

STUDIES IN NEOTROPICAL PALEOBOTANY. XIV. A PALYNOFLORA FROM THE MIDDLE EOCENE SARAMAGUACÁN FORMATION OF CUBA¹

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An assemblage of 46 fossil pollen and spore types is described from a core drilled through the middle Eocene Saramaguacán Formation, Camagüey Province, eastern Cuba. Many of the specimens represent unidentified or extinct taxa but several can be identified to family (Palmae, Bombacaceae, Gramineae, Moraceae, Myrtaceae) and some to genus (*Pteris*, *Crudia*, *Lymingtonia*?). The paleoclimate was warm-temperate to subtropical which is consistent with other floras in the region of comparable age and with the global paleotemperature curve. Older plate tectonic models show a variety of locations for proto-Cuba during Late Cretaceous and later times, including along the northern coast of South America. More recent models depict western and central Cuba as two separate parts until the Eocene, and eastern Cuba (joined to northern Hispaniola) docking to central Cuba also in the Eocene. All fragments are part of the North American Plate and none were directly connected with northern South America in late Mesozoic or Cenozoic time. The Saramaguacán flora supports this model because the assemblage is distinctly North American in affinities, with only one type (*Retimonocolpites* type 1) found elsewhere only in South America.

Key words: Cuba; Eocene; palynoflora; Saramaguacán Formation.

Cuba is the largest island bordering the Caribbean Basin and is a substantial part of the Antillean island chain forming a migratory pathway between the North and South American continents. Although a few paleobotanical studies were made earlier in the century (Berry, 1934, 1939; Hollick, 1928; Leon, 1929), and some later ones published on individual Mesozoic plant fossils (*Piazopteris*; Areces-Mallea, 1991; Vakhrameev, 1965, 1966), there have been no sustained investigations on plant megafossil floras from Cuba in modern times (Borhidi, 1996, p. 257).

A study of plant microfossils was begun by Areces-Mallea (1985, 1987, 1988, 1989, 1990; Areces-Mallea and García Rodríguez, 1990), and in 1993 the samples were sent to the KE (Kent State University) palynology laboratory for completion of the project. The material consisted of unprocessed rock, slides of processed material, and photographs. The palynomorphs were from a core ~30 cm long from the Saramaguacán Formation in the Sierra de Maraguán in east-central Cuba (Provincia de Camagüey), 2.5 km north of the road between Guanábana (Camagüey) and Sibanicú; Figs. 78, 79, 81). A buff-colored section of the core about ~8 cm long yielded the plant microfossils.

Areces-Mallea (1985, personal communication) provides the following information on the age and stratigraphic position of the Saramaguacán Formation. The stratigraphic sequence is described as follows:

Magantilla Formation (Miocene)
Saramaguacán Formation

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San Jacinto member
Santa Rosa member
El Capataz member
Guanábana member
Maraguán Formation (middle Eocene)

The Maraguán Formation is considered middle Eocene in age based on planktic and benthic foraminifera. The samples are part of the El Capataz member of middle late Eocene age because the benthic foraminifera *Nummulites floridensis* is present. This species is known also from the Santa Rosa member at the type section of the Saramaguacán Formation, and the Paleocene to middle Eocene benthic foraminifera *Ranikotalia* (*Nummulites*) *bermudezi* is known from the San Jacinto member.

Study of the Saramaguacán assemblage is complicated by the fact that several of the original specimens shown in the photographs are on slides presently in Cuba and are not available for study. In some cases similar specimens were recovered from material processed at KE and from which the morphology and size of the specimens in Cuba could be determined. Others, however, had to be described and identified from the photographs alone. In these instances, the subtle differences between colpate and colp(oid)ate (pores poorly developed), psilate-scabrate-microreticulate, and estimates of size and other quantitative features were often difficult to make depending on the preservation, orientation of the grains, and the focal level of the photographs. In cases where the morphology is distinctive, and similar to that of previously named specimens described from other Cenozoic palynofloras in the Gulf-Caribbean region, those names are used at the appropriate taxonomic level [viz., genus or genus/species; e.g., *Undulatisporites*, *Pteris dentata* (Nagy) Frederiksen, *Arecipites*, *Liliacidites*, etc.]. In instances where identity to previously described taxa is not clear from the photographs, the morphologically-based nomenclature developed by van der Hammen

(1956) is used (e.g., *Peripollenites*, *Retiaticolpites*). Eventually it may be possible to apply a more uniform nomenclature if the actual specimens become available for examination, but this appears unlikely in the near future. Considering the biogeographic importance of Cuba, the dearth of recent information on its vegetational, environmental, and geological history (there is a relatively recent geologic map of Cuba; Borkowska et al., 1988) and the fact that the available data do provide some insight on these histories, the results and preliminary interpretations are presented pending access to additional material.

MATERIALS AND METHODS

Much of the material described here is from slides and photographs originally studied and partly published by Areces-Mallea (1988). Samples at the CIDP (Centro de Investigación y Desarrollo del Petróleo, Havana, Cuba) were processed through HCl and HF to dissolve minerals. Schultze's reagent followed by KOH was used to remove organic debris. Palynomorphs were concentrated by flotation in a ZnCl_2 solution (specific weight 1.96), then stained with safranin and mounted in glycerine jelly. All specimens were examined and photographed at 400 \times magnification with a MBI-15 (Russian) microscope using ORWO NP-15 black and white film under blue light. Samples at KE were processed by standard methods described by Gray (1965) and Traverse (1988). The sediments were processed through HCl, HF, and HNO_3 to remove mineral and organic debris, then acetolyzed (nine parts acetic anhydride to one part concentrated H_2SO_4), preceded and followed by rinses in glacial acetic acid. Some residues were mounted unstained in glycerine jelly while others were stained with safranin and mounted in Protexx. The specimens at KE were examined and photographed at 400 \times magnification with a Leitz Orthoplan Photomicroscope using Ilford black and white film. Identifications were made by comparisons to a pollen and spore reference collection of 24 000 slides and a stratigraphic collection of previously studied Tertiary palynofloras from the Gulf/Caribbean region. Other identifications, primarily of distinctive morphological types from the southeastern United States, northern Mexico, Jamaica, Panama, and northern South America, are based on descriptions and illustrations in the literature. Location of specimens on the slides is by ESF (England Slide Finder) coordinates. In the descriptions "Photograph" designates microfossils presently available only from pictures provided by Areces-Mallea. Slides, residues, unprocessed samples, negatives, and duplicate prints are in the palynological collections at KE; other materials are in the Museo Nacional de Historia Natural in Habana, Cuba.

COMPOSITION

Monoletes—*Laevigatosporites* (Fig. 1). Reniform; monolete, laesura located on concave side of spore, straight, 25 μm long, extending 3/4 length of spore, inner margin entire; laevigate; size 35 \times 25 μm . Photograph.

This generalized spore type is produced by numerous species of the Blechnaceae, Polypodiaceae, and Pteridaceae. In instances where the spores first appear in a section, or where there is a significant increase in abundance, this may suggest development of swamp or marsh habitats or an increase in precipitation. However, the fossil spores have such a wide stratigraphic and geographic range that they are of limited value for stratigraphic correlation, age determination, or as paleoecological indicators.

Verrucatosporites usmensis van der Hammen (Figs. 2, 3). Reniform; monolete, laesura located on concave side of spore, straight, 25 μm long, narrow, extending 2/3 length of spore; inner margin entire(?); verrucate, verrucae conspicuous, shape irregular, 2–3 μm in diameter; size 35 \times 25 μm . Photograph.

These spores are also widespread in Gulf/Caribbean Cenozoic deposits (Germeraad, Hopping, and Muller, 1968). They

are produced by many genera in several families of ferns and have broad stratigraphic and geographic ranges.

Triletes—*Lygodiumsporites adriennis* (Potonie and Gelle-tich) Frederiksen (Fig. 4). Oblate, amb triangular, apices rounded; trilete, laesurae straight, 15 μm long, extending 3/4 distance to spore margin; laevigate; wall 2 μm thick; size 45 μm . Photograph.

These spores are also encountered in the literature under the name *Deltoidospora*. The particular type described here is more similar to the modern *Acrostichum* than to typical *Lygodium* but the biological affinities are uncertain.

Trilete fern spore type 1 (Fig. 5). This spore is similar to *Lygodiumsporites adriennis* and may represent the same taxon but it is noticeably smaller (30 μm). Photograph.

Undulatisporites concavus Kedves (Figs. 6, 7). Oblate, amb concavo-triangular, apices rounded; trilete, laesurae slightly sinuous, 15 μm long, extending nearly to spore margin, inner margin entire, bordered by lip 2–3 μm in width; indistinctly verrucate; wall 2 μm thick; size 32 μm . Photograph.

Similar spores are described by Frederiksen (1980a, p. 31, plate 2, fig. 6) from the upper Eocene Jackson Group of the southeastern United States.

