

# Middle Eocene Mangroves and Vegetation Changes in the Maracaibo Basin, Venezuela

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As a part of a general project that aims to reconstruct the paleosuccession of Paleogene mangroves of the Maracaibo Basin, this paper deals with the quantitative reconstruction of Middle Eocene mangrove communities, and their relation to potential forcing factors. Four palynological assemblages were found. These represent, respectively, inland forests (A1), back-mangrove herbaceous swamps (B1), mangroves (B2), and an unknown plant community dominated by the extinct *Echitriporites trianguliformis*. Mangroves were dominated by *Pelliciera* and *Nypa*; *Brevitricolpites variabilis*, which has been considered the dominant taxon of the early and middle Eocene mangroves in nearby areas, has not been found in this study. The succession of coastal vegetation, linked to sea-level changes, could be reconstructed from these assemblages. The trends constitute a palynocycle which began and ended with a low sea-level plant community dominated by unknown stands represented by *E. trianguliformis* and interpreted low paleosalinities; intermediate high sea-level vegetation is represented by mangroves and interpreted high paleosalinities. This cycle is correlated chronologically with the global eustatic cycle TE-JAS A 3.4, extending from 44 to 42.5 Ma (Lutetian). The floristic composition of middle Eocene mangroves was very different from those of the Oligocene to Recent. An important, probably worldwide, evolutionary change occurred during the late middle Eocene and the late Eocene in these communities. Pollen taxa botanically related to known and extant mangrove elements seem scarce for this time span.

## INTRODUCTION

Mangrove communities of the Caribbean region have changed noticeably through time. They have experienced a progressive diversification from 4 or 5 Eocene genera to about 15 in the Quaternary, to 27 in the present-day mangrove communities (Graham, 1995). The most common mangrove-forming genus of the present, *Rhizophora*, is known in coastal environments from the late Eocene, represented by the fossil pollen species *Zonocostites ramonae* (Germeraad et al., 1968). Other important components became established later, including *Avicennia* (Miocene), *Laguncularia* (Pliocene), and *Conocarpus* (Pleistocene) (Graham, 1995). During the Eocene, however, the mangrove components were different. According to Graham (1995), they were mainly *Nypa*, *Pelliciera*, the 'beach fern' *Acrostichum*, and the parent species of *Brevitricolpites variabilis*, which has been considered the ecological equivalent of *Rhizophora*. In the Late Eocene, *Nypa* (represented in the fossil record by *Spinizonocolpites prominatus*) disap-

peared from the Caribbean and, in general, from the Tethys area, although it is still important in the present-day Asian mangroves (Germeraad et al., 1968; Thanikaimoni, 1987). *Pelliciera* (represented by the fossil *Psilatricolporites crassus*) is now restricted to a small area in Central America (Wijmstra, 1968; Winograd, 1983; Jiménez, 1984), and *Acrostichum* is still present, widespread and abundant. Another important Eocene fossil pollen species commonly associated with mangrove vegetation is *Echitriporites trianguliformis*. It became extinct after the late Eocene and no botanical equivalent taxon is presently known, but its association with coastal marine sediments has led to the assumption that this pollen was derived from a mangrove element (Frederiksen, 1985).

A number of these findings are based on Venezuelan and northern South American fossil records, especially from the Maracaibo Basin (Kuyl et al., 1955; Germeraad et al., 1968; Lorente, 1986; Muller et al., 1987), but only qualitative studies are presently available. Detailed paleoecological successions based on quantitative analysis, botanical affinities, and comparison with modern sedimentation patterns are not available for Eocene mangroves. In northern South America, the main representatives of Paleocene and Eocene coastal communities have been considered to be *Deltoidospora adriennis*, *Echitriporites trianguliformis*, *Perisyncolporites pokorny*, *Retibrevitricolpites triangulatus*, and species of the genera *Spinizonocolpites* and *Proxapertites* (Rull, 1992a, 1997a; Colmenares and Terán, 1993). Important criteria for these assumptions have been the botanical affinities with present-day coastal elements, based on the pollen morphology, and the frequent association of these fossil taxa with coastal or near shore sediments. However, this procedure has two important constraints. On the one hand, almost half of these taxa are extinct or have no known modern botanical equivalent. On the other hand, there is no proof that community composition and structure have been constant through time. Significant changes in community composition during the last millenia have been recorded (Webb, 1987), suggesting significant changes in past times owing to evolution. Furthermore, a coastal habitat does not equate necessarily with the occurrence of mangroves, as can be seen along the present-day Caribbean coasts.

The present study is the first step of a broader study that aims to reconstruct palynologically the paleosuccession of Paleogene coastal assemblages of the Maracaibo Basin. Other goals are to establish the composition of the mangroves on the basis of objective, statistical associations among pollen and spore taxa prior to analyzing their respective botanical affinities, and to determine their patterns of occurrence in modern sediments. In addition, an attempt is made to associate paleovegetational trends

with paleoenvironmental fluctuations in order to determine potential forcing mechanisms, (i.e., climate and sea-level changes). Finally, a comparison of the geographic distribution of present and Eocene mangrove components is presented, and several biogeographical hypotheses are evaluated.

