

Palaeofloristic and palaeovegetational changes across the Paleocene/Eocene boundary in northern South America

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Abstract

A floral change occurring in northern South America at the Paleocene/Eocene boundary is analysed using palynological data. The sequence studied is an outcrop from the Venezuelan Maracaibo basin, deposited in shallow marine to coastal environments without apparent stratigraphic breaks. Significant pollen and spore counts from 237 samples were studied stratigraphically and statistically in order to compare Paleocene and Eocene palaeofloras and palaeoecological trends. The Late Paleocene/Early Eocene transition is the boundary between two floras which differ both qualitatively and quantitatively. However, the change is not sudden but stepped and gradual. Paleocene taxa seem to be of pantropical distribution, whereas Eocene assemblages are more restricted to the Neotropics. The global warming well documented elsewhere is proposed as the major cause for these changes. Trends in sporomorph diversity in this record appear to track changes in temperature documented in isotopic records from temperate regions. The extinct parent plant of *Echitriporites trianguliformis* is tentatively proposed to be intolerant to high temperatures, because of its absence during the Early Eocene warm phase. Palaeoecologically, although marsh and back-mangrove swamps dominated both Late Paleocene and Early Eocene assemblages, their taxonomic compositions were different, especially in the inland marsh forests. Mangrove components are scarce or absent through the whole sequence studied, suggesting the absence of these communities during the time-interval analysed. A palaeoecological subdivision into assemblage zones was not possible; instead, a recurrent pattern suggesting palynological cycles was observed. However, palynocycles could not be studied in detail due to the lack of knowledge of botanical affinities for many of the taxa involved and the apparent absence of mangrove assemblages. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The Late Paleocene/Early Eocene transition (P/E) has been recognised as one of the events of mass extinction occurred during the Cenozoic, on the basis of the high extinction rates of marine benthic organisms from bathyal and abyssal environ-

ments (Tjalsma and Lohman, 1983; Thomas, 1990; Molina, 1995), as well as land plants (Frederiksen, 1994a, 1998). One of the main causes proposed for such extinctions is the climate change documented by oxygen isotope analysis of cores from sea basins. Indeed, sea surface temperatures (SST) increased rapidly during the P/E passage, and attained a maximum, representing the absolute maximum recorded during the Tertiary, in the Early Eocene (Shakleton,

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1986; Miller et al., 1987). Among the proposed mechanisms for this climate change, greenhouse forcing due to higher atmospheric CO₂ concentrations has been proposed (Zachos et al., 1994). Other causes for the extinction such as increased submarine volcanic activity and sea level changes can not be discarded (Molina, 1995).

The impact of this climate shift on the Neotropical flora and vegetation is not known. By comparison with the Quaternary glacial–interglacial model, a similar or higher temperature change on land than in the sea might be assumed. For example, during the Last Glacial Maximum (LGM), the estimated SST for the Caribbean was between 2 and 4°C lower than today (Lin et al., 1997), whereas in northern South America, differences up to 8°C have been estimated for both the Andean high altitudes (Van der Hammen, 1988; Rull and Vegas-Villarúbia, 1996; Rull, 1998a), and the Amazon lowlands (Colinvaux et al., 1997). However, fossil evidence for this assumption is still lacking in the Paleogene. In northern South America, a number of works devoted to the Paleogene has contributed greatly to the development of tropical palynology. Among them, those developed in Brazil (Regali et al., 1974), Colombia (Van der Hammen, 1957, 1964; González, 1967; Van der Hammen and García de Mutis, 1966), Guyana (Van der Hammen and Wijmstra, 1964; Leidelmeyer, 1966; Wijmstra, 1971) and Venezuela (Kuyl et al., 1955; Germeraad et al., 1968; Muller, 1980, 1981; Muller et al., 1987) are worth mentioning. These works are mainly focused on the naming and description of relevant fossil taxa, as well as documenting their ranges through time. Some of them also consider quantitative variations and attempt palaeoenvironmental reconstruction. Although poorly documented, some basic observations can be made about the P/E boundary. Muller et al. (1987) provide a regional summary chart for this period. The P/E boundary is notable for the first occurrence of 14 marker taxa and the last appearance of 5 other. This represents a floral turnover of 50% (a total of 19 taxa pass through the boundary) in the marker taxa, which is lower than in other important boundaries like those of the Cretaceous/Paleocene or the Eocene/Oligocene. According to Van der Hammen (1957), the Paleocene and the Lower Eocene are two of the 10 Tertiary units that represent 2nd order

palynological cycles of 6 million years duration, controlled by climate (temperature). Within this frame, the P/E boundary is the limit between two climatic cycles, characterised by a peak of a group of palm pollen (*Monocolpites*), the drastic reduction (almost disappearance) in the abundance of other palms represented by *Proxapertites*, and the incoming and subsequent increase of ferns (*Psilamonoletes*, *Verrumonoletes*), during the Early Eocene. These cycles coincide approximately with the global 2nd order eustatic cycles Tejas A.2 and A.3 (Rull, 1997a). Colmenares and Terán (1993) reported a change from coastal to fluvial environments in the P/E transition. In addition, Upper Paleocene assemblages were less diverse and dominated by *Proxapertites* (coinciding with Van der Hammen's observations), whereas the Early Eocene was characterised by the absence of dominant types, and a higher sporomorph diversity. Another interesting feature is the appearance of the *Brevitricolpites* group, in the uppermost part of the Upper Paleocene. This genus has been considered the ecological equivalent of the modern mangroves and, therefore, a good indicator of brackish water environments (González, 1967) but, so far, it has been found only in Colombia (Rull, 1998b,d). Concerning mangroves, Paleocene and Early Eocene communities were poor in species. Only four pollen taxa have been related to them: *Deltoidospora adriennis*, *Brevitricolpites*, *Spinizonocolpites* and *Psilatricolporites crassus*, the last one having its first occurrence at the P/E boundary (Graham, 1995).

