A QUANTITATIVE PALYNOLOGICAL RECORD FROM THE EARLY MIOCENE OF WESTERN VENEZUELA, WITH EMPHASIS ON MANGROVES

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Abstract

The quantitative reconstruction presented in this paper documents paleoecological trends of the northern Maracaibo basin (western Venezuela), during the Early Miocene, through pollen analysis of drill core samples from the La Rosa (shallow marine) and Lagunillas (coastal plain) formations. Palynological assemblages were grouped statistically into three assemblages representing mangroves, herbaceous back-mangrove swamps, and inland palm/fern swamps. Mangroves were the local vegetation during the deposition of La Rosa Formation and, after a regressive event, were replaced by herbaceous back-mangroves during the sedimentation of Lagunillas Formation. The palynological assemblage representing palm/fern swamps dominates the entire sequence and is interpreted as a large background signal reflecting transport by rivers. Mangrove communities had few species, and represented a transitional phase in the mangrove community evolution, after the terminal Eocene biotic crisis.

INTRODUCTION

This paper presents a palynological study of Early Miocene La Rosa and Lagunillas formations from the NE of the Maracaibo basin in Venezuela, in order to reconstruct the paleosuccession of coastal plant communities, with emphasis on mangroves. It is a part of a broader project which is aimed at reconstructing coastal and mangrove communities and their paleosuccession in the Tertiary of the Maracaibo basin using quantitative pollen analysis and statistical paleoecological methods to increase the degree of objectivity in both the composition and the interpretation of palynological taphocenoses. Paleocommunities should be reconstructed from suitable taphocenoses, and not with qualitative or semi-quantitative data. In palynology, this is achieved through representative counts including all the palynomorph types present in samples (Rull, 1987), and comparison with modern analogs (Rull, 1998a). Furthermore, empirical associations based solely in the botanical affinities of the fossil taxa and the taxonomic composition of present communities (a common procedure) implicitly assume that communities have not changed through time, which is totally untrue, especially for mangroves (Graham, 1995; Rull, 1998b). To properly record past associations, more objective methods, such as statistical associations, should be applied, before looking at botanical affinities (Rull, 1998c). So far, several Paleocene and Eocene mangroves communities have been reconstructed with these methods (Rull, 1992; 1997b; 1998b; 1998c; 1999; 2000). However, post-Eocene mangroves, although well-known taxonomically (Lorente, 1986; Muller et al., 1987), have not yet been studied with these methods.

From a palynostratigraphic point of view, the Early Miocene in Venezuela is characterized by two zones (Lorente, 1986): Verrutricolporites and Psiladiporites, which are equivalent to the northern South American pollen zones Verrutricolporites rotundiporus–Echidiporites barbeitoensis, and Echitricolporites maristellae–Psiladiporites minimus, respectively (Muller et al., 1987). The zone of Verrutricolporites is an interval zone, having its base in the first occurrence of Verrutricolporites rotundiporus and its top below the first occurrence of Psiladiporites minimus or Echitricolporites maristellae. In addition, two other taxa: Bombacacidites zuatensis and Psilatricolporites pachydermatius have their first occurrence at the base of this zone. According to Lorente (1986), pollen assemblages for this zone are dominated in the entire basin by Zonocostites ramonae, the other important components being Psilatricolporites crassus, Bombacacidites baumfalki, Retitricolporites irregularis, Retitricolporites hispidus, Retitricolporites simplex, Jandufouria seamrogiformis, Verrucatosporites usmensis, Proxapertites operculatus, Monoporites annulatus, Mauritiidites franciscoi, Striatricolpites cataumbus, Psilatricolporites maculosus, and
Podocarpidites sp. The inferred sedimentary environment is coastal to shallow marine. The interval zone of Psiladiporites is defined by the first occurrence of Psiladiporites minimus, at the base. In western Venezuela, the first occurrence of Echitricolporites maristellae is also characteristic, and the zone is called Psiladiporites–Echitricolporites (Lorente, 1986). The top is defined by the first occurrence of Crassoretitriletes vanraadshooveni. In the Maracaibo basin, this zone can be subdivided into two well-differentiated intervals. The lower interval is dominated by Monoporites annulatus, Echitricolporites maristellae, Malvacipollis spinulosa, Psilatricolporites operculatus, Crototricolpites annemariae, Bombaccidites baculatus, Retimnonocolpites longicolpatus, Verrucatosporites usmensis, Magnastriatites grandiosus, Psilamonocolpites medius, Zonocostites ramonae, Mauritiidites franciscoi, and Retitricolporites guianensis, and was deposited under alluvial to lower coastal plain conditions, with some geographical variations. The upper interval is similar but in it Zonocostites ramonae decreases in abundance, and disappears in some areas. The sedimentary environments were alluvial to coastal plains, with more marine conditions in the south (Lorente, 1986).

