. Pollen of the various Compositae types (Figs. 13, 14) are referred to *Echitricolporites*, *Fenestrites*, and

other genera in the stratigraphic literature. In the Caribbean region they first appear in the latest Oligocene, become more common and diverse in the early Miocene, and are best represented, along with the Cheno/ams, beginning in the middle to late Miocene. Pollen of *Alchornea* (Fig. 9) is distinguished by an operculum within the colpus, and is one of the most frequent, but not abundant, components of Gulf/Caribbean Tertiary deposits. *Alchornea* is known in the stratigraphic literature as *Psilatricolporites operculatus* and ranges from middle Eocene to Recent. *Alchornea* is a common tree in the Gulf/Caribbean region, growing in moist lowland and premontane forests. *Alchornea* is represented in Haiti by the widespread *A. latifolia* Sw. in moist forests on limestone at elevations between about 930 to 1,370 m (Judd, 1987, p. 52). The presence of *Alfaroa/Oreomunnea* (Fig. 15) pollen in the late Tertiary of Haiti is of interest because neither genus presently occurs on the island. *Alfaroa* is a genus of about 7 species in the highlands of Mexico, Central America, and northern Colombia. *Oreomunnea* comprises two species in cloud forests from southern Mexico to central Costa Rica. It is known in the stratigraphic literature as *Momipites*, and in our studies ranges from middle(?) to late Eocene to Recent. *Oryctanthus* (Fig. 18) is a parasitic shrub of moist to drier, premontane forests and is widespread throughout the Gulf/Caribbean area. The Malpighiaceae (Fig. 16) is represented by pollen that presently cannot be referred to any one modern genus. *Allophylus* (Sapindaceae, Fig. 17) is a common member of the modern pine and cloud forests of Haiti (*A. rigidus* Sw., 950 to 4,000 m; *A. crassinervis* Radlk., 1,660 to 1,740 m; Judd, 1987). Three unknowns are also present whose affinities even at the family level have not been established.

## DISCUSSION

### Age of the Flora

Strata at the fossil plant locality are part of the Artibonite group (Woodring et al., 1924), which was considered at that time to consist of three formations: Madame Joie (basal), Thomonde, and Las Cahobas. The relationship of the plant-bearing beds to these formations was uncertain: "On the east side of the road from Mirebalais to Las Cahobas and immediately north of the small stream at the foot of the mountains, on the north side of the gap, soft sandy and clayey beds in the Thomonde formation strike N. 30° W and dip 32° NE. At the same locality but on the west side of the road, there is finely laminated buff or yellowish clay from which the plants ... were collected. The clay can hardly belong to the Thomonde formation because of its stratigraphic relations and because the Thomonde formation not far distant along the strike carries a relatively deep-water fauna. It may represent some part of the Miocene series not known elsewhere in the Central Plain. Its stratigraphic relations led to the supposition in the field that it was of Pliocene age, but overwhelming evidence shows that the sea withdrew from the area now embraced by the Central Plain before Pliocene time. It is unfortunate that the age of these beds is not known, as they furnish the largest collection of fossil plants obtained in the Republic" (Woodring et al., 1924, p. 166). The stratigraphic charts prepared by Cooke et al. (1943) place the Madame Joie Formation in the lower part of the lower Miocene, the Thomonde Formation in the upper lower Miocene, and the Las Cahobas Formation in the lower middle Miocene. Bowin (1975)

recognizes four formations within the Artibonite group, elevating the Maissade tongue of the Thomonde of earlier authors to formation status. The Madame Joie is considered late late Oligocene to early early Miocene in age; the Thomonde as middle early Miocene to middle Miocene; the Maissade as middle Miocene; and the Las Cahobas as late Miocene (Fig. 19). The position of the plant-bearing beds is not mentioned in these later publications.