The purpose of the present paper is to document floral and community changes across the P/E boundary in a western Venezuelan sequence by means of pollen data, and to discuss the possible causes. Late Paleocene and Early Eocene floras are compared using a palaeoecological approach, with special emphasis on the characterisation of coastal (mangrove?) palaeovegetation.

2. Study site and methods

The section studied is a river outcrop called Riecito Maché, situated at the northwestern part of the Maracaibo Basin (Fig. 1). During the Late Paleocene and Early Eocene, this area was situated at the land margin of a coastal environment, with

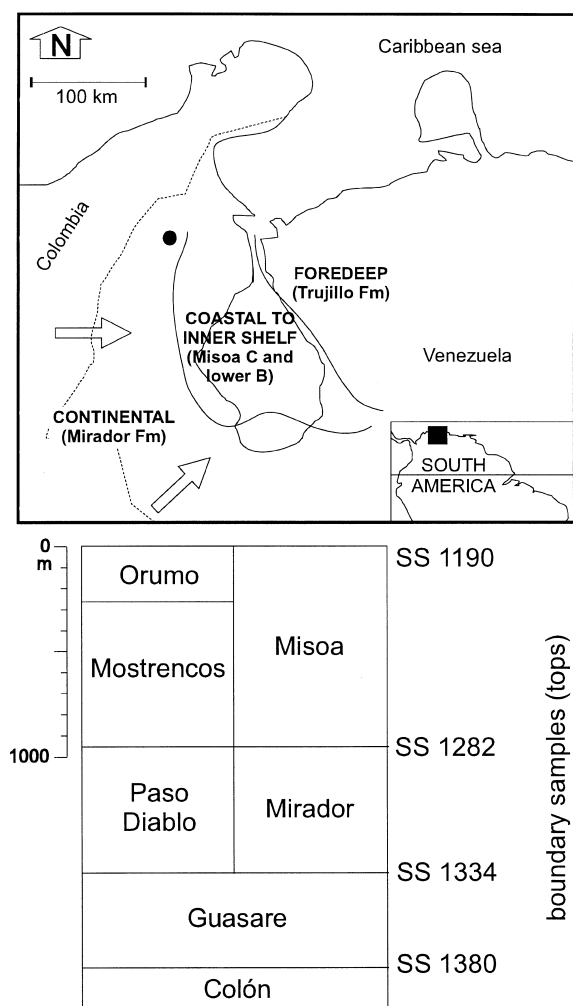


Fig. 1. Location map, palaeogeography and lithostratigraphy of the section studied.

the sediment source at the southwest, and the deeper part of the basin at the northeast. The sediments deposited during the time interval involved in this study constitute a supersequence (T1) up to 4000 m thick, characterised by two phases (Parnaud et al., 1995): an earlier regressive phase represented by the continental Mirador formation at the south and southwest and the turbiditic Trujillo formation at the northeast, and a later transgressive phase in which the transitional (inner shelf to shore) Misoa formation was deposited.

The *Riecito Maché* section embraces the Paso Diablo (= Mirador), and the Mostrencos and Orumo

(= Misoa) formations (Fig. 1). At the base, the Guasare and Colón formations, deposited in marine environments during the former Maastrichtian and Paleocene supersequences K6 and K7 (Parnaud et al., 1995) are present. The sampling was carried out by H.W. Stekhoven at more or less regular intervals of about 8 m average. The present study is concerned with a sequence of 237 samples, which was considered continuous (i.e. without evident hiatuses) in the field recognisance. These samples were analysed palynologically by E. Bradley and A. Ortega, after the usual chemical treatment (HF, HCl, centrifugation in zinc bromide, and mounting in glycerine-jelly). Barren and very poor samples were not included in the present work. Similarly, owing to the main aim of the survey (the Paleocene/Eocene boundary), only samples from Guasare, Mirador and Misoa formations were considered, excluding ten samples taken in the Cretaceous Colón formation.

The sporomorphs selected for the study were those reported in Germeraad et al. (1968) and Muller et al. (1987). Counts were conducted until a minimum of 200 per sample and the saturation of diversity, in order to minimize the confidence intervals for percentages (Rull, 1987). All the identified taxa were used in the range and diversity analysis, but not in palaeoecological analysis, because rare and scarce elements can create random noise in the statistical treatment (Birks, 1986). In order to select the significant components for quantitative analysis, a cut-off of 2% of the total pollen sum was employed (Rull, 1998b), the taxa whose total abundances (including all the samples) are below this value were discarded. Furthermore, marker taxa, whose presence/absence pattern is conditioned more by evolution than by environmental factors, were also excluded, even if they were over 2% of the total pollen sum. Similarly, samples were considered representative if counts are above 70–100 specimens (Germeraad et al., 1968). Percentages were calculated with respect to the total count.

The zonation and chronostratigraphic equivalence of Muller et al. (1987) were used. Plots were produced with RAGWARE (range charts) and PSIMPOLL 2.25 (percentage diagrams), and statistics was performed with MVSP 2.2. Percentages were log-ratio transformed prior to the statistical treatment (Aitchison, 1986). The similarity index of Gower

(1971) and the unweighted centroid agglomerative method were employed in the cluster analysis. Principal components were obtained from the uncentered correlation matrix.