In the mangrove communities, Zonocostites ramonae was abundant and geographically widespread in western Venezuela, during the Early Miocene. This form-species corresponds to the fossil pollen of Rhizophora, the dominant genus in present-day Neotropical mangrove communities (Chapman, 1976; Tomlinson, 1986). The fossil record shows that this pollen appeared in the Late Eocene in low quantities, and has been dominant in lower coastal mangrove communities from the Miocene to the present. Other mangrove-forming trees progressively appeared in the grove communities from the Miocene to the present. Other shows that this pollen appeared in the Late Eocene in low quantities (Chapman, 1976; Tomlinson, 1986). The fossil record of Zonocostites ramonae corresponds to the fossil pollen of Venezuela, during the Early Miocene. This form-species was abundant and geographically widespread in western environments were alluvial to coastal plains, with more marine conditions in the south. In the Maracaibo basin, this zone can be subdivided into two well-differentiated intervals. The lower interval is dominated by Monoporites annulatus, Echitricolporites maristellae, Malvacipollis spinulosa, Psilatricolporites operculatus, Crototricolpites annemariae, Bombaccidites baculatus, Retimnonocolpites longicolpatus, Verrucatosporites usmensis, Magnastriatites grandiosus, Psilamonocolpites medius, Zonocostites ramonae, Mauritiidites franciscoi, and Retitricolporites guianensis, and was deposited under alluvial to lower coastal plain conditions, with some geographical variations. The upper interval is similar but in it Zonocostites ramonae decreases in abundance, and disappears in some areas. The sedimentary environments were alluvial to coastal plains, with more marine conditions in the south (Lorente, 1986).

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MATERIAL AND METHODS

Study Site and Lithology

This study was carried out on core samples from well TJ located at the NE part of the Maracaibo basin, in western Venezuela (Text-Figure 1). The geological formations involved are La Rosa and lower Lagunillas. The La Rosa Formation unconformably overlies the Eocene Misoa Formation. It is approximately 200 m thick in the type locality, but can be as thick as 1000 m in the eastern part of the basin. It consists of greenish fossiliferous clayey shales with intercalated sandstone layers, and has been subdivided into four units: the basal Santa Bárbara Member (unconsolidated clayey sandstones), the La Rosa shales (with the typical lithology described for the formation), the Intermediate Sand (with a mixture of the main La Rosa lithologies) and the La Rosa sands (fine-grained sandstones, and shales with mollusks and foraminifers). The fossil content indicates an Early Miocene age, and initial deposition in a neritic environment. The Santa Bárbara Member represents the initial transgression on the eroded Eocene, later culminating in a shallow sea covering most of the Maracaibo basin. The Lagerstätte described for the formation, the ‘intermediate sand’ and the ‘La Rosa sand’ (informal names) were deposited in estuarine and beach, and ultimately deltaic environments, transitional to the overlying Lagunillas Formation (González de Juana et al., 1980).

The Lagunillas Formation is 300 to ~1000 m thick, consisting of unconsolidated sandstones, with intermingled clays, shales, and lignites. In the eastern part of the basin, it has been subdivided into three members: Lower Lagunillas (fine-grained sandstones with intercalated shales), Laguna (gray fossiliferous shales and gray sandstones), and Bachaquero (thick clayey sandstones with clays and shales). The Lagunillas Formation ranges from Lower to Middle Miocene in age, and represents the continuation of the regressive sequence initiated in the La Rosa Formation, although an intermediate increase of marine conditions are represented by the Laguna Member. The Lower Lagunillas Member was deposited in a deltaic environment, prograding from the S–SE, and the Bachaquero Member was deposited in fluvial and deltaic environments (González de Juana et al., 1980). In the present study, only the Lower Lagunillas member has been examined.

