

Ecostratigraphic Study of Paleocene and Early Eocene Palynological Cyclicality in Northern South America

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A quantitative palynological study of the Paleocene/Eocene transition in western Venezuela was undertaken to detect and analyze possible cyclic patterns. Two different methodologies were used, palynocycles and ecologs, and their results are compared. A total of 237 outcrop samples from three formations deposited in continental to coastal environments were analyzed for pollen and fern spores.

Several palynological cycles are recorded and correlated with third-order global eustatic cycles. A high-frequency cyclicality of ca. 220,000-year period also was found. Both methodologies recorded the same cyclic patterns and can be considered complementary. Ecologs are easier to use, but have less interpretative potential. Palynocycles are more complex, but also more descriptive and help detect small hiatuses. Diversity values reach maxima at cycle boundaries and their minima in the middle of cycles. This distribution has been interpreted in terms of different palynomorph sources under conditions of high and low sea level. During the Paleocene/Eocene transition, diversity shows a constant ascending trend, probably due to a long-term, worldwide climatic warming.

INTRODUCTION

Various temporal cycles in pollen assemblages have been detected in northern South America. The cyclic nature of the palynological record was first recognized by Van der Hammen (1957) in Colombia. Palynological cycles were evidenced by recurrent peaks in the abundance of palm pollen (*Monocolpites medius* group) that correlate with low-temperature phases. Within this framework, the Tertiary represented a single, first-order cycle of ~60 million years (my), embracing several second-order (6 my duration) cycles, of which the Paleocene and the lower Eocene were the first two representatives. In turn, each of these second-order cycles were subdivided into three cycles of 2 my duration (third-order cycles). According to Van der Hammen (1961), the cause for palynological cycles were temperature and sea-level oscillations produced by variations in the incoming solar radiation.

Poumot (1989) introduced the concept of palynocycles, connected to eustatic oscillations, for the African and Asian tropics. According to him, eustatic and climatic cycles are associated closely 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 lowermost 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 incipient prograding sandy deposits. Later, during maximum transgression, an increase of mangrove pollen occurs, owing to a combination of high sea-level stability and wetter climates. The beginning of the regressive phase is characterized by pollen from back-mangrove open forests growing under cooler climates. Finally, close to lowest sea-level stand, a phase of dominance by pollen of herbs or *Casuarina* (in South East Asia) indicates reduction of the mangrove fringe and its replacement by these communities. The palynocycle is closed by the return of the fern-spore phase. Poumot (1989) showed a good fit between palynocycles and the eustatic cycles of Haq et al. (1987) for the Neogene. In Venezuela, the same methodology allowed recognition of middle Eocene to Miocene palynocycles (Rull and Poumot, 1997; Rull, 1998). No attempts were made for the Paleocene and early Eocene.

More recently, Rull (1997a) used a paleovegetational approach based on the construction of ecologs. An ecolog is a time or depth curve based on quantitative data (usually frequencies) from fossil assemblages that reflects, in some way, the paleoecology of the ecosystems involved (Reyment, 1980). Two examples of ecologs are the tidal limit index (TLI) and the salinity index (SI). The TLI is defined as the ratio between the scores of two components from a principal components analysis (PCA) representing, respectively, coastal and inland vegetation zones; whereas, the SI is an additional tool that consists of the numerical relationship between marine palynomorphs (mainly dinoflagellate cysts and foram linings) and freshwater algal remains (*Pediastrum*, *Botryococcus*; Rull, 1992, 1997b). In this way, higher TLI and SI values represent inland displacements of the ecological belts resulting from marine transgressions, while lower values indicate the recolonization of the most seaward coastal terrains, related to low sea levels. The cycles obtained with this methodology for the Paleocene correlate well with global eustatic cycles (Rull, 1997a); no studies are available for the Eocene.

In a recent survey on the Paleocene/Eocene boundary in western Venezuela, a noticeable short-term variability in the abundance of palynological assemblages prevented the establishment of a useful palynostratigraphic zonation despite several attempts using quantitative methods (Rull, in press). Consequently, the author proposed that the palynological assemblages showed a cyclic behavior, but no further analyses were done at that time. The purpose of the present paper is to analyze in detail the same Paleocene/Eocene section to test this cyclic hypothesis. Additionally, a methodological comparison is made between palynocycles and the TLI ecolog. This question is not

about the usefulness of terrestrial sporomorphs to define cyclicity, which has been already treated elsewhere (Poumot, 1989; Rull 1997a; Poumot and Suc, 1994; Rull and Poumot, 1997), but on the evaluation of two different—both conceptually and mathematically—methodological approaches using sporomorph assemblages. In the case of Poumot's palynocycles, the assemblages are made solely on the basis of the botanical affinities of the fossil taxa and their assumed living representatives, whereas the TLI is derived primarily from objective statistical associations among fossil taxa. Botanical affinities are considered later to determine the ecological meaning of each statistical assemblage (Rull, 1998). On the other hand, palynocycles are simply sums and ecologs are the output of a more complex processes including multivariate analysis and logarithmic ratios; therefore, the variables resulting from one of these methods are not linear combinations of those obtained in the other. Hence, they are mathematically independent. Finally, palynocycles and ecologs are not computed using the same fossil taxa as variables. Indeed, palynocycles use any fossil with known botanical affinity, without considering their relative abundance. Ecologs, on the other hand, are built from quantitatively-significant taxa, independently of their botanical affinity (see methods).

Possible causes for the cyclicity also are considered, and an analysis of the relationships between cyclicity and diversity is presented.

STUDY SITE AND METHODS

The section studied is a river outcrop called Riecito Maché, situated in the northwestern part of the Maracaibo Basin (Fig. 1). During the Late Paleocene and early Eocene, this area was situated in a coastal environment with the sediment source to the southwest and the deeper part of the basin to the northeast (González de Juana et al., 1980). The sediments deposited during this time interval constitute a supersequence (T1) up to 4000 m thick, characterized by two phases (Parnaud et al., 1995): an earlier regressive phase represented by the continental Mirador Trujillo Formation at the south and southwest and the turbiditic Trujillo Formation to the northeast; and a later transgressive phase in which the transitional (inner shelf to shore) Misoa Formation was deposited.

The Riecito Maché is a composite section embracing the Paso Diablo (= Marcelina) and the Mostrencos and Orumo (= Misoa) formations (Fig. 1). At the base, the Guasare and Colón formations, deposited in marine environments during the Paleocene and Maastichtian, respectively, correspond to supersequences K6 and K7 (Parnaud et al., 1995). 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 from a part of the section of about 2,000 m thickness, containing the Misoa, Marcelina and Guasare formations. This sequence is considered to be continuous, based on the detailed (unpublished) field description of H. W. Stekhoven, who studied and sampled several outcrops along the river, in order to compile a complete sequence. All the samples were analyzed palynologically, following the usual chemical treatment (HF, HCl, centrifugation in zinc bromide, and mounting in glycerin-jelly). Barren samples