3. Results and interpretation

3.1. Range analysis and diversity

Fig. 2 shows the ranges of the sporomorph taxa for all the representative fossiliferous samples. Three taxon-range pollen zones could be identified: Zone 15 or *Gemmastephanocolpites gemmatus* (Early to Late Paleocene), Zone 16 or *Foveotricolpites perforatus* (Late Paleocene) and Zone 17 or *Rugutricolporites felix* (Early Eocene). The first two zones are characterised in the present study by the range of their marker species, but *Rugutricolporites felix* is only present at the top of Zone 17. The identification of this Zone is based on complementary characteristics such as the absence of *Stephanocolpites costatus* and *Foveotriletes margaritatus*, and the increase of *Retitricolporites irregularis*, *Striatricolpites catatumbus* and *Echistephanoporites alfonsi* (Muller et al., 1987). Lithological and palynostratigraphic boundaries are close, but do not coincide, with an offset between 40 and 120 m (Fig. 2). The Paleocene/Eocene boundary was found in sample SS 1287, at about 975 m below the top of the outcrop. In general, taxa can be informally subdivided into long-ranged (present throughout the interval considered), and characteristic (mainly or only present in either the Paleocene or the Eocene). Only four long-ranging taxa are important: *Proxapertites operculatus*, *Deltoidospora adriennis*, *Psilamonocolpites medius* and *Mauritiidites franciscoi*, extending up to recent times (Lorente, 1986; Muller et al., 1987). Among characteristic Paleocene taxa, the more abundant are *Concavisporites* sp., *Syncolporites lisamae*, *Foveotriletes margaritae*, *Gemmamonocolpites macrogemmatus*, *Longapertites vaneendenburgi*, *Gemmastephanocolpites gemmatus*, *Ctenolophonidites lisamae*, *Retidiporites botulus*, *Bombacidites annae* and *Foveotricolpites foveolatus*, while among those of the Eocene, *Echistephanoporites alfonsi*, *Psilatricolporites crassus*, *Retibrevitriporites triangulatus*, *Retitricolporites ir-*

regularis, *Striatricolpites catatumbus* and *Verrucatosporites speciosus* are worth mentioning. Other taxa are even more restricted (Fig. 2).

In order to analyse with more detail the Paleocene/Eocene passage, an arbitrary sample interval around it was considered, and the taxa which have their FAD (First Appearance Datum) or LAD (Last Appearance Datum) within this region were selected (Fig. 3). It is important to stress that only absolute FADs and LADs were considered, so the absence of Paleocene taxa after their LAD and Eocene ones before their FAD, was checked with classical palynostratigraphical works from the region (Gerreraad et al., 1968; Lorente, 1986; Muller et al., 1987). Thirteen taxa disappeared just before or in the boundary. It is interesting that no taxon was lost shortly after. On the other hand, twenty one taxa appear for the first time slightly before, in the boundary or slightly after. These changes occur in a gradual, somewhat stepped, manner. A single extinction and/or appearance event could not be observed. Considering that the total number of taxa analysed is 60, a floral turnover close to 40% can be estimated, since 26 taxa persisted across the limit.

In general, sporomorph diversity is lower in the Paleocene than in the Eocene (Fig. 4). During the Paleocene, an initial descending trend in diversity stops near the middle of the Mirador formation. Thereafter, a steady increase in diversity transgresses the P/E boundary, and attains a maximum in the lower half of the Lower Eocene. From the mid-Eocene onward, an oscillating trend in diversity is observed until the top of the section analysed. These trends in diversity are controlled by both richness and equitability; however, the first reduction in diversity after its Eocene maximum is apparently driven by loss of taxa, as equitability does not show any decrease (Fig. 4). No particular changes in diversity exist at the P/E boundary, where the increase initiated in the Late Paleocene continues.

3.2. Palaeovegetational analysis

This section deals with the quantitative establishment of palynological associations, and their interpretation in terms of palaeovegetation. Sporomorph assemblages are statistically defined prior to the botanical affinity analysis, in order to maintain ob-

