

## Diversification of Gulf/Caribbean Mangrove Communities through Cenozoic Time<sup>1</sup>

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### ABSTRACT

The mangrove community of the Neotropics shows a progressive increase in diversity through the Cenozoic. Palynofloras from the early Eocene ~50 Ma (million years ago) indicate that brackish-water coastal areas were occupied by four principal genera—*Acrostichum*, the extinct *Brevitricolpites variabilis*, *Nypa*, and *Pelliceria* (*Pellicera*). *Avicennia* is first reported in the late Miocene ~10 Ma. Extinctions, introductions, and adaptations varied the composition and increased net diversity to six mangrove and three associated genera by the middle Pliocene (~3.5 Ma)—*Acrostichum*, *Avicennia*, *Crenea*, *Laguncularia*, *Pelliceria*, *Rhizophora*; *Acacia*, *Hampea*/*Hibiscus*, and *Pachira*. Modernization continued in the Quaternary with the first microfossils of *Conocarpus*, and with the addition of eight possible associates, for a total of 15 genera. Twelve others, unknown as fossils, were added during the Cenozoic to constitute the present-day community of ~27 genera of mangroves and associates. The fossil record identifies a trend of increasing diversity that can be assessed as new assemblages are studied, and provides a first quantitative estimate of Neotropical history through the Cenozoic Era.

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### RESUMEN

La comunidad de manglares del neotrópico demuestra un incremento progresivo en diversidad durante el Cenozoico. Las palinofloras del comienzo del Eoceno (hace 50 millones de años) indican que cuatro generos ocuparon las áreas costeras de agua salobre: *Acrostichum*, el ahora extinto *Brevitricolpites variabilis*, *Nypa*, y *Pelliceria* (*Pellicera*). *Avicennia* se encuentra primero hacia el final del Mioceno hace 10 millones de años. Extinciones, introducciones, y adaptaciones variaron la composición de los manglares e incrementaron su diversidad neta, que llegó a seis géneros de mangle (*Acrostichum*, *Avicennia*, *Crenea*, *Laguncularia*, *Pelliceria*, *Rhizophora*) y tres géneros asociados (*Acacia*, *Hampea*/*Hibiscus*, y *Pachira*) hacia la mitad del Plioceno hace 3.5 millones de años. La modernización continuó durante el Cuaternario con los primeros microfósiles de *Conocarpus* y con la adición de ocho posibles asociados, alcanzando un total de 15 géneros. Otros doce géneros que no se conocen como fósiles se incorporaron durante el Cenozoico para constituir la comunidad actual de 27 géneros de mangles y asociados. Por medio del registro fósil se indentifica una tendencia hacia una diversidad creciente que se podrá evaluar a medida que se estudien nuevos grupos. El registro fósil también provee un primer estimado cuantitativo de la historia del manglar neotropical a través de la Era Cenozoica.

*Key words:* Cenozoic; history; mangroves; Neotropics; palynofloras.

THE MANGROVE COMMUNITY OF the Gulf/Caribbean region (Mexico, the Antilles, Central America, northern South America) consists of four principal components—*Avicennia germinans* L. (black mangrove), *Laguncularia racemosa* L. (white mangrove), *Rhizophora mangle* L. (red mangrove, plus other species and hybrids), and *Pelliceria rhizophorae* Planchon and Triana (palo de sal). The first three are widespread, while the last grows along the Pacific side of Costa Rica and Panama, along the eastern side of Panama and Nicaragua (Jiménez 1984, Roth & Grijalva 1991), and on the Pacific and Atlantic

coast of Colombia (Winograd 1983). *Conocarpus erectus* L. (buttonwood) is also commonly found in coastal brackish-water environments even though it lacks many of the morphological specializations typical of mangroves (aerial roots, vivipary). A second category includes mostly non-mangrove genera, but with one or more species that tolerate brackish water, grow marginal to the mangroves, and occasionally extend into that community (*Acacia*, *Dalbergia*, *Ficus*, *Hibiscus*, *Inga*). The first group consists mostly of plants that have a long geologic record as components of mangrove vegetation. The second category includes many plants with no fossil record, which probably have more recently developed a tolerance to brackish water or expanded their range into para-mangrove habitats.

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<sup>1</sup> Received 15 September 1993; revision accepted 4 March 1994.