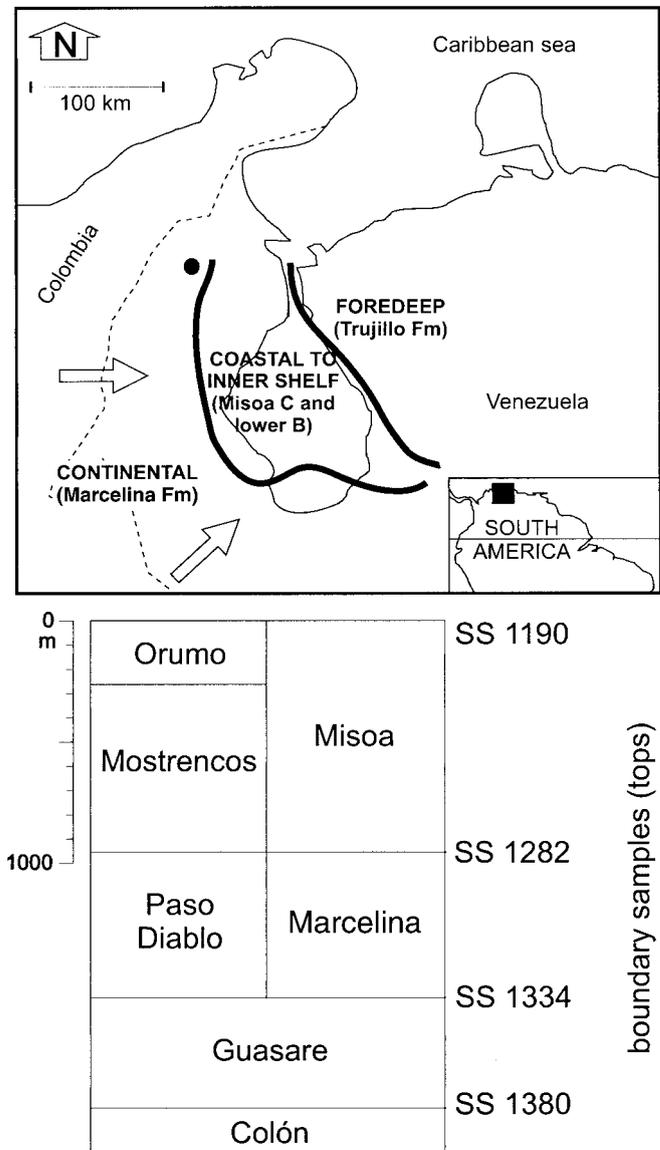


FIGURE 1—Location map, palaeogeography, and lithostratigraphy of the section studied. The sampling site is indicated by a black circle. Arrows show the main direction of sediment supply; paleoenvironmental boundaries are indicated by thick lines. In the lithostratigraphic column, the old local formational name (invalid) are placed at the left column; the accepted formal name occurs in the right column. Top samples for each formation are located at the right side (SS 1190 to SS 1380).

and others with poor recovery were not included in the range and paleoecological study, which are based on 138 samples (1 each ~14.5 m).

Although all the sporomorphs present were considered in the pollen sum, only those reported in Germeraad et al. (1968) and Muller et al. (1987) were initially selected for the range and diversity analysis (selection 1). A second selection was done for the paleoecological study in order to choose only the significant elements for statistical analysis. In this case, a cut-off of 2% abundance was employed (Rull, 1998); taxa with total abundance (including all the samples) below this value were discarded. Similarly, sam-

Riecito Maché - general range chart

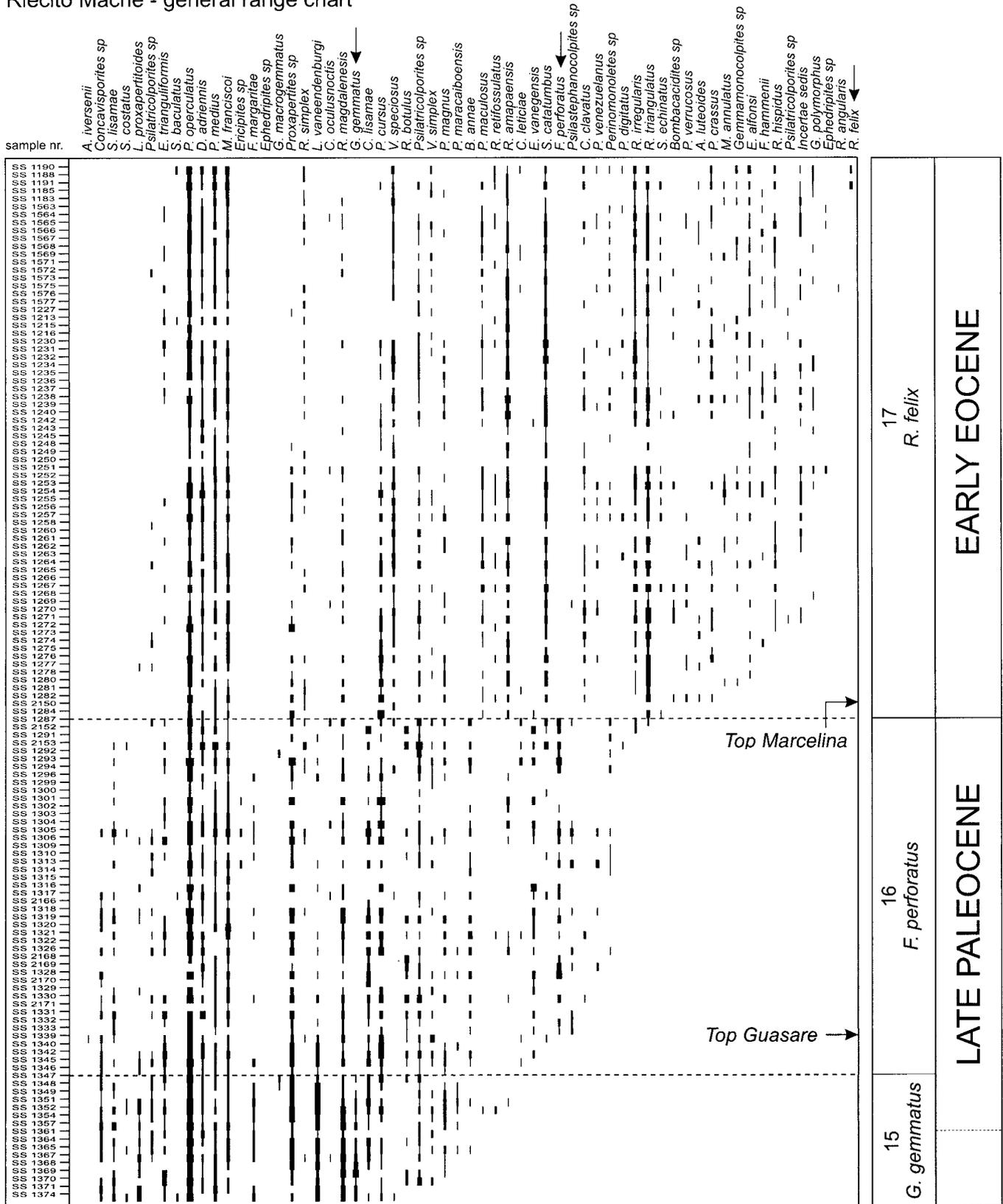


FIGURE 2—Range chart, palynological zones, and chronostratigraphy of the studied section, according to the zonation of Muller et al. (1987). Vertical arrows indicate the main chronostratigraphical markers. The corresponding formational tops are also noted. Samples correspond to the original field nomenclature, and are not to scale.