Riecito Maché - general range chart

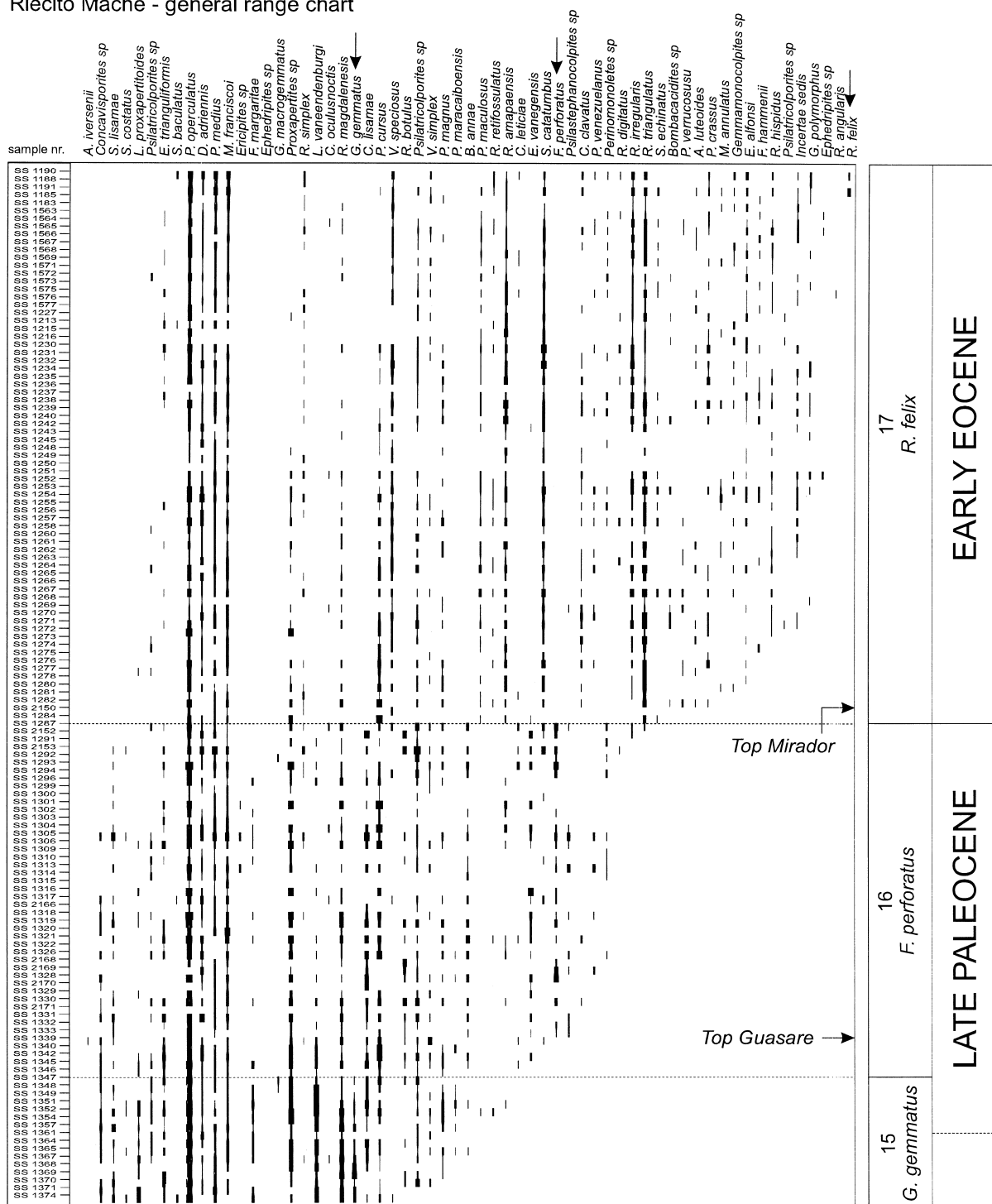


Fig. 2. Range chart, palynological zonation and chronostratigraphy.

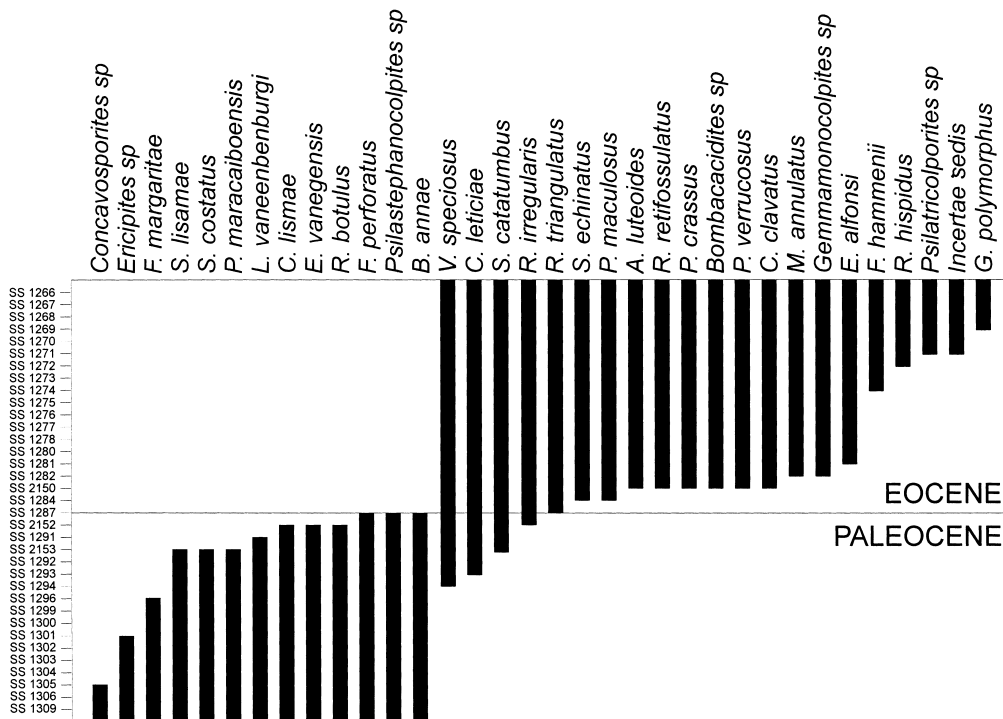


Fig. 3. Detail of the Paleocene/Eocene boundary, showing the taxa which have their FAD or LAD around it.

jectivity (Rull, 1998a,b). Paleocene and Eocene floras are studied separately for comparison purposes.

3.2.1. Paleocene

Twelve Paleocene taxa were found to be significant for quantitative treatment, but two of them were short-ranging markers (*Longapertites vaneemburgii* and *Foveotricolpites perforatus*), and were excluded. The remaining taxa were grouped into three objective assemblages, by means of cluster analysis (Fig. 5). Assemblage P1 is composed by *Proxapertites operculatus* and *Retidiporites magdalenensis*. There is a controversy about the botanical affinity of the first of these form-species. The proposal of Germeraad et al. (1968) of an extinct group of palms related to *Nypa* is not shared by Lorente (1986), who supports the assumption of Van der Hammen (1957), on the possibility that it is derived from another palm: *Astrocaryum*. Since *Nypa* is a mangrove palm and *Astrocaryum* grows in more continental environments, the results can be very different depending on who is right, but a definite answer is not avail-

able (Frederiksen, 1985). In a former analysis similar to the present, on Paleogene sediments, Rull (1992, 1997a) considered this pollen to have originated in continental environments, because it was not statistically associated with mangrove and coastal marsh components. The botanical affinity of *Retidiporites magdalenensis* is also uncertain (Thanikaimoni et al., 1984), although some superficial resemblance with *Banksia* and *Dryandra* (Proteaceae) has been suggested (Germeraad et al., 1968). The greatest morphological similarity found by the author in the literature is with *Bromelia* and *Aechmea* (Bromeliaceae) as depicted in Hallbritter (1992) and Erdtman (1972), respectively. A bromeliad affinity can not be discarded. Therefore, assemblage P1 is tentatively interpreted as an undefined continental association.

