Microfloral diversity patterns of the late Paleocene–Eocene interval in Colombia, northern South America

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ABSTRACT

The late Paleocene–early Eocene interval was characterized by a long period of global warming that culminated with the highest temperatures of the Tertiary. This interval was also associated with plant extinctions and a subsequent increase in plant diversity in temperate latitudes. However, tropical regions remain largely unknown. We compare the microfloral diversity of the late Paleocene with the late early to middle Eocene in flood plain, coastal plain, and estuarine facies of a section in the Colombian eastern Andes. Several techniques such as range-through method, rarefaction, bootstrap, detrended correspondence analysis, and Simpson index were used to assess the significance of the diversity pattern observed throughout the section. The microfloral record indicates a distinct, diverse Paleocene flora declining toward the end of the Paleocene, being replaced by a different and much more diverse Eocene flora. It is uncertain, however, how these floral changes correlate with the latest Paleocene thermal maximum and Eocene thermal maximum events.

Keywords: palynology, Colombia, tropical, vegetation, diversity, Paleogene.

INTRODUCTION

A long period of global warming characterized late Paleocene to early Eocene time, culminating in the Eocene thermal maximum at about 49 Ma. The warming has two distinct peaks, near the Paleocene-Eocene boundary (55.5 Ma) and in the middle to late early Eocene (Miller et al., 1987). The latest Paleocene thermal maximum is recognized by a rapid worldwide warming of high- to mid-latitude surface waters (e.g., Zachos et al., 1993), and correlates with a 35% decrease in plant diversity in mid-latitudes of North America (Wing, 1998).

The late early Eocene (or Eocene thermal maximum) was the warmest interval of the Tertiary (e.g., Miller et al., 1987). This event has been associated with increased plant diversity in middle to high latitudes (e.g., Wing, 1998). Increases in both greenhouse gases and oceanic heat transport have been proposed to explain this event (e.g., Sloan et al., 1995). Both mechanisms would generate changes in global climate, although the first would produce more changes in tropical regions (Sloan and Rea, 1995). Few data from terrestrial tropical regions are available to test these models. Here we present pollen and spore diversity data from the late Paleocene and the late early to middle Eocene epochs in the eastern Andes of Colombia.

METHODS

A stratigraphic section encompassing the late Paleocene–middle Eocene transition was studied in the Llanos Foothills, eastern Andes of Colombia, 73°1′W, 4°54′N. The section is exposed along the Piñalerita creek near Sabanalarga. There the sequence comprises, from older to younger, the Arcillas de El Limbo Formation (477 m thick), the Areniscas de El Limbo Formation (237 m), and the lower San Fernando Formation (72 m) (Fig. 1). Environments of deposition range from fluvial plain to lower coastal plain–estuarine deposits (Fig. 1). Sequence stratigraphic analyses indicate two sequences and five systems tracts (Fig. 1). The stratigraphic interval containing the Paleocene-Eocene boundary, as well as most of the early Eocene, was devoid of palynomorphs. Therefore, our study focuses on the comparison of the late Paleocene with the late early to middle Eocene palynofloras at this locality.

The word diversity is used to denote number of species (Rosenzweig, 1995). Pollen and spore diversity can be affected by three main factors (e.g., Holland, 1995): sample size (pollen grains per sample), sampling density for a given stratigraphic interval, and depositional environment. Several techniques have been used to take these factors into account. (1) Rarefaction, an interpolation technique, was used to estimate how many species would have been found had the sample been smaller than it actually was (Raup, 1975). Thus, diversity from small and large samples can be compared. Rarefaction was calculated with the Rarefaction calculator (Krebs and Brzustowski, 2000). (2) The unbiased Simpson index, or SI (Rosenzweig, 1995), was calculated to estimate underlying diversity independently of sample size. This index is adequate to estimate diversity of small samples regardless of sample size, and when used as ($-\log_e$ [SI]), it increases as the number of species does. (3) Bootstrap (Gilinsky, 1991) is a technique that allows comparison of the diversity of intervals with different sample density. (4) The range-through method (Boltovskoy, 1988) was used to estimate standing diversity. This method assumes that a taxon is present in a sample if it is present below and above the sample examined. It takes into account facies-related fossils and differences in capture probability for each taxon. (5) The overall floral composition throughout the section was observed using detrended correspondence analysis, or DCA (Hill and Gauch, 1980). DCA summarizes variation in the composition of the assemblages in a small number of dimensions (Wing, 1998). The ordination was performed on the raw abundance data excluding singletons and doubletons. Sample 475.2 was excluded because it is very different from all other samples affecting the overall DCA analysis by having it at one end of the first axis and packing all other cases together at the other. Analysis was performed in MVSP 3.0 (Kovach, 1998).