Riecito Maché. Selected taxa (>2%)

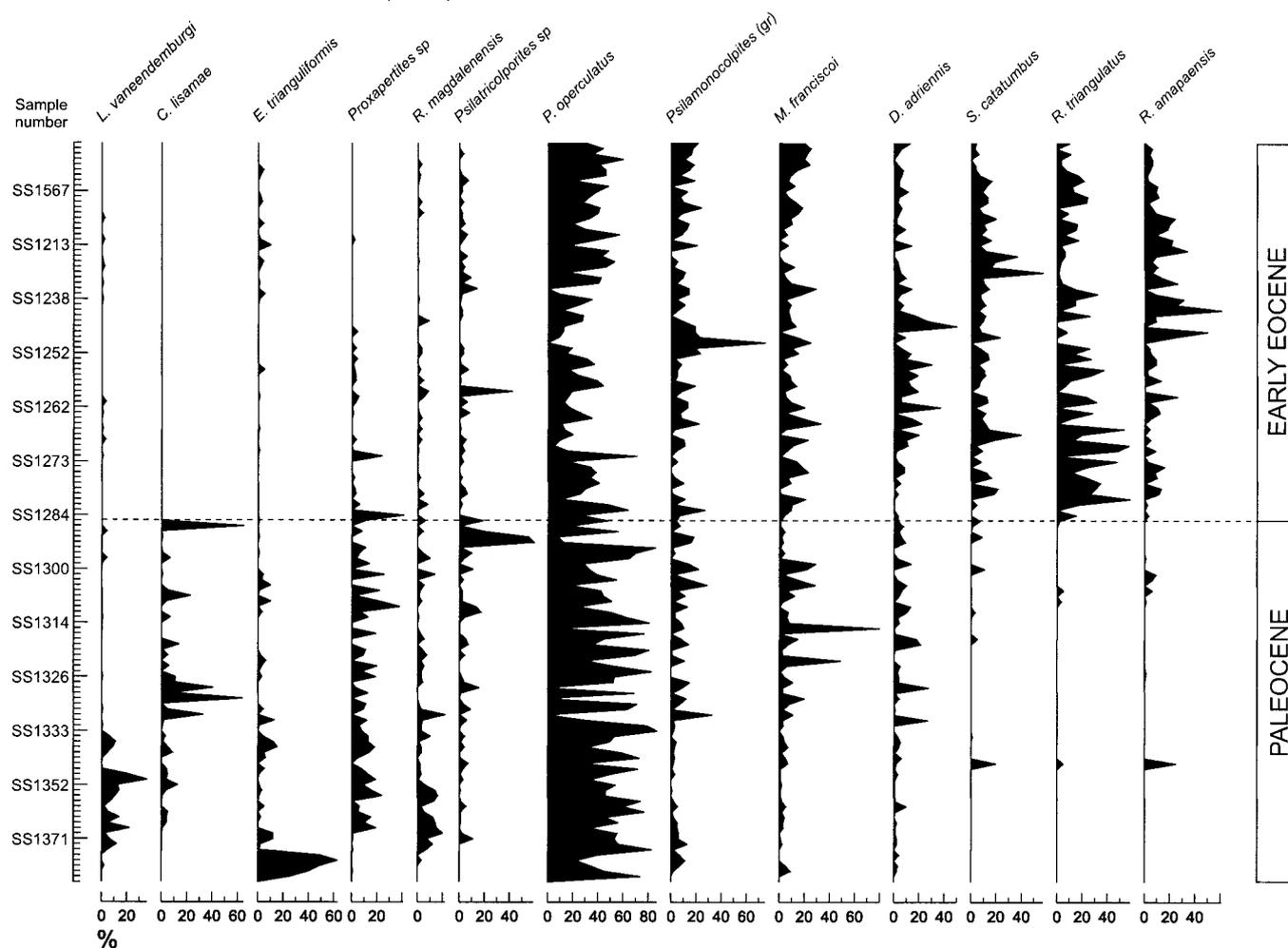


FIGURE 3—Percentage diagram of taxa of selection 2 (all which are above 2% of the total counts) used in the paleoecological analysis (see methods). Only some indicative samples are labelled (see Fig. 2 for the complete data set).

ples were considered representative if the pollen sum was over 200 (Rull, 1987), and the counts of taxa from the first selection were above 70–100 specimens (Germeraad et al., 1968). Percentages were calculated with respect to the total pollen sum. Statistical analyses were performed with Σ SIMSTAT and MVSP. The diversity was analyzed using the Shannon-Weaver index (H'), which considers both taxa richness (number of taxa) and equitability (the evenness with which the grains are distributed among these taxa). Thus, a hypothetical sample in which all the grains belong to the same taxon has no diversity, while one in which every individual belongs to a different type has the maximum diversity. On the other hand, given two completely even samples, the one with the larger number of types has the greater diversity. Similarly, if two samples have the same number of types, the more even is also the more diverse (Pielou, 1966, 1975). The equitability is the ratio between the diversity measured in a given assemblage (H') and the maximum H' possible with the same richness; that is, if all the taxa have the same relative abundance. By definition, this ranges from 0 to 1.

RESULTS AND INTERPRETATION

The raw data used in this analysis are presented in Figures 2 and 3. Figure 2 shows the stratigraphic ranges of taxa from selection 1, and Figure 3 displays the percentages of taxa from the second selection. A floristic and vegetational change across the Paleocene/Eocene boundary is evident. This change is analyzed by Rull (1999) wherein details about palynological zonation, chronostratigraphy, and smoothing are presented.

To search for possible palynocycles in the sense of Poumot (1989), pollen and spores were arranged in ecological groups proposed by this author, considering the botanical affinities of sporomorphs selected (Table 1, Appendix 1). A constraint for the application of this methodology is the unknown affinity of around 60% of the taxa involved. This, in part, explains the scarcity of mangrove and herb groups (Fig. 4). However, the Poumot method was attempted because the counts of known taxa in each sample were always a significant percentage of the total (70% on average). A group of 'unknown affinity' was added because of

TABLE 1—Composition of ecological groups of Poumot, considering the botanical affinities of sporomorphs from selection 1 (Fig. 2).

Spores	Palms	Mangroves	Forests	Herbs	Unknown
<i>V. speciosus</i>	<i>Psilamonocolpites</i>		<i>Bombacacidites</i>		
<i>D. adriennis</i>	<i>Proxapertites</i>		<i>R. simplex</i>		
<i>F. margaritatus</i>	<i>Longapertites</i>	<i>P. crassus</i>	<i>R. irregularis</i>		
<i>Concavisporites</i>	<i>M. franciscoi</i>	<i>Spinizonocolpites</i>	<i>R. hispidus</i>		
			<i>P. maculosus</i>	<i>C. oculusnoctis</i>	
			<i>S. catatumbusa</i>	<i>Ephedripites</i>	<i>E. trianguliformis</i>
			<i>B. annae</i>	<i>M. annulatus</i>	<i>B. triangulatus</i>

its numerical and probable paleoecological importance. This group is dominated by *Echitriporites trianguliformis*, an extinct taxon of unknown botanical affinity, and considered an important component in the establishment of palynocycles for the Paleogene of northern South America (Rull, 1998).

A megapalynocycle is suggested (Fig. 4) in which the initial spore phase is missing (situated probably earlier in the Paleocene), its end being located in the lower Eocene. A second megapalynocycle starts in the lower Eocene, but it is represented only by the spore phase and probably a small part of the palm phase. The first megapalynocycle can be subdivided into 7 palynocycles, of which the first three (1 to 3) are Paleocene and well-defined. However, in palynocycle 2, two palm peaks may reflect the presence of more than one palynocycle. In the Paleocene/Eocene transition, four palynocycles (4 to 7) are identified, but lack the initial spores stage. Finally, palynocycles 8 to 10 correspond to the second megapalynocycle in the lower Eocene. A further subdivision into high-frequency cycles is still

possible using non-smoothed raw data (Fig. 5). A good example following this procedure is shown for palynocycle 10 (lower Eocene), which comprises at least four minor cycles (A to D). Some isolated peaks may indicate the occurrence of a greater number of cycles which could become more evident with increased sampling.

