

THE CURRENT STATUS OF THE LEGUME FOSSIL RECORD IN THE CARIBBEAN REGION

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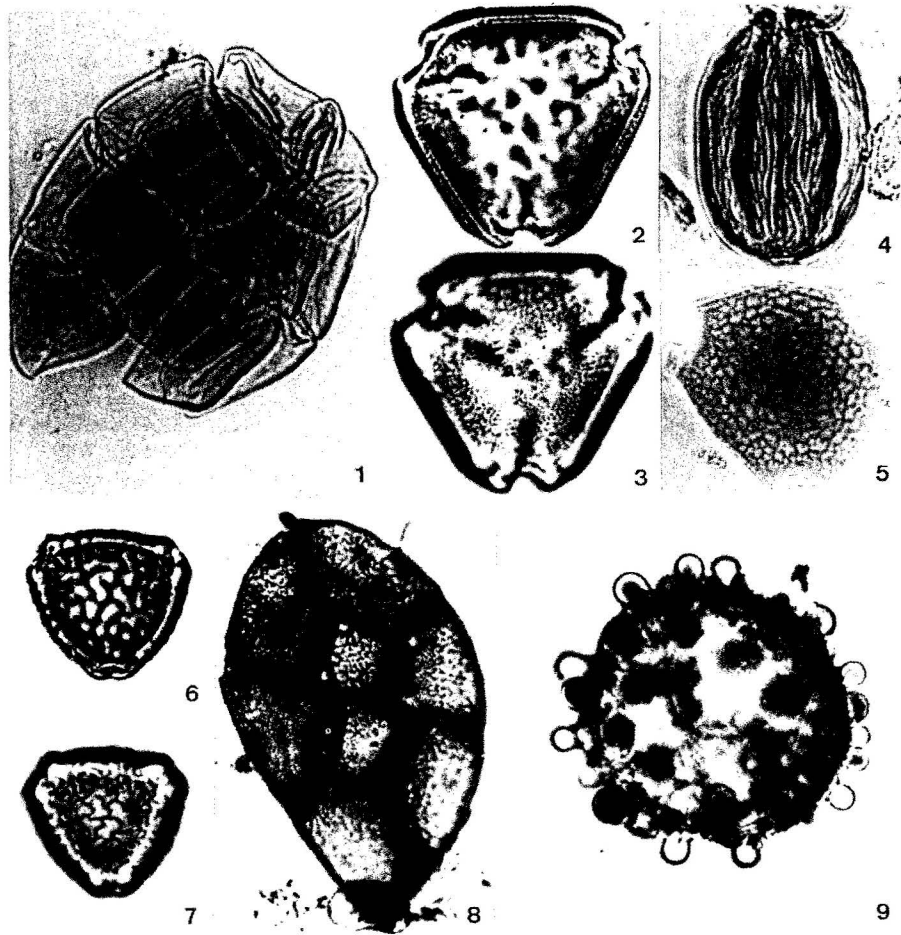
Abstract

Thirty-one genera of legumes have been reported from the megafossil and microfossil record of the Caribbean region (Mexico, Central America, the Antilles), but because of errors likely in the identification of many fragmentary and poorly preserved leaf specimens described in the older literature, the actual number is probably considerably fewer. Among more recent reports are *Acacia* from the Oligo-Miocene Simojovel Group of Chiapas, Mexico (leaflets preserved in amber), and from the Miocene of the Dominican Republic (flowers in amber); and *Hymenaea* from the Eocene of the Dominican Republic (flowers in amber). The Tertiary pollen records are *Crudia* (middle(?) to upper Eocene, lower Miocene, middle Pliocene of Panama), *Acacia* (including cf. *Acacia*; Oligocene of Puerto Rico, lower Miocene and middle Pliocene of Panama), *Mimosa* (middle Pliocene of Veracruz state, Mexico), *Desmanthus* (middle Pliocene of Veracruz state, Mexico), and *Erythrina* (middle Pliocene of Panama). Late-Glacial and Holocene microfossil records are *Acacia*, *Caesalpinia*, *Calliandra*, Mimosoideae polyads and tetrads, *Erythrina*, *Canavalia*, *Copaifera*, *Drepanocarpus lunatus*-type, *Leucaena multicapitula*, *Mucuna*, *Pterocarpus*-type, *P. officinalis*-type, and *Swartzia*.