Laboratory and Analytical Methods

Palynological analyses were carried out on all the shaly intervals of the selected cores (31 samples). Samples were digested in HF and HCl, and centrifuged with ZnBr₂, before mounting in glycerin-jelly. In order to have statistically-representative proportions, counts were done on random transects until the saturation of diversity (Rull, 1987). Final average counts were 424 for spormorphs (pollen and fern spores) and 497 for the total, which include fungal spores, freshwater algal remains (Pediastrum, Botryococcus,
Pseudoschizaea) and marine microplankton (dinoflagellate cysts, foraminiferal linings, acritarchs). The most important taxa identified are shown in Plates 1 to 4. Range analysis was based on the chronostratigraphically-meaning taxa, according to the Lorente (1986) and Muller et al. (1987) zonations. Percentages were computed with respect to the 'pollen sum', which included pollen and fern spores. Diagrams were plotted with PSIMPOLL (Bennett, 1994). Palynological assemblages were obtained from cluster analysis using the Gower (1971) similarity coefficient on log-e transformed percentages and the unweighted centroid agglomerative method, using Multivariate Statistical Package (MVSP) software (Kovach, 1989). Only taxa over 1% of the total were selected for cluster analyses, in order to avoid random noise in paleoecological interpretation (Rull, 1997a; 1998c). Botanical affinities, modern analogs, and vegetational patterns used in the paleoecological and paleoenvironmental interpretation are from Lindeman (1953), Muller (1959), van der Hammen (1963), Germeraad et al. (1968), Wijmstra (1968), Caratini et al. (1973), Murillo and Bless (1974), Anderson and Muller (1975), Gastony and Tryon (1976), Muller (1981), Sheihing and Pfefferkorn (1984), Thanikaimoni et al. (1984), Frederiksen (1985), Lorente (1986), Tomlinson (1986), Muller et al. (1987), Tissot et al. (1988), Thanikaimoni (1987), Westgate and Gee (1990), Roubik and Moreno (1991), Srivastava and Binda (1991), Tryon and Lugardon (1991), Hoorn (1994), Velásquez (1994), Rull (1997b, 1998a, d), Rull and Vegas-Vilarrúbia (1999), and Graham (1999).

Text-Figure 1. Location map showing the approximate distribution of the formations involved, according to the updated version (on-line) of the Venezuelan Stratigraphic Code (www.intevep.pdv.com:80/~ibc03/).
RESULTS AND INTERPRETATION

Palynostratigraphy

The section studied was subdivided into the two Early Miocene palynostratigraphic zones described by Lorente (1986) and Muller et al. (1987) for northern South America (Text-Figure 2). The *Verrutricolporites* zone was recognized between the base of the section and the first occurrence of *Echitricolporites maristellae*, which defines the *Psiladiporites–Echitricolporites* zone, until the top of the sequence. The *Verrutricolporites* zone coincides with the La Rosa Formation, while the *Psiladiporites–Echitricolporites* zone corresponds to the part of the Lower Lagunillas Member considered in this study. Few rare species are restricted to each zone. It is also worth mentioning the occurrence of

Text-Figure 2. Presence/absence distribution chart and palynostratigraphical interpretation, for the La Rosa and Lagunillas formations.
several Paleogene taxa, such as *Spinizonocolpites echinatus*, *Spinizonocolpites baculatus*, *Echitriporites trianguliformis*, *Proxapertites cursus*, *Foveotriporites hammenii*, and *Retidiporites magdalenensis*. They usually show single occurrences in isolated samples, and can be assumed to be reworked from older upstream paleo-outcrops.

**Paleoecology and Paleoenvironments**

Fern and allied spores are generally dominant throughout the whole section (Text-Figure 3). Pollen and fungal spores show lower values, and aquatic elements (freshwater and marine together) are only important in the La Rosa Forma-

![Text-Figure 3](image-url) Percentage diagram for the major groups of palynomorphs.
Text-Figure 4. Percentage diagram of the palynomorphs selected for cluster analysis (>1%).

EARLY MIOCENE

| Palynofloras | Palynofloras
<table>
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<tr>
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<tbody>
<tr>
<td>Verrutricolporites</td>
<td>Verrutricolporites</td>
</tr>
<tr>
<td>Psiladiporites-Echitricolporites</td>
<td>Psiladiporites-Echitricolporites</td>
</tr>
</tbody>
</table>

La Rosa Fm.

SAMPLES

Lagunillas Fm.