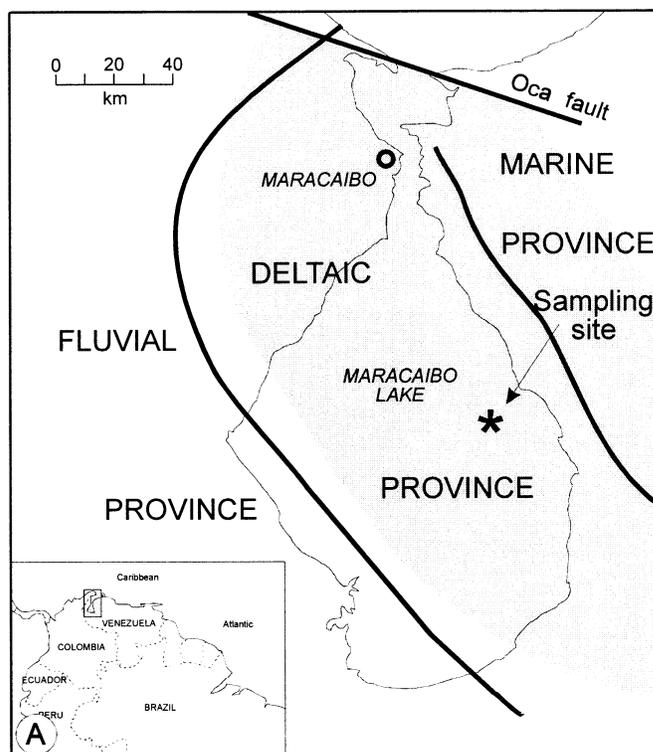
### STRATIGRAPHIC AND PALEOGEOGRAPHIC FRAMEWORK

The sediments under study belong to the Misoa Formation, a sequence of gray quartzitic sandstones intercalated with micaceous and carbonaceous laminated shales. It is situated unconformably between the underlying Paleocene Guasare Formation, deposited in neritic shelf environments, and the overlying Paují Formation, deposited in deep-marine environments (Fig. 1). The Misoa Formation is about 5000 m in maximum thickness, and is considered a sequence of fluvio-deltaic to marginal marine sediments (González de Juana et al., 1980), although an alternative interpretation of more neritic conditions has been published recently (Higgs, 1996). This formation has been divided into upper and lower intervals called, respectively, 'B' and 'C'. The B interval, in turn, has been further subdivided into lower B, a highstand systems tract deposited in deltaic environments, and upper B, deposited on a shallow shelf (Parnaud et al., 1995). The sediments in the present work represent the upper-B/lower-B transition (Fig. 1) and, therefore, afford a high probability of recording palynologically significant environmental changes.

### MATERIALS AND METHODS

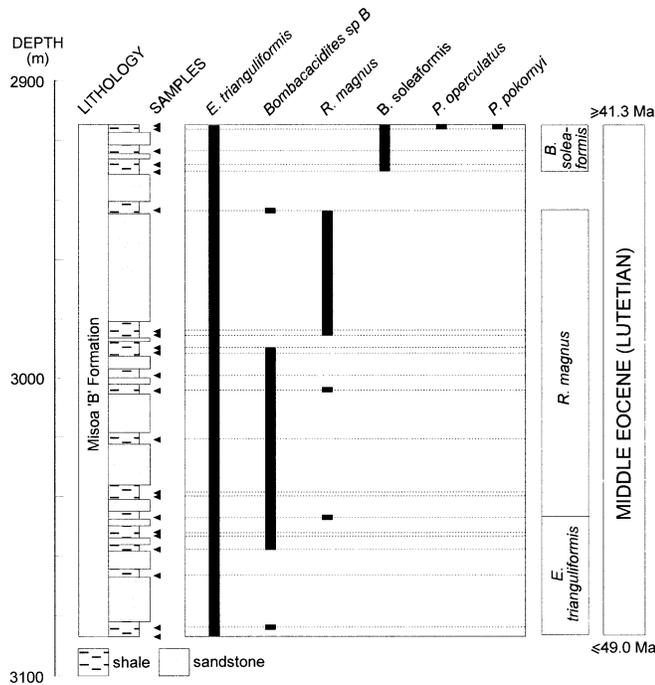
Twenty two samples were taken from well cores. These consist of dark gray to black shales intercalated with more or less thick sandstone layers (Fig. 2). An average of four grams per sample were treated with HCl and HF, followed by centrifugation in a zinc-bromide density gradient. The residues were mounted in glycerine jelly and stored in ethyl alcohol. Counts of pollen, fern spores, fungal spores, algae remains, dinoflagellate cysts, and foraminiferal linings were made according to the criteria of Rull (1987), to standardize the data for further statistical treatment. Identifications were based on literature with descriptions and illustrations of Paleogene taxa from northern South America (Van der Hammen and Wijmstra, 1964; González, 1967; Regali et al., 1974; Germeraad et al., 1968; Muller et al., 1987; Colmenares and Terán, 1993), as well as the MARAVEN type collection. The palynological zonation of Muller et al. (1987) for northern South America was used as the framework.

Diagrams were plotted with PSIMPOLL (version 2.25) and statistical analysis were done using MVSP (version 2.1). For statistical treatment, percentages with respect to the pollen sum (including all the pollen and spores counted) were used, but only taxa above 2% of the total in at least one sample were considered in order to avoid random 'noise' produced by rare taxa (Birks, 1986). In the cluster analysis, Gower's (1971) similarity coefficient and the unweighted centroid agglomerative method were used (Kovach, 1989). Detrended correspondence analysis (DCA) was carried out according to Hill and Gauch (1980), using the reciprocal averaging algorithm. Percentages were log-



	SYSTEM	SERIES	FORMATION
EOCENE		UPPER	Paují
		MIDDLE	Misoa B
		LOWER	C
PALEOCENE		UPPER	Guasare
		LOWER	Guasare

FIGURE 1—Paleogeography and Stratigraphy. (A) Paleogeographical reconstruction of the Middle Eocene in the Maracaibo Basin. Shaded areas represents the present approximate distribution of the Misoa Formation. (B) Stratigraphic relationships of the Misoa Formation. The approximate stratigraphical position of the sequence studied is shaded. Dashed pattern indicates absence of sediments in the area. Simplified from Zambrano et al. (1970), González de Juana et al. (1980), and Parnaud et al. (1995).



**FIGURE 2**—Stratigraphical ranges of the selected markers and the corresponding palynological zones of Muller et al. (1987). General lithostratigraphy and samples are indicated. *B* = *Bombacacidites*, *E* = *Echitriporites*, *P* = *Psilatricolporites (operculatus)*, *Perisyncolporites (pokorny)*, *R* = *Retitricolporites*.

ratio transformed previous to all statistical analyses (Aitchison, 1982). Paleosalinity indices were computed according to Rull (1992a, 1997b), as the natural logarithm of the ratio between the abundances of marine (bulk dinoflagellate cysts and foraminiferal linings) and freshwater (*Pediastrum* and *Botryococcus*) plankton components. Val-

ues of 3 indicate normal marine salinity, whereas values of  $-3$  represent freshwaters. Intermediate values correspond to several degrees of brackish water.

## RESULTS AND INTERPRETATION

Among the taxa recorded, 23 were selected in the present paper (Table 1), owing to their chronostratigraphic or paleoecologic significance. All the remaining taxa together are commonly under 10% of the pollen sum (which includes only pollen and fern spores), and none of them attain 2% individually.

