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NEW ANGIOSPERM RECORDS FROM THE CARIBBEAN TERTIARY[1]

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ABSTRACT

Thirteen taxa represented by fossil palynomorphs that either have no previous fossil record or were unknown as microfossils in the region have been recovered from Gulf/Caribbean Tertiary deposits and processed by acetolysis. Twelve of these are from the Pliocene Gatun Formation in the Canal region of Panama: *Aegiphila* (Verbenaceae), cf. *Bucida* (Combretaceae), *Cabomba* (Cabombaceae/Nymphaeaceae), *Casimiroa* (Rutaceae), *Cosmibuena* (Rubiaceae), *Cymbopetalum* (Annonaceae), *Faramea* (Rubiaceae), Mutisieae type (Compositae), *Petrea* (Verbenaceae), *Posoqueria* (Rubiaceae), and *Symplocos* (two types, Symplocaceae). The other (*Hygrophila*, Acanthaceae) is from the Miocene Artibonite Group of Haiti. These new records support emerging concepts concerning the biogeography and paleoenvironments of proto-Central America based on previous studies: a Tertiary vegetation with predominantly Central American and Mexican affinities; little evidence of extensive arid or savanna vegetation; a paleophysiography of low to moderate altitudes; and an essentially modern tropical climate for the southern part of present-day Central America, which on the basis of plate tectonic evidence, consisted mostly of volcanic islands until about 3.8 Myr.

DURING A STUDY of palynofloras from Tertiary deposits in the Caribbean region, 13 angiosperm pollen types were identified that either were new reports for the area or had no previous fossil record. Twelve of these (*Aegiphila*, Verbenaceae; cf. *Bucida*, Combretaceae; *Cabomba*, Cabombaceae/Nymphaeaceae; *Casimiroa*, Rutaceae; *Cosmibuena*, Rubiaceae; *Cymbopetalum*, Annonaceae; *Faramea*, Rubiaceae; Mutisieae type, Compositae; *Petrea*, Verbenaceae; *Posoqueria*, Rubiaceae; *Symplocos* (two types), Symplocaceae) were from the Gatun Formation of the of the Canal region of Panama. The other (*Hygrophila*, Acanthaceae) was from the Artibonite Group of Haiti.

The Gatun Formation outcrops extensively on the north (Caribbean) side of the Canal, but all known surface exposures are marine. However, well cores drilled by the Panama Canal Commission in 1962 encountered subsurface Gatun sediments consisting of near-shore, estuarine deposits that contained a rich pollen and spore assemblage. The cores were from Gatun Lake at latitude 9°16′N, longitude 79°52′W, and the specimens were recovered at depths of 178′, 253′, and 255.5′ (depths in feet following original log data; see Graham, Stewart, and Stewart, 1985 for discussion of the geology of the fossil-bearing deposits). Until recently the Gatun Formation has been considered middle Miocene in age (Woodring, 1957–1982) and is so designated on the Geologic Map of the Panama Canal and Vicinity (Stewart and Stewart, 1980). Current studies of ostracoda (van den Bold, personal communication) and foraminifera (Vokes, 1983; personal communication) now suggest the Gatun Formation is probably Pliocene in age.

The material from Haiti was obtained from the outer matrix of megafossil specimens in the collections of the United States National Museum. These collections were made in the early 1900s by W. P. Woodring and sent to E. W. Berry for study (Berry, 1923). They are from the Department de l'Ouest, along a road cut from Mirebalais to Las Cahobas (latitude 18°55′N, longitude 72°36′W). Bowin (1973) presents a series of geologic transects for the general area, but none are from the Mirebalais-Las Cahobas region specifically, and it is unlikely new geologic information will be forthcoming in the near future. Strata in the vicinity of the fossil locality are part of the Artibonite Group (Bowin, 1975; Woodring, Brown, and Burbank, 1924), which includes four formations—Madame Joie (latest Oligocene to earliest Miocene), Thomonde (early to middle Miocene), Maissade (middle Miocene), and Las Cahobas (late Miocene). The fossils are from a clay above the Thomonde Formation, but in the opinion of Woodring et al. (1924) the clay

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does not belong to that formation. It is likely an unnamed unit, and possibly a facies of the Las Cohobas Formation. Berry (1923) thought the megafossil specimens indicated a late Miocene age, and the microfossils are consistent with a late Tertiary age assignment. The pollen assemblage contains a relatively large and diverse Compositae component, and in the Gulf/ Caribbean region these first appear in abundance in the Miocene.

MATERIALS AND METHODS—Samples were broken in a mortar and pestle, transferred to Nalgene plastic beakers, and covered with 10% hydrochloric acid for 1 hour to remove carbonates. The samples were transferred to 50 ml Nalgene centrifuge tubes, washed four times with distilled water (1,500 rpm for 4 minutes), and covered with hydrofluoric acid for 1 hour to remove silicates. The samples were then treated with concentrated nitric acid (overnight, oxidation of organic debris), 10% potassium hydroxide (3 minutes), and acetolyzed for 3 minutes (nine parts acetic anhydride to one part concentrated sulfuric acid; preceded and followed by washes in glacial acetic acid), with four washes in distilled water between each step. The samples were drained for 1 hour, melted glycerine jelly added, and ten slides prepared from each sample. The slides were sealed with CoverBond, labeled, and photographed with a Leitz Orthoplan photomicroscope using Panatomic X film. Location of the specimens on the slides is given in the plate legends by England Slide Finder coordinates. Comparisons were made with acetolyzed material in a modern reference collection of about 25,000 slides. Materials are deposited in the palynological collections at Kent State University.

RESULTS—Descriptions are provided for each microfossil, together with the geographic range and ecological conditions under which the modern analogs grow. Any previous fossil record and the stratigraphic range for each type is also listed. Terminology for vegetation types follows Holdridge (1947; Holdridge et al., 1971).

Aegiphila (Verbenaceae, Figs. 1, 2)—Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (9–12 μm, apex to equator), inner colpi margins entire to slightly diffuse; echinate, echinae short (ca. 1 μm), moderately dense and uniformly distributed; tectate, wall ca. 1–1.5 μm thick; E 45 μm.