Introduction

The Leguminosae are one of the most important components of the modern Caribbean vegetation. In Panama 430 species are listed for the native flora (D'Arcy, 1987), and on Trinidad *Mora excelsa* Benth. forms nearly pure stands. Among four field stations in Central America (La Selva, Barro Colorado Island) and Amazonian South America (Cocha Cashu, Ducke), Gentry (1990) notes that the Leguminosae is the most diverse family in all the lowland tree plots. The family occupies habitats ranging from deserts and near-deserts (*Acacia*, *Cercidium*, *Mimosa*, *Parkinsonia*, *Prosopis*), to tropical rain forest trees (*Brownea*, *Crudia*, *Enterolobium*, *Lonchocarpus*, *Machaerium*, *Pithecellobium*) and vines (*Entada*), to genera with hundreds of species occupying a wide range of habitats (*Cassia*, *Erythrina*, *Inga*). Yet for all its diversity, extensive geographical distribution, and broad ecological range, the family is infrequent, and never abundant, in Caribbean Cenozoic deposits.

A number of factors account, at least in part, for the relatively meager representation of the family in the microfossil and megafossil record. Pollen production is low among the entomophilous species, and the closed forest habitat of many legumes is not conducive to extensive representation in lowland basins of deposition that constitute the primary source of the Tertiary and several Quaternary palynofloras. Pollen diversity is high in the legumes, but it is countered by the large size of the family, and a number of fossil pollen types are not definitely assignable to individual legume genera, even though they are suspected as belonging to the family. There are many generalized tricolporate reticulate pollen forms in the Leguminosae, and these and other types often overlap with related



FIGS. 1-9. Fossil Leguminosae pollen from Cenozoic deposits in northern Latin America. Palynomorph sizes are given in microns. 1. *Acacia*, lower Miocene Culebra Formation, Panama. 54 μm . (Graham, 1988a); 2, 3. *Canavalia*, Quaternary, Gatun Lake, Panama. 55 μm . (Bartlett & Barghoorn, 1973); 4. *Crudia*, middle Pliocene Gatun Formation, Panama. 46 x 30 μm . (Graham, 1991); 5. *Erythrina*, middle Pliocene Gatun Formation, Panama. 35 μm . (Graham, 1991); 6, 7. *Erythrina*, Quaternary, Gatun Lake, Panama. 35 μm . (Bartlett & Barghoorn, 1973); 8. *Calliandra*, Quaternary, Gatun Lake, Panama. 215 μm . (Bartlett & Barghoorn, 1973); 9. *Bauhinia*, Quaternary, Gatun Lake, Panama. 110 μm . (Bartlett & Barghoorn, 1973).

families (e.g., Rosaceae). Consequently, additional records may exist among the 'unknowns' in Cenozoic paleopalynological assemblages from the Caribbean region. However, these unknowns are typically represented by only one to a few specimens because the more abundant types, belonging to familiar tropical plants, have mostly been

identified. Therefore, even when new legume records are suspected among the unidentified material, there are usually only a few specimens. This reduces the number of well-preserved palynomorphs that are available for examination, precludes establishing the range of variation for the microfossils, and makes comparison with pollen of modern taxa more difficult.

The scant megafossil record is a reflection of the fact that tropical environments, characterized by rapid decay of organic material, are not ideal for the preservation of leaf, flower, fruit, and seed material. Many leaf or leaflet types are also of a generalized morphology, especially within the context of the size of the family.

As a result of these factors, it is likely that assembling a reliable fossil record for the Leguminosae from the Caribbean region that is adequate for biogeographic, paleoecologic, and phylogenetic purposes, will be a long-term process involving the slow accumulation of individual records. One possible source of new material is from fossil woods. These are abundant around the village of Ocu in western Panama, where the facade of the Posada San Sebastian is built of fossil wood of Oligocene(?) age. During a visit in 1963–64 with Elso Barghoorn, he distinguished several types with a hand lens, some of which he thought were legumes. These woods now form part of the Hankins collection at Harvard University and have not been studied in detail. Another potential source of new material is the relatively extensive San Sebastian megafossil (leaf) flora of middle to late Oligocene age from Puerto Rico which has not been studied since the original work of Hollick (1928).