TABLE 1. Fossil record of common mangroves (m) and mangrove associates in the Cenozoic of the Gulf/Caribbean region. Present occurrences (first column) are after Gentry (1982) and Tomlinson (1986). Listing under Modern only (second column) means there are no fossils reported from the region. For references to fossil occurrences see Table 2.

	Modern	Quaternary	Pliocene	Miocene	Oligocene	Eocene
<i>Amphitecna</i>	x					
<i>Dalbergia</i>	x					
<i>Inga</i>	x					
<i>Lycium</i>	x					
<i>Mora</i> (m)	x					
<i>Mouriria</i>	x					
<i>Muelleria</i>	x					
<i>Pavonia</i>	x					
<i>Phyryganocydia</i>	x					
<i>Tabebuia</i>	x					
<i>Ternstroemia</i>	x					
<i>Tuberosyles</i>	x					
<i>Cassipourea</i>	xxxxxxxxxx					
cf. <i>Clusia</i>	xxxxxxxxxx					
<i>Conocarpus</i> (m)	xxxxxxxxxx					
<i>Ficus</i>	xxxxxxxxxx					
<i>Pterocarpus</i>	xxxxxxxxxx					
<i>Randia</i>	xxxxxxxxxx					
<i>Laguncularia</i> (m)	xxxxxxxxxxxxxxxxxxxxxxxx					
<i>Avicennia</i> (m)	xx					
<i>Pachira</i>	xx					
<i>Acacia</i>	xx					
<i>Crenea</i> (m)	xx(?)					
<i>Hampea/Hibiscus</i>	xx					
<i>Rhizophora</i> (m)	xx					
<i>Pelliceria</i> (m)	xx					
<i>Nypa</i> (m)						xxxxx
<i>Brevitricolpites variabilis</i> (m)						xxx
<i>Acrostichum</i> (m)	xx					

A data base of Cenozoic plant fossils from the Gulf/Caribbean is slowly accumulating and is sufficient to address certain questions of vegetational and environmental history. Initially these records provided low resolution data on individual elements, paleocommunities, and paleoenvironments at localities widely scattered geographically and stratigraphically through the region. It is now possible to focus on more specific questions, such as the time of emergence of the isthmian land bridge (Graham 1992a), paleoaltitudes and landscape evolution (Graham 1989a), paleotemperatures of coastal waters (Graham 1994, in press), the geologic record of individual plant groups (e.g., the Leguminosae, Graham 1992b), and the history of various modern vegetation types (e.g., the tropical dry forest; Graham & Dilcher, in press). The data are also beginning to suggest a trend in the development of Neotropical mangrove vegetation.

A list of 29 mangrove and mangrove-associated genera in northern Latin America is presented in Table 1. The list was compiled from Gentry (1982)

and Tomlinson (1986), and is representative of Neotropical vegetation presently growing in and marginal to the mangrove environment. They are arranged in Table 1 according to their time of appearance in Cenozoic palynofloras from the Gulf/Caribbean region, the sequence used in the following discussion. The fossil records are based on palynofloras because no extensive, recently studied macrofossil floras are available. Literature references to reports of fossil mangrove pollen in the Neotropics are provided in Table 2, and the history of New World mangrove genera occurring outside the Neotropics is discussed by van Steenis (1962), Muller (1964), Leopold (1969), Muller and Caratini (1977), and Caratini *et al.* (1980).

Tracing the Cenozoic history of plants or communities in the Gulf/Caribbean area based on paleopalynology is constrained by identifications that can mostly be made only to genus, and by the meager fossil record. It is particularly difficult to establish initial appearances because floras of late Mesozoic and early Cenozoic age are unknown for

many regions. For example, there are no published Paleocene or early Eocene assemblages from Mexico, Central America, or the Antilles, so the record in northern Latin America begins with the middle Eocene Chapelton flora of Jamaica, and the middle(?) to late Eocene Gatuncillo flora of Panama. Plant microfossils are known from the middle Eocene Saramaguacan Formation of Cuba, but the study is mostly unpublished (Araces Mallea 1985, 1987, 1988) and it is now being investigated jointly (Araces Mallea & Graham, pers. obs.). As yet no pollen of mangroves has been recovered.