Aegiphila is a large genus of about 160 species of trees, shrubs, and lianas growing in Mexico, Central America, the Antilles, and South America (Brazil, Colombia, Venezuela, the Guianas, Peru). Twenty-one species are listed for Panama (D'Arcy, 1987; Moldenke, 1973) and these occur primarily in moist forest types (tropical moist, tropical wet, premontane moist, premontane wet). The microfossils are similar to *A. elata* Sw. (Table 1), a widespread species (Mexico, Central America, the Antilles, the Guianas, Venezuela) found along the margins of woods and streams. *Aegiphila* has not been reported previously in the fossil record.

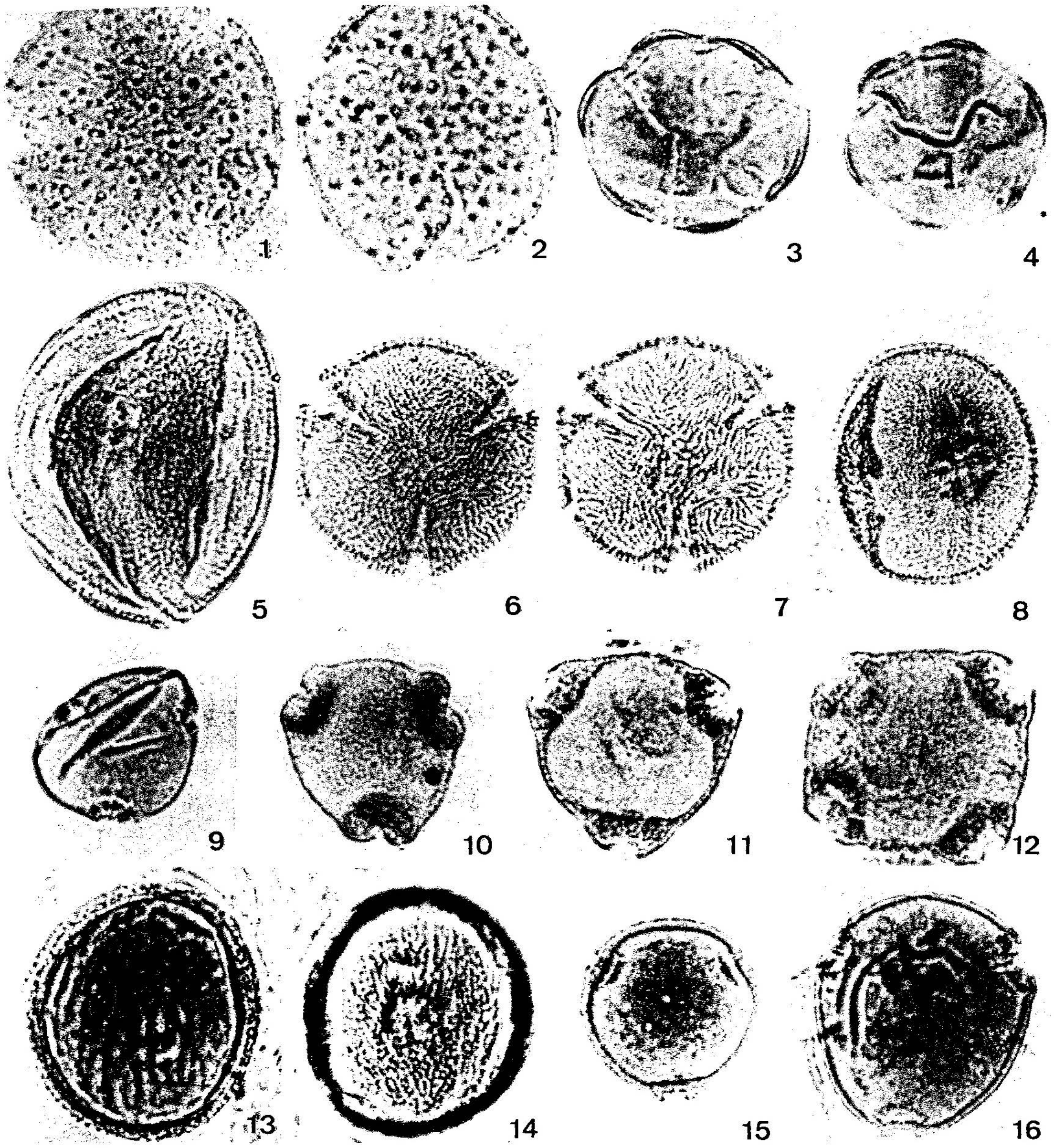
cf. Bucida (Combretaceae, Figs. 3, 4)—Prolate-spheroidal, amb circular, lobate due to thinning of wall at apertures; tricolporate with three pseudocolpi, colpi equatorially arranged, meridionally elongated, equidistant, ca. 15 μm long (apex to equator), narrow, colpus margin entire to slightly dentate, pseudocolpi similar, slightly shorter (ca. 12 μm apex to equator), pores circular, 3 μm in diameter, situated at midpoint of colpus; scabrate; tectate, wall 2 μm thick; E 30 μm.

Bucida presently occurs from south Florida to Central America and the Antilles. Of the four species, one is listed for Panama (*B. buceras* L.), a small tree or shrub growing in wet forests and strand thickets at elevations from sea level to about 1,000 m throughout the range of the genus. Leaves identified as *Bucida* have been reported from the Eocene Wilcox Formation of Kentucky (*B. eocenica* Berry, 1941) and from the Tertiary of the Dominican Republic (*B. sanchezensis* Berry, 1921). Reinvestigation of other leaf material from these early studies (e.g., Dilcher, 1973) has shown that many identifications are incorrect. The genus has not been reported previously in the microfossil record.

The specimens most resemble *Bucida* in our reference collection, particularly in the relatively large size (30 μm) for this type grain, but scabrate, tricolporate grains with three pseudocolpi, although frequently smaller (ca. 20–28 μm), occur in several families of the Myrtales (Combretaceae, Lythraceae, Melastomataceae); hence the provisional cf. identification.

Cabomba (Cabombaceae/Nymphaeaceae, Fig. 5)—Reniform; monocolpate, colpus 45 μm long, bordered by faint, narrow (ca. 2 μm) margo; striate, striae appearing finely beaded due to underlying columellae; tectate, wall 2 μm thick; P 58 × E 34 μm.