To obtain the ecolog used in the present study, the tidal limit index (TLI; Rull, 1997a) was determined from Principal Components Analysis on the uncentered covariance matrix obtained from pollen percentages. The first three components embrace more than 80% of the total variance (Table 2). Component loadings show a strong influence of *Proxapertites operculatus* on component 1. In conjunction with the affinity of this taxon with the palm *Astrocaryum* (Van der Hammen, 1963; Lorente, 1986), component 1 is interpreted as a continental factor (Rull, 1992). Component 2 is related positively to taxa better represented in the Eocene section (e.g., *Retibrevitricolpites triangulatus*, *Striatricolpites catatumbus*, and *Retitricolporites amapaensis*) and negatively to others that are more abundant in the Paleocene (*Proxapertites* sp., *Ctenolophonidites lisamae*, *Longapertites vaneendemburgi*, and *Retidiporites magdalenensis*). Component 2 reflects the floral change that occurred during the Paleocene/Eocene transition (Fig. 6). Although taxa restricted either to the Eocene or the Paleocene previously were removed from the analysis, differences in abundance of some elements still cause chronostratigraphic 'noise' in the paleoenvironmental interpretation. As a consequence, component 2 was not considered in the construction of the TLI ecolog. Finally, component 3 is associated almost exclusively with back-mangrove palms (represented by *Psilamonocolpites* spp. and *Mautitiidites franciscoi*) and ferns (*Deltoidospora adriennis*). This association has been found commonly in the Tertiary of Venezuela, and is considered representative of the wetlands behind the mangroves near the limit of tidal influence (Rull, 1992, 1997a, b, 1998). However, some of its constituents (*D. adriennis* and *Psilamonocolpites*) can be transported to near shore environments, as has been shown by modern analogue studies (Muller, 1959). As a result of the interpretation of this PCA analysis, component 3 was used as the coastal factor. The resulting curve (Fig. 7) shows eight TLI cycles (A to H), with four corresponding to the Paleocene and four within the Lower Eocene section. Minor peaks of the non-smoothed curve probably reflect TLI cycles of shorter duration.

In order to search for possible regularity in the TLI cyclicity, autocorrelation analysis was conducted. Correlations were found to be significant only for the shortest lags, with a noticeable maximum in the lag 3 (Fig. 8);

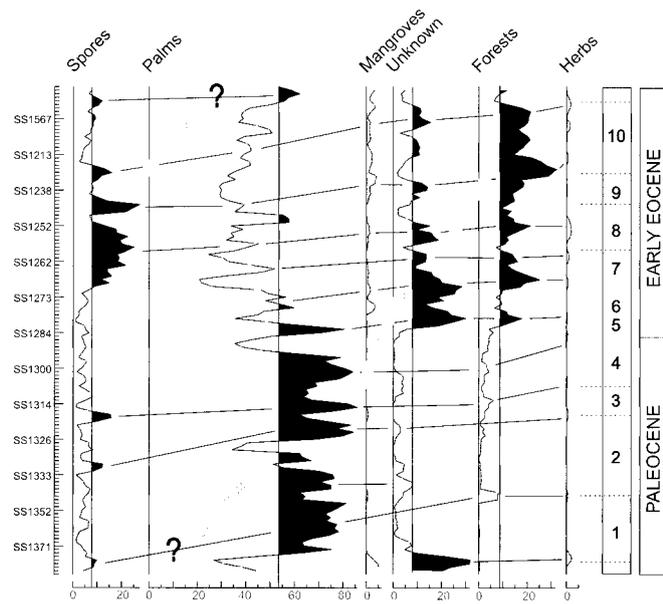


FIGURE 4—Poumot diagram showing the megapalynocycles and the interpreted palynocycles, following 6-point polynomial smoothing. Black areas represent values above the mean (under visual resolution in herbs). Palynocycle trends are represented by solid lines, and megapalynocycles by grey bars. Question marks indicate that the cycle should continue, but there is no evidence within the analyzed data set. Palynocycles are labelled from 1 to 10. Only some indicative samples are labelled (see Fig. 2).

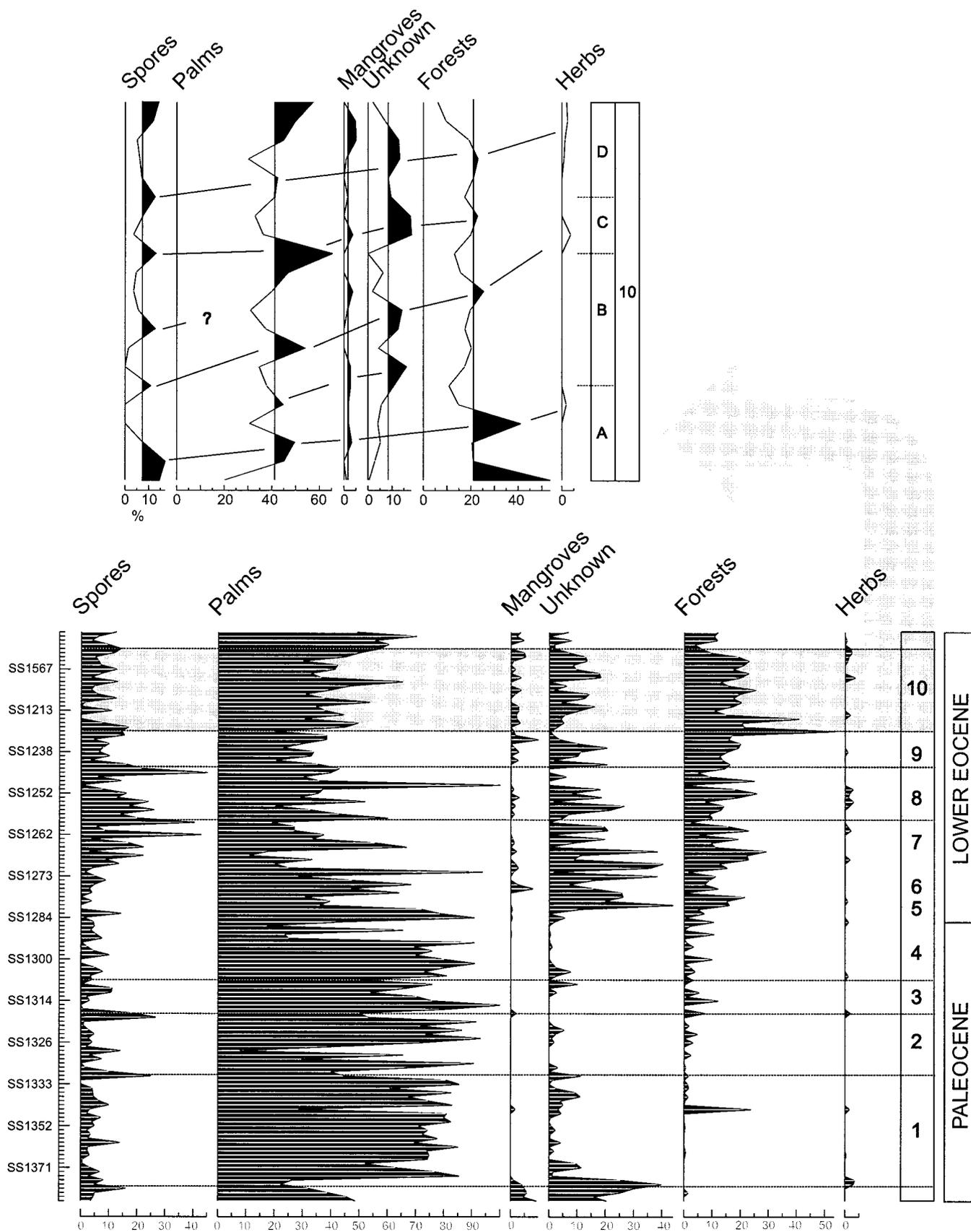


FIGURE 5—Non-smoothed Poumot diagram showing the decomposition of one palynocycle (in grey) into minor cycles (upper diagram). In the upper diagram, black areas indicate values above the mean (under visual resolution in the herbs), and solid lines represent the trends of palynocycles. Only some indicative samples are labelled (see Fig. 2).