### Paleogene records

**Mangroves.** The oldest occurrences of a possible mangrove component from the Gulf/Caribbean region are fern spores described under the artificial genus *Deltoidospora*. The biological affinity of these generalized trilete spores (those with a Y-shaped mark on the proximal surface) is not known, but they are morphologically similar to those of *Acrostichum aureum* L., which is the principal fern presently growing within mangrove vegetation. The spores are common in lignites deposited under brackish, coastal conditions, and are frequently found in assemblages containing abundant *Rhizophora* pollen. Similar spores extend back into the Paleozoic, and although it is not certain which ones represent *Acrostichum*, the associated vegetation, sediment type, and depositional environment suggest that the genus probably has been a member of Neotropical strand vegetation throughout the Cenozoic.

Prior to the late Eocene one of the most abundant pollen types in coastal deposits was *Brevitricolpites variabilis*. Its affinities are unknown, but it dominated the habitat now occupied by *Rhizophora* and was clearly the ecological equivalent of that genus. It disappeared from the region in the middle Eocene.

*Spinozonocolpites baculatus* / *S. echinatus* represents pollen similar to the Old World mangrove palm *Nypa*. The oldest occurrence there, and in northern South America, is Late Cretaceous (Senonian). It is reported from the middle Eocene Laredo Formation of Texas. Pollen of *Nypa* is not known from the New World after the Eocene; specimens from younger deposits in South America are redeposited (Lorente 1986). *Nypa* has not been found in the intervening area of Mexico, Central America, or the Antilles. An illustration in an unpublished report from the Oligo-Miocene La Quinta Forma-

TABLE 2. *Literature on mangroves and mangrove associates in the Cenozoic of the Gulf/Caribbean region. Additional references summarizing stratigraphic ranges for northern South America are Germeaad et al. (1968, fig. 15) Lorente (1986, tables 11–13), and Muller et al. (1987, table II).*

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Quaternary	
Panama (Gatun Lake)—Bartlett and Barghoorn (1973)	
Costa Rica (Deep Sea Drilling Project core 565, western C.R.)—Horn (1985)	
Tertiary	
Pliocene (including Mio-Pliocene)	
Mexico (Veracruz, Paraje Solo Formation)—Graham (1976)	
Panama (Gatun Formation)—Graham (1991a, b, c)	
Miocene	
Panama (Culebra, Cucaracha, La Boca formations)—Graham (1988a, b, 1989b)	
Costa Rica (Uscari sequence)—Graham (1987)	
Oligocene (including Oligo-Miocene)	
Puerto Rico (San Sebastian Formation)—Graham and Jarzen (1969)	
Mexico (Chiapas, Simojovel Group)—Langenheim et al. (1967)	
Eocene	
Panama (Gatuncillo Formation)—Graham (1985)	
Jamaica (Chapelton Formation)—Graham (1993, 1994)	
Texas (Laredo Formation)—Westgate and Gee (1990)	

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tion of Chiapas, Mexico (Biaggi 1978) is not adequate to confirm its presence there, and the specimen may be malvaceous (E. Martínez-Hernández, pers. comm.).

*Psilatricolporites crassus* was described from the Tertiary of the Guiana Basin (van der Hammen & Wijnstra 1964), and it is now known to represent pollen of the mangrove *Pelliceria*. The oldest records are from the early Eocene of northern South America. It has also been reported from the middle Eocene of Jamaica, middle(?) to late Eocene of Panama, Oligocene of Puerto Rico, Oligo-Miocene of Chiapas, Mexico, and the early Miocene of Panama (Graham 1977). It disappeared from the northern limits of its range beginning in the Miocene, but persisted into the Miocene in northern South America (Wijnstra 1968). Pollen of *Pelliceria* was not recovered from the Mio-Pliocene Gatun Formation of central Panama, or the middle Pliocene Paraje Solo Formation of southeastern Veracruz, Mexico; by that time *Pelliceria* had probably attained its near-modern distribution.

In the late Eocene a new element appeared that

by the end of that epoch had replaced *Brevitricolpites variabilis* to become the most frequent and abundant plant microfossil in Neotropical coastal deposits. Pollen described in the stratigraphic literature as *Zonocostites ramonae* represents *Rbizophora*, and constitutes 96 percent of the plant microfossils in samples from the Oligocene San Sebastian Formation (Graham & Jarzen 1969, table 1) and from the Pliocene Paraje Solo Formation (Graham 1976, table 1). In one sample from the lower Miocene Culebra Formation of Panama (A. Graham, pers. obs.) it is present to the exclusion of virtually all other pollen. In addition, it is known from the middle(?) to upper Eocene Gatuncillo Formation of Panama (at a maximum of 10% when it was just becoming the dominant mangrove in the region), the Simojovel Group of Mexico, the Uscari sequence of Costa Rica, and the Cucaracha, La Boca, and Gatun formations of Panama. It has been the principal mangrove component in the Neotropics since the Eocene.