Depth (m)

1070 1080 1090 1100 1110 1120 1130 1140

SAND

SHALE

Fungal spores
V. Rull: A quantitative palynological record from the Early Miocene of western Venezuela, with emphasis on mangroves

In the percentage diagram for selected taxa (>1%), a clearer differentiation can be seen than using only presence/absence data (Text-Figure 4). Dominant and less abundant elements show little variations across the section, although *Laevigatosporites vulgaris* is slightly more abundant in the Lagunillas Formation (*Psiladiporites–Echitricolporites* zone). Other elements with intermediate abundance, however, are clearly distinctive. Characteristic of the La Rosa Formation are the mangrove elements, *Psilatricolporites crassus* and *Zonocostites ramonae*, the marine representatives (foraminiferal linings and acritarchs) and the freshwater alga *Botryococcus*, indicating sedimentation in coastal and shallow marine environments, close to mangrove vegetation. *Botryococcus*, although more typical of freshwater environments, can also occur in slightly brackish water, due to its tolerance to salinity (Rull, 1997b). The main elements that characterize the Lower Lagunillas Member of the Lagunillas Formation are fern spores (*Magnastriatites grandiosus, Laevigatosporites catanejensis, Perinomonoletes* sp.), together with *Retitricolporites guianensis* (of unknown affinity), and the freshwater alga *Pediastrum*. This is consistent with the presence of alluvial and coastal plain environments flooded by freshwater.

Cluster analysis provided 3 groups, EM1–3, which were interpreted according to the known botanical affinities of their components and the available modern analog studies (see Table 1 for a summary). Group EM1 is also recognized in the percentage diagram, and is typical of the La Rosa Formation (Text-Figures 5 and 6). From a vegetational point of view, it is considered to be a mangrove assemblage deposited near the mangrove belt or in adjacent shallow brackish water. The lower Lagunillas Member is characterized by group EM2 (Text-Figure 6), which is composed of elements typical of vegetation flooded by fresh or low-salinity water (*Magnatriatites grandiosus, Deltoidospora adriennis, Laevigatosporites catanejensis, Pediastrum*). It also includes other elements with a wide range of environmental conditions, which also present in coastal swamps and marshes (*Monoporites annulatus, Perisyncolporites pokornyi*), and a form-species with unknown botanical affinity and environmental requirements (*Retitricolporites guianensis*). The majority of these components are ferns or herbs, hence, they probably represent herbaceous swamps and marshes behind the mangrove belt. Group EM3 is composed of palms (*Mauritiidites franciscoi, Psilamonocolpites* sp.), ferns (*Verrucatosporites usmensis, Laevigatosporites vulgaris*), and fungal spores, representing another type of coastal swamps (palm/herb swamps) common in the Neotropics. The palm *Mauritiidites franciscoi* typically develops almost monotypical stands (*‘morichales’*) in the freshwater swamps of upper coastal plains and savannas, beyond the limit of tidal influence. Therefore, this assemblage is thought to represent the more inland vegetation recorded in this study.

The succession of these assemblages through time shows a dominant ‘background’ pollen signal from palm/fern–back-mangrove swamps (EM3) with little changes,

![Cluster analysis on the percentages of selected palynomorphs (>1%).](image-url)
and the replacement of mangroves (EM1) by herbaceous back-mangrove swamps (EM2), in the La Rosa–Lagunillas transition. Indeed, during deposition of the La Rosa Formation (*Verrucicocolporites* zone), pollen sedimentation was almost exclusively composed of palm/fern swamp sporomorphs and pollen locally deposited under or in front of the mangrove fringe, with a negligible contribution from herbaceous back-mangrove swamps. During deposition of the Lagunillas Formation (*Psiladiporites–Echitricolporites* zone), although sporomorphs under 1%, with significant correlation.

Text-Figure 6. Percentage diagram showing the quantitative assemblages established, and the sporomorphs under 1%, with significant correlation.

1, 2 *Deltoidospora adriennis* (Potonié & Gelletich 1933) Frederiksen 1983. 3572' (106.4–17.6), 3673' (76.3–25.0).
3, 4 *Foveotriletes ornatus* Regali et al., 1974. 3481' (84.1–1.5).
5, 6 *Magnastritites grandiosus* (Kedves & Solé de Porta) Dueñas 1980. 1963. 3551' (85.0–22.3); 3686' (108.8–2.6); bar = 16 µm for these two specimens.