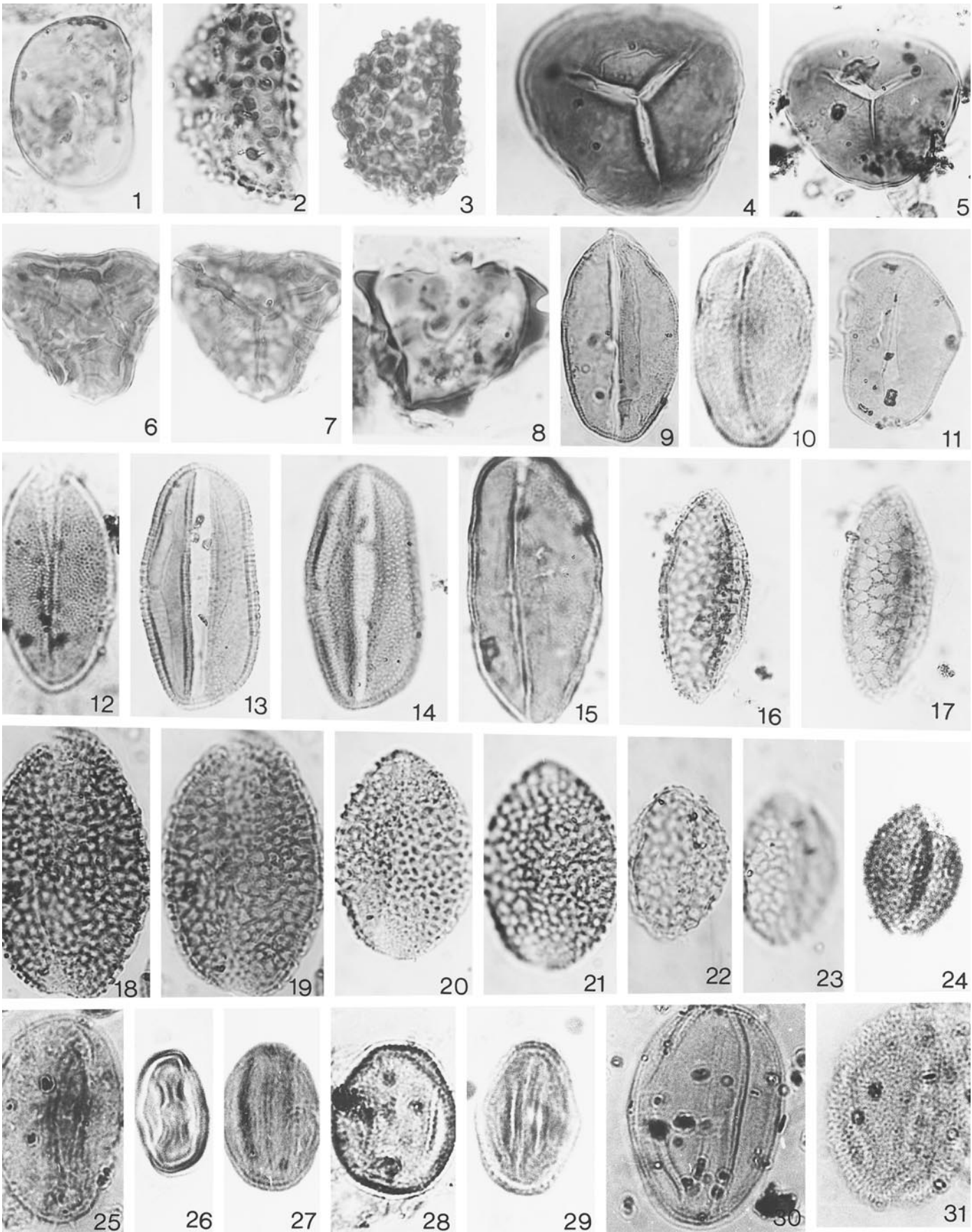
cf. *Pteris dentata* (Nagy) Frederiksen (Pteridaceae; Fig. 8). This specimen is fragmentary but enough remains to recognize it as a spore of the tropical fern *Pteris*. Frederiksen (1980a, p. 32, pl. 3, figs. 5, 6) described similar spores from the Jackson Group (upper Eocene) of the southeastern United States, and they are frequent in Tertiary deposits throughout the Gulf-Caribbean area. Photograph.

Monosulcates—*Arecipites* (Palmae; Figs. 9–15). Greatest diameter often slightly off of equator (grains then wedge-shaped); monosulcate, sulcus straight, narrow, 30–40 μm long, extending entire length of grain, inner margin entire to slightly lobate to dentate; finely reticulate, muri smooth, straight, width of muri approximately equal to diameter of lumina (1 μm or less); tectate-perforate, columellae just evident in median optical section (at 400 \times magnification), wall 1–2 μm thick; size 42–54 \times 25–32 μm . Slide A4, ESF X-36 (Fig. 10); Slide A2, ESF Z-36,1; slide Y-25, S-32; and photograph.

Palm pollen is the most diverse and numerically the most abundant plant microfossil in the Saramaguacán assemblage. Although several studies have been made on the pollen of modern palms (Harley, 1989, 1990; Harley and Morley, 1995; Thanikaimoni, 1966), the size of the family (estimated 2500 species), its pantropical distribution, and the subtle morphological differences in pollen between many taxa still make it impossible to identify most fossil specimens to genus. Among the Saragaguacán fossils there are slight differences in size, wall thickness, and distinctiveness of the microreticulum and all specimens are presently referred to the form genus *Arecipites*.

Liliacidites (Figs. 16, 17). Monosulcate, sulcus straight, narrow, 33 μm long, extending nearly entire length of grain, inner margin entire to slightly dentate due to overlying sculpture elements; reticulate, muri smooth, sinuous, width (1 μm) considerably less than diameter of lumina (4–5 μm) producing a delicate, open reticulum; tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 1–2 μm thick; size 42 \times 18 μm . Photograph.

Monosulcate pollen of this type has not been described from the Paleogene of the southeastern United States or from north-



ern South America. Despite the etymology of the generic name its affinities can only be ascribed to the monocotyledons (Liliaceae, Amaryllidaceae, Bromeliaceae, et al.).

Retimonocolpites type 1 (Figs. 18, 19). Monosulcate, sulcus straight, 50 μm long, extending entire length of grain, inner margin dentate due to overlying sculpture elements, narrow margo formed by finer sculpture bordering sulcus; reticulate, muri smooth, slightly sinuous, width (1 μm) narrow in relation to diameter of lumina (5 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 2 μm thick; size 75 \times 40 μm . Slide A4, ESF S-25; photograph.

González-Guzmán (1967, pp. 51–52, pl. XXV, figs. 2, 2a) describes and illustrates a specimen from the lower to middle Eocene of the Tibú area of Colombia that appears similar to the Saramaguacán specimen.

Retimonocolpites type 2 (Figs. 20, 21). This specimen differs from *R.* type 1 in being distinctly smaller (45 μm). Photograph.

Retimonocolpites type 3 (Figs. 22, 23). This specimen is distinguished by the open and fine reticulum and its comparatively small size (30 μm). Photograph.

Retimonocolpites type 4 (Fig. 24). This specimen is small (20 μm) and densely microreticulate. Photograph.

Retimonocolpites(?) type 5 (Fig. 25). The distinguishing features of *R.*(?) type 5 are the apparent small echinae (e.g., evident along the bottom margin of the specimen illustrated). Slide X24, ESF P-34,2–4.

Tricolpates—*Cupuliferoidaepollenites liblarensis* (Thompson) Potonié (Fig. 26). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 23 μm long; psilate to faintly scabrate; tectate, wall homogeneous in median optical section (at 400 \times magnification), moderately thick (2 μm); size 26 \times 16 μm . Slide A4, ESF R-27.

A similar specimen is described and illustrated by Frederiksen (1980a, pp. 46–47, pl. 9, fig. 23) from the Upper Eocene Jackson Group of the southeastern United States. Its biological affinity is unknown but possibly with the Fagaceae.

Fraxinoipollenites cf. *F. scoticus* (Simpson) Frederiksen (Fig. 27). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 30 μm long, inner margin entire; reticulate to slightly striato-reticulate, muri smooth, straight, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, individual columellae just evident in median optical section (at 400 \times magnification), wall 1 μm thick; size 33 \times 24 μm . Slide A1, ESF N-40,2.

Frederiksen (1980a, p. 48, pl. 10, fig. 18) describes and illustrates a similar specimen from the upper Eocene Jackson Group of the southeastern United States. Despite the etymology of the generic name the biological affinity is unknown and probably not with *Fraxinus*.

Echitricolpites (Fig. 28). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 22 μm long, inner margin slightly dentate due to overlying sculpture elements; minutely and densely echinate, echinae short (1 μm or less); tectate, wall homogeneous in median optical section (at 400 \times magnification), 1–2 μm thick; size 35 \times 30 μm . Slide X24, ESF N-38,2.