On the basis of the plant megafossil material, Berry considered the flora to be Miocene in age, and probably late Miocene, consistent with estimates by Woodring et al. (1924) based on field observations and other paleontological evidence. Efforts at age determination from the plant microfossil assemblage are equally equivocal. As noted earlier, the types of Compositae pollen recovered from the Artibonite strata first appear in the Gulf/Caribbean region in the uppermost Oligocene, but do not become abundant (as in the Artibonite assemblage) until the early Miocene. Compositae pollen in association with that of the Chenopodiaceae/Amaranthaceae is typical of even later floras. For this reason, the microfossil flora is regarded as probably late Miocene to possibly Pliocene in age, and the strata may represent a facies of the Las Cahobas Formation.

#### Paleocommunities and Paleoenvironments

The composition of the fossil flora suggests a mosaic of pine and cloud forests. All genera presently occur in that vegetation type, either in Haiti, or in the case of *Alfaroa/Oreomunnea*, in similar communities elsewhere in the Caribbean.

There were no representatives of the xerophytic vegetation that now characterizes many lowland areas to the lee of mountains (e.g., in the Artibonite Plain southeast of Grande-Saline, Woodring et al., 1924, pl. IV; Cul-de-Sac Plain near Pont Beudet, pl. V; northeast of Gonaines, pl. V). No pollen of the Gramineae was recovered, a family which is the principle component of savannas (e.g., southwest of St.-Michel de l'Atalaye; Woodring et al., 1924, pl. VI). Based on studies of other Gulf/Caribbean Tertiary microfossil floras (Figs. 20, 21), it is likely that savannas and dry to arid communities developed in the Pliocene and Quaternary, with maximum range expansion in very recent times as a result of anthropogenic factors.

Little is known of the lowland paleocommunities except for the nine genera of megafossils reported by Berry (1923; Table 1). In evaluating the megafossil record it must be noted that in the few instances where a re-study has been made of these older works, the percentage of misidentifications is high. In the Eocene Wilcox flora of the southeastern United States, Dilcher (1973) estimates that 60% of Berry's determinations may be incorrect, and the figure likely would not be any lower for the Haiti material. None of the genera identified by Berry were encountered as microfossils (Table 1). If the megafossil assemblage were larger and more diverse, it would be possible to suggest broad paleoclimatic conditions based on leaf physiognomy (Wolfe, 1971). For the few fragmentary specimens in Berry (1923), all are described as entire-margined and coriaceous to subcoriaceous in texture, two have prominent drip tips, and size ranges from 3.25 x 1.1 cm to 9 x 3 cm. These specimens are probably remnants of a lowland paleocommunity growing close to the margins of the depositional basin.

General parameters for the late Tertiary paleoclimate of Haiti can be established from modern temperature and rainfall records at sites bracketing the altitude ranges suggested by the fossil flora (to the extent these data are available for Haiti). Pétionville (18° 31' N, 72° 17' W; altitude 400 m) is located just to the southeast of Port-au-Prince. The average monthly temperature, based on an eight year record from 1909 to 1916 (Woodring et al., 1924, p. 39), ranges from a December/January minimum of 23.1° C to a July maximum of 26.5° C. At Furcy (18° 25' N, 72° 17' W; altitude 1,540 m) the values are a December/January minimum of 17.5° C and a summer maximum of 19.8° C. Records from Port-au-Prince (18° 32' N, 72° 26' W), Pétionville, and Furcy indicate an average lowering of the annual mean temperature of about 1° C for each 150 m increase in altitude (at its present latitude of ca. 18° N). Annual rainfall at Pétionville (based on 20-21 year records) is 1,327.5 ml, with the driest months (December/January) receiving 26.1 and 28.9 ml, respectively, and the wettest months (April/May) receiving 183.2 and 220.6 ml. Comparable rainfall figures are not available for Furcy, but annual rainfall is about 2,100 ml, with December/January dry and April/May wet periods. Mirebalais (18° 55' N, 72° 36' W; 100 m elevation), closest to the fossil locality, is one of the wettest places in Haiti, receiving about 2,659 ml of annual rainfall, while the driest is at Gonaives (19° 27' N, 72° 41' W; 524 ml). None of these extremes support (or, rather, supported in the recent past) vegetation similar to the paleocommunities, especially the deserts near Gonaives.