Assemblage P2 contains *Ctenolophonidites lisamae*, the modern equivalent of *Ctenolophon* (Ctenolophonaceae), a genus that was extinct in South America in the Eocene. Two living congeners, *Ctenolophon englerianus* and *Ctenolophon parvifolius*, are endemic to the tropical freshwater swamp

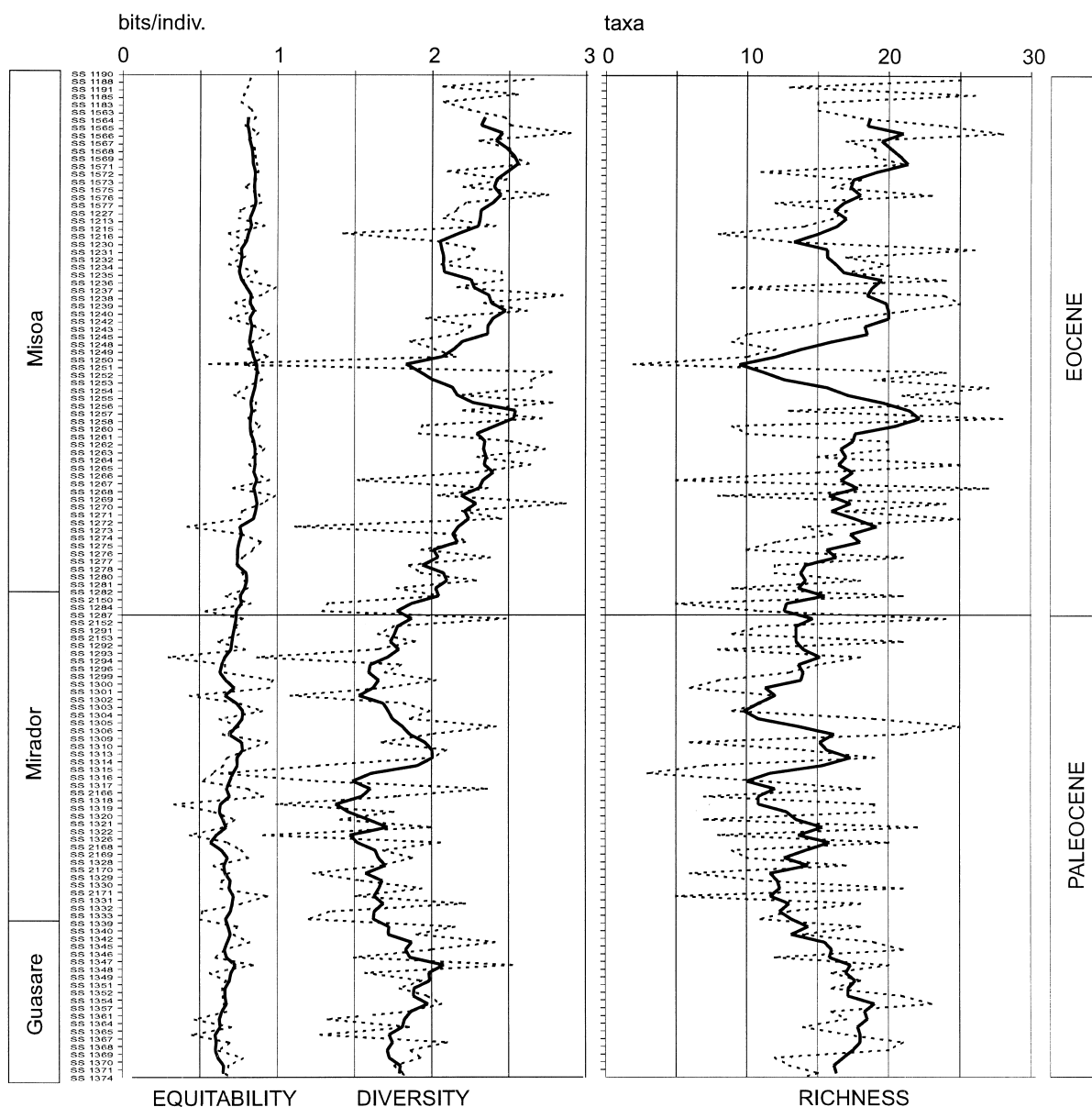


Fig. 4. Diversity (H , Shannon–Weaver index), equitability (H/H_{\max}), and richness (number of taxa) trends. Dotted lines = actual values; solid lines = 6-step smoothing.

forests of West Africa (Thanikaimoni et al., 1984; Van der Ham, 1989), suggesting that *Ctenolophondites lisamae* may have been a freshwater species. The extinct form-species *Echitriporites trianguliformis* is also controversial. Although some similarity with Proteaceae has been mentioned (Germeraad et al., 1968), *Echitriporites trianguliformis* has no

clear modern equivalents. Based on the pattern of occurrence in the sedimentary record, a coastal habitat has been proposed for its ancestral plant (Frederiksen, 1985), but recent studies do not support this hypothesis and favor a continental environment (Rull, 1998b). Finally, *Proxapertites cursus* and *Proxapertites* sp. are very similar in morphology (they are

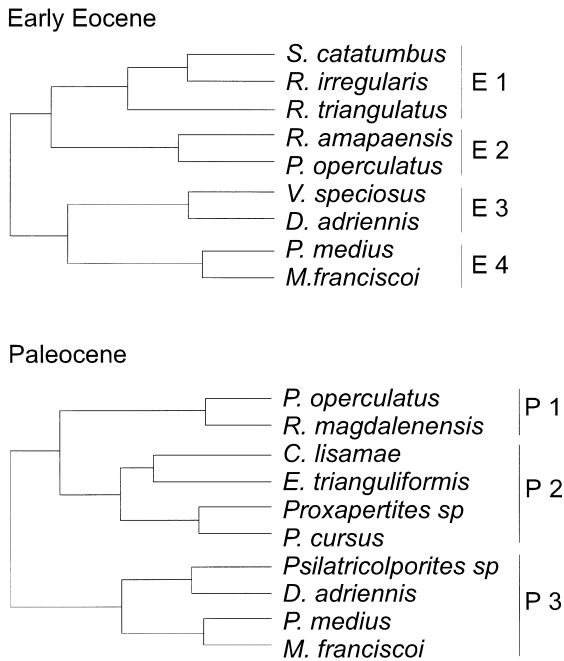


Fig. 5. Results of cluster analysis.

different only in the size of their reticula, larger in the former) and can be treated together. From a botanical and palaeoecological point of view, these taxa are considered very similar to *Proxapertites operculatus* (Germeraad et al., 1968; Lorente, 1986). The composition of assemblage P2 is consistent with a continental environment, that was forested and probably flooded by freshwater.