TABLE 2—Component loadings and cumulative variance of the first three principal components.

Taxa	Component 1	Component 2	Component 3
<i>S. catatumbus</i>	0.240	0.417	-0.207
<i>C. lisamae</i>	0.081	-0.248	0.106
<i>R. triangulatus</i>	0.241	0.435	-0.347
<i>E. trianguliformis</i>	0.117	-0.191	0.048
<i>Psilatricolporites</i> sp	0.176	-0.040	-0.008
<i>R. amapaensis</i>	0.215	0.351	-0.303
<i>Proxapertites</i> sp	0.175	-0.411	-0.307
<i>P. operculatus</i>	0.643	-0.305	-0.219
<i>R. magdalenensis</i>	0.148	-0.266	-0.124
<i>Psilamonocolpites</i> (gr)	0.334	0.097	0.547
<i>M. franciscoi</i>	0.352	0.103	0.425
<i>L. vaneendemburgi</i>	0.078	-0.230	-0.136
<i>D. adriennis</i>	0.282	0.092	0.274
Cumulative var. (%)	67.18	78.97	84.25

hence, only these very short cycles can be considered to have a regular duration. They coincide with the minor palynocycles and TLI cycles found using non-smoothed data (Figs. 5 and 7).

CORRELATIONS AND DISCUSSION

The correlation between palynocycles and TLI cycles found after smoothing is shown in Figure 9. The cycles co-

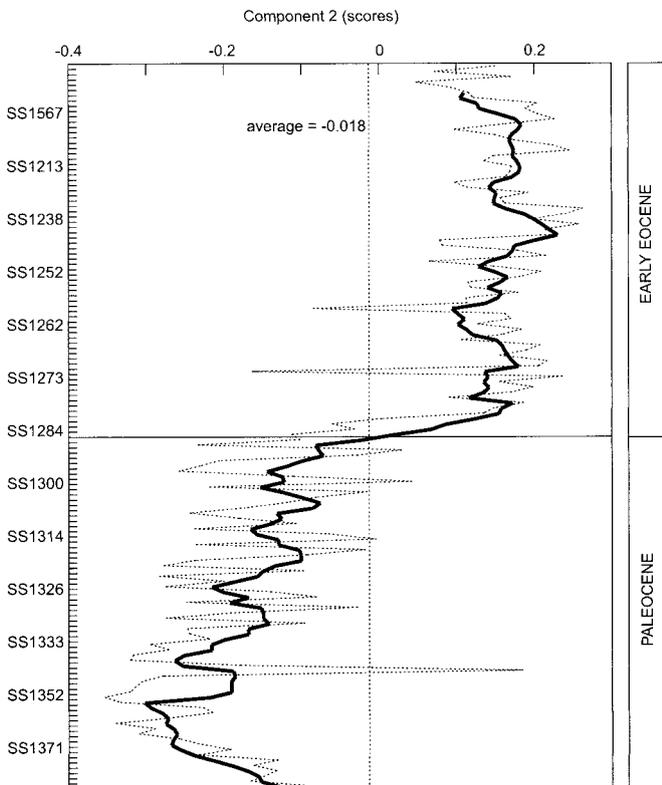


FIGURE 6—Scores of the second component from the PCA. The dotted line represents the raw data and the solid line depicts the 6-point polynomial smoothing. Only some indicative samples are labelled (see Fig. 2) set.

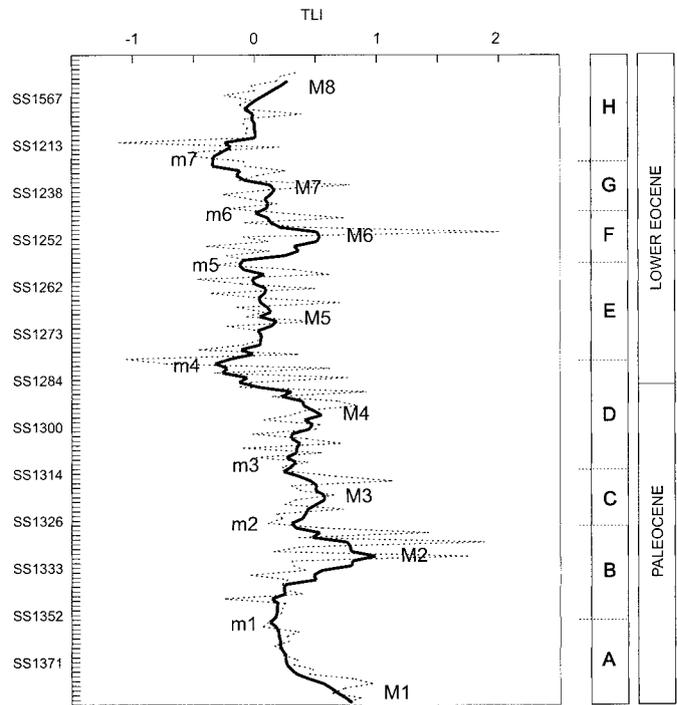


FIGURE 7—Tidal limit index (TLI) curve, calculated according to Rull (1992, 1997a), and inferred cycles (labelled from A to H). Dotted line shows the raw data and solid line depicts the 6-point polynomial smoothing. M—Maxima, m—minima. Only some indicative samples are labelled (see Fig. 2).

incide satisfactorily, except for the central region (the Paleocene/Eocene transition) in which four undefined palynocycles and two TLI cycles tentatively are identified. The correlation between them is not clear, but it is possible that palynocycles 4 to 7 are of lower order than D and E. There are also small out-of-phase relationships in the correlation of Paleocene palynocycles 2–3 and B–C. Greater correspondence between palynocycles and TLI cycles was found in the Eocene. At least 8 palynological cycles could be defined by a combination of both methodologies, suggesting that both palynocycles and TLI cycles are expressions of the same cyclicity. However, the interpretation in terms of paleovegetational changes is slightly different. Indeed, the TLI curve only records the recurrent alternation of two ecological belts—the more coastal and the more

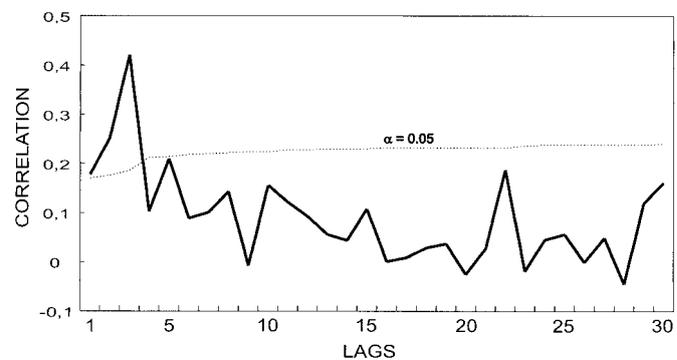


FIGURE 8—Autocorrelation diagram on the non-smoothed tidal limit index (see Fig. 7).