The Caribbean Record

A compilation of legume records based on megafossils from Cenozoic deposits in the Caribbean region (Table 1) provides 17 names: *Acacia*, *Acacioxylon*, *Caesalpinia*, *Caesalpinites*, *Cassia*, *Copaifera* (including *Copaiva*), *Cynometra*, *Dalbergia*, *Dioclea*?, *Gymnocladus*, *Hymenaea*, *Inga*, *Leguminosites*, *Lonchocarpus*, *Pithecellobium* (including *Pithecolobium*), *Sophora* (including *Sophora*?), and *Taenioxylon*. In view of the age of most of the reports, none of which have been verified or restudied, the fragmentary and poorly preserved nature of the specimens, and the success rate for identification of other tropical material by the same authors, the reliable megafossil record of the Leguminosae for the entire Caribbean region can be considered as consisting of *Acacia* (Miranda, 1963; Dilcher et al., 1990, this volume), and *Hymenaea* (Hueber & Langenheim, 1986).

The microfossil record (Table 1) consists of 15 genera: *Acacia* (including cf. *Acacia*), *Bauhinia*, *Caesalpinia*, *Calliandra*, *Canavalia*, *Copaifera*, *Crudia*, *Desmanthus*, *Drepanocarpus* (= *Machaerium*, as *D. lunatus*-type), *Erythrina*, *Leucaena multicapitula*, *Mimosa* (including Mimosoideae tetrad, polyad), *Mucuna*, *Pterocarpus*-type (including *P. officinalis*-type), and *Swartzia*. These reports as a group are likely more accurate than those for the megafossils because they are based on more recent studies. However, they contribute relatively little to the history of the family because nine of the 12 are exclusively post-Glacial (Holocene) reports and all but *Crudia* (mostly Amazonian South America, extending into the Antilles) presently grow in the vicinity of the northern Latin American deposits. The oldest report is of *Crudia* from the middle(?) to late Eocene of Panama. Other reports include *Acacia* from the middle to upper Oligocene of Puerto Rico, *Mimosa* and *Desmanthus* from the middle Pliocene of Veracruz, Mexico, and *Erythrina* from the middle Pliocene of Panama. The oldest fossil flora from northern Latin America (Mexico, Central America, the Antilles) within the time range of the angiosperms is a megafossil assemblage from Coahuila (northern Mexico) of Maastrichtian (Late Cretaceous) age, and no legumes are reported (Weber, 1972).

In summary, the most reliable reports of fossil Leguminosae in the Caribbean region are *Acacia*, *Crudia*, *Desmanthus*, *Erythrina*, *Hymenaea*, and *Mimosa* from the Tertiary, and *Bauhinia*, *Caesalpinia*, *Calliandra*, *Canavalia*, *Copaifera*, *Drepanocarpus*, *Erythrina*, *Leucaena*,

TABLE 1. Fossil Record of Leguminosae in Cenozoic Deposits of Northern Latin America. Comments on the provisional status of megafossil reports provided by Patrick Herendeen.