The third assemblage (P3) has already been described (except for the unnamed *Psilatricolporites* sp.) from the Paleogene and Neogene of western Venezuela (Rull, 1992, 1997a,b), and represents the transition between coastal plains and alluvial plains. The presence of *Deltoidospora adriennis*, representing the modern mangrove fern *Achrostichum* (Tomlinson, 1986), may indicate a tidal influence, but the occurrence of *Mauritiidites franciscoi*, related to the living *Mauritia*, which can not tolerate salinity (Rull, 1998c), suggests that flooding waters are mostly fresh. This is not incompatible with the presence of *Acrostichum*, since it grows well in inland terrains flooded by freshwaters (Velásquez, 1994).

Despite many attempts, including the quantitative methods provided by PSIMPOLL (Bennett, 1996), a

subdivision of the diagram into a few useful assemblage zones was not possible (Fig. 6). As a general trend, the dominance of assemblage P1 throughout the sequence is worth mentioning, mainly due to *P. operculatus*, but no particular assemblage dominates any part of the sequence enough to be characterised by this fact.

3.2.2. Early Eocene

Among the Eocene taxa, eleven were over 2% of total abundance, but two were not used because their absence in the upper half of the Lower Eocene is due to their real LAD; these are *Proxapertites cursus* and *Proxapertites sp.* The other nine components were grouped into four assemblages (Fig. 5). In assemblage E1, two elements are related to wetland forests. Indeed, *Striatricolpites catatumbus* has been associated to *Crudia* (Fabaceae), a tree that grows in river banks and freshwater swamps, while *Retitricolporites irregularis* is related to *Amanoa* (Euphorbiaceae), from similar environments (Germeraad et al., 1968; Lorente, 1986). No modern affinity is known for *Retibrevitricolpites triangulatus*, which was extinct at the Eocene/Oligocene boundary (Muller et al., 1987), but in the Middle Eocene, it is statistically associated with a continental assemblage dominated by *Echitriporites trianguliformis* (Rull, 1998b). Therefore, assemblage E1 likely represents inland marshy forests. Assemblage E2 resembles the Paleocene assemblage P1 because of the dominance of *Proxapertites operculatus*. Since the botanical affinity of *Retitricolpites amapaensis* is not known (Lorente, 1986), the same environment (i.e. undefined continental) is assumed for E2. Finally, assemblages E3 and E4 are equivalent to P3 if they are considered together, but they are separated in this cluster. This separation is meaningful, because the ancestral parent plants of *Verrucatosporites* and *Deltoidospora* (E3) were more salinity tolerant and occupy a more distal position, reaching the mangrove itself (Van der Hammen, 1963; Ellison, 1989). In contrast, the combination of *Psilamonocolpites medius* and *Mauritiidites franciscoi* represent back-mangrove palm swamps flooded with slightly brackish or fresh waters (Muller, 1959; Tissot et al., 1988; Rull, 1998c). As in the Paleocene, a zonation of the percentage diagram was not achieved (Fig. 7).