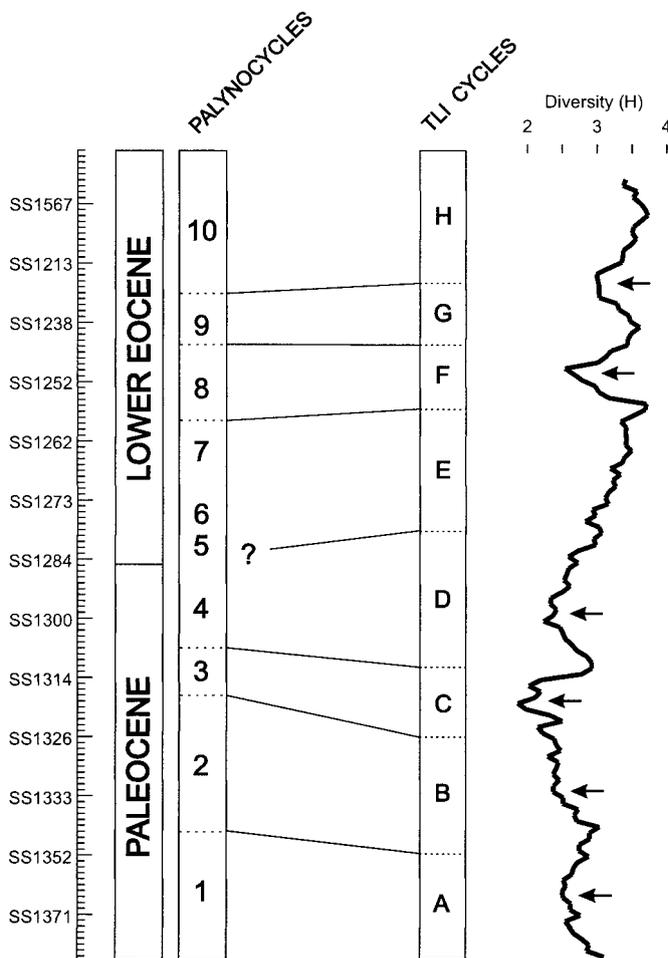


FIGURE 9—Correlation between palynocycles and TLI cycles, and comparison with diversity trends represented by the Shannon-Weaver index (Rull, in press). Diversity in bits/indiv; arrows indicate diversity minima. Only some indicative samples are labelled (see Fig. 2).

continental one—while the palynocycles describe the entire vegetational sequence involved in the eustatic oscillations. This makes the palynocycle methodology more complex because of the need for a greater knowledge of the botanical affinities of fossil taxa, as well as the response of different ecosystems to transgressions and regressions. For example, in the present study it is suspected that mangrove and herb representatives could not be fully defined (see above). Furthermore, the paleoecological expertise of the palynologist is a key factor in this methodology. However, its potential is high, because it can detect more subtle small-scale events as, for example, ecological successions and small hiatuses (Poumot, 1989; Poumot & Suc, 1994). The TLI method, in contrast, is easier to perform, but does not have the same interpretative power in terms of vegetational succession. As a consequence, although both are based on terrestrial vegetation, these methods seem to be complementary in their utilization.

The identified palynological cycles tentatively can be correlated with others found previously, and also with global eustatic cycles, using the age of the palynological zones involved. The base of the section studied is Late Paleocene or slightly older (Fig. 2). Hence, the four Paleocene

cycles could correspond to those found by Rull (1997a) using the same ecolog method, and may correlate with the four third-order global eustatic cycles reported by Haq et al. (1987) for the Late Paleocene (TA1.3 to TA2.3, 60 to 54.2 my BP). Similarly, the Early Eocene palynological cycles can be correlated with the first 4 of the 7 global Early Eocene cycles, which are also of the third order (TA2.4 to TA2.7, 54.2 to 50.5 my BP). The minor palynological cycles recorded in the non-smoothed curves (Figs. 5 and 7) possibly could correspond to fourth-order eustatic cycles (Poumot, 1989; Rull and Poumot, 1997). Based on the delimited cycles and the chronology of Haq et al. (1987), a duration of approximately 10 my (see above) can be estimated for the section. On the other hand, a maximum duration for the interval can be obtained by assuming that all palynological zones (Fig. 2) are present. According to the chronostratigraphic correlation of Lorente et al. (1997), this results in a maximum duration of about 12 my. Considering the 3-lag regularity, this time would embrace 46 minor cycles averaging about 220,000 to 260,000 years duration. The first value is more credible because, most probably, not all identified pollen zones are complete. According to Schwartzacher (1993), cycles of periods longer than 100,000 years are found in stratigraphic records where the cyclicity is caused by eccentricity; i.e., the changes in the elliptical shape of the Earth's orbit. Therefore, astronomically-induced climate changes (Milankovitch cyclicity) should be considered as one of the possible controlling factors for the high-frequency cyclicity found in the present work. However, other type of cyclical forcing factors would be involved, because of the differences between Milankovitch and the recognized periodicities circumscribed here in. Further research is necessary to demonstrate these or other relationships.

It is interesting to analyze the diversity trends within this cyclical frame. A regular pattern consisting of a diversity minima is present near the middle of each palynological cycle (when sea level is high) in the Paleocene (Fig. 9). During the Paleocene/Eocene transition, there is an increasing trend. In the Early Eocene, two minima are recorded again, the first one at the middle of a cycle, and the second in the boundary between two cycles. Diversity peaks always are located at the base of the cycles or near the boundaries (corresponding to low sea level), except for the last one which is in the middle of cycle H (or 10). On the other hand, diversity is correlated with the continental component 1 ($r = 0.750$, $\alpha < 0.001$), but not with the coastal component 3 ($r = -0.152$, $\alpha > 0.05$). Furthermore, richness is positively correlated with component 1 ($r = 0.519$, $\alpha < 0.001$) and negatively correlated with component 3 ($r = -0.419$, $\alpha < 0.001$). This indicates that the continental component is related to higher diversities controlled by richness which, in turn, is inversely related to the coastal component. A possible explanation may be found in the different sedimentary patterns in low and high sea-level. According to Poumot (1989), changes in sea level determine not only lateral, but also topographical variations. Indeed, during low sea-level phases, most or all of the shelf is exposed, and the space for the occurrence of the distal-most mangrove belt (which requires shallow and quiet saline or brackish waters, protected from the wave influence) is notably reduced or absent. Furthermore, a lowering in the base level of rivers occurs, and their transport

capacity is increased, thus favoring the costal sedimentation of a greater variety of sporomorphs (which increase richness), originating from most of the ecosystems present in the catchment area. Conversely, during a high sea level phase, an increase in shelf space is available for mangroves and other coastal biocoenoses, which form more extensive communities. This, together with the diminished transport energy, due to both the smoothed river gradients and the flatness of the shelf depositional sites (inner and middle shelf, mainly), favor the dominance of autochthonous sporomorph assemblages in coastal areas, the components of which represent mainly the adjacent plant communities.

This assumption is supported by the results of Hoorn (1997) from the recent Amazon fan. Here, the sediments corresponding to the phase of low sea-level were deposited during the Last Glacial Maximum, around 18–20 ka before present. Within these deposits are a mixture of Andean, tropical lowland, and reworked Cretaceous and Tertiary palynomorphs. These assemblages are characterized by larger quantities of fern and allied spores, corroded taxa, and fungal spores, due to the higher amount of erosion resulting from the lowering of fluvial base level. On the contrary, interglacial sediments—corresponding to high sea levels—have a low continental content (low sporomorph richness) and are dominated by autochthonous and marine representatives.

However, richness is not always responsible for the diversity oscillations. Overall, diversity is equally affected by both richness ($r = 0.671$, $\alpha < 0.001$) and equitability ($r = 0.642$, $\alpha < 0.001$). Therefore, both floral turnover and variations in the relative frequencies of taxa influence changes in diversity over this interval. A more detailed analysis (Fig. 10) shows that some diversity minima are due to a decrease in equitability (e.g., the first and last ones in the Paleocene), while others are a consequence of low richness (e.g., the two intermediate ones of the Paleocene, and the first one in the Eocene). Still others are caused by both factors (e.g., the last one in the Eocene). A possible explanation of decreasing diversity due to low equitability is that, although richness is the same or higher, one or a few assemblage components are dominant and many are rare. This is compatible with the former assumption that there is more autochthonous contribution during high sea level, because coastal communities commonly are dominated by few species adapted to live in high and fluctuating salinities, as is the case of mangrove-forming trees.