Cabomba is a genus of six species of aquatic herbs occurring in warm temperate to tropical



Figs. 1–16. Fossil pollen from the Gatun Formation (Panama) and the Artibonite Group (Haiti). **1, 2.** *Aegiphila,* Gatun core SL-103, 253′, slide 12, ESF J-26; slide 9, ESF T-48. **3, 4.** cf. *Bucida,* Gatun core SL-103, slide 6, ESF G-25; slide 1, ESF M-39. **5.** *Cabomba,* Gatun core SL-103, 253′, slide 1, ESF J-51. **6–8.** *Casimiroa,* Gatun core SL-103, 253′, slide 1, ESF P-40. **9.** *Cosmibuena,* Gatun core SL-103, slide 1, ESF M-44. **10–12.** *Faramea,* Gatun core SL-103, 253′, slide 1, ESF H-37; slide 9, ESF H-20; slide 2, ESF F-42. **13, 14.** *Hygrophila,* Artibonite, slide 7, ESF E-44. **15.** *Symplocos, S. chiriquensis* type, Gatun core SL-103, 178′, slide 2, ESF E-35. **16.** *Symplocos, S. pychantha* type, Gatun core SL-103, 253′, slide 5, ESF V-33.

areas of the New World (the Antilles, Central America, South America). In Panama it is represented by *C. piauhyensis* Gardner which has pollen similar to the specimen. The genus has been reported as a megafossil from the Paleocene Ft. Union Formation of North Dakota (see listings in LaMotte, 1952, p. 89). This is the first report of fossil pollen.

Casimiroa (Rutaceae, Figs. 6–8)—Prolate-spheroidal, amb circular; tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, 30 μm long, colpus margin entire to faintly dentate, narrow (ca. 3–4 μm wide), tapering to acute apex, bordered by costae colpi ca. 4–5 μm wide, pore equatorially elongated, ca. 2 × 3 μm, bordered by costae pori ca. 2

μm wide; finely striate-reticulate, arranged in swirl pattern, striae/muri occasionally appearing minutely beaded due to underlying columellae; tectate-perforate, wall ca. 1.5 μm thick, columellae clearly evident; P 45–50 × E 35–40 μm.

The genus consists of six species of trees and shrubs in Mexico and Central America but is not listed for Panama (D'Arcy, 1987). Among the species examined (Table 1), the pollen is most similar to *C. tetrameria* Millsp. *Casimiroa* has not been reported previously in the fossil record.

Cosmibuena (Rubiaceae, Fig. 9)—Oblate, amb circular; tricolporate, colpi equatorially arranged, oriented parallel to equator (as observed in polar view), equidistant, ca. 12 μm long, inner margin entire, pore circular, 3–4 μm in diameter, situated at midpoint of colpus, bordered by beaded annulus of fine, discontinuous ektexine elements; psilate; tectate, wall 1.5 μm thick; E 28 μm.

In *Cosmibuena* the colpi are elongated equatorially rather than meridionally and are thus difficult to observe consistently in polar view. There appears to be a colpus extending from the lower pore of the specimen illustrated in Fig. 9. The genus consists of about 12 species growing in Central and tropical South America. In Panama it is represented by the trees *C. ovalis* Standley and the more widely distributed *C. skinneri* (Oerst.) Hemsley. The latter occurs from Mexico to Colombia and possibly Brazil, growing in the tropical moist, premontane wet, and premontane rain forests. Bartlett and Barghoorn (1973, p. 226, pl. XII) record pollen similar to *Cosmibuena paludicola* Standley from surface samples in Gatun Lake near the shore of Barro Colorado Island. They illustrate a grain in equatorial view showing the equatorially elongated colpus. The genus has not been reported previously in the fossil record.

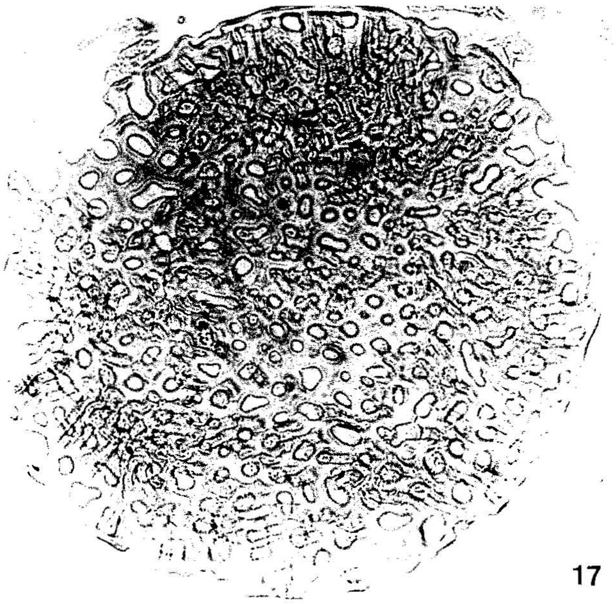
Cymbopetalum (Annonaceae, Fig. 17)—Oblate, amb circular; nonaperturate(?); psilate/reticulate; tectate-perforate, tectal perforations large, circular to irregular in outline, constituting ca. 40–50% of grain surface, columellae conspicuous, ca. 15 μm long; E 180 μm.

The pollen of modern *Cymbopetalum* species are in polyads of eight, but these easily separate into individual grains. Modern pollen of *Cymbopetalum* and the six other genera in its tribe have been studied by Walker (1971a–c, 1972). The genus consists of 11–13 species of trees and shrubs distributed from Mexico to tropical South America. Three species are recorded for Panama: *C. brasiliense* (Vell.) Benth., *C. costaricense* (D. Smith) R. E. Fries, and *C. lanuipetalum* Schery. Tiffney and McClammer (1988) have reviewed the fossil seed record of the Annonaceae (oldest records are from the latest Cretaceous, Nigeria), and Muller (1981) has summarized the fossil pollen record (Maestrichtian and Paleocene of Colombia). Pollen identified as *Annona*? *foveoreticulata* Elsik (1974) from the early and middle Eocene Reklaw Formation of Texas is said to be similar also to *Cymbopetalum* (Muller, 1981, p. 7, based on personal communication from Canright; also discussed by Taylor, 1988). The Reklaw specimens (Elsik, 1974, pl. 1, Figs. 16, 17), however, are quite different in size and morphology from the Gatun specimens. *Annona* pollen has also been reported from the middle Eocene of Tennessee (Elsik and Dilcher, 1974), but these specimens are different from the Texas specimens and are not considered to be similar to *Cymbopetalum* by Muller (1981, p. 7), as may be suggested from Taylor (1988, pp. 267, 268). *Cymbopetalum* has not been reported previously in the fossil record.