Retitricolpites type 1 (Fig. 29). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 24 μm long, costae colpi 2 μm wide; finely reticulate, muri smooth, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, columellae evident in optical section (at 400 \times magnification), short, relatively thick (0.5 μm), wall 1 μm thick; size 36 \times 26 μm . Slide A4, ESF X-40,2.

Retitricolpites type 2 (Fig. 30). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, 50 μm long, narrow costae colpi 1 μm wide, inner margin slightly dentate due to overlying sculpture elements; finely reticulate, muri smooth, straight, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 1 μm thick; size 54 \times 34 μm . Slide X24, ESF Q-34.

This specimen differs from *R.* type 1 in being larger (54 μm vs. 36 μm) and the wall is thinner relative to the size of the grain.

Retitricolpites type 3 (Fig. 31). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 27 μm long, inner margin dentate due to overlying sculpture elements; finely reticulate, muri smooth, straight, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), long (2–3 μm), wall 3 μm thick; size 46 \times 30 μm . Slide Y25, ESF R-40,4.

Retitricolpites type 4 (Fig. 32). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 39 μm long, inner margin slightly dentate due to overlying sculpture elements; finely reticulate to striato-reticulate, muri smooth, straight, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), short, broad, apices rounded, wall 1 μm thick; size 54 \times 32 μm . Slide X24, ESF M-36,3–4.

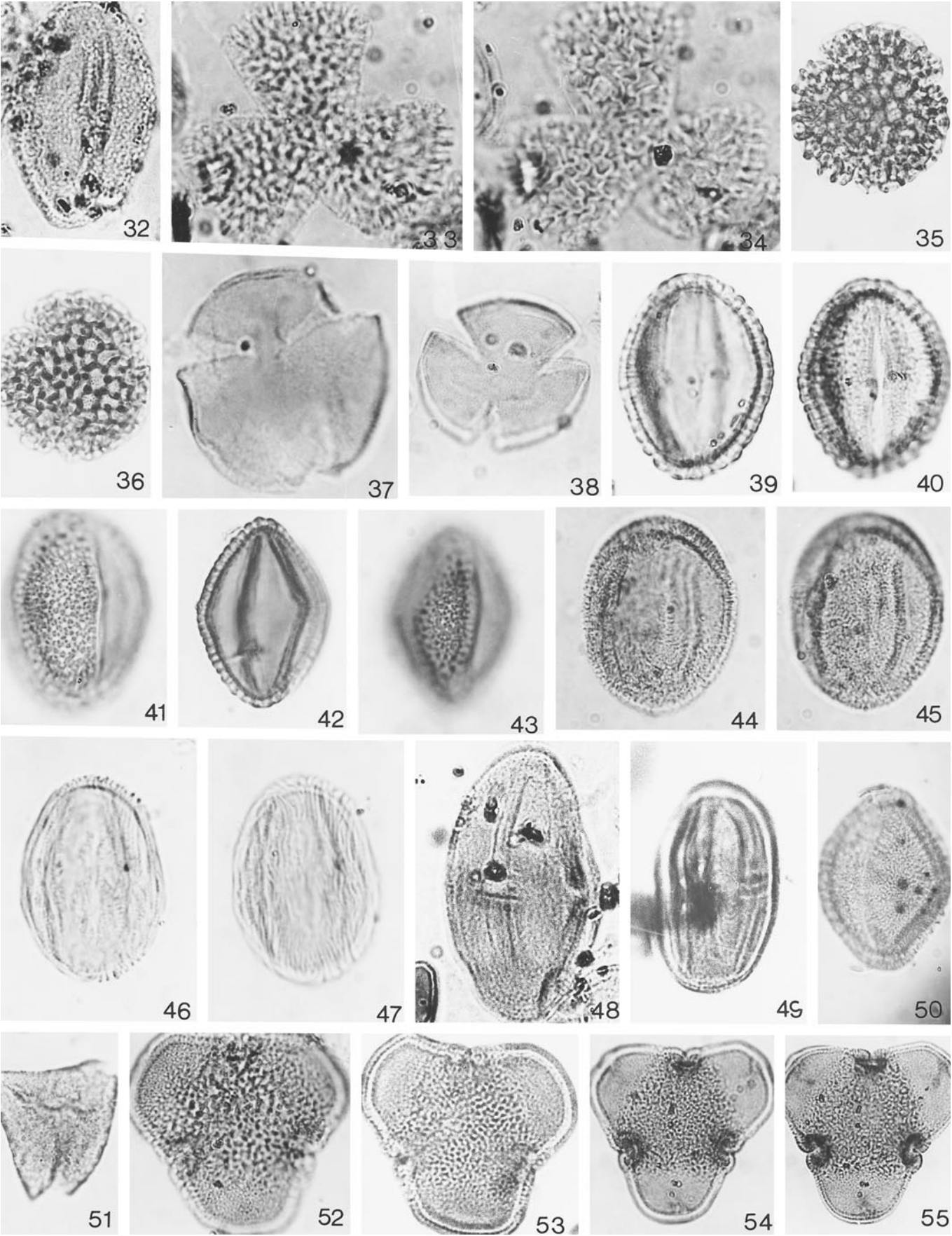
Retitricolpites type 5 (Figs. 33, 34). Oblate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, 15 μm long (apex to equator), margin entire; reticulate, muri smooth, sinuous, width of muri (1 μm) narrow in relation to diameter of lumina (4 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), long, narrow, wall 2–3 μm thick; size 50 μm . Photograph.

Retitricolpites type 6 (Figs. 37, 38). Oblate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, 15 μm long (apex to equator), tapering to acute apex, margin entire; psilate (microreticulate?); tectate (tectate-perforate?), columellae evident in median optical section (at 400 \times magnification), wall 1–1.5 μm thick; size 30 (Fig. 38) to 50 μm (Fig. 37). Photograph.

Reticulataepollis cf. *intergranulata* (Potonié) Krutzsch

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Figs. 1–31. Fossil spores and pollen grains from the middle Eocene Saramaguacán Formation, Cuba. See text for descriptions and measurements, and Table 1 for numerical representations. Photographs 1–24 are by Areces-Mallea. 1. *Laevigatosporites*. 2–3. *Verrucatosporites usmensis*. 4. *Lygodiumsporites adriensis*. 5. Trilete fern spore type 1. 6–7. *Undulatisporites concavus*. 8. Cf. *Pteris dentata*. 9–15. *Arecipites*. 16–17. *Liliacidites*. 18–19. *Retimonocolpites* type 1. 20–21. *R.* type 2. 22–23. *R.* type 3. 24. *R.* type 4. 25. *R.*(?) type 5. 26. *Cupuliferoidaepollenites liblarensis*. 27. *Fraxinoipollenites* cf. *F. scoticus*. 28. *Echitricolpites*. 29. *Retitricolpites* type 1. 30. *R.* type 2. 31. *R.* type 3.



(Figs. 35, 36). Oblate-spheroidal, amb circular; tricolate, colpi equatorially arranged, meridionally elongated, equidistant, short, 5 μm (apex to equator), inner margin entire; reticulate, muri smooth, sinuous, width of muri (1 μm) narrow in relation to diameter of lumina (2–3 μm), lumina polygonal, floor granular; tectate-perforate, columellae evident in median optical section (at 400 \times magnification), long (3 μm), wall 3 μm thick; size 30 μm . Photograph.

Otherwise comparable specimens among modern and fossil taxa often have a pore along the colpus but this feature is obscure in the photograph. Frederiksen (1980a, p. 60, pl. 14, figs. 23–26) describes and illustrates similar specimens from the upper Eocene of the southeastern United States.

Tricolporoidites—*Retitricolporoides* type 1 (Figs. 39–41). Prolate; tricolporoidate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 34 μm long, extending nearly entire length of grain, inner margin entire, costae colpi 3 μm wide; reticulate, reticulum regular, muri smooth, straight, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), apices rounded, wall 2 μm thick; size 35 \times 28 μm . Photograph.

This generalized type of prolate, tricolpor(oid)ate, reticulate grain is widespread throughout the Cenozoic in the Gulf/Caribbean region. It is produced by members of the Anacardiaceae, Euphorbiaceae, Rutaceae, and others. If a distinct pore is present, as there appears to be in a similar grain illustrated in Fig. 50, the moderately large size and comparatively heavy wall suggest possible affinities with *Coccoloba* (Polygonaceae).

Retitricolporoides type 2 (Figs. 42, 43). This specimen is similar to *R.* type 1 but it has a slightly thinner wall and is smaller (25 μm). Photograph.

Retitricolporoides type 3 (Figs. 44, 45). Prolate; tricolporoidate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 34 μm long, extending 3/4 length of grain, inner margin slightly dentate due to overlying sculpture elements; finely reticulate and in places arranged into a slightly swirled pattern, muri smooth, slightly sinuous, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 2 μm thick; size 40 \times 32 μm . Photograph.

Striatricolpites cataumbus González Guzmán (Leguminosae, Caesalpinioideae; Figs. 46, 47). Prolate; tricolporoidate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 30 μm long, extending 3/4 to nearly entire length of grain, inner margin entire; striate, striae sinuous, densely arranged; tectate, wall 1 μm thick; size 40 \times 27 μm . Photograph.