7, 8 *Laevigatosporites vulgaris* Potonié 1934. 3727' (89.9–3.6), 3623' (81.3–17.3).
9, 10 *Laevigatosporites catanejensis* Muller et al., 1987. 3713' (108.3–8.2), 3673' (94.3–18.8).
11, 12 *Verrucatosporites usemensis* (van der Hammen 1956) Germeraad et al., 1968. 3767' (75.7–5.0).
13, 14 *Perinomonoletes* sp. Krutzsch 1967. 3673' (110.5–7.5), 3760' (112.2–19.9).
morphs from palm/fern swamps continued to be dominant, sporomorphs from herbaceous swamps increased, and the pollen from mangroves was substantially reduced to very few grains, probably transported landward by wind. Therefore, the replacement of mangrove assemblage EM1 (coastal) by assemblage EM2 (continental) across the boundary between the La Rosa and the Lagunillas formations (Text-Figure 6) can be interpreted as a regressive trend, from shallow shelf to back-mangrove environments of deposition.

**TABLE 1.** Pearson product-moment coefficients between the palynomorph assemblages and the taxa below 1%. Significance level ($\alpha$): * 0.05, ** 0.01, *** 0.001.

<table>
<thead>
<tr>
<th></th>
<th>EM1</th>
<th>EM2</th>
<th>EM3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bombacacidites baumfalki</td>
<td>0.1096</td>
<td>-0.1441</td>
<td>-0.1388</td>
</tr>
<tr>
<td>Bombacacidites brevis</td>
<td>0.1923</td>
<td>-0.5312**</td>
<td>0.0998</td>
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<td>Clavamonocolpites lorentei</td>
<td>0.1286</td>
<td>0.0905</td>
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<tr>
<td>Corsinipollenitesocuslus-noctis</td>
<td>0.3186</td>
<td>-0.0051</td>
<td>-0.3785*</td>
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<td>Echitricolporites maristellae</td>
<td>-0.4762**</td>
<td>0.7853***</td>
<td>-0.0028</td>
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<td>Foveotritiletes ornatus</td>
<td>0.0665</td>
<td>-0.0098</td>
<td>-0.1311</td>
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<td>0.1859</td>
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<td>Malvacipollis spinulosa</td>
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<td>Perforotricolpites digitatus</td>
<td>-0.1354</td>
<td>0.3478</td>
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<td>Podocarpidites sp.</td>
<td>0.4691**</td>
<td>-0.3523</td>
<td>-0.4291*</td>
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<td>Proteacidites triangulosus</td>
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<td>0.6771***</td>
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<td>Psilatricolporites operculatus</td>
<td>-0.3077</td>
<td>0.6683***</td>
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<td>Psilatricolporites venezuelanus</td>
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<td>-0.3527</td>
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<td>Retistephanoporites crassianulatus</td>
<td>0.3406</td>
<td>-0.3669*</td>
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<tr>
<td>Retitricolpites simplex</td>
<td>0.3580*</td>
<td>-0.0305</td>
<td>-0.3996*</td>
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<td>Retitricolporites hispidus</td>
<td>0.3617*</td>
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<td>Retitricolporites irregularis</td>
<td>0.5083**</td>
<td>-0.3890*</td>
<td>-0.4308*</td>
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<td>-0.2323</td>
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<tr>
<td>Echitriletes muelleri</td>
<td>0.5745***</td>
<td>-0.1980</td>
<td>-0.5522**</td>
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<tr>
<td>Polypodiaceoisporites sp.</td>
<td>0.1249</td>
<td>-0.0403</td>
<td>-0.2356</td>
</tr>
</tbody>
</table>

**PLATE 2**

2, 3. Podocarpidites sp. Cookson 1947 ex Couper 1953. 3492' (104.2–5.4), 3760' (102.1–1.4).
4, 5. Psilamonocolpites spp. van der Hammen & García de Muriis 1965. 3673' (79.0–14.9), 3755' (104.6–8.4).
7, 8. Echidiporites barbeitoensis Muller et al., 1987. 3673' (11.2–11.2).
10, 11. Psilatricolporites maculosus Regali et al 1974. 3551' (72.8–11.5), 3673' (93.5–20.2).
12, 13. Zonocostites ramonae Germeraad et al., 1968. 3486' (91.6–23.0), 3755' (98.1–3.7), 3589' (92.5–18.0).
15. Psilatricolporites operculatus van der Hammen & Wijmstra 1964. 3673' (89.7–6.3), 3673' (94.3–3.6).
16, 17. Psilatricolporites venezuelanus Lorente 1986. 3551' (98.7–21.0).
18. Perfotricolpites digitatus González 1967. 3572' (98.5–3.9).
Minor taxa