MEGAFOSSILS				
Caesalpinioideae				
Taxon	Age	Country	Reference	Comments
<i>Caesalpinia</i>	Miocene	Cuba	Berry, 1939	
<i>Caesalpinites</i>	Miocene	Cuba	Berry, 1939	
<i>Cassia</i>	Tertiary Miocene Oligocene	Panama Cuba Puerto Rico	Berry, 1918 Berry, 1939 Hollick, 1928	leaflet, legume? ¹ leaflets, all poor specimens, some incomplete, legume?
<i>Copaifera</i>	Oligocene	Puerto Rico	Hollick, 1928	leaflet, incomplete, probably legume
<i>Copaiva</i> (= <i>Copaifera</i>)				
<i>Cynometra</i>	Oligocene	Puerto Rico	Hollick, 1928	leaflet, incomplete, probably legume, possibly caesalpinoid
<i>Gymnocladus</i>	Miocene	Oaxaca, Mexico	Berry, 1923	(as the fern <i>Gymnogramme</i> ; see Maldonado-Koerdell, 1950)
<i>Hymenaea</i>	Eocene	Dominican Republic	Hueber & Langenheim, 1986	flowers in amber
Mimosoideae				
<i>Acacia</i>	Oligo-Miocene Miocene	Chiapas, Mexico Dominican Republic	Miranda, 1963 Dilcher et al., 1990, this volume	
<i>Acacioxylon</i>	Tertiary	Oaxaca, Mexico	Felix & Nathorst, 1893	probably mimosoid
<i>Inga</i>	Tertiary Tertiary Miocene Oligocene	Costa Rica Dominican Republic Veracruz, Mexico Puerto Rico	Berry, 1921a Berry, 1921b Berry, 1923 Hollick, 1928	leaflet, incomplete, legume? leaflet, incomplete, legume? leaflets, most incomplete, some specimens probably legume
<i>Pithecellobium</i>	Tertiary	Dominican Republic	Berry, 1921b	leaflet, incomplete & poor specimen, legume?
<i>Pithecolobium</i> (= <i>Pithecellobium</i>)				
Papilionoideae				
<i>Dalbergia</i>	Miocene	Cuba	Berry, 1939	
<i>Dioclea?</i>	Miocene	Oaxaca, Mexico	Berry, 1923	
<i>Lonchocarpus</i>	Oligocene	Puerto Rico	Hollick, 1928	leaflet, generalized morphology, legume?
<i>Sophora</i>	Tertiary Miocene	Dominican Republic Cuba	Berry, 1921b Berry, 1939	leaflet, not <i>Sophora</i> , legume?
<i>Sophora?</i>	Oligocene	Puerto Rico	Hollick, 1928	leaflet, incomplete, legume
Subfamily Unassigned				
<i>Leguminosites</i>	Miocene	Veracruz, Mexico	Berry, 1923	
<i>Taenioxylon</i>	Tertiary	Panama	Berry, 1918	legume affinities cannot be confirmed without evidence of vestured pits

TABLE 1 Continued

MICROFOSSILS			
Caesalpinoideae			
Taxon	Age	Country	Reference
<i>Crudia</i>	middle(?) to upper Eocene, lower Miocene middle Pliocene	Panama Panama Panama	Graham, 1985 Graham, 1988b, 1989 Graham 1991
<i>Bauhinia emarginata</i>	Quaternary	Panama	Bartlett & Barghoorn, 1973
Mimosoideae			
<i>Acacia</i>	Oligocene lower Miocene middle Pliocene Quaternary	Puerto Rico Panama Panama Guatemala	Graham & Jarzen, 1969 Graham, 1988a Graham, 1991 Tsukada, 1966
cf. <i>Acacia</i>	middle Pliocene	Veracruz, Mexico	Graham, 1976
<i>Mimosa</i>	middle Pliocene	Veracruz, Mexico	Graham, 1976
<i>Caesalpinia</i>	Quaternary	Haiti	Higuera-Gundy, 1989
<i>Calliandra</i>	Quaternary	Panama	Bartlett & Barghoorn, 1973
Mimosoideae polyad	Quaternary	Costa Rica	Horn, 1985
Mimosoideae tetrad	Quaternary	Costa Rica	Horn, 1985
Papilionoideae			
<i>Desmanthus</i>	middle Pliocene	Veracruz, Mexico	Graham, 1976
<i>Erythrina</i>	Quaternary middle Pliocene	Panama Panama	Bartlett & Barghoorn, 1973 Graham, 1991
<i>Canavalia</i>	Quaternary	Panama	Bartlett & Barghoorn, 1973
<i>Copaifera</i>	Quaternary	Panama	Bartlett & Barghoorn, 1973
<i>Drepanocarpus lunatus</i> -type (= <i>Machaerium</i>)	Quaternary	Panama	Bartlett & Barghoorn, 1973
<i>Leucaena multicapitula</i>	Quaternary	Panama	Bartlett & Barghoorn, 1973
<i>Mucuna</i>	Quaternary	Panama	Bartlett & Barghoorn, 1973
<i>Pterocarpus</i> -type	Quaternary	Panama	Bartlett & Barghoorn, 1973
<i>P. officinalis</i> -type	Quaternary	Panama	Bartlett & Barghoorn, 1973
Swartzieae			
<i>Swartzia panamensis</i> -type	Quaternary	Panama	Bartlett & Barghoorn, 1973

¹ "Legume ?" indicates that the family identification is uncertain because of incomplete or poorly preserved specimens and/or generalized morphology.

Mimosoideae, *Mucuna*, *Pterocarpus*, and *Swartzia* from the Holocene. This data base is meager but it is more accurate than the extensive record implied in the older literature.

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