These grains are similar to those produced by *Crudia* although the biological equivalency of the modern taxon and these ancient microfossils is not certain. The microfossils are frequent but not abundant in early and middle Tertiary deposits of the Gulf-Caribbean region, and megafossils (fruits) have

been found in the Eocene of the southeastern United States (Herendeen and Dilcher, 1990).

Tricolporates—*Retitricolporites* type 1 (Fig. 49). Prolate; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 42 μm long, extending 3/4 to nearly entire length of grain, inner margin entire, narrow costae colpi (1–2 μm wide), pores situated at mid-point of colpus, equatorially elongated (1 \times 4 μm); finely reticulate, muri smooth, straight, width of muri approximately equal to diameter of lumina (1 μm); tectate-perforate, columellae just evident in median optical section (at 400 \times magnification), wall 2 μm thick; size 48 \times 27 μm . Slide A4, ESF V-27,1–3.

Retitricolporites type 2 (Fig. 48). Prolate; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight 45 μm long, narrow costae colpi (1–2 μm wide), pores situated at midpoint of colpus, equatorially elongated, 4 \times 9 μm ; finely reticulate to striato-reticulate, muri smooth, slightly sinuous, width of muri approximately equal to diameter of lumina (1 μm) to lumina slightly elongated; tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 1 μm thick; size 60 \times 34 μm . Slide X24, ESF L-35,4.

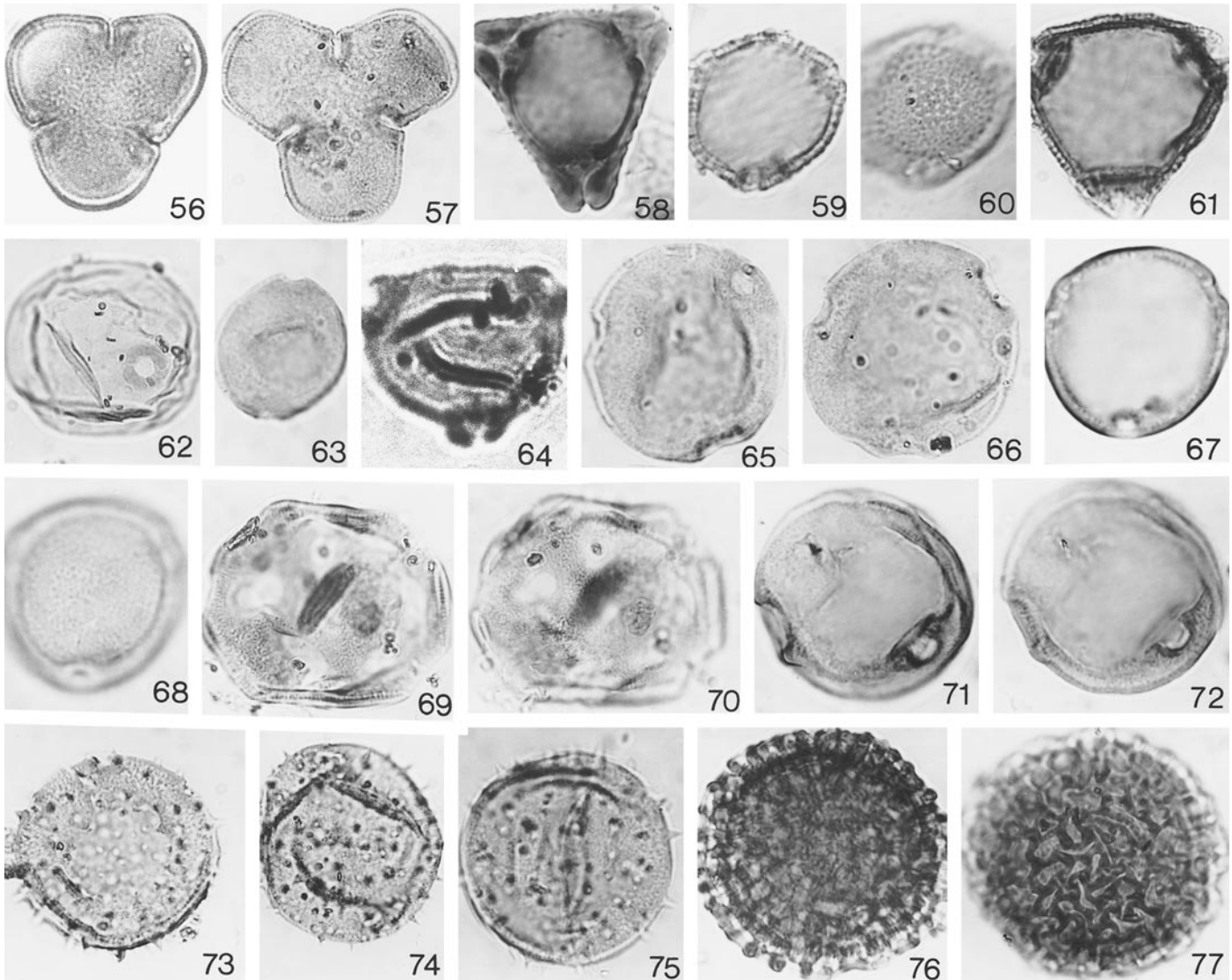
Retitricolporites type 3 (Fig. 50). This grain is similar to those described under *Retitricolporoidites* but a faint pore is more evident (center of left colpus in Fig. 50). Photograph.

Trisyncolporate—*Myrtaceidites* cf. *parvus* Cookson and Pike (Myrtaceae; Fig. 51). Oblate, amb triangular, apices acute; trisyncolporate, colpi equatorially arranged, meridionally elongated, equidistant, 14 μm long (apex to equator), straight, margin slightly diffuse, fused at the poles, pores indistinct; scabrate; tectate, size 25 μm . Photograph.

These grains are similar to those produced by *Eugenia*, *Myrcia*, and other genera of the Myrtaceae but they can not be assigned to any one modern genus. They are frequent but never abundant in the Gulf/Caribbean Tertiary. The Saramaguacán specimens differ from *M. parvus* described and illustrated by Frederiksen (1980a, p. 58, pl. 14, figs. 9–11) in being more distinctly triangular and scabrate.

Brevitricolpates/Brevitricolporates—*Bombacacidites* cf. *tilioides* Krutzsch (Bombacaceae; Figs. 52–55). Oblate, amb triangular, apices rounded; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, situated in inter-apical area, short (6 μm , apex to equator), costae pori (3 μm wide), pores situated at midpoint of colpus, meridionally elongated; reticulate in polar region grading to more finely reticulate/scabrate at apices; tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 2 μm thick; size 48 μm . Photograph.

The biological affinities of these grains are with the Bombacaceae which is presently a family typical of warm-temperate to tropical environments. They are common in the Saramaguacán flora, and similar microfossils are frequent in the Tertiary of the Gulf/Caribbean region. Frederiksen (1980a, p.



Figs. 56–77. Fossil pollen grains from the middle Eocene Saramaguacán Formation, Cuba. See text for descriptions and measurements, and Table 1 for numerical representations. Except for figs. 56 and 64 all photographs are by Areces-Mallea. **56.** *Bombacacidites* type 1. **57.** *B.* type 2. **58.** *Basopollis*/cf. *Choanopollenites*. **59–60.** *Retibrevitricolpites*. **61.** *Porocolpollenites*. **62.** *Graminidites gramineoides*. **63.** *Psiladiporites redundatis*. **64.** *Brosipollis* cf. *striata*. **65–66.** *Tripopollenites* type 1. **67–68.** *T.* type 2. **69–70.** *Lymingtonia* cf. *L. rhetor*. **71–72.** *Pericolporites*. **73–75.** *Malvacipollis tschudyi*. **76–77.** *Retipollenites* cf. *confusus*.

59, pl. 14, fig. 15) reports pollen of *B. nacimientoensis* (Anderson) Elsik from the Eocene of the southeastern United States; [see also Elsik (1968) for a record from the Paleocene Rockdale lignite of Texas]. Germeraad, Hopping, and Muller (1968) report a different form [*B. annae* (van der Hammen) Leidelmeier] in the Paleocene of the Maracaibo region of Venezuela. Because the Saramaguacán form slightly differs from typical *B. tilioides*, Areces-Mallea (1985) described it as a different species (*B. mirabilis* Areces). González Guzmán (1967) does not list it for the Eocene of the Tibú area of Colombia, but it is reported by Lorente (1986) for the Upper Tertiary of Venezuela. Generally, the Saramaguacán specimens are more similar to those from the southeastern United States than to those from northern South America.

B. type 1 (Fig. 56). This specimen differs from *B. tilioides* in being more uniformly and finely reticulate. If the reticulum is interpreted as uniform across the entire surface the specimen

would be identified as *B. nanobrochatus* Frederiksen. If the reticulum is viewed as slightly finer at the corners it would be *B. fereparilis* Frederiksen. Both species, like *B. tilioides*, are known from North America (Frederiksen, 1983). Slide A1, ESF A-24,4.