DATING THE LA PIÑALERITA SECTION

Dating Tertiary continental sections in the neotropics is difficult because of the absence of planktonic foraminifera, magnetic stratigraphy, or isotope studies. Biostratigraphic data are restricted to pollen and spores that may be regionally endemic. Here, we use pollen and spores coupled with the method of graphic correlation (Shaw, 1964; Edwards, 1989) to date the studied

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section. This method allows the true stratigraphic range of a taxon to be determined. A composite section was developed by analyzing the pollen and spore stratigraphic distribution of five sections in eastern Colombia. The Piñalerita section was chosen as the reference section. A detailed description and analysis of this composite section can be found in Jaramillo and Dilcher (2000).

Because no magnetic, isotope stratigraphy, or radiometric ages are available for the composite section, we calibrated the composite section using better-dated sections in Nigeria that contained planktonic foraminifera data and a radiometric age coupled with palynology. Several palynologists have noticed floristic similarities between northern South America and tropical western Africa during the Paleocene-Eocene (e.g., Germeraad et al., 1968). Therefore, correlation with the Nigerian sections probably should provide a general idea of the timing of pollen and spore succession in northern South America.

The foraminifera data indicate that the interval P4–P5 is located between composite units 0 to 420 (Fig. 2A). The position of the Paleocene-Eocene boundary is then tentatively located at composite unit 420, although it could be located in an interval between composite units 420 and 465. The sample at 475.2 m in the Piñalerita section (composite unit 465 in composite section) contains an assemblage that lacks typical late Paleocene taxa such as *Foveotricolpites perforatus*, *Retidiporites magdalenensis*, and *Bombacacidites annae*. The early Eocene (zones P5–P7) would be represented between composite units 420 and 590 (Fig. 2A), although the exact position of the early-middle Eocene boundary remains uncertain. This calibration of the composite section was then used to date the Piñalerita section (Fig. 2B).

RESULTS

We recovered between 21 and 500 grains per sample (Table 1). Using rarefaction, we calculated number of species per sample after counting 75 and 115 grains (Table 1; full range chart is in the

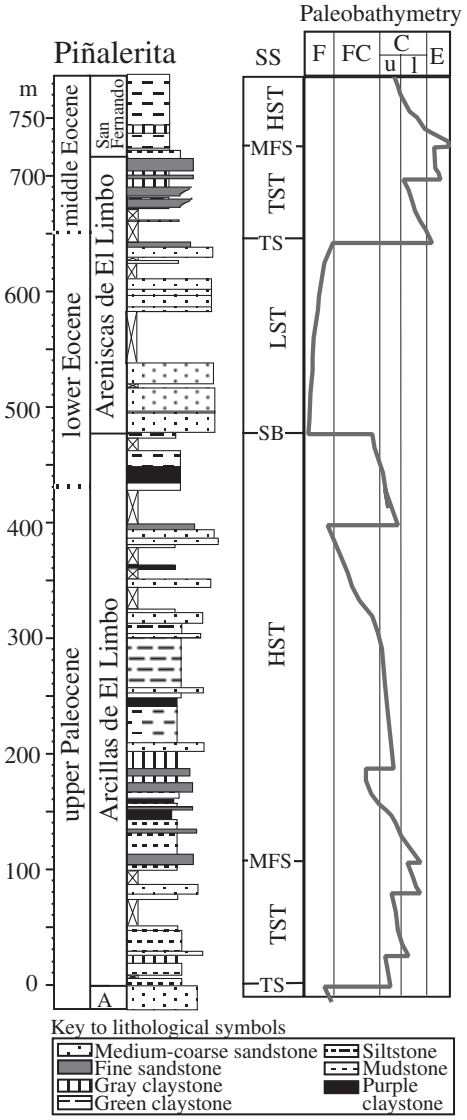

Figure 1. Sequence stratigraphy for Piñalerita section, eastern Cordillera, Colombia (after Jaramillo, 1999). A—Areniscas de El Morro Formation, F—fluvial plain, FC—fluvial to coastal plain, uC—upper coastal plain, lC—lower coastal plain, E—estuarine, SS—sequence stratigraphy, LST—lowstand systems tract, TST—transgressive systems tract, HST—highstand systems tract, TS—transgressive surface, MFS—maximum flooding surface, SB—sequence boundary.