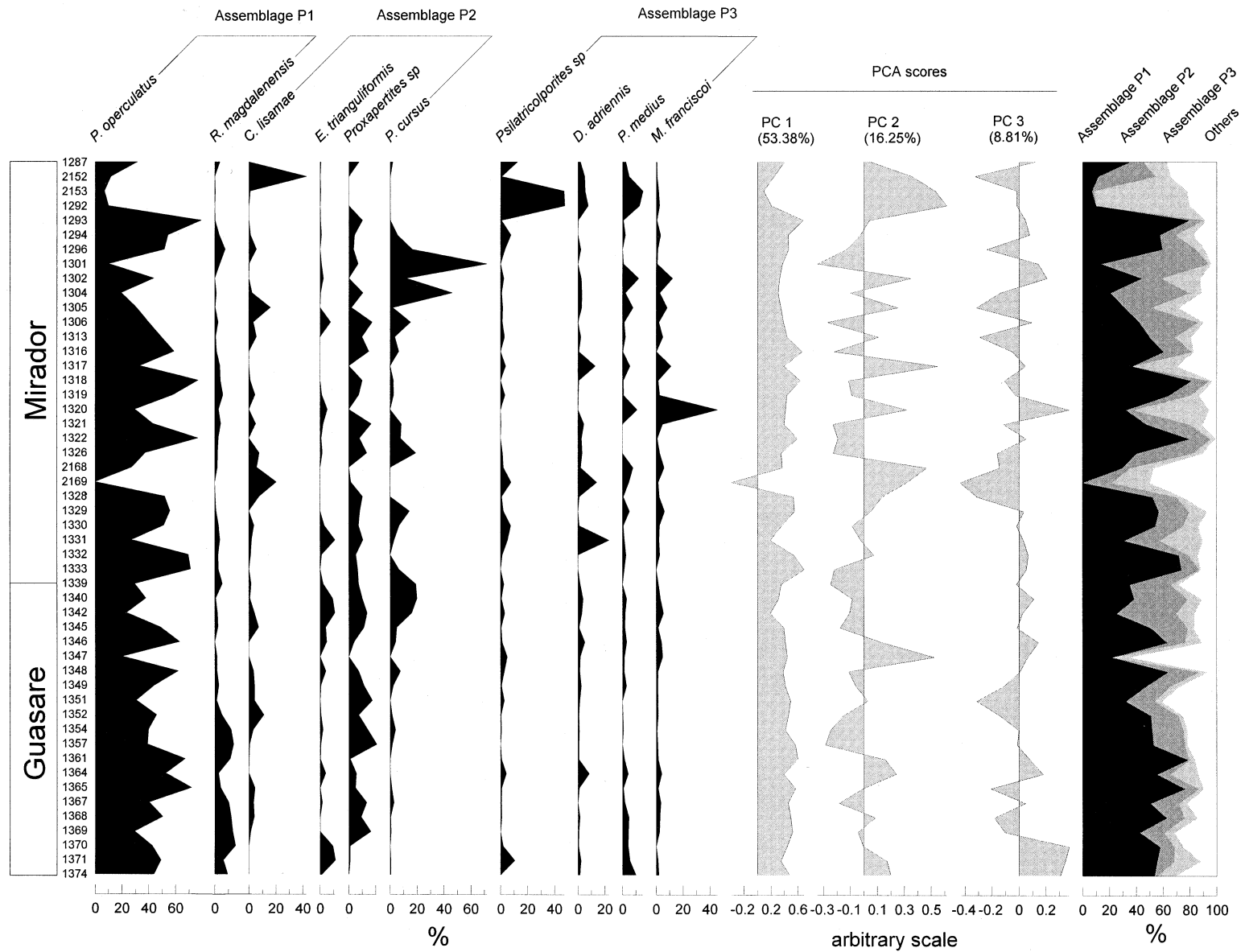


Fig. 6. Percentage diagram of the significant Paleocene taxa arranged according to the associations and cumulative percentage of the assemblages.

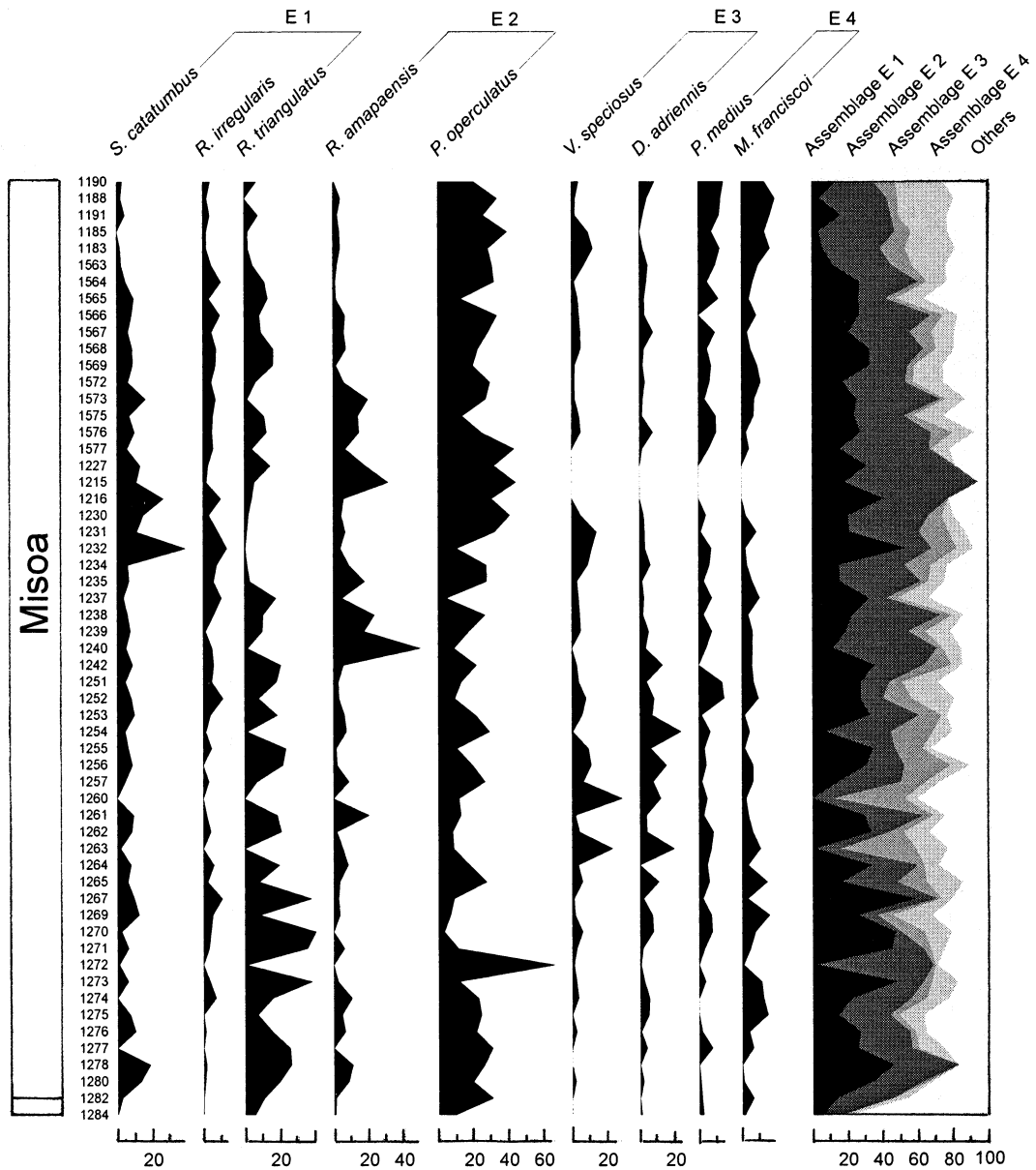


Fig. 7. Percentage diagram of the significant Eocene taxa arranged according to the associations and cumulative percentage of the assemblages.