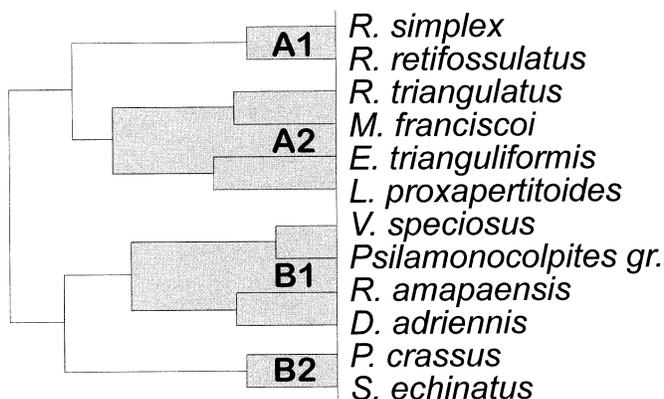
### Palynological Zonation and Chronostratigraphy

Using the occurrence ranges of the marker species defined by Muller et al. (1987), three Eocene pollen zones could be defined (Fig. 2). The lowermost part of the section is assigned to the *Echitriporites trianguliformis* Zone based on the occurrence of the marker species and the absence of markers for the upper and lower zones. Other important taxa present are *Verrustephanocolpites simplex* and *Retitricolporites irregularis*, while *Gemmamonocolpites* sp., *Gemmastephanoporites polymorphus*, and *Monoporites annulatus* occur occasionally. A gradual floral change marks the transition to the *Retitricolporites magnus* Zone, in which the species characteristic of the underlying zone become more scarce, while *Bombacacidites* sp. B and *Gemmamonocolpites* sp. are more frequent. Finally, a more intense floral change is recorded, representing the transition to the *Bombacacidites soleaformis* Zone. In it, a floral replacement takes place. All the taxa of the former zones, except *E. trianguliformis*, are absent or scarce, whereas the marker species together with *Psilaperiporites robustus*, *Psilatricolporites operculatus*, and *Perisyncolporites pokorny*, have their first occurrences.

These three zones correspond to the lower half of the

**TABLE 1**—List of fossil taxa used and probable botanical affinities.

Taxa	Affinity
<i>Bombacacidites soleaformis</i> Muller, DiGiacomo and Van Erve	Bombacaceae
<i>Bombacacidites</i> sp. B Muller, DiGiacomo and Van Erve	Bombacaceae
<i>Deltoidospora adriennis</i> (Potonié et Gelletich) Frederiksen	<i>Acrostichum aureum</i>
<i>Echitriporites trianguliformis</i> Van Hoeken-Klinkenberg	Unknown
<i>Gemmamonocolpites</i> Van der Hammen and García de Mutis	Unknown
<i>Gemmastephanoporites polymorphus</i> González	Unknown
<i>Longapertites proxapertitoides</i> Van der Hammen and García de Mutis	Palmae
<i>Mauritiidites franciscoi</i> (Van der Hammen) Van Hoeken-Klinkenberg	<i>Mauritia</i>
<i>Monoporites annulatus</i> Van der Hammen	Gramineae
<i>Perisyncolporites pokorny</i> Germeraad, Hopping and Muller	Malpighiaceae
<i>Psilamonocolpites</i> Van der Hammen and García de Mutis	Palmae
<i>Psilaperiporites robustus</i> Regali, Uesugui and Santos	Chenopodiaceae-Amaranth.
<i>Psilatricolporites crassus</i> Van der Hammen and Wijmstra	<i>Pelliciera</i>
<i>Psilatricolporites operculatus</i> Van der Hammen and Wijmstra	Euphorbiaceae
<i>Retibrevitricolpites triangulatus</i> Van Hoeken-Klinkenberg	Unknown
<i>Retimonocolpites retifossulatus</i> Lorente	Palmae
<i>Retitricolpites amapaensis</i> Regali, Uesugui and Santos	Unknown
<i>Retitricolpites magnus</i> González	Unknown
<i>Retitricolpites simplex</i> González	Anacardiaceae
<i>Retitricolporites irregularis</i> Van der Hammen and Wijmstra	Euphorbiaceae
<i>Spinizonocolpites prominatus</i> (= <i>S. echinatus</i> ) (McIntyre) Stover and Evans	<i>Nypa</i>
<i>Verrucatosporites</i> c.f. <i>V. speciosus</i> Harris	Polypodiaceae
<i>Verrustephanoporites simplex</i> Leidelmeyer	Unknown



**FIGURE 3**—Dendrogram showing the results of the cluster analysis on statistically significant taxa and their assemblages. *D* = *Deltoidospora*, *E* = *Echitriporites*, *L* = *Longapertites*, *M* = *Mauritiidites*, *P* = *Psilatricolporites*, *R* = *Retitricolporites* (*simplex*, *amapaensis*), *Retimonocolpites* (*retifossulatus*), *Retibrevitricolpites* (*triangulatus*), *S* = *Spinizonocolpites*, *V* = *Verrucatosporites*.

middle Eocene (Muller et al., 1987), most probably within the Lutetian Stage. According to Berggren et al. (1995), this stage spans the interval between 49 and 41.3 Ma.

#### Paleoecological Analysis

##### *Palynological Assemblages and Paleoecological Succession*

The statistically significant taxa (above 2% of the total) were grouped mathematically into two assemblages, each of which were further divided into two subassemblages (Fig. 3). The first subassemblage (A1) is composed of *Retitricolporites simplex* and *Retimonocolpites retifossulatus*. According to González (1967), *R. simplex* could be derived from some Anacardiaceae species, a family containing numerous neotropical trees from inland forests (Aristeguieta, 1973). *Retimonocolpites retifossulatus* has no clear affinity, but it has been tentatively related to the palm family (Palmae or Arecaceae) by Lorente (1986). Therefore, subassemblage A1 most probably represents inland communities. The second subassemblage (A2) is composed by *Retibrevitricolpites triangulatus*, *Echitriporites trianguliformis*, *Mauritiidites franciscoi*, and *Longapertites proxapertitoides*. The first two species are now extinct and there are no known modern equivalents, despite the superficial resemblance of *E. trianguliformis* to some Proteaceae pollen (Germeraad et al., 1968). *Mauritiidites franciscoi*, in contrast, corresponds most probably to one or more species of *Mauritia*, a palm genus typical of the neotropical lowlands and common in the back-mangrove communities flooded with fresh water (Muller, 1959; Van der Hammen, 1963; Tissot et al., 1988; Rull, in press). Finally, *L. proxapertitoides* is similar to the pollen of *Eugeissona*, a palm from the present Asian lowland evergreen forests (Thanikaimoni et al., 1984). Hence, subassemblage A2 seems related to back-mangrove palm swamps.