*Verrutricolporites rotundiporis* is similar to the pollen of *Crenea*, although the faint pseudocolpi (non-germinal furrows in the pollen wall) present on modern forms (Graham *et al.* 1985, figs. 14, 34) are not evident on fossil specimens illustrated by Germeraad *et al.* (1968, pl. XVI, figs. 5–7; Graham & Graham 1971), or on those examined by the author in the Shell Oil collections at The Hague where the Germeraad *et al.* material is preserved. These structures are frequently obscure, however, and in other respects the fossils resemble *Crenea*. It is a shrub to small tree growing on frequently inundated mud flats, occasionally at or even beyond the zone of *Rbizophora* and is, therefore, an expected component of fossil mangrove assemblages. Today it is distributed along the coast of Colombia to the juncture with Panama, then along the northeast coast of South America (Lourteig 1986); it is not presently known from Central America. In the stratigraphic range chart of Germeraad *et al.* (1968, fig. 15; p. 278) it is listed from the late Eocene to Recent in the Caribbean region, but in Muller *et al.* (1987, table II) it goes back only to the base of the Oligocene.

Mangrove associates. A possible mangrove associate is *Echiperiporites estelae*. The pollen is similar to that of *Hampea* and *Hibiscus* (Malvaceae). One species of *Hibiscus* (*H. tiliaceous* L.) is widely distributed on tropical beaches and in mangrove swamps (Robyns 1965, p. 504). Another, *H. sororius* L.f., occurs in marshy areas, on floating mats, and in strand vegetation. Microfossils are known from the Culebra (lower Miocene), Gatun (Mio-Pliocene),

and Paraje Solo (middle Pliocene) formations of Panama and Mexico, and in northern South America they range from the late Eocene to the Recent.

*Acacia* (*Polyadipollenites mariae*) is another mangrove associate, with species that grow marginal to that community or extend into zones occasionally inundated by brackish water. Pollen has been recovered from the San Sebastian, Culebra, Gatun, and Paraje Solo (as *cf. Acacia*) formations. In northern South America its range according to the text in Lorente (1986, p. 210) is “the entire stratigraphic interval included in this study” (Oligocene to Recent) but in the charts (Lorente 1986, tables 11–13) its oldest occurrence is early Miocene. Its range in the Gulf/Caribbean region is from the middle Oligocene (San Sebastian Formation) to Recent.

### Neogene records

Mangroves. *Avicennia* is a true mangrove whose pollen has been reported from the late Miocene of northern Latin America (as *Avicennia* type; Muller *et al.* 1987) and from the Quaternary of Panama and Costa Rica. *Laguncularia* occurs in the Paraje Solo Formation.

Mangrove associates. *Pachira* (*Bombacacidites baculatus*) is known from the Oligo-Miocene Simojovel Group of Chiapas, Mexico (as *Pachira* type), and from the Quaternary of Panama. Its stratigraphic range in northern South America is from the middle Miocene to Recent.

### Quaternary records

Pollen of several mangroves and many possible mangrove associates is encountered in the Quaternary. *Rbizophora* is abundant in sediments from Costa Rica and Panama, *Avicennia* and *Laguncularia* are known from the Quaternary of Costa Rica, and *Cassipourea* and *Conocarpus* occur in sediments from Gatun Lake, Panama. An occasional pollen grain of *Ficus* is recovered from Quaternary sediments deposited in lowland coastal habitats (Horn 1990), but it is not certain whether the species is one that occasionally extends into the mangrove community, or one that only grows in adjacent lowland areas. *Ficus* pollen has been reported from the Quaternary of Panama and Costa Rica, and from several sites in South America (Absy 1979; Liu & Colinvaux 1985, 1988; Bush & Colinvaux 1988; Colinvaux *et al.* 1988; Frost 1988). A small, diporate (2-pored), psilate (smooth walled) specimen from the Eocene Gatuncillo Formation of Panama has been referred to *cf. Ficus* (Graham 1985,