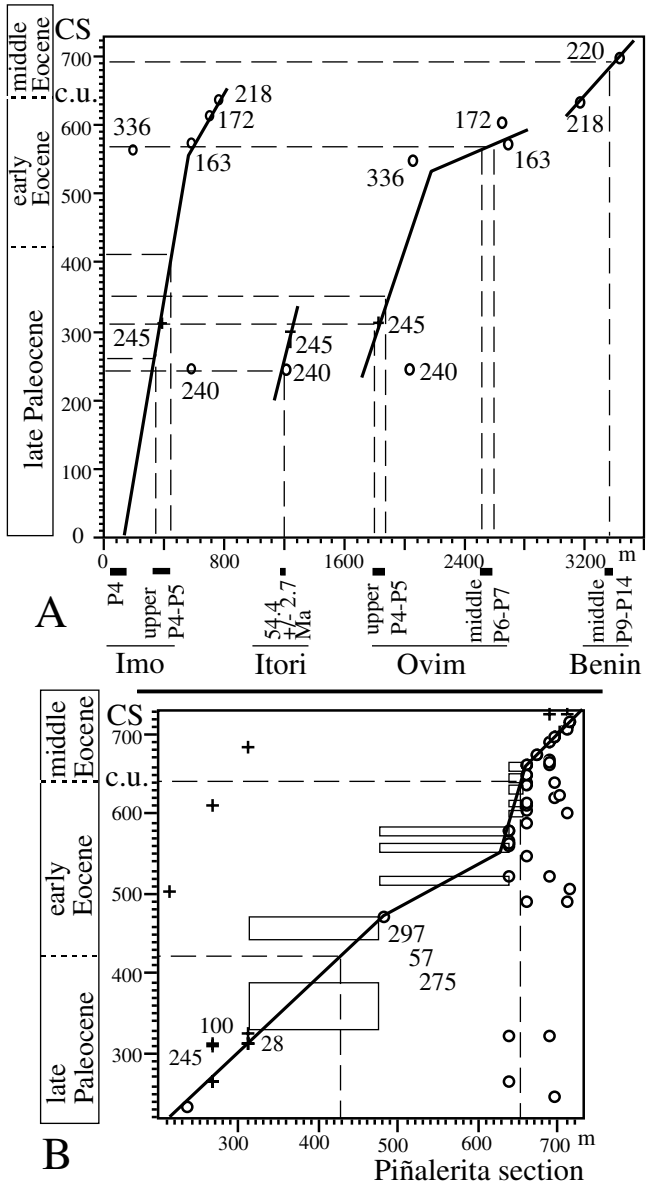

Figure 2. Dating of Piñalerita section. A: Summary of calibration datums for composite section. Line of correlation of composite section versus four sites in Nigeria: Itori well (pollen and bentonite radiometric data from Adegoke et al., 1970; Jan du Chêne et al., 1978), and the Imo, Ovim, and Benin sections (foram and pollen data from Germeraad et al., 1968). B: Line of correlation of composite section versus Piñalerita section. Boxes indicate strata down to next lower sample for first appearance datums and up to next higher sample for last appearance datums to take into account large gaps in sample interval. P—planktonic foraminifera zones of Berggren et al. (1995); c.u.—composite units; circles—first occurrence datums. Crosses—last occurrence datums. Pollen species: *Striatopollis catatumbus* (336), *Siltaria mariposa* (297), *Tricolpites clarensis* (275), *Retidiporites magdalenensis* (245), *Retibrevitricolpites triangulatus* (240), *Ranunculacidites operculatus* (220), *Lanagiopollis crassa* (218), *Perisyncolporites pokornyi* (172), *Monoporopollenites annulatus* (163), *Foveotricolpites perforatus* (100), *Cricotriporites guianensis* (57), *Bombacacidites annae* (28). Imo and Ovim sections contain *Planorotalites (Globorotalia) pseudomenardii* zone of Germeraad et al. (1968) that is equivalent to P4 zone, and *Morozovella velascoensis–Morozovella acuta* zone that is equivalent to upper P4–P5 zone. *Morozovella formosa* zone of Germeraad et al. (1968) is equivalent to range of *M. formosa–formosa*, (middle P6–P7). *Truncorotaloides rohri* zone of Germeraad et al. (1968) is equivalent to range of *T. rohri* (middle P9–P14).