Elements under 1% (called here minor taxa) were also investigated for paleoenvironmental and paleoecological purposes by computing their correlations with the three assemblages found (Rull, 1991). For this analysis, the reworked sporomorphs and the very sparse taxa with only single occurrences in a few samples, such as *Bombacacidites baculatus*, *Bombacacidites bellus*, *Crototricolpites annemariae*, *Echidiporites barbeitoensis*, *Jandufouria seamrogiformis*, *Kuylisporites waterbolki*, *Perfotricolpites digitatus*, *Proxapertites tertiaria*, *Psilatricolporites pachydermatus*, *Retitricolporites maristellae*, *Retitricolporites hispidus*, and *Retitricolporites irregulares* were excluded. Four minor taxa have highly significant correlations (α < 0.01) with the mangrove assemblage (Table 1, Text-Figure 6): *Podocarpidites*, *Psilatricolporites maculosus*, *Retitricolporites irregularis*, and *Echitricolporites muelleri*. The first taxon is the pollen of the gymnosperm tree genus *Podocarpus*, living in highland rain forests of northern South America; its pollen is widely dispersed by wind. The form-species *Proxapertites irregularis* corresponds to *Amanoa* (Euphorbiaceae), a tree from upper delta environments (Germeraad et al., 1968; Lorente, 1986). Little ecological information is available for *Psilatricolporites maculosus* and *Echitricolporites muelleri*, that have been related to the families Sapotaceae and Selaginellaceae respectively, with wide ranges of occurrence (Van der Hammen, 1963; Lorente, 1986). Two other taxa (*Retitricolpites simplex* and *Retitricolporites hispidus*) show lower but still significant correlations (α < 0.05). They are similar to the pollen of inland forest trees of the families Anacardiaceae and Flacourtiaceae respectively (Lorente, 1986; and observations of the author from herbarium material). Rull (1998c) included *Retitricolpites simplex* in an Eocene assemblage representing inland forest communities.

Two taxa show highly significant correlations with the back-mangrove herb swamps component: *Echitricolporites maristellae* and *Psilatricolporites opeculatus*. The first one is a marker species having its first occurrence at the base of *Psilatricolporites–Echitricolporites* zone; therefore, the significant correlation could be due in part to evolutionary and not environmental factors. However, when only the range of occurrence of the species is considered, the correlation is still significant (r = 0.6772, α < 0.001), indicating a real statistical association. The botanical affinity of *Echitricolporites maristellae* is not well established, although it has been related to the Malvaceae or Bombacaceae (Lorente, 1986). The most probable botanical affinity of *Proxapertites opeculatus* is with the palm *Astrocaryum*, from inland and back-mangrove communities (van der Hammen, 1963; Lorente, 1986). None of the taxa considered have a positive significant relationship with the assemblage EM3. However, the negative correlations of some elements are worth mentioning. Almost all the taxa with significant positive correlations with the mangrove assemblage are negatively associated to the assemblage EM3, except for *Retitricolporites hispidus* (Table 1).