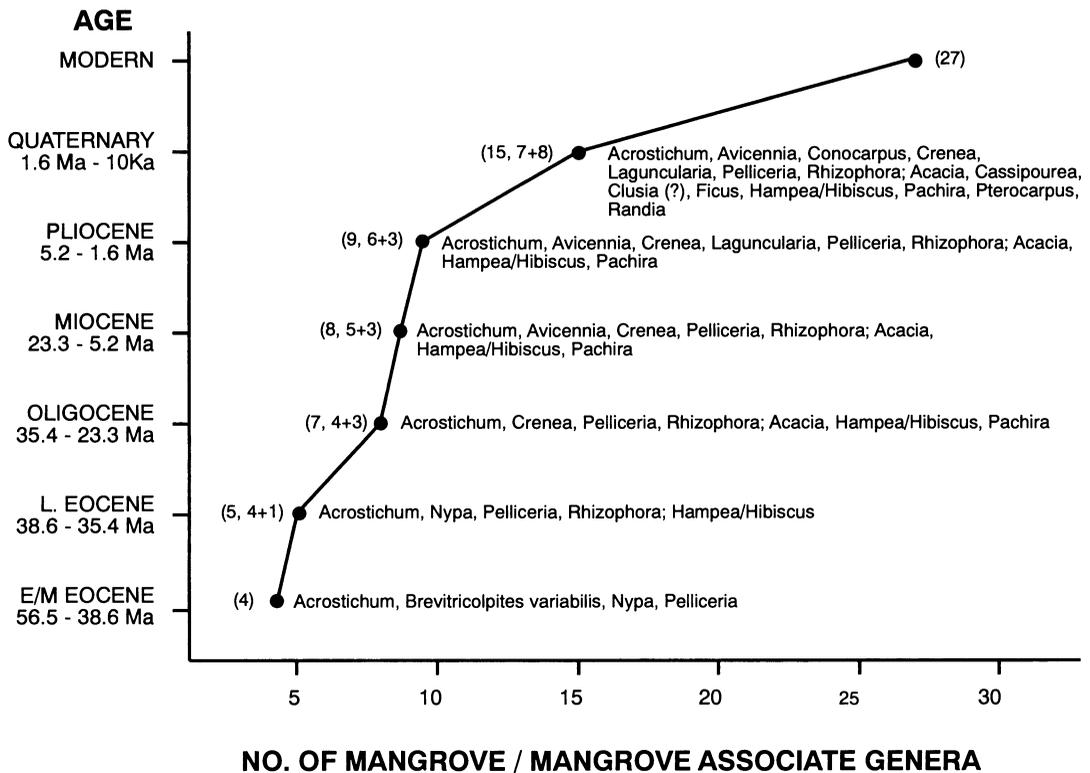


FIGURE 1. Progressive diversification and possible adaptation trend in Cenozoic mangrove communities from the Gulf/Caribbean region. Figures in parentheses indicate total number of genera, then mangrove plus associate genera represented in each epoch. Time scale is after Harland *et al.* (1989).

fig. 58). Pollen similar to *Pterocarpus* occurs in Quaternary deposits of Panama (*Pterocarpus*-type, *P. officinalis*-type), and *Randia* has been found in the same material. The current fossil pollen record of *Clusia* does not pertain to mangrove history. It is present in Quaternary sediments from the High Plain of Bogotá (Hooghiemstra 1984), but there is no record from coastal deposits.

## DISCUSSION

Cenozoic plant microfossil assemblages from the Gulf/Caribbean region reflect a trend of increasing diversity of genera adapted to the mangrove environment (Fig. 1). In the early Eocene, macrophyte mangrove vegetation included at least four elements—the palm *Nypa*, now found only in the Old World tropics; *Pelliceria*, which was widespread in the early Tertiary but is now restricted to southern Central America and northern South America; the extinct *Brevitricolpites variabilis*; and probably, the fern *Acrostichum*. There is no paleobotanical evi-

dence that any of the mangrove associates listed in Table 1 were adapted to the mangrove habitat or had developed tolerance to brackish water in the early Eocene.