Faramea (Rubiaceae, Figs. 10–12)—Oblate, amb oval triangular; tri- to tetraporate, pores equatorially arranged, equidistant, circular to slightly oval, ca. 4 μm in diameter, inner margin entire to faintly dentate, surrounded by conspicuous annulus 5–6 μm wide; scabrate; tectate, wall 1.5 μm thick; E 27–36 μm.

Faramea is a large genus of about 120 species of tropical trees and shrubs distributed from northeastern Mexico to South America and in the Antilles. Seventeen species are recorded for Panama, including the widespread *F. occidentalis* (L.) A. Rich., which produces pollen similar to the Gatun specimens. It grows in the tropical moist, premontane moist, and premontane wet forests.

The pollen of *Faramea* can vary from small, thick-walled forms to larger, thinner-walled forms, with two to four apertures, among grains on a single slide. Triporate pollen has been reported from the Oligocene San Sebastian Formation of Puerto Rico (Graham and Jarzen, 1969, Fig. 21) and from the Pliocene Paraje Solo Formation of Mexico (Graham, 1976, Figs. 179, 180). The heavier-walled, diporate type has been reported from the Middle(?) to Upper Gatuncillo Formation of Panama (Graham, 1985, Figs. 64, 65). Bartlett and Barghoorn (1973, pl. XII, Fig. 7) illustrate another form from Quaternary deposits in Gatun Lake, Panama. The Gatun Formation specimens (Figs. 10, 11) are slightly different but most similar to the Paraje Solo specimens. They can-



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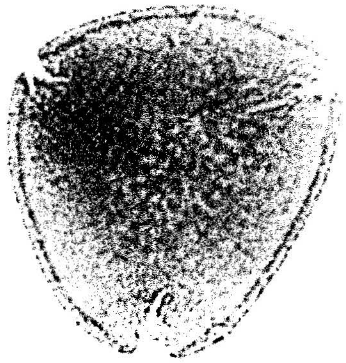

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Figs. 17–20. Fossil pollen from the Gatun Formation (Panama). **17.** *Cymbopetalum,* Gatun core SL-103, 253′, slide 16, ESF N-26. **18.** Mutisieae type, Gatun core SL-103, 253′, slide 14, ESF J-35. **19.** *Posoqueria,* Gatun core SL-103, 253′, slide 4, ESF P-19 (note surface view inset in center of photograph). **20.** *Petrea,* Gatun core SL-103, 255.5′, slide 5, ESF S-34.

not be referred to any individual modern species but fall within the range of variation of *F. occidentalis* pollen, including the occurrence of tetraporate grains (Fig. 12).

Hygrophila (Acanthaceae, Figs. 13, 14)— Prolate-spheroidal; tricolporate with numerous pseudocolpi (sexine segments arranged in vertical bands ca. 2 μm wide), colpi equatorially arranged, meridionally elongated, equidistant, ca. 25 μm long (estimated), pore circular, 4 μm in diameter, situated at midpoint of colpus; faintly and irregularly reticulate; tectate, columellae fine, wall 2 μm thick; P 45 × E 39 μm.

Hygrophila is a genus of about 80 species of herbs to 1 m tall found in both the New and Old World tropics. In Latin America it is distributed from Mexico through Central America and the Antilles to central Argentina. 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) which, among others, produces pollen similar to the Haitian specimens. Pollen of the genus is known from the Miocene of Senegal (Médus, 1975; see Muller, 1981, p. 97; 1984, p. 430) as *Hydrophila* type. It has not

been reported in the megafossil record, and this is the first report of microfossils in the New World.

Mutisieae type (Compositae, Fig. 18)—Prolate to prolate-spheroidal; tricol(por?)ate (pores obscure), colpi equatorially arranged, meridionally elongated, equidistant, ca. 45–48 μm long; echinate, echinae ca. 2 μm long, broad at base; tectate, wall 8–9 μm thick, inner wall 4–5 μm, outer wall (including ca. 2 μm spines) 3–4 μm; P 68 × E 60 μm.

According to Cabrera (1977), "The Mutisieae is a tropical or, essentially, neotropical tribe, with great concentration of genera and species in mountainous and arid regions." Neither condition was extensive in southern Central America until the late Tertiary, and then only to a limited extent. Thus it is not surprising that the tribe is poorly represented in the fossil record of the region.

The principal center of species concentration is in the tropical Andes of Peru, Bolivia, and northwestern Argentina (31 genera), followed by the central Andes of Chile (17 genera), and in arid Patagonia (18 genera). Fossil floras from the Gulf/Caribbean region show limited affinity with these areas until later in the Tertiary, and especially in the Quaternary. Within the region of southern United States, Mexico, Central America, the Antilles, and northern South America (Venezuela, outside Guyana) there are seven genera (Cabrera, 1977, p. 1046): *Acourtia, Chaptalia, Gochnatia, Jungia, Lycoseris, Onoseris,* and *Trixis.* Pollen of species in each genus, except *Onoseris,* was examined (Table 1), and none resembled the fossil specimen. *Gochnatia* is most similar, but differs in being more oblate, smaller (ca. 50–55 μm), and in having shorter, more densely arranged columellae. In the subtribe Mutisiinae, Cabrera (1977, p. 1043) lists 17 New World genera. Pollen from eight was available for study (Table 1), and that of *Mutisia* was most similar to the specimen.