**DISCUSSION**

The ‘background’ palynological assemblage from palm/fern swamps is considered to be transported from inland communities, probably upper delta environments, considering that 1) it originated in these environments, 2) the major transport agents for palynomorphs in coastal environments are water currents flowing towards the sea, and 3) the La Rosa and Lagunillas Formations were deposited in more distal environments (mangroves and back-mangroves, respectively). The large amounts of this background signal, however, are surprising. In modern analog studies from northern South America, such quantities are never attained in shelf environments (Rull, 1998a). This can be explained by an increased water-transport capacity, which involves a very humid climate, the existence of a major fluvial system, or both. Current paleogeographic reconstructions support these points. According to Díaz de Gamero (1996), during the Early Miocene, the proto-Orinoco fluvial system drained most of the western part of northern South America and its delta was situated in the northeast Maracaibo basin.
The Early Miocene mangrove communities are represented in this study by the assemblage EM1 of the Verrucitolporites zone (La Rosa Formation), and probably associated minor taxa. The only known mangrove-forming trees present were Rhizophora (Zonocostites ramostellae) and Pelliciera (Psilatricolporites crassus), forming an intermediate association between typical Eocene and post-Eocene mangroves, and representing a transitional phase after the terminal Eocene impoverishment of these communities and their progressive Neogene enrichment (Rull, 1998b; Graham, 1995). None of the minor taxa statistically associated with the mangrove assemblage in the present study has been previously considered a mangrove or mangrove-related element (Graham, 1995). In the case of Podocarpus, the correlation can be explained by wind transport to coastal environments (Muller, 1959). A potential source in the southeast could have been the incipient northern Andes, where uplift was initiated shortly before, during the late Oligocene (Rull, 1997b). Some of the other minor elements also correspond to present montane taxa (Sapotaceae, Alchornea and Anacardiaceae) and have been found in modern mangrove sediments (Rull and Vegas–Vilarrúbia, 1999). Therefore, in the study area, Early Miocene mangroves seem to have been of low diversity. However, more work is needed to establish the botanical affinities of many minor taxa in order to infer a better paleovegetational history.

Compared with modern analog studies, in which the mangrove pollen commonly ranges from 20% to more than 70% (Muller, 1963; van der Hammen, 1963; Tissot et al., 1988), the mangrove signal found in this study is not strong (Text-Figure 4). The same is true for several sites of the region (Root et al., 1998). This probably indicates that the sediments were deposited some distance away from any dense mangrove vegetation, although both marine palynomorphs (Text-Figure 4) and micropaleontological analysis clearly indicated a shallow-water (0–20 m depth) coastal environment of deposition (Echeverría and Ruiz, 1999). Therefore, mangroves were probably reduced and/or were not dense in the region, contrasting with other areas of the same basin and eastern Venezuela, where mangrove pollen is abundant in the Early Miocene (Lorente, 1986). A ‘dilution’ effect due to the background EM3 assemblage is undoubtedly present, but insufficient to explain such low values. A possible explanation for Pelliciera emerges after the consideration of its biogeography. Aside from doubtful records in Europe and Africa (Muller, 1981), Pelliciera is known to be common in Eocene to Miocene records of Central America, northern South America and the Caribbean–Gulf of Mexico region (Text-Figure 7). A dramatic reduction began in the Miocene (Wijmstra, 1968), leading to its present relict distribution. It disappeared from the northern limits of its range beginning in the Miocene (Graham, 1995), but remained as a scarce element in northern South America until the Pleistocene. Therefore, the Early Miocene mangrove communities of the Maracaibo basin were probably affected by the initial reduction.

The relative scarcity of Rhizophora, however, remains to be explained. In the available modern analog studies for the region that include mangroves, similar numbers of this pollen occur only inland, in freshwater environments, most probably due to wind transport (Muller, 1959; ten Broek and Nijssen, 1971). However, inland fluvial paleoenvironments for the La Rosa Formation are unlikely because of the abundance of marine palynomorphs (Text-Figure 4), and the micropaleontological evidence (see above). Low percentages of Rhizophora pollen have been also found within a disturbed mangrove stand surrounded by montane forests (Rull and Vegas–Vilarrúbia, 1999; Rull et al., 1999). These modern pollen assemblages, however, are very different from those found in the present work, because they are dominated by herbaceous pollen (Gramineae, Cyepraceae, Chenopodiaceae) with negligible percentages of marine elements. On the other hand, it is known that Rhizophora can survive in low-saline, even in freshwater, where is not as abundant as in truly brackish and marine ones (Lindeman, 1953; Van der Hammen, 1963). Therefore, the possibility of shallow marine environments of low