These analyses indicate that the increasing diversity trend across the Paleocene/Eocene boundary is anomalous because it does not fit with third- and fourth-order cyclicity. It is influenced by both richness and equitability (Fig. 10), suggesting a continued increase in the number of species and a decrease in dominance. A major climatic shift is known worldwide across the P/E boundary. Sea-surface temperatures (SST) increased and attained a maximum in the early Eocene, representing the absolute maximum recorded during the Tertiary (Shackleton, 1986; Miller et al., 1987). Therefore, it is possible that the influence of long-term climate trends on ecosystem diversity was more intense and obscured the effect of sea-level oscillations.

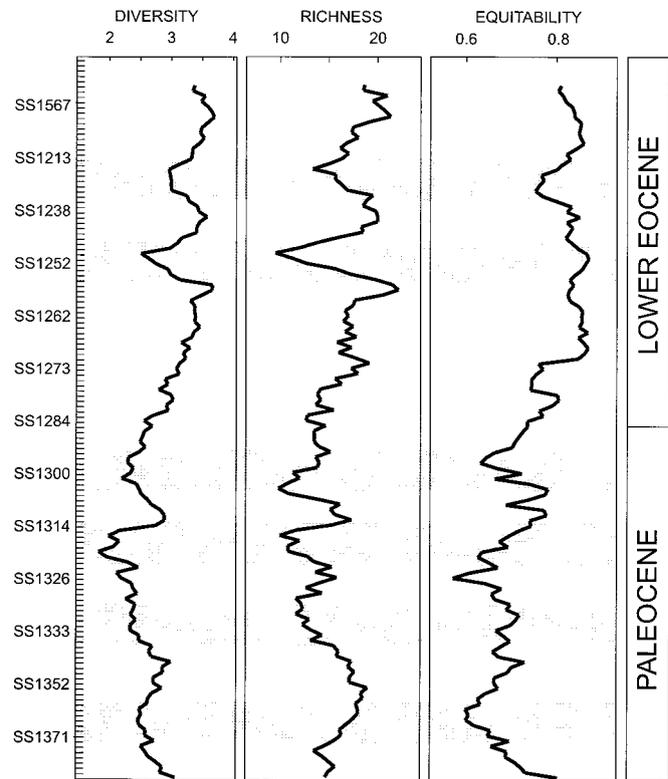


FIGURE 10—Diversity, richness, and equitability curves. Diversity is in bits/individ.; richness is in number of taxa, and equitability is the proportion of the maximum possible diversity for a given richness (see methods for details). The shaded areas correspond to the diversity minima, and occur in the middle of palynological cycles. Only some indicative samples are labelled (see Fig. 2).

CONCLUSIONS

Palynological cyclicity in a Late Paleocene/Early Eocene sequence from western Venezuela is described using of palynocycles and ecologs. At least 8 palynological cycles have been delimited and correlated with third-order global eustatic cycles. A high-frequency cyclicity with a period of ca. 220,000–260,000 year has been detected and related to recurrent climatic changes, possibly related to Milankovitch cyclicity (eccentricity), in combination with other unknown forcing mechanisms. Evaluation of the results from both methods result in the same patterns. Ecologs are easier to use and interpret, but have less interpretative potential. Palynocycles are more complex, but reveal all the phases of the cycles, including small hiatuses. These two methodologies can be considered complementary. Diversity values show their maxima in the cycle boundaries, and their minima in the middle of the cycles. This pattern may be linked to different palynomorph sources during the two extreme sea-level positions. When sea level is low, the rivers have more transport capacity and gather palynomorphs from the ecosystems of the catchment area. In contrast, during the high-sea level phases, pollen and spores come mainly from the adjacent coastal ecosystems, usually dominated by a few salt-tolerant taxa. In the Paleocene/Eocene transition, diversity shows a constant ascending trend which does not correlate with cyclicity. This

is probably due to the superimposition of long-term global climatic warming.

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REFERENCES

- FREDERIKSEN, N.O., 1985, Review of early Tertiary sporomorph palaeoecology: American Association of Stratigraphic Palynologists Contributions Series, no. 15, p. 1–92.
- GERMERAAD, J.H., HOPPING, C.A., and MULLER, J., 1968, Palynology of Tertiary sediments from tropical areas: Review of Palaeobotany and Palynology, v. 6, p. 189–348.
- GONZÁLEZ DE JUANA, C., ITURRALDE, J.M., and PICARD, X., 1980, Geología de Venezuela y de sus cuencas petrolíferas (vols. I, II): FONINVEST, Caracas, 1031 p.
- HAQ, B.U., HANDERBOL, J., and VAIL, R.P., 1987, Chronology of fluctuating sea levels since the Triassic: *Science*, v. 235, p. 1156–1167.
- HOORN, C., 1997, Palynology of the Pleistocene glacial/interglacial cycles of the Amazon fan (holes 940A, 944A, and 946A): in FLOOD, R.D., PIPER, D.J.W., KLAUS, A., and PETERSON, L.C., eds., Proceedings of the Ocean Drilling Program, Scientific Results, v. 155, p. 397–409.
- LORENTE, M.A., 1986, Palynology and palynofacies of the upper Tertiary in Venezuela: *Dissertationes Botanicae*, v. 99, p. 1–222.
- LORENTE, M.A., RULL, V., RUIZ, M., DURÁN, I., TRUSKOWSKI, I., and DI GIACOMO, E., 1997, Nuevos aportes para la datación de los principales eventos tectónicos y unidades litoestratigráficas de la cuenca de Maracaibo, Venezuela occidental: *Boletín de Geología*, v. XVIII, no. 31, p. 33–50.
- MILLER, K.G., FAIRBANKS, R.G., and MOUNTAIN, G.S., 1987, Tertiary oxygen isotope synthesis, sea-level history/continental margin erosion: *Paleoceanography*, v. 2, p. 1–19.
- MULLER, J., 1959, Palynology of recent Orinoco delta and shelf sediments: *Micropalaeontology*, v. 5, p. 1–32.
- MULLER, J., DI GIACOMO, E., and VAN ERVE, A.W., 1987, A palynological zonation for the Cretaceous, Tertiary, and Quaternary of Northern South America: American Association of Stratigraphic Palynologists Contributions Series, v. 19, p. 7–76.
- PARNAUD, F., GOU, Y., PASCUAL, J.-C., CAPELLO, M.A., TRUSKOWSKI, I., and PASSALACQUA, H., 1995, Stratigraphic synthesis of western Venezuela: American Association of Petroleum Geologists Memoir, no. 62, p. 681–698.
- PIELOU, E.C., 1966, Species-diversity and pattern-diversity in the study of ecological diversity: *Journal of Theoretical Biology*, v. 10, p. 370–383.
- PIELOU, E.C., 1975, *Ecological diversity*: J. Wiley & Sons, Inc., New York, 165 p.
- POUMOT, C., 1989, Palynological evidence for eustatic events in the tropical Neogene: *Bulletin des Centres de Recherches Exploration-Production Elf Aquitaine*, v. 13, p. 437–453.
- POUMOT, C., and SUC, J.-P., 1994, Palynofaciès et dépôts séquentiels dans des sédiments marins au Néogène: *Bulletin des Centres de Recherches Exploration-Production Elf Aquitaine*, v. 18, p. 107–119.
- REYMENT, R.A., 1980, *Morphometric Methods in Biostratigraphy*: Academic Press, London, 168 p.
- RULL, V., 1987, A note on pollen counting in palaeoecology: *Pollen et Spores*, v. 29, p. 471–480.
- RULL, V., 1992, Paleoeología y análisis secuencial de una sección deltaica Terciaria en la Cuenca de Maracaibo: *Boletín Sociedad Venezolana Geólogos*, v. 46, p. 16–26.
- RULL, V., 1997a, Sequence analysis of Western Venezuelan Cretaceous to Eocene sediments using palynology. Chrono-palaeoenvironmental and palaeovegetational approaches: *Palynology*, v. 21, p. 79–90.
- RULL, V., 1997b, Oligo-Miocene palynology of the Rio Chama sequence (western Venezuela), with comments on fossil algae as palaeoenvironmental indicators: *Palynology*, v. 21, p. 213–229.
- RULL, V., 1998, Middle Eocene mangroves and vegetation changes in the Maracaibo basin: *PALAIOS*, v. 13, p. 287–296.
- RULL, V., 1999, Palaeofloristic and palaeovegetational changes across the Paleocene/Eocene boundary in Northern South America: *Review of Palaeobotany and Palynology*, v. 107, p. 83–95.
- RULL, V., and POUMOT, C., 1997, Eocene to Miocene palynocycles from western Venezuela, and correlations with global eustatic cycles: *Memorias VIII Congreso Geológico Venezolano*, v. II, p. 343–349.
- SCHWARTZACHER, W., 1993, *Cyclostratigraphy and the Milankovitch Theory*: Elsevier, Amsterdam, 225 p.
- SHACKLETON, N.J., 1986, Paleogene stable isotope events: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 57, p. 91–102.
- THANIKAIMONI, G., CARATINI, C., VENKATACHALA, B.S., RAMANUJAM, C.G.K., and KAR, R.K., 1984, Selected Tertiary Angiosperm pollens from India and their relationship with African Tertiary pollens: *Institut Français de Pondichéry travaux de la section scientifique et technique*, v. 19, p. 1–92.
- VAN DER HAMMEN, T., 1957, Climatic periodicity and evolution of South American Maastrichtian and Tertiary floras: *Boletín Geológico*, v. 5, p. 49–91.
- VAN DER HAMMEN, T., 1961, Upper Cretaceous and Tertiary climatic periodicities and their causes: *Annals of the New York Academy of Sciences*, v. 95, p. 440–448.
- VAN DER HAMMEN, T., 1963, A palynological study on the Quaternary of British Guiana: *Leidse Geologische Mededelingen*, v. 29, p. 125–180.
- WIJMSTRA, T.A., 1968, The identity of *Psilatricolporites* and *Pelliciera*: *Acta Botanica Neerlandica*, v. 17, p. 114–116.