Pollen morphology of the Mutisieae was studied by Wodehouse (1928, 1929a, b, 1935), Carlquist (1957), Barroso and Maguire (1973), Stix (1960), and Skvarla et al. (1977). Additional illustrations are provided in Heusser (1971, pl. 23), Markgraf and D'Antoni (1978, pl. 18, 19), and Wingenroth and Heusser (1983, pl. 8, 9). Based on this survey, which does not include all representatives of the tribe, the pollen of *Mutisia* can be distinguished from that of other genera. For example, *Acourtia, Aphyllocladus, Chaetanthera, Chaptalia, Gerbera, Jungia, Lycoseris,* and *Trixis* lack the comparatively conspicuous spines of the Gatun specimen. Other genera have a thicker, more elaborate inner wall layer and are commonly larger. These include species of *Chaetanthera, Achnopogon, Dinoseris, Gongyolepis,* and *Hyaloseris.* Skvarla et al. (1977) note that "Stix (1960) established eight [nine] Mutisieae pollen-types: *Onoseris, Saussurea, Berardia, Dicoma, Erythrocephalum, Mutisia, Ameghinoa, Oxyphyllum,* and *Trixis*; each type being confined to its own genus." On the basis of this limited survey, the Gatun specimen appears most similar to *Mutisia.* It is possible, however, that the specimen may represent some genus outside the Mutisieae not encountered in our survey. Also, the fossil material is limited (a single specimen), and its presence in Central America in the middle Pliocene is unexpected, considering the paleoclimatic and paleophysiographic conditions prevailing there at the time. For these reasons, a record of the grain is placed in the literature, and it is provisionally referred to the tribe Mutisieae until additional information becomes available.

Petrea (Verbenaceae, Fig. 20)—Oblate, amb oval-triangular, tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–8 μm apex to equator), margin entire to minutely dentate; scabrate; tectate, wall 3 μm thick; E 52–56 μm.

The genus consists of about 30 species of lianas widespread in tropical America, distributed from northern Mexico to southern Brazil and the Antilles. In Panama it is represented by four species (D'Arcy, 1987), including *P. aspera* Turcz., which produces pollen similar to the specimens. This species occurs throughout the range of the genus, and in Panama is known from the tropical moist forest. Megafossils identified as *Petrea* are reported from the late Eocene La Porte flora of California (Potbury, 1935).

Posoqueria (Rubiaceae, Fig. 19)—Spherical to oblate-spheroidal, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, short (12 μm apex to equator), broad at midpoint (9–12 μm), colpi faint and frequently obscure, pore circular, conspicuous (7–9 μm in diameter), situated at midpoint of colpus, bordered by conspicuous annulus 4–5 μm wide; reticulate, reticulum irregular, lumen circular, 6–8 μm in diameter in equatorial region, becoming finer and disrupted at poles, columellae supporting reticulum long (3–4 μm), clavae with smaller clavae-baculae occupying lumina of reticulum, muri smooth, slightly sinuous; tectate-perforate, wall 3–4 μm thick; E 68–70 μm.

Posoqueria comprises about 15 species of trees and shrubs distributed in Mexico, Central and tropical South America, and the Antilles. In Panama it is represented by the widespread *P. latifolia* (Rudge) R. & S., found mostly in the tropical moist forest, but also in the tropical wet, premontane wet, premontane moist, and tropical dry forests. The genus has not been reported previously in the fossil record.

Symplocos (S. chiriquensis Pitt. type, Symplocaceae, Fig. 15)—Oblate, amb oval-triangular to nearly circular; triporate (or tricolporate but with colpi short and obscure), pores equatorially arranged, equidistant, circular, 3 μm in diameter, annulus 3 μm wide; psilate to faintly scabrate; tectate, wall 3 μm thick; E 28 μm.

Symplocos (S. pychantha Hemsley type, Symplocaceae, Fig. 16)—This grain is similar to the above type, but is larger (E 38 μm) and in that regard compares closely to pollen of *S. pychantha.*

Symplocos is a large genus of about 350 species of trees and shrubs found in the tropics and subtropics of the New and Old World. Three species are listed for Panama, with *S. chiriquensis* producing pollen similar to the smaller specimens, and *S. pychantha* producing pollen similar to the larger ones. The genus has been reported in the megafossil record as *S. oregona* by Chaney and Sanborn (1933) from the late Eocene Goshen Formation of Oregon; *S. exilis* MacGinitie from the middle Eocene Green River flora of Colorado and Utah (MacGinitie, 1969); and *S. incondita* MacGinitie from the middle Eocene Wind River Basin by MacGinitie (1974). As a microfossil it is reported as *Triporopollenites andersonii* and *T. scabroporus* by Chmura (1973) from the Maestrichtian of California (see also Newman, 1965, Campanian of Colorado). According to Muller (1981, p. 42), these species compare closely with *S. pringlei* and *S. stellaris,* respectively. There are no previous reports of this pollen type identified as *Symplocos* in the fossil record of northern Latin America.

DISCUSSION—Twelve of the 13 taxa reported are components of a large plant microfossil assemblage from the Gatun Formation that exceeds 100 pollen and spore types. Paleoenvironmental reconstructions and biogeographic considerations ultimately will be based on the total flora and placed within the context of Tertiary paleotemperature patterns (Savin, 1977; Savin and Douglas, 1985; Savin, Douglas, and Stehli, 1975), sea level curves (Haq, Hardenbol, and Vail, 1987; Vail and Hardenbol, 1979; Vail et al., 1977), vertebrate and invertebrate histories (Stehli and Webb, 1985), and plate tectonic (Malfait and Dinkelman, 1972; Molnar and Sykes, 1969; Wadge and Burke, 1983) and biogeographic models (Buskirk, 1985; Rosen, 1985). It is interesting, however, to look at these new records in terms of geographic affinities, climates, and altitudes suggested for proto-Central America by the five Tertiary floras already studied: Gatuncillo, Uscari, Culebra, Cucaracha, and La Boca (Graham, 1987).