**PLATE 4**

| 1 | Retitricolporites guianensis | van der Hammen & Wijmstra 1964. 3623' (86.7–1.9). |
| 2, 3, 4, 5 | Retitricolporites irregularis | van der Hammen & Wijmstra 1964. 3693' (99.3–24.1), 3686' (78.0–10.8). |
| 6, 7, 8 | Striatricolpites catatumbus | González 1967. 3600' (110.2–14.5), 3481' (104.1–17.4). |
| 9 | Ilexpollenites sp. | Thiegart 1937 ex Potomí 1960. 3481' (75.0–19.6). |
| 10, 11 | Echitricolporites maristellae | Muller et al., 1987. 3628' |
| 12 | Psilaperiporites minimus | Regali et al., 1974. 3636' (105.1–20.8). |
| 13, 14 | Perisyncolporites sp. | Germeraad et al., 1968. 3628' (90.4–17.4). |
| 15 | Perisyncolporites pokornyi | Germeraad et al., 1968. 3628' (90.4–17.4). |
| 16 | Malvacipollis spinulosa | Frederiksen 1983. 3673' (77.8–8.4). |
salinity should not be neglected. This could be supported in part by the fact that *Pelliciera* can also live in low-salinity water (Fuchs, 1970; Jiménez, 1984). According to the available paleogeographical reconstructions, shallow brackish-water environments could have existed in the northern Maracaibo basin during the Early Miocene. Saline water would have been provided by the marine connection located at the north of the basin (Hoorn, 1994), whereas freshwater was probably carried by the large proto-Orinoco fluvial system (Díaz de Gamero, 1996).

ACKNOWLEDGMENTS

The author wishes to thank Drs. M. Antonieta Lorente, Francisca Oboh-Ikenobe, and David Pocknall for their comments and suggestions that improved the clarity and quality of the manuscript. Special thanks to the former editor of *Palynology*, David Goodman, for his excellent job during these years.

REFERENCES CITED

ANDERSON, J.A.R., and MULLER, J.

BENNETT, K.D.

CARATINI, C., BLASCO, F., and THANIKAIMONI, G.

CHAPMAN, V.J.

DÍAZ DE GAMERO, M.L.

ECHEVERRÍA, L., and RUIZ, M.
1999 *Estudio micropaleontológico de las formaciones La Rosa y Lagunillas en el noroeste de la cuenca de Maracaibo*. PDVSA Internal report, Caracas.

FREDDERIKSEN, N.O.

FUCHS, H.P.

GASTONY, G.J., and TRYON, R.M.
V. Rull: A quantitative palynological record from the Early Miocene of western Venezuela, with emphasis on mangroves

GERMERAAD, J.H., HOPPING, C.A., and MULLER, J.

GONZÁLEZ DE JUANA, C., ITURRALDE DE AROZENA, J.M., and PICARD, X.
1980 Geología de Venezuela y sus cuencas petrolíferas. FONINVES, Caracas. 1031 pgs.

GOWER, J.C.

GRAHAM, A.

GRAHAM, A.

HOORN, C.

JIMÉNEZ, J.A.
1984 A hypothesis to explain the reduced distribution of the mangrove Pelliciera rhizophorae Tr. & Pl. Biotropica, 16: 304–308.

KOVACH, W.L.

LINDEMAN, J.C.
1953 The vegetation of Suriname. Van Eedenfonds, Amsterdam. 135 pgs.

LORENTE, M.A.

MULLER, J.


MULLER, J., DI GIACOMO, E., and VAN ERVE, A.W.

MURILLO, M.T., and BLESS, M.J.M.

PARES, M., UESUGUI, N., and SANTOS, A.

ROOT, S.A., CURRY, R.P., and RODGERS, B.K.

ROUBIK, D.W., and MORENO, J.E.

RULL, V.


RULL, V., and VEGA-VILARRÚBIA, T.

RULL, V., VEGA-VILARRÚBIA, T., and ESPINOZA DE PERNÍA, N.

SHEIHING, M.H., and PFEFFERKORN, H.W.
SRIVASTAVA, S.K., and BINDA, P.L.

TEN BROEK, A.N.Ch., and NIJSSEN, L.

THANIKAIMONI, G.
1987 Mangrove palynology. *Institut français de Pondichéry, travaux de la section scientifique et technique*, 24: 1–100.

THANIKAIMONI, G., CARATINI, C., VENKATACHALA, B.S., RAMANUJAM, C.G.K., and KAR, R.K.

TISSOT, C., DJUWANSAH, M.R., and MARIUS, C.

TOMLINSON, P.B.

TRYON, A.F., and LUGARDON, B.

VAN DER HAMMEN, T.

VELÁSQUEZ, J.
1994 *Plantas acuáticas vasculares de Venezuela*. Universidad Central de Venezuela, Caracas. 992 pgs.

WESTGATE, J.W., and GEE, C.T.

WIJMSTRA, T.A.

WIJMSTRA, T.A.

WINOGRAD, M.