B. Type 2 (Fig. 57). This specimen is finely reticulate across the entire surface and is distinctly concave in outline. A similar specimen is reported by Frederiksen (1980b, p. 170, pl. 3, fig. 31) from the Paleogene of the southeastern United States. Photograph.

Basopollis/cf. *Choanopollenites* sp. (Fig. 58). Oblate, amb triangular, apices acute; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, situated at apices, straight, short (6 μm), vestibulate, conspicuously protruding (7–8 μm), pores situated at midpoint of colpi, distinct annulus (3–4 μm wide); finely verrucate/fossulate; tectate-perforate, wall 2 μm thick; size 32 μm . Photograph.



Fig. 78. Index map of Cuba with provinces and site of the Saramaguacàn drill hole (Isle of Pines= Isla de la Juventud, Isle of the Youth).

This grain belongs to the Normapolles group of pollen, an extinct assemblage with affinities possibly with the Juglandaceae, and characteristic of eastern North America and western Europe during the Cretaceous and Paleogene. It was described from Cuba as *Basopollis* by Areces-Mallea (1989), while Frederiksen (personal communication) believes it is similar to *Choanopollenites* as described by Tschudy (1973). It represents one of the several elements of the Cuban Eocene flora with affinities to North America.

Retibrevitricolpites (Figs. 59, 60). Oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (2–3 μm apex to equator), inner margin entire, surrounded by costae colpi (2 μm wide); finely reticulate, muri smooth, straight, width of muri approximately

equal to slightly wider than diameter of lumina (1 μm); tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 2 μm thick; size 25 μm . Photograph.

Porocolpopollenites (Fig. 61). Oblate, amb oval-triangular, apices acute; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, situated at apices, straight, short (3 μm apex to equator), pores situated at midpoint of colpi, surrounded by costae porae 3 μm wide; finely reticulate; tectate-perforate, columellae evident in median optical section (at 400 \times magnification), wall 1 μm thick; size 32 μm . Photograph.

This grain is similar to those of the modern genus *Symplocos* described by Frederiksen (1980a) from the Eocene of the

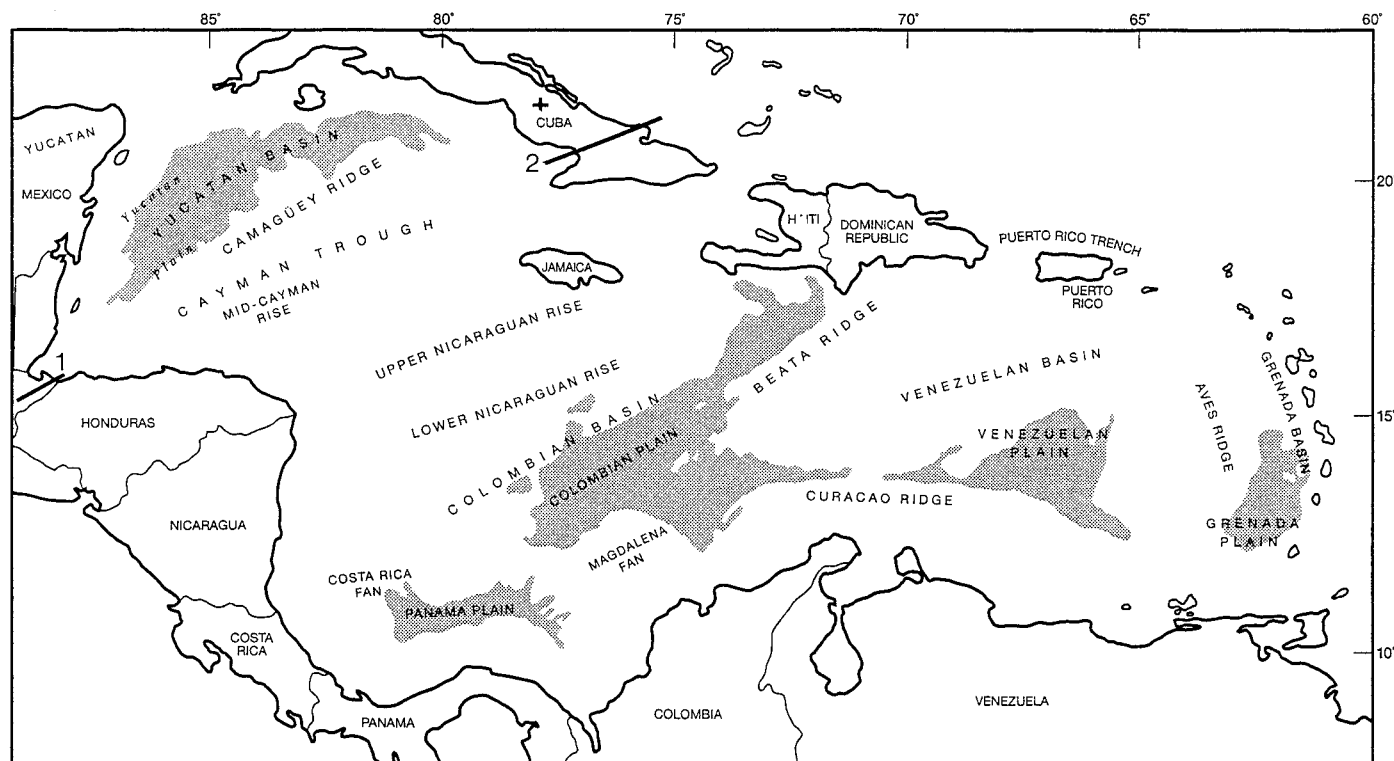


Fig. 79. Physiographic diagram of the Caribbean Basin and surrounding lands. + = site of the Saramaguacàn drill hole; dark line (1)= on-land continuation of the Cayman Trough as the Polochic/Motagua fault system of Guatemala; dark line (2)= Cauto Basin delimiting the eastern fragment (Sierra Maestra region) from central and western Cuba.

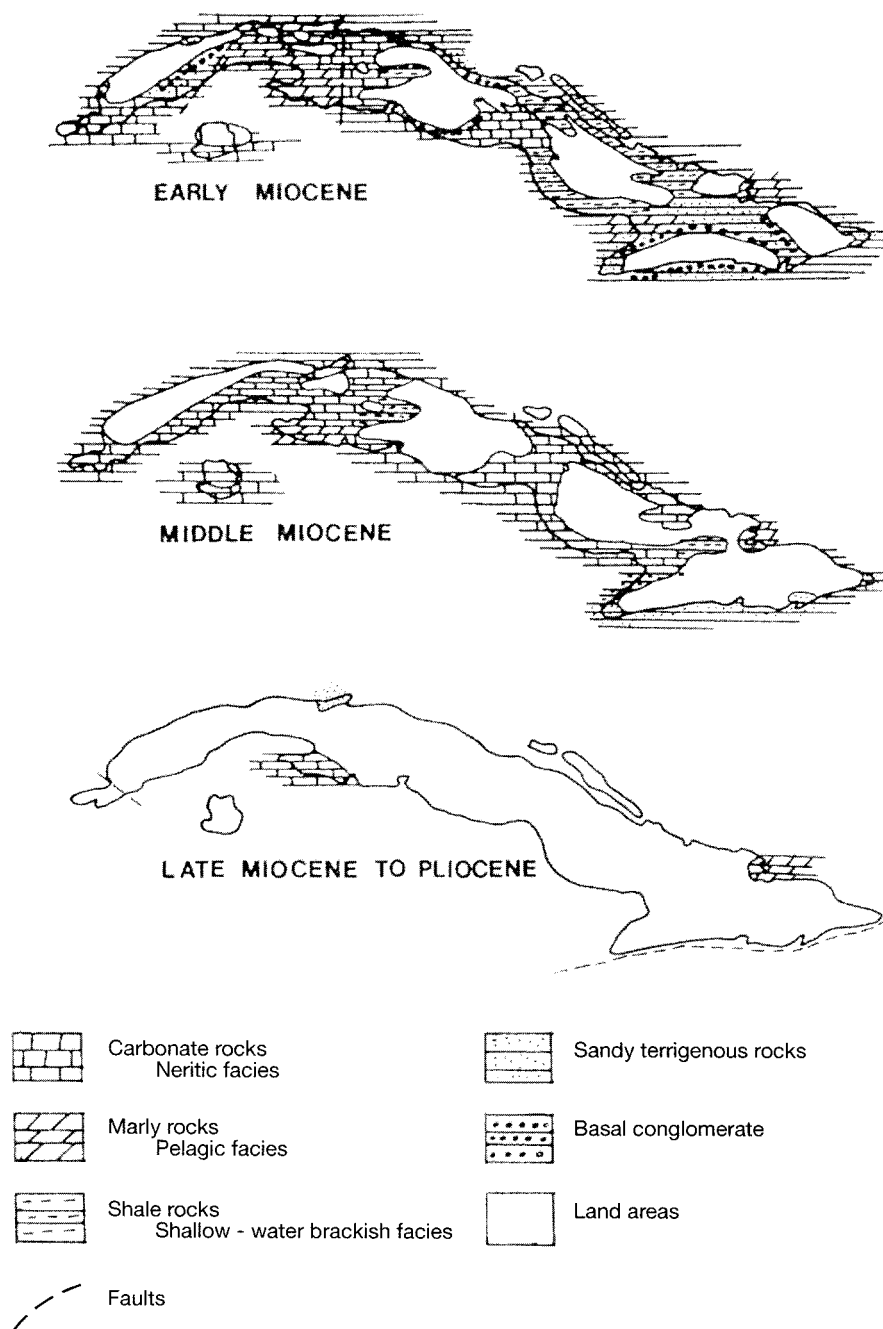


Fig. 80. Generalized paleogeography of Cuba in the Miocene (after Iturralde-Vinent, 1978; see also Lewis and Draper, 1990, p. 93).

southeastern United States. It is similar also to one listed as "unidentified porocolpate pollen" by Elsik and Dilcher (1974, pl. 29, figs. 84–85) from the middle Eocene of Tennessee.