Subassemblage B1 is defined by two fern spore types, the *Psilamoncolpites* group and *Retitricolporites amapaensis*. The botanical affinities of the last is not known (Lorente, 1986). However, although many palm genera have psilate, monocolpate pollen (Thanikaimoni, 1970), some of them from present-day back-mangrove areas are common-

ly referred to *Psilamoncolpites*, especially *Euterpe*, *Manicaria*, *Maximiliana*, and *Jessenia* (Muller, 1959; Van der Hammen, 1963; Tissot et al., 1988). Concerning the ferns, there is little doubt that species of *Verrucatosporites* are derived from some Polypodiaceae. Among them, *Stenochlaena palustris*, a climbing species from the swamps behind the outermost mangrove belt, produces the same spore type (Germeraad et al., 1968; Hasseldonckx, 1977; Lorente, 1986; Thanikaimoni, 1987; Tissot et al., 1988; Ellison, 1989). *Deltoidospora adriennis* has been considered the analog of *Acrostichum aureum* (the so-called 'fern beach'), which is typical of the inner mangrove zone, especially in more open and disturbed areas (Van der Hammen, 1963; Westgate and Gee, 1990; Ellison, 1989). Finally, subassemblage B2 is defined by two form-species clearly related to mangrove communities. *Psilatricolporites crassus* is the pollen of *Pelliciera* (Pellicieraceae), a mangrove-forming tree now restricted to Central America (Graham, 1995). *Spinizonocolpites prominatus* is identical to the pollen of *Nypa*, a palm from the modern Asian mangroves in brackish and salt-water environments (Germeraad et al., 1968; Frederiksen, 1985; Thanikaimoni, 1987). It is important to note that *Brevitricolpites variabilis*, as described and depicted by González (1967), has not been found in this study.

Studies on modern pollen deposition as related to vegetation in coastal sediments complement the deductions from fossil affinities, and provide an interesting differentiation between palm-dominated and herbaceous back-mangrove swamps (Muller, 1959; Van der Hammen, 1963; Tissot et al., 1988). For example, in the Orinoco delta, the pollen assemblages from the palm-dominated swamps are dominated by palm pollen, with *Mauritia* locally very abundant in the 'morichales' (almost pure *Mauritia* palms swamps). In contrast, *Polypodium* spores are the more abundant and widespread type in the sediments of the extensive herbaceous fern swamps (Muller, 1959). This indicates that the two subassemblages that characterize the back-mangrove communities can be differentiated into those corresponding to palm swamps with 'morichales' (A2) and fern swamps (B1). However, this interpretation is more evident in the case of B1, because A2 is dominated by an extinct species with unknown affinity (*E. trianguliformis*), and not by palms. In summary, three of the four palynological assemblages recognized through statistical methods represent inland communities (A1), herbaceous fern swamps (B1), and mangroves (B2); the character of the fourth assemblage (A2) remains unknown.

Four assemblage-pollen zones (E-1 to E-4) were obtained using the same clustering methods, but this time constrained in order to maintain the stratigraphical arrangement of samples (Fig. 4). The more noteworthy features of assemblage Zone E-1 are the absolute dominance of *E. trianguliformis* and *M. franciscoi*, together with the absence of *P. crassus*. This indicates the absence of mangroves and 'morichales' during this interval (*E. trianguliformis* Zone), and the dominance of unknown communities in which the parent species of *E. trianguliformis* was the major component. A slight increase of mangroves and back-mangrove fern swamps took place in assemblage Zone E-2 (lower *R. magnus* Zone), but the *E. trianguliformis* vegetation was still dominant. Mangrove vegetation attained its maximum development in assemblage Zone