These five floras are all older (middle(?) to late Eocene to early Miocene) than the Gatun flora (Pliocene), and their geographic affinities are almost completely with Central and North America. This is the expected pattern because at the beginning of the Eocene South America was isolated about midway between Africa and North America, and final connection with North America was not established until about 3.8 Myr (Stehli and Webb, 1985). The Gatun flora is probably about 4–6 Myr old and certainly deposited closer to the time of closure between North and South America than any of the previous floras studied from the region. Nonetheless, 11 of the 12 genera from the Gatun Formation, excluding the problematic Mutisieae type, all occur in the modern vegetation of Central America, and two (cf. *Bucida, Casimiroa*) do not presently extend into South America. Furthermore, 27 angiosperm families represented in the Gatun flora (Graham, unpublished data) were also analyzed by Raven and Axelrod (1974) as to probable North America to South America and South America to North America introductions during the Tertiary. Of these 27 families, 23 are considered likely north to south introductions. The newly identified taxa are consistent with and support previous interpretations that the Tertiary vegetation of proto-Central America was predominantly North American in affinity.

Paleoclimatic interpretations based on previously studied floras suggest the vegetation of the volcanic islands constituting proto-Central America during the Tertiary was distinctly tropical, with little evidence of extensive cool, dry (savanna), or arid (desert) habitats. All 11 of the new Gatun taxa presently occur in moist vegetation types, such as the tropical moist, tropical wet, premontane moist, and premontane wet forests (*Cabomba* is an aquatic herb, and *Hygrophila* grows in marshes). The rest of the dicot component of the Gatun flora (Graham, unpublished data) also suggests predominantly tropical conditions, but with better representation of temperature elements (e.g.,

TABLE 1. *List of species examined*

Species	Collection
Aegiphila	
A. alba Mold.	Gentry 28530, Equador, MO
A. amazonica Mold.	Prance et al. 25522, Brazil, MO
A. anomala Pittier	Gentry 4928, Panama, MO
	Dressler et al. 3976, Panama, MO
A. brachiata Vell.	Silva & Cordeiro 201, Brazil, MO
A. bracteolosa Mold.	Prance et al. 25522, Brazil, MO
A. brasiliensis Mold.	Hatschbach 22189, Brazil, MO
A. candelabrum Briq.	Hatschbach & Guimaroes 19157, Brazil, MO
A. cephalophora Standley	Croat 11465, Panama, MO
	Shattuck 988, MO
	Liesner 3203, Costa Rica, MO
A. deppeana Steudel	Ortiz 714, Guatemala, MO
	Dodge & Thomas 6189, Costa Rica, MO
A. elata Sw.	Croat 5506, Panama, MO
	Gentry 8601, Belize, MO
A. falcata D. Smith	Grayum 2393, Costa Rica, MO
	Harmon 2408, Guatemala, MO
A. integrifolia (Jacq.) Jackson	Broadway 6682, Trinidad, MO
A. mollis Kunth	Woodson et al. 1174, Panama, MO
	Davidse 24124, Costa Rica, MO
A. monstrosa Mold.	Gentle 948, Br. Hondruas, MO
	Liesner & Dwyer 1632, Belize, MO
A. panamensis Mold.	Ebinger 243, Panama, MO
	Dwyer et al. 450, Nicaragua, MO
	Breedlove 28551, Mexico, MO
A. schimpfii Mold.	OSU exchange
A. skutchii Mold.	Breedlove 26369, Mexico, MO
A. sufflava Mold.	Klug 2076, Peru, MICH
A. sellowiana Cham.	Aluaich 2850, Brazil, MO
cf. *Bucida*	
B. buceras L.	Ekman 8574, Cuba, US
	Innes 229, Br. Honduras, MO
	Vara & Arias 262, Mexico, MO
	Duke 15478, Panama, MO
	Proctor & Gillis 33377, Bahamas, MO
B. macrostachys Standley	Dwyer 120, Br. Honduras, MO
Cabomba	
C. caroliniana A. Gray	McFarland 3649, Florida, GH
C. piauhyensis Gardner	Killip 37677, Venezuela, GH
Casimiroa	
C. calderonii Chiang & Madrano	Medrano et al. F-1259, Mexico, MO
	Chiang et al. F-203, Mexico, MO
C. edulis Llave	Rose 2678, Mexico, US
	Cruz WB-00444, El Salvador, MO
	Calderon 72, El Salvador, MO
	Pringle 3861, Mexico, MO
C. pringlei (S. Wats.) Engl.	Gonzalez M. et al. 8589, Mexico, MO
F. vaginata Griseb.	Webster 3837, Cuba, US
Hygrophila	
H. costata Nees	Guzman et al. 1175, Nicaragua, MO
H. guianensis Nees	White 277, Panama, GH
	Fairchild 2105, Panama, MO
	Wasshausen & Encarnacion 1045, Peru, MO
Compositae—Mutisieae	
Achnopogon	
A. steyermarkii Aristeg.	Huber & Medina 8527, Venezuela, MO
Acourtia	
A. alamani Hemsley	Arsene 2106, Mexico, MO