4. Conclusions and discussion

According to the results of the present work, Late Paleocene and Early Eocene floras differed both qualitatively and quantitatively. A conspicuous ecological change took place at the Paleocene/Eocene

boundary. Among the major floral components, only four long-ranging taxa remained unchanged, whereas two characteristic Paleocene and Early Eocene floras can be differentiated on the basis of no less than sixteen restricted taxa, considering only the most abundant ones. The characteristic Paleocene flora is

almost identical to that of nearby Neotropical regions (Van der Hammen and García de Mutis, 1966; Leidelmeier, 1966; Regali et al., 1974), and very similar to the low-latitude Asian assemblages (Frederiksen, 1994b), showing its Pantropical character. Contrasting this, the Lower Eocene flora is geographically more differentiated, owing to a higher proportion of restricted elements, caused by both the regional extinction of Paleocene taxa and the incoming of new components. These changes may result from the closure of the Tethys seaway progressively isolating the eastern and western hemispheres. Despite its magnitude, the change across the P/E boundary, however, was not sudden, but gradual (possibly stepped). On the one hand, LADs and FADs of the restricted elements occurred in a progressive way, and on the other hand, diversity shows a continuous increase that crosses the boundary. A stepped pattern has been also found in temperate areas of North America, and related to the asynchrony between different extinction and immigration events, controlled by warming (Wing, 1998). Within the Tertiary, the floral change that occurred at the P/E boundary seems to be slightly lower than that of the Eocene/Oligocene boundary, where the floral turnover is of about 50% and marks a break point between the very different Eocene and post-Eocene floras (Rull, 1997b, 1998d). Concerning the causes of the P/E floristic change, its gradual shape is not compatible with a sudden mass extinction, and the well-documented general warming seems the most reasonable explanation. In this sense, it is interesting that diversity roughly follows a similar trend as global temperature estimates and increases across the P/E boundary attaining a maximum in the Early Eocene (Fig. 4). However, diversity and temperature are not always directly related. Indeed, Wing (1998) reports that, in the Late Paleocene, richness (based on plant macrofossil data) decreases with estimated temperatures increase, whereas during the Early Eocene, these parameters follow the same ascending trends. Furthermore, Frederiksen (1995) shows that, in southeastern North America, the diversity maximum may have lagged 8 m.y. behind peak temperature. Contrarily, in Western Europe, taxa impoverishment preceded the global Early Eocene maximum temperature event. Frederiksen (1995) suggested that palaeogeography determined different extinction and migratory responses to changing

climate. In Europe, floral interchange was limited, and local extinction favoured, due to land fragmentation and the existence of sea barriers; whereas in North America, the large terrestrial landmass was suitable for east–west migrations. Therefore, other factors related to the palaeogeography must be considered. Interestingly, *Echitriporites trianguliformis* appears to locally have extinct as climate warmed (Fig. 2), suggesting that this form-species does not tolerate high temperatures. Indeed, it diminishes at the P/E boundary (coinciding with the temperature increase), disappears at the beginning of the Early Eocene, reappears thereafter, and attain its maximum values in the Middle Eocene, when the temperature was lower again (Zachos et al., 1994). These comparisons, however, are made using isotope curves from other areas. In order to have more conclusive evidence, in situ isotope studies are needed.

From a palaeovegetational point of view, two similar assemblages, representing undefined continental communities (P1–E2) and back-mangrove swamps (P3–E3/E4), were present in both the Paleocene and Early Eocene; whereas one is exclusively Paleocene (P2) and the other occurs only in the Early Eocene (E1), both representing inland marshy forests. Attempts to determine useful assemblage zones did not succeed. Instead, several palynocycles could be defined, suggesting a cyclic forcing mechanism controlling vegetational changes. Compared with other Paleogene assemblages, the statistical association among *Psilamonocolpites medius*, *Mauritiidites franciscoi*, *Deltoidospora adriennis* and *Verrucatosporites* (back-mangrove swamps) has been previously documented in other localities from the same basin (Rull, 1992, 1997a,b, 1998b), in the Paleocene and Middle Eocene. However, *Mauritiidites* sometimes falls in other, more inland, associations. The fact is noteworthy that none of the associations found in this study represents mangroves. The more common and abundant Eocene mangrove taxa, *Psilatricolporites crassus* and *Spinizonocolpites echinatus*, are present in the Early Eocene (Fig. 2), but in very low numbers, as compared with the middle Eocene (Rull, 1998b). Their numbers are not enough to be included in the statistical analysis. In the Paleocene, only *Spinizonocolpites baculatus* occurs, but in very few samples and in negligible quantities. The placement of the sediments studied on inland

environments is unlikely, since it is well known that the Guasare formation is a shallow marine accumulation, and the Misoa formation is a deltaic deposit (González de Juana et al., 1980), two environments where the pollen of mangroves is always present, even abundant (Muller, 1959). Therefore, mangrove communities were almost absent during the Paleocene and Early Eocene, in the site studied. If palaeoenvironments are not responsible for this fact, evolution and/or climate are possibly the cause. The FAD of *Psilatricolporites crassus* is at the P/E boundary and, therefore, the only known mangrove taxon of the Paleocene is *Spinizonocolpites baculatus* [according to Graham (1995), *Deltoidospora adriennis* is also a mangrove taxon, but it occurs mostly in the inner belt, and disturbed sites (Tomlinson, 1986)], but it is very scarce. Therefore, the absence of mangroves in the Paleocene could be largely due to evolutionary causes. On the other hand, mangroves need a tropical, humid climate to develop (Chapman, 1976); hence, the existence of dry conditions could be an alternative or complementary explanation. Whatever the cause, if we combine the results of the present study with those of Rull (1998b), the first regular record of mangrove vegetation (although poorly developed) in western Venezuela is at the P/E boundary, and its full development was not attained until the middle Eocene.

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