## Selected taxa (&gt;2%)

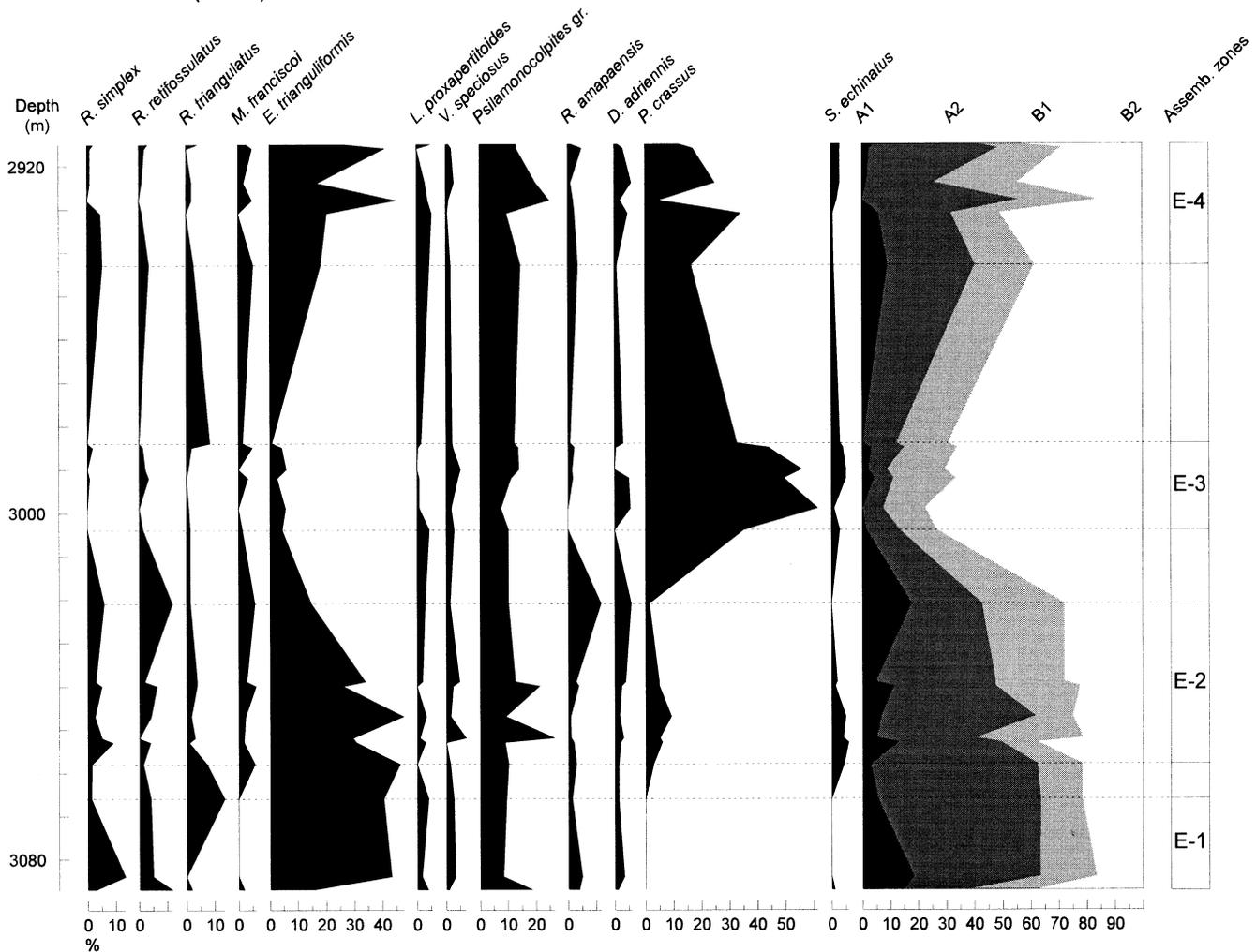


FIGURE 4—Percentage pollen diagram of selected taxa and their assemblages, with the assemblage zones indicated. Genera abbreviated as in Figure 3.

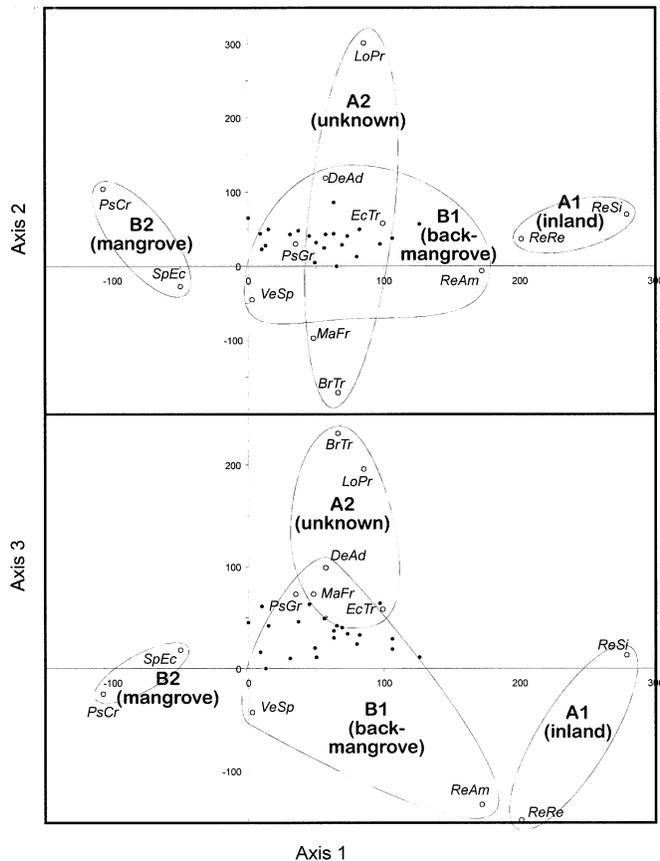
E-3 (upper *R. magnus* Zone). During this time, mangroves were probably *in situ*. This is inferred because in subassemblage B2 they reach almost 80%, whereas in inland assemblage A they reach around 5%. From here, a progressive decrease in the mangrove assemblage occurred, with a corresponding trend towards assemblage A2. This lasted until assemblage zone E-4 (*B. soleaformis* Zone), where both B2 and A2 are co-dominant but *Psilamonocolpites* is important again.

In summary, a successive replacement of two major assemblages took place in a cyclic process. It began with the dominance of inland (?) communities of *E. trianguliformis*, and culminated in the middle of the section with a maximum in mangrove development before the return to inland assemblages. This suggests a displacement of coastal vegetation communities that was probably related to a transgressive-regressive cycle.

#### Paleocommunity and Paleosalinity Trends

The following analysis is based on the concept of attraction domains. Holling (1973) introduced the concept of re-

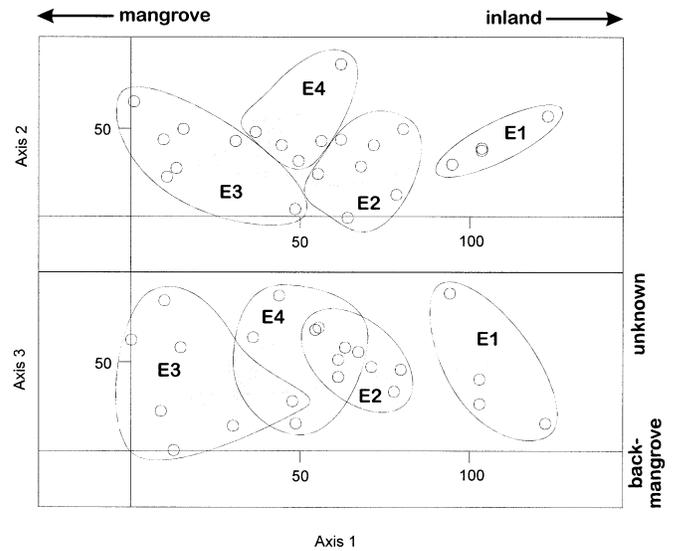
silience as the property of ecological systems to absorb disturbances and to persist. Holling's concept is based on the existence of several possible states for an ecosystem and is opposed to the stability concept, which involves only one possible equilibrium status. The abstract domain embracing the possible states is called the attraction domain of the ecosystem (Gilpin and Case, 1976). Rull (1992a, 1996) used multivariate statistical methods to graphically display the attraction domains for several neotropical communities. These techniques allow visual appreciation of the domains of the communities involved in a study, as well as their temporal trends. Since the simultaneous plotting of both taxa and samples is required, the recommended tool is detrended correspondence analysis (DCA). The results of a DCA on the data of the present study are shown in Figure 5. The attraction domain for each paleocommunity is represented by the region defined by its corresponding assemblage. In this way, mangroves are situated at the left of the plot (assemblage B2), back-mangrove swamps in the center (B1), and inland communities at the right (A2), defining a coastal to inland trend along axis 1.