TABLE 1. *Continued*

Species	Collection
	Actinoseris
A. polymorpha (Less.) Cabrera	Macedo 2746, Brazil, MO
	Aphyllocladus
A. ephedroides Cabrera	Cabrera 24473, Argentina, MO
A. spartioides Wedd.	Renvoize 3408, Argentina, MO
	Barnadesia
B. berberoides Sch.	Peyton 1563, Peru, MO
B. caryophylla (Vell.) Blake	Stein & Todzia 2351, Peru, MO
	Brachyclados
B. lycioides Don.	Paci 737, Argentina, NY
B. polyacantha Wedd.	Nee 36717, Bolivia, NY
	Chaetanthera
C. apiculata (Remy) Meigen	Werdermann 627, Chile, MO
C. chilensis (Willd.) DC.	Zollner 8687, Chile, MO
C. elegans Phil.	Werdermann 1256, Chile, MO
C. sapota Oerst.	Arsene 10474, Mexico, US, MO
	Rzedowski exchange, Mexico, ENCB
	Novelo et al. 424, Mexico, MO
C. tetrameria Millsp.	Enriquez 294, Mexico, US
	Novelo 194, Mexico, US
	Tonruz 11924, Costa Rica, CR
	Haber 508, Costa Rica, MO
	Cosmibuena
C. grandiflora Rusby	Harvard exchange, GH
C. paludicola Standley	Johnston 1598, Panama, GH
C. skinneri (Oerst.) Hemsley	Ebinger 917, Panama, MO
	Cymbopetalum
C. brasiliense (Vell.) Benth.	Smith 10084, Trinidad, US
C. costaricense (D. Smith) R. E. Fries	Burger & Stolze 5847, Costa Rica, CR
	Skutch 4928, Costa Rica, GH
C. penduliflorum (Dunal) Baillon	Lundell 6371, Br. Honduras, TEX
	Faramea
F. calophylla Standley	Killip & Garcia 33239, Colombia, US
F. coarinensis Muell.-Arg.	Krukoff 1416, Brazil, MICH
F. hyacinthina Mart.	Paris exchange
F. jefensis Dwyer & Hayden	Dwyer et al. 7279, Panama, MO
F. luteouirens Standley	Croat 5217, Panama, MO
F. occidentalis (L.) A. Rich.	Blum 2329, Panama, MO
	Allen 1849, Panama, GH
F. platycarpa Dwyer & Hayden	Porter et al. 4162, Panama, MO
F. scalaris Standley	Davidson 436, Panama, GH
F. talamancarum Standley	Kirkbride et al. 496, Panama, US
C. limbata Legg.	Kuntze 192, Chile, NY
	Chaptalia
C. hintoni Bullock	Hinton 3465, Mexico, MO
C. nutans (L.) Polak	Huston 0646, Br. Hondruas, MO
	Breedlove 39993, Mexico, MO
	Hamilton 784, Panama, MO
	Nee 8588, Panama, MO
	Chuquiraga
C. jussieui J. F. Gmelin	Maguire & Maguire 61737, Ecuador, NY
	Dasyphyllum
D. brasiliense (Spruce) Cabrera	Nee & Moraes 31441, Bolivia, NY
	Dinoseris
D. salicifolia Griseb.	Casas 7805, Bolivia, NY

TABLE 1. *Continued*

Species	Collection
	Gerbera
G. hieracioides (Kunth) Zardini	Cap E-3391, Ecuador, NY
	Gochnatia
G. paucifloscula (Wurd. & Hitch.) Jervis	Correll 43500, Bahamas, NY
	Gongyolepis
G. benthamiana Schomb.	Bunting & Holmqvist 4637, Venezuela, NY
	Hyaloseris
H. cinerea Gris.	Burkart 20870, Argentina, NY
	Jungia
J. ferruginea L.f.	Allen 1520, Panama, MO
	D'Arcy 10683, Panama, MO
	Cassas & Molero 6552, Bolivia, NY
	Lycoseris
L. latifolia (D. Don.) Benth.	Ducke 9536, Panama, MO
	Warner 189, Panama, MO
L. triplinervia Less.	Greenman 5136, Panama, MO
	Curran 39M, South America, NY
	Mutisia
M. acerosa Poepp.	Morrison 16859, Chile, GH
	Zollner 11617, Chile, MO
M. acuminata Ruíz & Pavón	Stork & Horton 9133, Peru, GH
	Ferreyra 3455, Peru, MO
	Solomon 13292, Bolivia, MO
M. campanulata Less.	Henry 35635, Brazil, MO
M. clematis L.	Schultes 7021, Colombia, GH
	Linden 64, New Granada, MO
M. coccinea A. St.Hil.	Hester 87803, Uruguay, GH
	Smith & Klein 13644, Brazil, MO
	Shepherd et al. 5753, Brazil, NY
M. comptoniaefolia Rusby	Baug 795, Bolivia, GH
M. decurrens Cav.	Cabrera 5967, Argentina, GH
M. friesiana Cabrera	Cabrera 15322, Argentina, GH
M. grandiflora H. & B.	Cuatrecasas 20917, Colombia, GH
M. hamata Reiche	Cabrera 15152, Argentina, GH
	Asplund 3057, Bolivia, MO
M. kurtzii Friis	Cabrera 13959, Argentina, GH
M. lanata Ruíz & Pavón	Pennell 14142, Peru, GH
M. latifolia D. Donn.	West 3964, Chile, GH
M. ledifolia Decne.	Cabrera 7799, Argentina, GH
M. madoniana Wedd.	Mandon 8, Bolivia, GH
M. orbignyana Wedd.	Buchtien 341, Bolivia, GH
M. sinuata Cav.	Jaffuel 3512, Chile, GH
M. spectabilis Phil.	Wagenknecht 121, Chili, GH
M. spinosa Ruíz & Pavón	Cabrera 5991, Argentina, GH
M. subspinosa Cav.	Mexia 4388, Argentina, GH
M. vicia Koster	Cardenan 2309, Bolivia, GH
M. viciaefolia Cav.	Saunders 55, Peru, TEX
	Pachylaena
P. atriplicifolia Don.	Hastings 446, Chile, NY
	Perezia
P. wrightii A. Gray	L. & J. Shultz 1353, N.M., NY
	Trichicline
T. macrocephala Less.	Reitz 4194, Brazil, NY
	Trixis
T. antimenorrhoea (Schrank) Mart.	Nee 35269, Bolivia, NY
T. inula Crantz	Croat 21892, Panama, MO
T. radialis (L.) Kuntze	Allen 201, Panama, MO