The paleoaltitude for the Artibonite flora cannot be established from the limited information available. The modern analogs grow between sea level and 2,300 m, with an average lower elevation of 700 m and an average higher elevation of 1,900 m. A zone from about 1,200 to 1,300 m would accommodate all components of the flora. The present altitude at Mirebalais is only 100 m, so the palynoflora probably reflects an upland community growing on slopes adjacent to the depositional basin. No pollen of mangroves (*Rhizophora*, *Avicennia*, *Conocarpus*, *Laguncularia*), or plants with species associated with the mangroves (*Hibiscus*, *Mimosa*, *Sapium*, and others), which do occur in other Gulf/Caribbean Tertiary floras, were found in the Haiti material.

Paleoenvironmental reconstructions, and especially biogeographic models, for the Caribbean must take into account the former position and the submergent/emergent history of the islands. In the case of Hispaniola, its northern and southern portions, divided at the Cul-de-Sac--Enriquillo Basin (Pindell & Dewey, 1982; Mann & Burke, 1984), have had similar but independent histories. Southern Hispaniola is constituted of uplifted ocean floor emergent only since the Pliocene. Several models show southern Hispaniola, and Jamaica, moving "several hundred kilometers eastward into their present positions during the last 30 million years", at an estimated rate of about 3 cm/year (Buskirk, 1985). Collision of southern Hispaniola with northern Hispaniola occurred in the late Miocene. It is not possible to reconstruct paleophysiographic detail to the degree of locating precisely the fossil site during this period. However, the reconstructions suggest the locality may have been on the southern shore of the northern fragment of proto-Hispaniola, with the fossil flora being deposited during or just prior to the accretion of southern Hispaniola. Most tectonic models for the early and middle Tertiary (see