Monoporate—*Graminidites gramineoides* (Meyer) Krutzsch (Gramineae; Fig. 62). Spherical, amb circular; monoporate, pore circular, 3 μm in diameter, inner margin entire, surrounded by annulus 2 μm wide, outer margin diffuse; psilate to scabrate; tectate, wall 1–2 μm thick, homogeneous in median optical section (at 400 \times magnification); size 30 μm . Photograph.

Pollen of the Gramineae (also known in the stratigraphic

literature as *Monoporites annuloides* van der Hammen; see, e.g., Germeraad, Hopping, and Muller, 1968, p. 294, pl. 3, fig. 3) is common in parts of the Saramaguacán section, as judged from the number of photographs of specimens processed at Havana, but none were found in the material processed in the KE laboratory so percentages could not be calculated. Certainly, ferns, grasses, palms, and Bombacaceae were prominent in the middle Eocene vegetation of east-central Cuba.

Diporate—*Psiladiporites redundantis* González Guzmán (Moraceae; Fig. 63). Elliptical, amb oval; diporate, pores situated at opposite poles of the grain, circular, 3 μm in diameter,

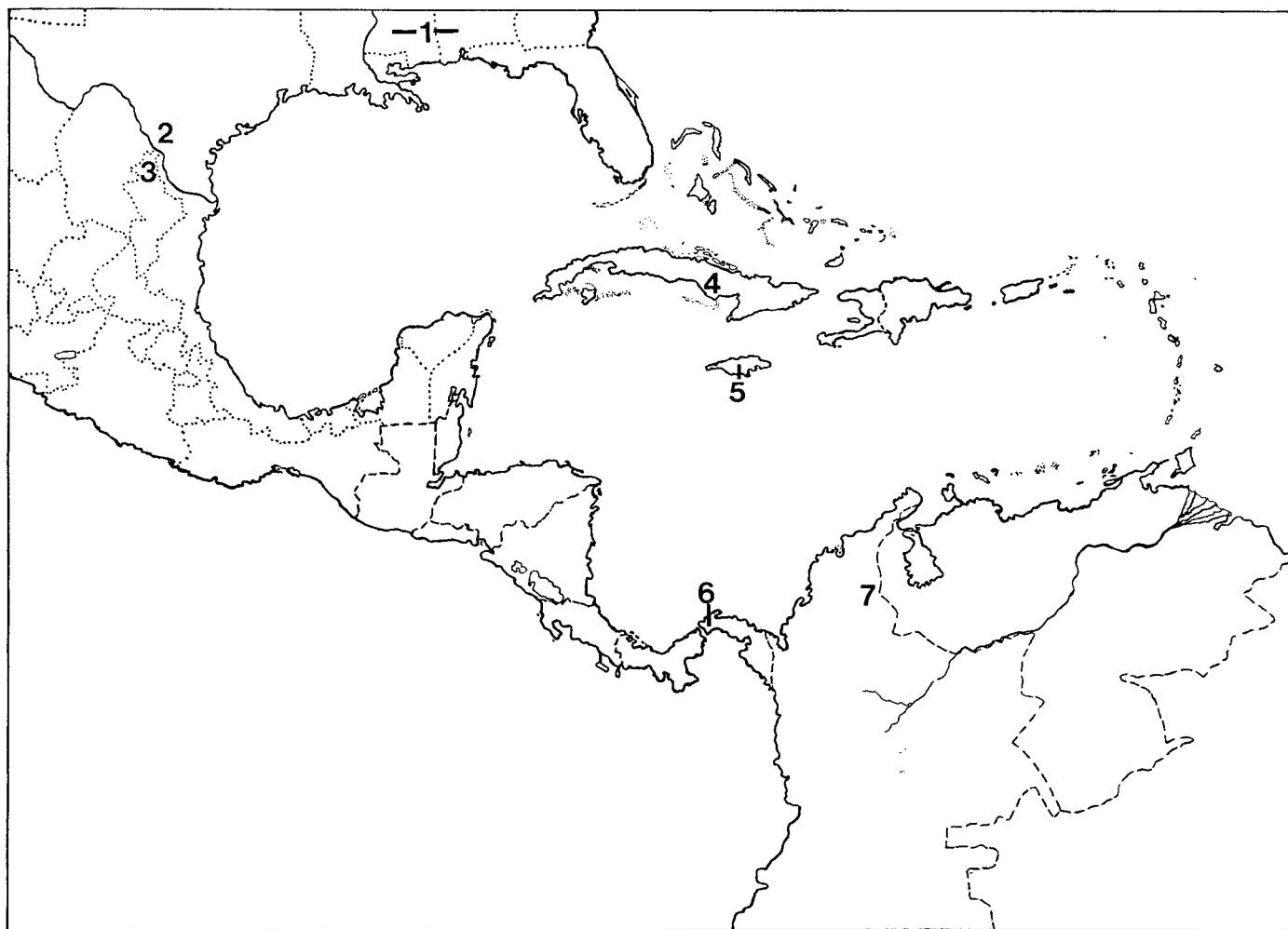


Fig. 81. Geographic distribution of middle to late Eocene palynofloras mentioned in the text. 1= Jackson Group (Frideriksen, 1980a, b, 1988); 2/3= Laredo Formation, Texas (Westgate and Gee, 1990)/Burgos Basin, Nuevo Leon, Mexico (Martínez-Hernández, Hernández-Campos, and Sánchez-López, 1980); 4= Saramaguacán flora, Cuba (present study); 5= Guys Hill Member, Chapelton Formation, Jamaica (Graham, 1993); 6= Gatuncillo flora, Panama (Graham, 1985); 7= includes both the Los Cuervos and Mirador Formations, Colombia (González Guzmán, 1967).

sourrounded by faint annulus 1 μm in diameter; scabrate; tectate, wall 1 μm thick, homogeneous in median optical section (at 400 \times magnification); size 23 \times 20 μm . Photograph.

These grains are similar to ones produced by several members of the Moraceae. In addition to the occurrence in South America (González Guzmán, 1967), similar grains are known from the Eocene of Panama (Graham, 1985, p. 518–519, fig. 58) and from Paleogene sediments of the Gulf Coast of the southeastern United States [Frederiksen, 1988, p. 48, pl. 1, fig. 17; Elsik, 1974, pl. 2, figs. 35, 36 reports a somewhat similar type from the Eocene of the Texas Gulf Coast as *Ficus?* Spp. (Moraceae)].

Triporates—*Brosipollis* cf. *striata* Frederiksen (Fig. 64). Oblate, amb triangular; triporate, pores situated at apices of grain, circular to oval, 4 μm in diameter, equatorially arranged, equidistant, protruding 5 μm , surrounded by annulus 2–3 μm wide; scabrate to possibly faintly striate; tectate, wall homogeneous to columellae just evident in median optical section (at 400 \times magnification), 2 μm thick; size 33 μm (excluding pores). Slide Y25, ESF U-38,3.

Frederiksen (1988, p. 52, pl. 3, figs. 23–26; pl. 4, figs. 1–3) describes the species from the Paleogene of the Gulf Coast of eastern United States and considers its affinities probably to be with *Bursera*, which has finely striate pollen.

Triporopollenites type 1 (Fig. 65, 66). Spherical, amb circular; triporate, pores equatorially arranged, equidistant, circular (3 μm in diameter), inner margin entire, surrounded by costae pori (1–2 μm wide), outer margin of annulus slightly diffuse; scabrate; tectate, wall 2 μm thick; size 45 μm . Photograph.

Triporopollenites type 2 (Figs. 67, 68). Oblate-spheroidal, amb circular; triporate, pores equatorially arranged, equidistant, circular, 3 μm in diameter, inner margin entire, surrounded by costae pori 2 μm wide; scabrate; tectate, wall 2 μm thick, columellae evident in median optical section (at 400 \times magnification); size 40 μm . Photograph.