**FIGURE 5**—Samples (black dots) and taxa (white dots) represented in the space of the three first axes obtained using DCA: Taxa are grouped according to the palynological assemblages of Figure 3. *PsCr* = *Psilatricolporites crassus*, *SpPr* = *Spinizonocolpites prominatus*, *VeSp* = *Verrucatosporites cf. speciosus*, *PsGr* = *Pilamonoletes* group, *MaFr* = *Mauritidites franciscoi*, *BrTr* = *Brevitricolpites triangularis*, *EcTr* = *Echitriporites trianguliformis*, *DeAd* = *Deltoidospora adriennis*, *ReAm* = *Retitricolpites amapaensis*, *LoPr* = *Longaperites vaneedenburgi*, *ReRe* = *Retimonocolpites retifossulatus*, and *ReSi* = *Retitricolpites simplex*.

Axis 2 does not contribute very much to the separation of attraction domains, but assemblages A2 (unknown) and B1 are well discriminated by axis 3.

In order to follow the paleocommunity trends, samples were grouped according to assemblage zones E-1 to E-4 (Fig. 4) and connected by an arrow representing time (Fig. 6). Using the same plot, the values of the paleosalinity index were added, according to four classes, from more saline to almost freshwater: 0 to -0.5, -0.5 to -1, -1 to -2 and < -2 (Fig. 7). In this way, changes in paleocommunities and paleosalinity can be resolved at the same time. A trend from the inland region to the mangrove one is recorded from E-1 to E-3. This is paralleled by a conspicuous increase in paleosalinities, which attained their maximum in assemblage zone E-3 where the maximum of the mangrove assemblage occurs (Fig. 4). However, fully marine salinities (index = 3) have not been reached. Later (E-4), an abrupt reversal to the inland region is observed. The trend stops at the A2 region (unknown assemblage dominated by *E. trianguliformis*), where the minimum salinity values are recorded, which suggests an inland environ-

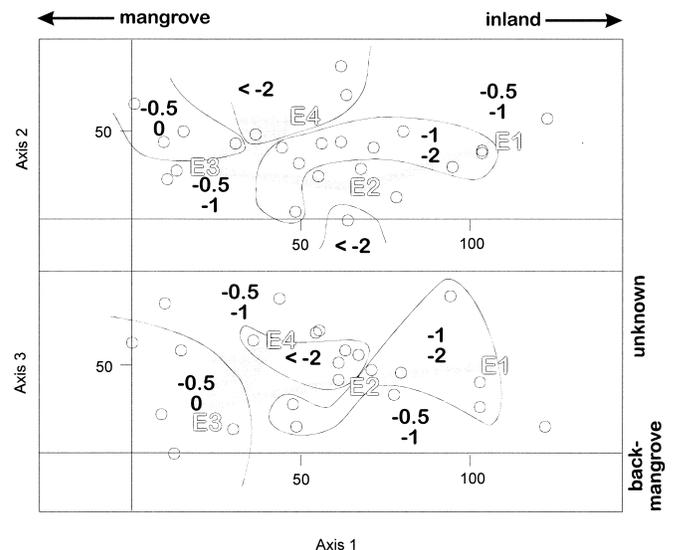


**FIGURE 6**—Magnification of the central region of plot in Figure 5, showing the samples grouped according to the palynological zones of Figure 4. The arrow represents the direction of time.

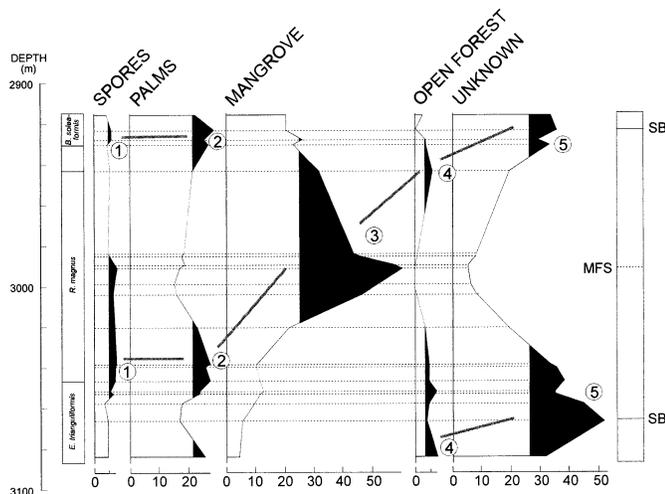
ment connected to freshwater flooding for the corresponding paleocommunity. Once again, a recurrent trend involving mangroves and inland communities has been observed, this time associated with paleosalinity variations that support the existence of a transgressive-regressive cycle.

## CYCLICITY

The concept of cycles in the fossil pollen record was introduced by Van der Hammen (1957). He proposed a single first-order cycle of 60 million years represented by the whole Tertiary, a second-order category characterized by cycles with a 6-million-year period, and minor third-order cycles with a 2-million-year period. These cycles were evi-



**FIGURE 7**—Magnification of the central region of plot in Figure 5, showing the paleosalinity index areas (see text).

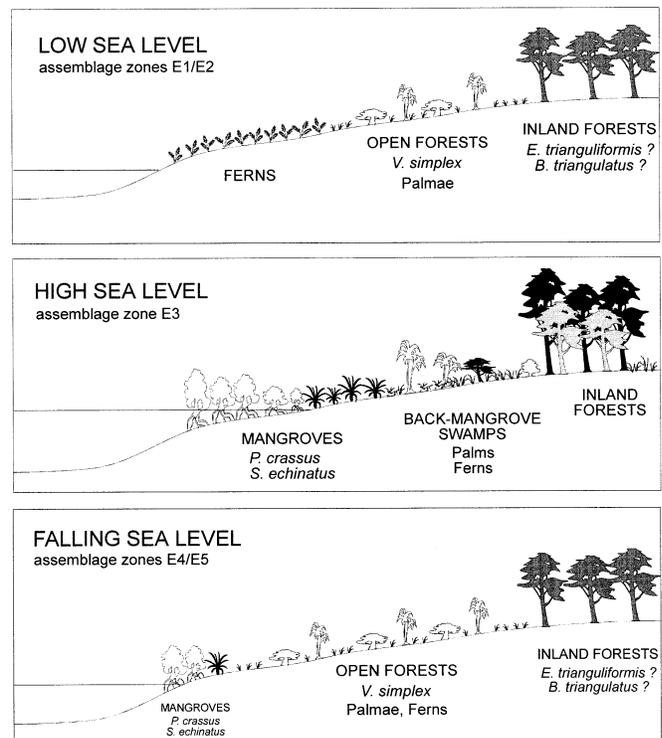


**FIGURE 8**—Percentage pollen diagram grouped according to Poumot (1989). Curves are 3-point smoothed. Black areas represent the values above the mean within each group. Numbers refer to the sequence of Poumot (1989).