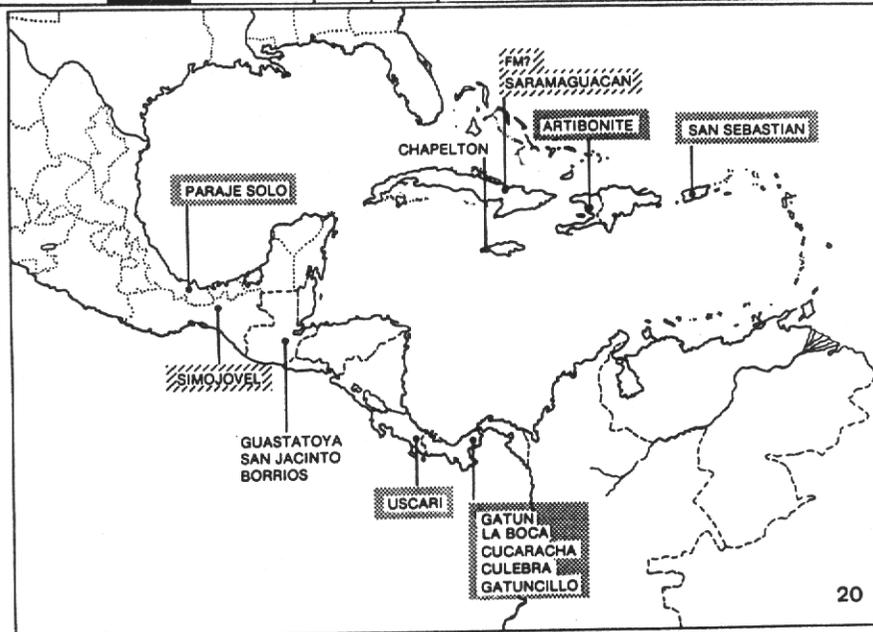
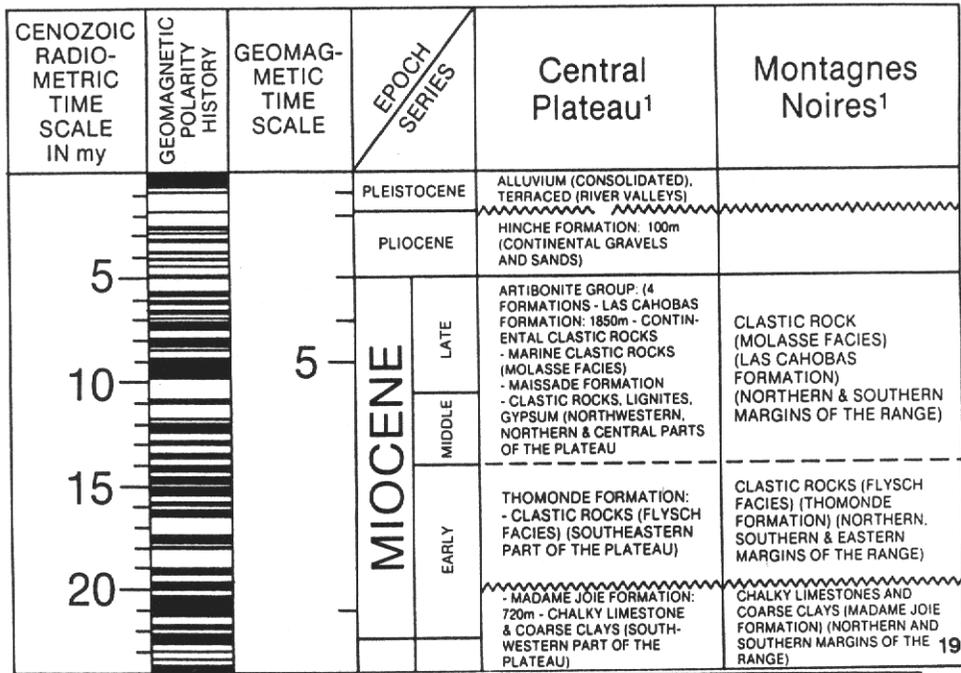


Figure 19. Stratigraphic relations of the Artibonite group formations. After Bowin (1975, used with permission).

Figure 20. Geographic distribution of Caribbean microfossil floras. Stippling indicates study complete.

Figure 21. Stratigraphic distribution of Caribbean microfossil floras; position does not imply formal correlation.

summary in Buskirk, 1985; Rosen, 1985) show the Greater Antilles further to the west, off the southern coast of Mexico, and moving east along the Motagua-Polochic/Cayman fault zone. In this case the affinities of early and middle Tertiary fossil floras should be primarily with Mexico and northern Central America, with a South American component becoming progressively more prominent in latest Tertiary and Quaternary times. Although the data base is meager, the Antillean Tertiary floras studied to date (Figs. 20, 21) have almost exclusively northern Central American and Mexican affinities. This observation forms one component of a preliminary biogeographic model to be tested as future studies are completed.

In summary, the twenty-five fossil palynomorphs recovered from the Artibonite flora, in association with other limited paleontological and stratigraphic evidence, suggest an age of late Miocene to possibly middle Pliocene. The principal paleocommunities were pine and cloud forests, with a fringing fern marsh. Annual paleotemperatures are estimated from 23° C to 26° C at elevations of about 400 m, and from 17° C to 19° C at elevations of about 1,400 m. Rainfall is estimated at 1,300 ml and was seasonal. All modern analogs of the Artibonite flora grow between sea level and about 1,200 to 1,300 m, consistent with values based on Tertiary paleopalynological evidence from other Caribbean localities. The affinities of the Artibonite flora are with northern Central America and Mexico, as opposed to South America, supporting reconstructions that place the proto-Greater Antilles to the west along southern Mexico during the lower and middle Tertiary.

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