These grains are similar to *Celtis* (*Celtipollenites*) listed by Frederiksen (1988, pl. 3, figs. 7–11) from the upper middle Eocene Lisbon Formation of southeastern United States.

Periporate—*Lyningtonia* cf. *L. rhetor* Erdtman (Nyctagi-

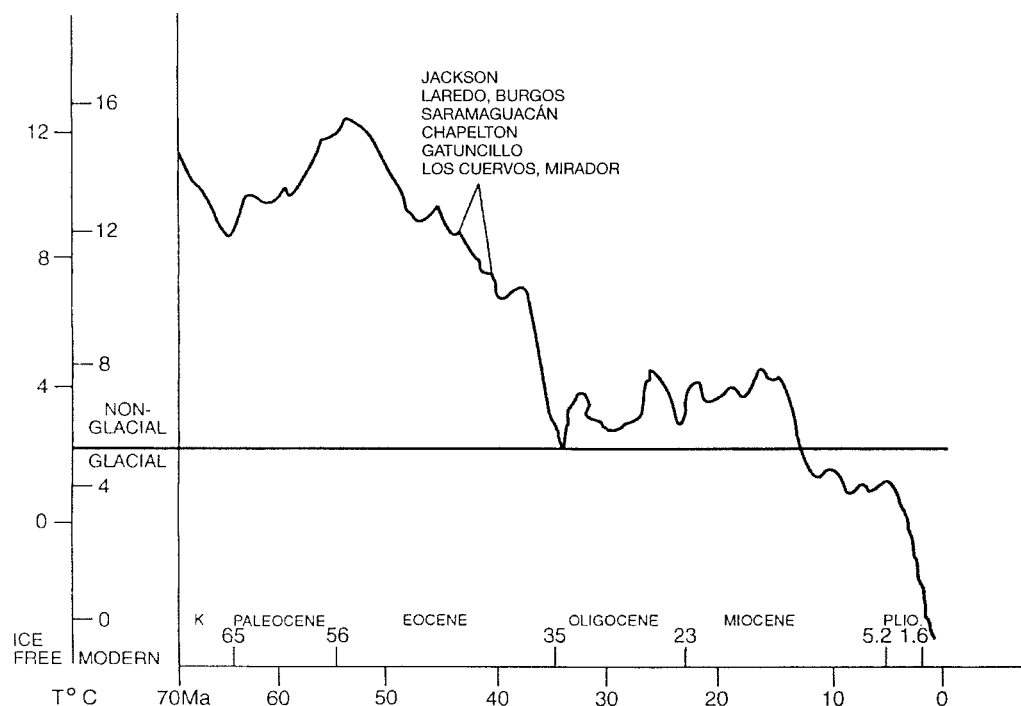


Fig. 82. Global benthic paleotemperature curve showing temperature context for middle to late Eocene palynofloras in northern Latin America. Curve follows Miller, Fairbanks, and Mountain (1987).

naceae; Figs. 69, 70). Oblate, amb polygonal (eight sided); periporate, pores equally spaced, circular, 4 μm in diameter, inner margin entire; scabrate (or psilate with heads of columellae apparent through thin tectum); tectate, wall 2–3 μm thick; size 45 μm . Photograph.

Frederiksen (1980a, p. 44, pl. 9, figs. 1–3; see also Elsik and Dilcher, 1974) describes and illustrates a similar specimen from the upper Eocene Jackson Group of the southeastern United States. The grains are similar to some Nyctaginaceae (e.g., *Phaeoptilum*).

Pericolporate—*Pericolporites* (Figs. 71, 72). Oblate spheroidal, amb circular; pericorporate, apertures equidistant, colpi 20 μm long (apex to mid-point of pore), margin slightly diffuse, tapering to acute apex, pores situated at mid-point of colpus, circular, 3 μm in diameter, inner margin entire, annulus 2–3 μm wide; scabrate; tectate, wall 2 μm thick, homogeneous to columellae just evident in median optical section (at 400 \times magnification); size 45 μm . Photograph.

Stephanoporate—*Malvacipollis tschudyi* Frederiksen (Figs. 73–75). Oblate-spheroidal to spherical, amb circular; stephanoporate, pores circular, 2 μm in diameter, inner margin entire, equidistant, surrounded by narrow costae pori; echinate, echinae short (2 μm), straight; tectate, wall 1–2 μm thick, columellae just evident in median optical section (at 400 \times magnification); size 30–35 μm (excluding spines); Slide Y25, ESF U-38.2; and photograph.

This pollen type is common in the fossil assemblage but it is not always possible to determine aperture number and arrangement from those represented only by photographs. The biological affinities are possibly with the Malvaceae.

Nonaperturate—*Retipollenites* cf. *confusus* González Guz-

mán (Figs. 76, 77). Spherical, amb circular; nonaperturate; reticulate, reticulum coarse (open), heavy, muri thick (2 μm), flat, smooth, slightly sinuous, lumina 3–4 μm in diameter; tectate-perforate, columellae coarse (clearly evident median in optical section at 400 \times magnification), spaced 3–4 μm , 3 μm long; size 45 μm . Photograph.

DISCUSSION

Geologic history—The history of the Caribbean Basin and adjacent lands is complex and, indeed, the area is one of the last regions whose evolution is still controversial in terms of the plate tectonic paradigm (Lewis and Draper, 1990). The models of Pindell and Barrett (1990) and Pindell (1994) are widely accepted, as are those derived from earlier, unpublished versions (e.g., Ross and Scotese, 1988), although criticisms and modifications have recently been proposed (Iturralde-Vinent, 1994; Meschede, 1998; Meschede and Frick, 1998; G. Draper, Florida International University). With regards specifically to Cuba its history is becoming more clear, especially as earlier reconstructions showing movement of the island over great distances from the south are discarded. For example, Corral (1939) shows Cuba and other islands of the Greater Antilles located along the north coast of South America as recently as the late Miocene (Borhidi, 1996, p. 257).

The current consensus is that western and central Cuba were separate until early to middle Eocene time. The northern part consisted of the Bahama Bank, a continental margin that was composed of Jurassic to Cretaceous shallow, continental platform to deeper-water, continental rise deposits; the southern part consisted of a Cretaceous volcanic island arc (Draper and Barros, 1994; Lewis and Draper, 1990). The arc collided with the continental margin in early to middle Eocene time causing widespread thrust faulting and folding of the Bahamian sedi-

ments and the emplacing of both ocean crust and the arc onto the Bahamian margin.

The tectonic evolution of the Oriente region (Holguin-Granma-Santiago-Guantanamo provinces; Fig. 78) is still controversial. The ophiolites (ocean floor material) seem to have been emplaced at the very end of the Cretaceous onto arc crust rather than continental crust. It is likely that Oriente was joined to northern Hispaniola and formed a separate block that did not dock against central Cuba until the Eocene (G. Draper, Florida International University). The block includes the present Sierra Maestra region (Fig. 79). Since the middle Eocene Cuba has mostly been tectonically quiescent (Draper and Barros, 1994). The Saramaguacán locality is west of the suture and was part of the island arc. Hispaniola separated in the middle to late Eocene with activation of the Cayman Trough fault system. The on-continent continuation of the Cayman Trough is the Polochic-Montagua fault system of northeastern Guatemala (Fig. 79).

During the middle Tertiary there was further uplift in proto-Cuba so that by the early Miocene it had the configuration shown in Fig. 80. By the late Miocene the various parts had coalesced into essentially the modern geography of Cuba and the island was emergent except for the Zapata Peninsula to the northwest and parts of Oriente Province. By this scenario western and central Cuba have always been part of the North American plate; eastern Cuba came from the vicinity of the Yucatan Peninsula/northern Central America; and no part was ever directly connected with South America.

The light brown color and the fine-grained nature of the sediments, together with fossil remains of a diverse terrestrial vegetation, indicate the Saramaguacán assemblage is a freshwater swamp or marsh community deposited beyond the influence of marine waters. The middle Eocene represents a transition period in the Caribbean Tertiary between times when many palynomorphs can be assigned to modern genera (late Eocene and younger) and when most appear distinct from extant taxa (early Eocene and older). By the late Eocene pollen of the mangrove *Rhizophora* was widespread in brackish-water habitats along the Caribbean coasts (Graham, 1995) and often constitutes 90% of palynofloras in lignites deposited under brackish-water conditions. Earlier, in the Paleocene and early Eocene, a different pollen type (*Brevitricolpites variabilis*) often reaches these same percentages in brackish-water lignites and presumably it is the ecological equivalent of *Rhizophora*. Neither *Rhizophora* nor *B. variabilis* pollen was recovered from the Saramaguacán flora. The absence of mangroves, the composition of the flora, the light brown color and fine-grained texture of the sediments, and the geologic history indicates the Saramaguacán assemblage represents an inland swamp or marsh community growing along the northeastern margin of the proto-Cuba island arc which was then near its present position.