denced by the relative abundance of *Monocolpites medius* (palm pollen) and related by Van der Hammen to temperature changes conditioned by periodic variations in incoming solar radiation. The middle Eocene represents a second-order cycle (48 to 42 million years before present), subdivided into three third-order cycles (A, B, and C) with boundaries at 46 and 44 my BP, respectively. Recently, Poumot (1989) introduced the concept of a palynocycle or pollen cycle, which he connected to eustatic oscillations. According to him, eustatic and climatic cycles are closely associated and determine variations in the coastal plant communities that can be followed through pollen assemblages. Five main phases were recognized in this process. During the low sea-level phase, erosion and transport predominate and the coastal pollen assemblages are dominated by fern spores from both coastal swamps and water-transported from inland forests. At the beginning of sea-level rise, a peak of palm pollen is recorded. This is related to the ability of several tropical palms to become established in the incipient prograding sandy accumulations. Later, during maximum transgression, an increase of mangrove pollen is typical, owing to a combination of high sea-level stability and wetter climate. The regressive phase is characterized by pollen from back-mangrove open forests due to the cooler climate. Finally, close to the lowest sea-level stand, a phase of dominance of herbs or *Casuarina* (in South East Asia) pollen indicates reduction of the mangrove fringe and its replacement by these communities. The palynocycle is closed by return of the fern-spore phase.

Poumot (1989) showed a good fit between palynocycles and eustatic cycles of Haq et al. (1987) for the Neogene of Asia and Africa. In Venezuela, the same methodology allowed the recognition of the main Eocene to Miocene palynocycles (Rull and Poumot, 1997). During the middle Eocene (49.5 to 39.5 my), palynocycles PCY1 to PCY6 were correlated with third-order cycles TEJAS A 3.1 through 3.6.

In the present work, pollen assemblages were arranged



**FIGURE 9**—Hypothetical sequence of coastal vegetation in relation to sea level during the Lutetian Stage.

according to the ecological groups of Poumot (1989), following the criteria established by Rull and Poumot (1997). The derived groups, however, did not differ significantly from those obtained in the cluster analysis. The spore group is constituted by *V. speciosus* and *D. adriennis*, while the palm group is composed of *M. franciscoi*, *L. proxapertitoides*, *R. retifossulatus* and psilate palm pollen. Mangroves include *P. crassus*, *S. prominatus*, and *R. amapaensis*, and the open forest is represented by *R. simplex*. Finally, a group of unknowns is defined by *E. trianguliformis* and *R. triangulatus* in an attempt to test their behavior in this scheme. Figure 8 represents the stratigraphical ordination of these assemblages. Curves are 3-point smoothed using polynomial regression, and the values above the mean are highlighted. The sequence begins with the end of a former cycle within the *E. trianguliformis* Zone. A complete palynocycle is then recorded up to the *B. soleaformis* Zone, where the beginning of a third cycle emerges. The maximum transgression is recorded at the middle of the *R. magnus* Zone in the mangrove peak. It is noteworthy that the peaks of spores and palms are simultaneous, whereas the transition from mangrove to open forest is sequential. This suggests that the low sea-level phase is notably shorter than the maximum sea-level phase, or that spores and palms in this case co-occur (Burnham, pers. comm.). A tentative community reconstruction for the paleosuccession of coastal communities is shown in Figure 9, following the rules of Poumot (1989).

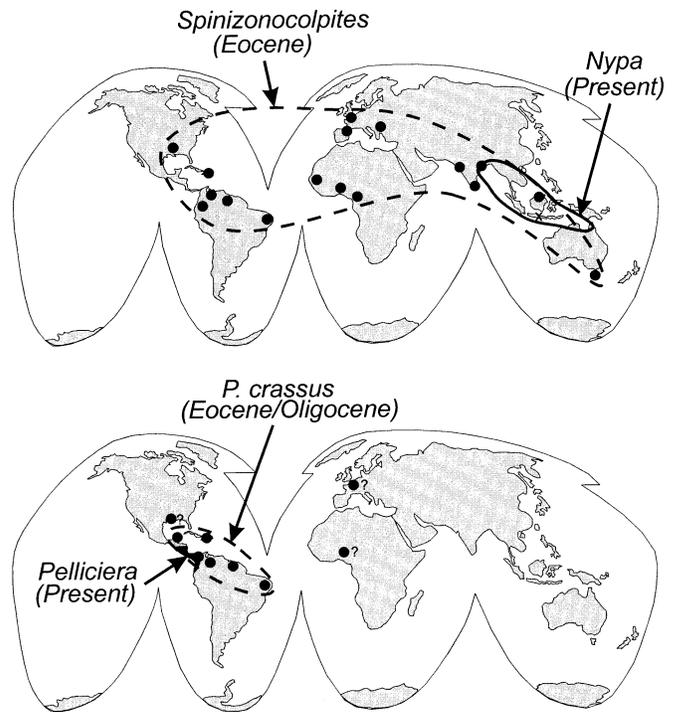
The palynocycle recorded here is in the same stratigraphical position as the PCY4 of Rull and Poumot (1997) with respect to the pollen zones. Therefore, it can be considered its chronostratigraphic equivalent. PCY4 is corre-

lated with the third-order cycle TEJAS A 3.4 of Haq et al. (1987), which is the last within the Lutetian, and has sequence boundaries (SB) at 44 and 42.5 my BP. The mangrove peak, coinciding with maximum estimated paleosalinities (Fig. 7) probably corresponds to the maximum flooding surface (MFS) of 43 my. By this correlation, the cycle also corresponds to cycle 'C' of the middle Eocene in the framework of Van der Hammen (1957).