At the beginning of the late Eocene *B. variabilis* disappeared and was replaced by *Rhizophora* as the dominant mangrove. *Acrostichum*, *Nypa*, and *Pelliceria* were still present, and a possible mangrove associate first appeared if some of the *Hampea/Hibiscus* pollen was contributed by plants ecologically similar to *Hibiscus tiliaceus*. By the end of the Eocene microfossils similar to those of four mangroves (*Acrostichum*, *Nypa*, *Pelliceria*, *Rhizophora*) and one possible associate (*Hampea/Hibiscus*) were found in the region (Fig. 1).

By the Oligocene *Nypa* disappeared, and *Crenea* became established after a possible late Eocene appearance. *Acacia* was present by the middle Oligocene (San Sebastian flora), and *Pachira* appeared in the Oligo-Miocene (Simojovel flora). At this time the community consisted of at least four mangrove components (*Acrostichum*, *Crenea*, *Pelliceria*, *Rhi-*

*zophora*) and three potential mangrove associates (*Acacia*, *Hampea/Hibiscus*, *Pachira*).

In the Miocene pollen of the mangrove *Avicennia* is first recorded, and *Laguncularia* pollen appears in the middle Pliocene (Paraje Solo Formation). It is at this time (~3.5 Ma) that the fossil record first reveals a mangrove community of near-modern composition consisting of the dominants *Avicennia*, *Laguncularia*, *Rhizophora*, *Crenea*, and probably *Acrostichum*, with the previously widespread *Pelliceria* confined to the southern Caribbean region. According to the current microfossil record, the composition of the modern mangrove community became established in the Quaternary with the first report of *Conocarpus*. Possible associates at this time included *Acacia*, *Cassipourea* (in the Rhizophoraceae but more typical of forested hillsides and freshwater margins), possibly *Clusia* (see previous discussion), *Ficus*, *Hampea/Hibiscus*, *Pachira*, *Pterocarpus*, and *Randia*. These 15 genera have been augmented at various times during the Cenozoic by the 12 additional genera listed in Table 1 (first column) that are presently unknown as fossils.

The near-linear increase in diversity with time depicted in Figure 1 is only a general reflection of the complex history of mangrove development. As noted previously, the record is based solely on plant microfossils, which are mostly identifiable only to genus, and the fossil floras are few in number and scattered both geographically and stratigraphically. In addition, potential components such as grasses cannot be recognized below family based on pollen characters, pollen of the important tropical family Lauraceae does not fossilize, and pollinating mechanisms in other genera (e.g., *Ficus*) preclude an adequate representation as microfossils. Clearly, information from macrofossil floras would add substantially to the history of mangrove vegetation, but the only such flora known for the region is from the middle Oligocene Sebastian Formation of Puerto Rico, and it has not been revised since the original study (Hollick 1928). Continued studies of regional palynofloras will provide refinements in the presently general outline of mangrove history. For ex-

ample, Rull (1993) notes that in the Maracaibo Basin of Venezuela, *Nypa* pollen begins to disappear in the early/middle Eocene, while *Rhizophora* does not become abundant until the late Eocene. During this gap of about 10 Ma, a pollen type identified as *Echitriporites trianguliformis* is abundant, and although its biological affinities are presently unknown, Frederiksen (1983) suggests it may have occupied the mangrove habitat. For the present, the microfossil record can best be read as reflecting an Eocene mangrove vegetation substantially different in composition from the present, and consisting of 4 or 5 genera. In the Oligocene, pollen of 7 mangroves is recovered. By the Mio-Pliocene, 8 or 9 components were present, and in the Quaternary, at least 15 genera are recorded in the fossil record that were available to the mangrove community.

The nature of paleofloristic/paleoenvironmental studies often precludes addressing predefined questions of biotic history. Rather, each flora provides varied information on lineages, communities, climate, and physiography for a specific time and place. Eventually the aggregate floras may come to suggest trends of development through time. It is worthwhile to record these early indications because they identify one of a broad spectrum of subjects that can be explored as new floras are discovered; the studies are long-term and there is no certainty as to when additional relevant data will be forthcoming; and in the meantime, the trends can be assessed and refined from other independent lines of inquiry. In the case of mangrove history, a summary of the existing fossil record documents, for the first time, that diversification (and possibly adaptation to the mangrove environment), has progressively increased through Cenozoic time, and reveals something of the quantitative nature of this history.

## ACKNOWLEDGMENTS

The author gratefully acknowledges the helpful review comments provided by N. O. Frederiksen, J. Langenheim, and L. C. Roth. Research supported by NSF grant DEB 920674.

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