Paleoclimates—Relatively little can be said about the middle Eocene terrestrial climates of Cuba based on plant microfossil evidence because the palynomorphs mostly can not be referred to modern taxa. Even when generic identifications are possible it is not certain that these ancient entities are biologically equivalent or had the same ecological requirements as similar modern forms. Nonetheless, several lines of independent evidence provide an approximation of terrestrial Eocene paleoclimates in the northern Caribbean region. The composition and numerical representations of the flora are shown in

TABLE 1. Composition, numerical representation, and geographic affinities of the Saramaguacán palynoflora. Percentages are based on counts of 200 palynomorphs from slide X24. Fern spores and grasses were not encountered in material processed at KE but were common in the flora as suggested by the number of photographs from material presently housed at the Museo Nacional de Historia Natural in Habana, Cuba. Na = North America, Sa = South America, W = widespread, E? = endemic?.

Taxon	%	NA	SA	W	E?
<i>Laevigatosporites</i>				x	
<i>Verrucatosporites usmensis</i>				x	
<i>Lygodiumsporites adriennis</i>				x	
Trilete fern spore type 1				x	
<i>Undulatisporites concavus</i>		x			
cf. <i>Pteris dentata</i>		x			
<i>Arecipites</i>				x	
<i>Liliacidites</i>	50.5				x
<i>Retimonocolpites</i> type 1	0.5		x		
R. type 2				x?	
R. type 3				x?	
R. type 4				x?	
R.(?) type 5	1				x
<i>Cupuliferoidaepollenites liblarensis</i>					
<i>Fraxinopollenites</i> cf. <i>F. scoticus</i>		x			
		x			
<i>Echitricolpites</i>	3.5				x
<i>Retitricolpites</i> type 1				x	
R. type 2	8				x
R. type 3	4.5				x
R. type 4	7				x
R. type 5					x
R. type 6					x
<i>Reticulataepollis</i> cf. <i>intergranulata</i>		x			
<i>Retitricolporoides</i> type 1				x	
R. type 2	1.5			x	
R. type 3				x	
<i>Striatricolpites cataumbus</i>				x	
<i>Retitricolporites</i> type 1	0.5			x	
R. type 2					x
R. type 3				x	
<i>Myrtaceidites</i> cf. <i>parvus</i>				x	
<i>Bombacacidites</i> cf. <i>tillioides</i>					
B. type 1	9	x			
B. type 2		x			
<i>Basopollis</i> /cf. <i>Choanopollenites</i>		x			
		x			
<i>Porocolpollenites</i>		x			
<i>Retibrevitricolporites</i>		x			
<i>Graminidites gramineoides</i>				x	
<i>Psilodiporites redundantis</i>				x	
<i>Brosipollis</i> cf. <i>striata</i>	1.5	x			
<i>Tripoporipollenites</i> type 1					x
T. type 2	5.5				x
<i>Lymingtonia</i> cf. <i>L. rhetor</i>	11	x			
<i>Pericolporites</i>					x
<i>Malvacipollis tschudyi</i>	6	x			
<i>Retipollenites</i> cf. <i>confusus</i>		x			
Totals	100	16	1	18	11

Table 1. The most abundant microfossils, based on counts of processed material at KE, and on the number of photographs from samples presently housed in Cuba, are Palmae, ferns, Bombacaceae, and grasses. Two genera that can most reliably be assigned to modern genera are the tropical fern *Pteris* and the primarily Amazonian rain forest genus *Crudia*. Collectively, the composition of the palynoflora suggests a warm-temperate to tropical climate.

Associated floras of similar age in the region suggest a similar paleoclimate. The localities for eight middle to late Eocene floras from the Gulf/Caribbean region are shown on Fig. 81. Taxa include *Selaginella*, *Ceratopteris*, *Deltoidospora* (cf. *Acrostichum*, often associated with *Rhizophora* in modern mangrove swamps), *Pteris*, *Palmae* (including cf. *Mauritia*), cf. *Tillandsia*, *Casearia*, *Coccoloba*, *Combretum/Terminalia*, *Eugenia/Myrcia*, *Faramaea*, cf. *Ficus*, *Lisianthus*, *Psilatricolporites crassus* van der Hammen and Wijmstra (*Pelliceria*), and others. These regional paleofloras all reflect warm-temperate to tropical terrestrial climates in the middle to late Eocene.

Context information is provided by the global benthic paleotemperature curve (Fig. 82; Miller, Fairbanks, and Mountain, 1987). This curve is based on $^{18}\text{O}/^{16}\text{O}$ ratios in the shells of marine invertebrates and is, therefore, independent of reconstructions based on fossil plant evidence. More ^{18}O is taken up as the water cools, and deep-sea cores provide a record of the ratios from the past 100 Ma. The curve clearly shows warm climates only slightly cooler than those of the early Eocene thermal maximum. Thus, composition, associated floras, and context information are all consistent in suggesting warm-temperate to tropical climates in the middle Eocene of the Caribbean region.

North America vs. South America Affinities—One geological question which the Saramaguacán study can address is whether the composition of the flora suggests stronger affinities with North America, consistent with recent plate tectonic models, or with northern South America as suggested in older models. Comparisons with North America are limited mostly to the southeastern United States which has the largest and most completely studied palynofloras of middle to late Eocene age.

Table 1 shows that of the 46 palynomorphs recognized for the Saramaguacán flora, 18 are widespread, 16 are similar to ones reported from the southeastern United States, and only one (*Retimonocolpites* type 1) is similar to a form described from northern South America. Further comparisons with regions in Mexico, Central America, and other islands of the Antilles (Fig. 81) are constrained by the mostly smaller size and the few middle to late Eocene floras available. The plant microflora of the Guys Hill Member of the Chapelton Formation in Jamaica (Graham, 1993) is geographically the closest to the Saramaguacán flora and it is about the same age (middle Eocene). However, it was deposited under different ecological conditions as evidenced by the presence of the mangrove *Psilatricolporites crassus* (*Pelliceria*) and several marine dinoflagellates. *Deltoidospora* (*Lygodiumsporites*), *Arecipites* (*Palmae*), and *Bombacacidites* are abundant in the Chapelton and Saramaguacán floras.

The Burgos Basin flora (Martínez-Hernández, Hernández-Campos, and Sánchez-López, 1980) in northeastern Mexico (Fig. 81) is also a small assemblage with several palynomorphs similar to those from Saramaguacán. These include *Monocolpopollenites* (= our *Arecipites*, Fig. 11), *Liliacidites* (=possibly our Figs. 16, 17), *Bombacacidites*, *Jussitriporites* (=our *Brosipollis* cf. *striata*, Fig. 64), and *Nudopollis* (our *Basopollis*/cf. *Choanopollenites*, Fig. 58). The Burgos Basin flora differs in the presence of *Ilexpollenites* (*Ilex*) and *Momipites* (*Juglandaceae*, cf. *Alfaroa*, *Engelhardia*, *Oreomunnea*).

In the slightly younger middle(?) to late Eocene Gatuncillo flora (Graham, 1985) in Panama there are several palynomorphs similar to those of the Saramaguacán and other Eocene

floras to the north. These include *Pteris*, *Lygodiumsporites* (=Trilete fern spore type 3 in the Gatuncillo flora), *Arecipites*, *Striatricolpites catumbus* (= *Crudia*), *Cyrtaceidites* (= *Eugenia/Myrcia*), and *Psiladiporites* (=cf. *Ficus*). The Gatuncillo flora also includes the mangroves *Pelliceria* and *Rhizophora* indicating deposition under coastal brackish-water environments rather than the fresh-water swamp/marsh conditions of the Saramaguacán flora.

All of these floras, collectively and individually, are more similar to one another than to any floras of comparable age known from northern South America. In particular, the Normapolles *Basopollis*/cf. *Choanopollenites* (Areces-Mallea, 1990) is a distinctive form characteristic of eastern North America and has not been reported from sites belonging to the Caribbean or other southern plates. These results are consistent with plate tectonic reconstructions showing the island arc and fragment comprising western and central Cuba as part of the North American plate, and the fragment presently constituting eastern Cuba as originating in the vicinity of the Yucatan Peninsula/northern Central America.

A point that can be raised for preliminary consideration is the extent of paleoendemism (Table 1). Endemics are a characteristic feature of the Caribbean islands. Borhidi (1996, p. 216) gives the number of endemic plant taxa on Cuba as 3178 or 49.9% of the total flora and 53% of the native flora. Howard (1973) lists 40 genera found only on Cuba. In all the Tertiary palynofloras studied from northern Latin America there are specimens from each assemblage that presently have not been found in any other. Of the 46 palynomorph types in the Saramaguacán flora 11 (24%) are unique to that flora. There is not a sufficient number of fossil floras known from the Caribbean Basin to determine which forms are likely paleoendemics. As more fossil floras are studied, however, it is worthwhile to track these unique forms which may eventually provide an approximation of the extent of endemism in the Antilles at different times in its history.

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