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APPENDIX 1

List of taxa referred with living relatives.

Pollen taxon	Living relative	Reference
<i>Anacolosidites luteoides</i>	<i>Anacolosa</i> (Olacaceae)	Germeraad et al. (1968)
<i>Annutriporites iversenii</i>	Unknown Angiosperm	
<i>Bombacacidites sp</i>	Bombacaceae	
<i>Bombacacidites annae</i>	<i>Bombax</i> (Bombacaceae)	Germeraad et al. (1986)
<i>Clavainaperturites clavatus</i>	Unknown	
<i>Clavatricolporites leticiae</i>	Unknown Angiosperm	
<i>Concavisporites sp</i>	Unknown fern	
<i>Corsinipollenites oculusnoctis</i>	<i>Jussiaea</i> (Onagraceae)	Lorente (1968)
<i>Ctenolophonidites lisamae</i>	<i>Ctenolophon</i> (Ctenolophonaceae)	Germeraad et al. (1968)
<i>Deltoidospora adriennis</i>	<i>Acrostichum</i> (Pteridaceae)	Lorente (1986)
<i>Echistephanoporites alfonsi</i>	Unknown Angiosperm	
<i>Echitriporites trianguliformis</i>	Unknown Angiosperm	
<i>Ephedripites sp</i>	<i>Ephedra</i>	Frederiksen (1985)
<i>Ephedripites vanegensis</i>	<i>Ephedra</i>	Frederiksen (1985)
<i>Ericipites sp</i>	Ericaceae?	Lorente (1986)
<i>Foveotricolpites perforatus</i>	Unknown Angiosperm	
<i>Foveotriletes margaritae</i>	Unknown fern	
<i>Foveotroporites hammenii</i>	Unknown Angiosperm	
<i>Gemmamonocolpites macrogemmatus</i>	Unknown Angiosperm	
<i>Gemmastephanocolpites sp</i>	Unknown Angiosperm	
<i>Gemmastephanocolpites gemmatus</i>	Unknown Angiosperm	
<i>Gemmastephanocolpites polymorphus</i>	Unknown Angiosperm	
<i>Longapertites proxapertitoides</i>	<i>Eugeissona?</i> (Arecaceae)	Thanikaimoni et al. (1984)
<i>Longapertites vaneendeburgi</i>	<i>Eugeissona</i> (Arecaceae)	Thanikaimoni et al. (1984)
<i>Mauritiidites franciscoi</i>	<i>Mauritia</i> (Arecaceae)	Lorente (1986)
<i>Monoporites annulatus</i>	Poaceae	Germeraad et al. (1968)
<i>Perfotricolpites digitata</i>	<i>Merremia</i> (Convolvulaceae)	Germeraad et al. (1968)
<i>Perinomonoletes sp</i>	Unknown fern	
<i>Proxapertites sp</i>	Arecaceae?	
<i>Proxapertites cursus</i>	Arecaceae?	Germeraad et al. (1968)
<i>Proxapertites magnus</i>	Unknown Angiosperm	
<i>Proxapertites maracaiboensis</i>	Unknown Angiosperm	
<i>Proxapertites operculatus</i>	<i>Astrocaryum</i> (Arecaceae)	Van der Hammen (1957)
<i>Psilamonocolpites sp</i>	Arecaceae	Lorente (1986)
<i>Psilamonocolpites medius</i>	Arecaceae	Lorente (1986)
<i>Psilastephanocolpites sp</i>	Unknown Angiosperm	
<i>Psilastephanocolpites verrucosus</i>	Unknown Angiosperm	
<i>Psilatricolporites sp</i>	Unknown Angiosperm	
<i>Psilatricolporites crassus</i>	<i>Pelliciera</i> (Pellicieraceae)	Wijmstra (1968)
<i>Psilatricolporites venezuelanus</i>	Unknown Angiosperm	
<i>Psilatricolporites maculosus</i>	<i>Chrysophyllum</i> (Sapotaceae)	Lorente (1986)
<i>Retibrevitricolpites triangulatus</i>	Unknown Angiosperm	
<i>Retidiporites botulus</i>	Unknown Angiosperm	
<i>Retidiporites magdalenensis</i>	Unknown Angiosperm	
<i>Retimonocolpites retifossulatus</i>	Unknown Angiosperm	
<i>Retisyncolporites angularis</i>	Unknown Angiosperm	
<i>Retitricolpites amapaensis</i>	Unknown Angiosperm	
<i>Retitricolporites hispidus</i>	Unknown Angiosperm	
<i>Retitricolporites irregularis</i>	Unknown Angiosperm <i>Amanoa</i> (Euphorbiaceae)	Germeradd et al. (1968)
<i>Retitricolpites simplex</i>	Anacardiaceae?	Lorente (1986)
<i>Rugutricolporites felix</i>	Unknown Angiosperm	
<i>Spinizonocolpites baculatus</i>	<i>Nypa</i> (Arecaceae)	Germerad et al. (1968)
<i>Spinizonocolpites echinatus</i>	<i>Nypa</i> (Arecaceae)	Germerad et al. (1968)
<i>Stephanocolpites costatus</i>	Unknown Angiosperm	
<i>Striatricolpites catatumbus</i>	<i>Crudia?</i> (Fabaceae)	Germeraad et al. (1968)
<i>Syncolporites lisamae</i>	Unknown Angiosperm	
<i>Verucatosporites speciosus</i>	Unknown Angiosperm	
<i>Verrustephanoporites simplex</i>	Unknown Angiosperm	