TABLE 1. *Continued*

Species	Collection
	Petraea
P. arborea Kunth	Leyden exchange, Venezuela
P. aspera Turcz.	Croat 5731, Panama, MO
	Pittier et al. 15430, Venezuela, US
	Pittier 6531, Panama, GH
	Hunter & Allen 658, Panama, MO
P. bracteosa Steud.	Harvard exchange
P. volubilis L.	Bartlett 7417, Guatemala, GH
	Moldenke 8004, Mexico, MO
	Liesner 4644, Costa Rica, MO
	Posoqueria
P. coriaceae Mart. & Gal.	Leyden exchange, Venezuela
P. latifolia (Rudge) R. & S.	Shell exchange, Suriname
	Jarzen exchange
	Croat 5143, Panama, MO
	Pittier 4579, Panama, US
	Robleto 568, Nicaragua, MO
	Martinez S. 18225, Mexico, MO
	Symplocos (New World collections only)
S. amplifolia Brand.	Teran 1077, Venezuela, MO
S. arechea L'Heritier	Shell exchange, Peru
	Klug 3624, Peru, MO
S. austinsmithii Standley	Hartshorn 2247, Costa Rica, MO
S. brenesii Standley	Haber 218, Costa Rica, MO
S. celastrinea Mart.	Shell exchange, Brazil
	Hassler 10295, Paraguay, MO
S. chiriquensis Pitt.	Harvard exchange, Panama, GH
	Skutch 4362, Costa Rica, MO
	Woodson et al. 1110, Panama, MO
S. citrea Lex.	Shell exchange, Panama
	Cabrera 5997, Mexico, MO
S. coccinea H. & B.	Shell exchange, Mexico
S. costaricana Hemsley	Amoco exchange
	Haber 343, Costa Rica, MO
S. flavifolia Lundell	Sousa et al. 9341, Mexico, MO
S. guyanensis (Aubl.) Gurcke	Webster 24023, Suriname, MO
S. hartwegii A. DC.	Shell exchange, Mexico
	Breedlove & Smith 31851, Mexico, MO
	Williams et al. 41726, Guatemala, MO
S. johnsonii Standley	Breedlove 38000, Mexico, MO
S. jurgensenii Hemsley	Shell exchange, Mexico
S. klotzschii Brand.	Hessler 4487, Paraguay, MO
S. laeviramulosa Elm.	Harvard exchange, GH
S. lanceolata DC.	Shell exchange, Paraguay
S. latifolia Krug & Urban	Shell exchange, Puerto Rico
S. laxifolia Benth.	Shell exchange, Brazil
S. limoncillo H. & B.	Koptur SK-308, Costa Rica, MO
S. lindeniana Krug & Urban	Shell exchange, Cuba
S. lundii DC.	Shell exchange, Brazil
S. martinicensis Griseb.	Shell exchange, Mexico
	D'Arcy 714, Tortola, W.I., MO
	Aguilar H. 217, Guatemala, MO
S. mathewsii DC.	Shell exchange, Bolivia
S. matudae Lundell	Breedlove & Smith 32715, Mexico, MO
S. molinae L. Williams	Webster et al. 11979, Honduras, MO
S. nitens (Pohl.) Benth.	Shell exchange, Paraguay
S. octopetala Sw.	Urban 4270, Puerto Rico, MO
S. pringlei Robinson	Shell exchange, Mexico
S. prionophylla Hemsley	Rzedowski exchange, Mexico, ENCB
	Hinton et al. 15367, Mexico, GH
	Torres C. 2064, Mexico, MO
	Pringle 9125, Mexico, MO

TABLE 1. *Continued*

Species	Collection
S. pubescens Klotzsch	Shell exchange, Brazil
	Jarzen exchange, Brazil, MO
S. pycnantha Hemsley	Shell exchange, Mexico
S. rhamnifolia DC.	Shell exchange, Brazil
S. salicifolia Griseb.	Shell exchange, Cuba
S. serrulata H. & B.	Churchill & Kuijt 5089, Panama, MO
S. speciosa Hemsley	Shell exchange, Guatemala
	Martin 672, Mexico, MO
	Clewell 3800, Honduras, MO
S. spruceana Guerke	Shell exchange, Peru
S. suaveolans Klotzsch	Shell exchange, Venezuela
S. tenuifolia Brand.	Jarzen exchange, Brazil
S. theaeformis (L.f.) Guerke	Shell exchange, Colombia
S. tetrandras Mart.	Shell exchange, Brazil
S. uniflora (Pohl) Benth.	Shell exchange, Paraguay
	Jarzen exchange, Argentina, MO
S. uruguensis Brand.	Jarzen exchange, Argentina, MO
S. vernicosa L. Williams	Hernandez M. 6907, Mexico, MO
	Molina R. 25537, Honduras, MO

Quercus, making its first appearance in the Panama Tertiary flora, along with *Ilex* and *Alfaroa/Oreomunnea*). This suggests that the middle to late Miocene cooling trend slightly expanded available temperate habitats in proto-Central America. Nonetheless, these newly described elements of the Gatun flora, together with the preliminary assessment of the total flora, still suggest primarily tropical climates, comparable to those of the present, for most of the area.

Previous studies also suggest the physiography of the landscape was low-lying, with little evidence of high altitudes (Graham, 1987, 1989). The modern analogs of all genera previously reported grow at elevations between sea level and about 1,200 to 1,400 m. The same is true for these new genera from the Gatun flora, which grow primarily in tropical lowland to premontane habitats. Preliminary study of the dicot component (Graham, unpublished data) indicates a somewhat greater variety of habitats for the Gatun flora than for those of the earlier Tertiary. Grass pollen first reaches significant percentages in the Gatun flora, and overall diversity increases from 55, 21, and 54 types in the Culebra, Cucaracha, and La Boca floras to over 100 types in the Gatun flora. Some effect from the late Tertiary cooling trend, together with increased physiographic diversity, probably accounts for most of the differences between the older floras and the Gatun assemblage. However, none of the Central American floras suggest elevations that would support high altitude or paramo vegetation, and thus provide continuous or near-continuous habitats for interchange of temperate elements between North and South America. High elevations are a recent feature of the southern Central American landscape.

The 13 taxa reported here are from Miocene and middle Pliocene deposits and are not sufficiently old to contribute information directly relevant to the origin or phylogeny of the respective genera or families, or to stratigraphic correlation between Gulf/Caribbean Tertiary strata (Fig. 21). They do, however, represent a first step in the lengthy process of building such a record. Furthermore, in association with other members of the Gatun and Artibonite floras, they provide an expanded data base for developing biogeographic and paleoenvironmental models for the Gulf/Caribbean region.

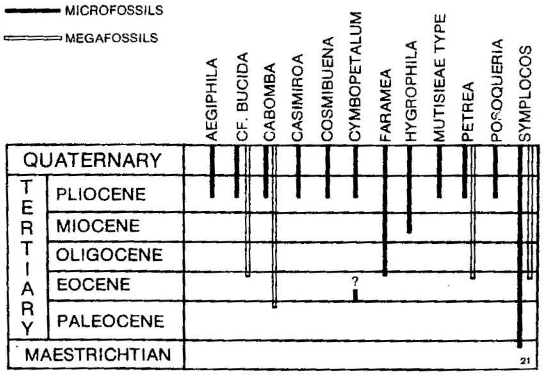

Fig. 21. Stratigraphic distribution of newly reported taxa.

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