#### HISTORICAL BIOGEOGRAPHY

Only one of the common middle Eocene mangrove taxa remains as an important element of these communities in the Neogene of the Maracaibo Basin—the 'beach fern' *Acrostichum aureum* (*D. adriennis*). Since the late Eocene/early Oligocene, *Rhizophora* (*Zonocostites*) species have been dominant both floristically and physiognomically in the mangroves of this area (Germeraad et al., 1968). *Pelliciera* has become less important since the late Eocene and has disappeared from the Maracaibo Basin at the Pliocene/Pleistocene boundary (Lorente, 1986), whereas *Nypa* disappeared near the Eocene/Oligocene boundary (Muller, 1980). Thus, an important biogeographic change took place in these communities in the Eocene/Oligocene transition, enough to completely reorganize these floras. The reduction of two important Eocene mangrove components, *Pelliciera* and *Nypa*, was a worldwide phenomenon. Indeed, *Nypa* (*Spinizonocolpites*) was present on all the continents during the Eocene but, at present, it only occurs in the Indo-Malesian region (Fig. 10). In contrast, *Pelliciera* (*P. crassus*) was present in the Caribbean area and the Atlantic coasts of Guyana and Brazil during Eocene-Oligocene times (its occurrence in Europe and Africa is unsettled), but now it is restricted to a small area of Central and Northern South America (Fig. 10). According to Germeraad et al. (1968), the extinction of *Nypa* in the Tethys region was caused by a drier, more seasonal climate, whereas the limited distribution of *Pelliciera* is a consequence of its low tolerance to high salinities caused by increased evaporation in dry climates (Jiménez, 1984). It is interesting that both taxa are presently common in back-mangrove areas. If they were dominant in the Eocene, a change in ecological preference from euryhaline to brackish water is implied. Also, *Nypa* seemingly did not coexist with *Rhizophora*, since their last and first occurrence, respectively, took place near the Eocene/Oligocene boundary (Muller, 1980). In contrast, *Pelliciera* co-occurred with the Neogene and present dominant genera of the Caribbean mangroves until the Miocene, as *Avicennia* in the present (Wijmstra, 1968). This indicates that mangroves experienced not only changes among their species, but that changes also occurred within communities, despite the fact that the taxonomic elements remained the same.

More studies on the late middle Eocene and late Eocene of the Maracaibo Basin are needed for a definitive assessment. However, there is an apparent lack of pollen of some recognized mangrove taxa in these records (Rull, 1993, 1997b). The possibility that *E. trianguliformis* was an important mangrove component has been suggested by Frederiksen (1985) and Rull (1993). However, the results of the present work do not support this hypothesis. During this interval, the first occurrence of another unknown, *Retitricolpites guianensis*, is recorded in the Maracaibo Basin.



**FIGURE 10**—Present (shaded areas) and Eocene (black circles) geographic distribution of *Nypa*, *Pelliciera*, and their fossils: *Spinizonocolpites* spp. and *P. crassus*. After Germeraad et al. (1968), Muller (1980, 1981), Thanikaimoni et al. (1984), Frederiksen (1980, 1985, 1988), Thanikaimoni (1987), Westgate and Gee (1990), Graham (1995), Pole and Macphail (1996).

This taxon remained an important component of the flora until at least the Miocene (Germeraad et al., 1968; Lorente, 1986; Muller et al., 1987). According to Germeraad et al. (1968) *R. guianensis* resembles the pollen of several Sterculiaceae and Tiliaceae, which occupy a wide range of environments (Lorente, 1986). However, paleoecologically-oriented studies are not available to test its possible association with mangrove communities. During the Neogene, the mangroves of the Maracaibo Basin seemingly did not undergo significant floristic changes (Lorente, 1986). Rather, they show a gradual trend of enrichment, as in other areas of Gulf/Caribbean region (Graham, 1995).

#### GENERAL CONCLUSIONS

A paleoecological reconstruction of middle Eocene coastal communities from the eastern Maracaibo Basin defines four subassemblages based on the association of significant taxa: A1, inland forest communities; A2, an unknown plant community also from inland, freshwater swamps, and dominated by *E. trianguliformis*; B1, back-mangrove herbaceous swamps dominated by ferns, and B2, mangroves. The mangroves were dominated by *Pelliciera* and *Nypa*, while *Brevitricolpites variabilis*, which has been considered the dominant taxon of the early and middle Eocene mangroves in nearby areas, has not been found in this study. These four subassemblages allow reconstruction of the sequence of coastal vegetation development, using quantitative zonation of the percentage pollen diagram, graphical multivariate paleocommunity analysis,

and quantitative study of paleosalinity trends. The four assemblage zones found with these procedures (E-1 to E-4) show a cyclic alternation of palynological assemblages: Unknown A2 dominates E-1 and E-2, and the salinity is low; B1 (mangroves) is dominant in E-3, coinciding with maximum salinity; and A2 is dominant again in E-4, where salinity attained its minimum values (Fig. 9). These trends fit well with the phases of a Poumot palynocycle, suggesting that the recurrent trend reflects the lateral displacement of coastal ecological belts connected to apparently eustatic sea-level variations. The lowest sea level coincided with the dominance of unknown *E. trianguliformis* communities (A2) and low paleosalinities, whereas maximum sea level was characterized by mangroves (B2) and high paleosalinities. Based on the identification of corresponding palynological zones defined through marker taxa, the transgressive-regressive cycle recorded in this way has been correlated chronologically with the eustatic cycle TEJAS A 3.4, extending from 44 to 42.5 my BP (Lutetian). The continued presence and quantitative importance of *E. trianguliformis* in the Middle Eocene indicates that it could be very important paleoecologically. Further study is needed on the botanical affinities of this taxon.

The floristic composition of middle Eocene mangroves is very different from that of the Oligocene to Recent ones in the Maracaibo Basin. An important biogeographic change is suggested to have occurred in these communities during the upper middle Eocene and the late Eocene. Pollen taxa botanically related to known mangrove elements seem scarce for this time span, but studies are few. The change seems to have been worldwide in scope, as indicated by the widespread geographical distribution of *Pelliciera* and *Nypa* during the Eocene, compared with their present-day endemic centers.

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