GSA Data Repository[1]). Results at 75 grains cutoff show an average of 20 species per sample (standard deviation, SD, = 5) for upper Paleocene samples and 27 species per sample (SD = 7) for lower-middle Eocene samples. The isolated sample in the lowermost Eocene (at 475.2 m) was not included in the Eocene average and shows a diversity of five species per sample. At 115 grains cutoff, there is an average of 21 species per sample (SD = 5) for upper Paleocene and 32 species per sample (SD = 6) for lower-middle Eocene samples (see footnote 1). The isolated sample at 475.2 m shows six species per sample. Rarefaction at 75 cutoff was used to test for influence of lithology on diversity using a factorial ANOVA test (age $p = 0.021$, lithology $p = 0.37$, interaction age and lithology $p = 0.40$, $n = 24$, lithologies are given in range chart; see footnote 1).

Bootstrapping of the 115 grain cut-off data set (4999 iterations), also excluding the 475.2 m sample, indicated a diversity average of 31.71 (confidence interval 28.69–34.70) for Eocene samples and 21.71 (confidence interval 18.31–25.01) for Paleocene samples. Average diversity does not overlap at 95% confidence interval ($p = 0.0008$).

The average unbiased Simpson index (SI, expressed as $-\log_e$[SI]) for Paleocene samples is 2.09 (SD = 0.48); Eocene samples have a mean of 2.54 (SD = 0.63) (see footnote 1). The 475.2 m sample has an index of 0.71 and was not included in the mean Eocene index. The SI also was calculated for samples arranged according to their position in a systems tract (for stratigraphic position of systems tracts see Fig. 1). The average SI for the Paleocene transgressive systems tract is 1.90 (SD = 0.38), for the Paleocene highstand systems tract it is 2.28 (SD = 0.45), for the Eocene transgressive systems tract it is 2.47 (SD = 0.75), and for the Eocene highstand systems tract it is 2.58 (SD = 0.39).

Detrended correspondence analysis shows that axis 1 values (explains 17.5% of the variation) in Paleocene strata range from 3.09 to 6.51 (mean 4.26), and values in Eocene strata fluctuate between –0.48 and 2.92 (mean 1.41; Table 1).

We calculated standing diversity for each sample throughout the entire stratigraphic interval using the range-through method (Table 1; Fig. 3). Because taxa with single occurrences can introduce noise to the diversity pattern (Wing, 1998), the standing diversity was calculated excluding taxa with single occurrences. The upper Paleocene samples have an average of 38 species (SD = 9), the late early-middle Eocene has 73 species (SD = 14), and the lowermost Eocene sample (475.2 m) has a standing diversity of 26 species.

Species were separated into three categories: those whose stratigraphic ranges are restricted to the Paleocene, those restricted to the Eocene, and those in both Paleocene and Eocene strata (Fig. 3). Species data indicate a flora of 18 species per sample (SD = 4) that occurs in both Paleocene and Eocene strata, a late Paleocene flora of 20 species per sample (S = 6), and an early-middle Eocene flora of 53 species per sample (SD = 21). Proportion of first and last occurrences versus standing diversity was calculated (Table 1). An increase in proportion of last occurrences occurs in uppermost Paleocene (0.33 and 0.23 of standing diversity), and an increase in first appearances occurs in early to lowermost middle Eocene samples (0.37 and 0.35).

DISCUSSION

The underlying vegetation change recorded by pollen and spores can be masked by many factors (e.g., sampling size and density and lithofacies; e.g., Holland, 1995). Therefore, an analysis of pollen and spore diversity must take into account these factors before any inference can be made from the diversity pattern observed.

Major problems in estimating diversity are sample size and sample density. Rarefaction, Simpson index (SI), and bootstrap results indicate that, regardless of the sample size and sample density, there is a distinct and marked difference in diversity between late Paleocene and early to middle Eocene samples. Eocene samples are, on average, 1.4 times more diverse than Paleocene samples.

Holland (1995) found that the stacking of depositional environments in systems tracts affects diversity patterns. The pattern of increase in diversity from Paleocene to Eocene is maintained even when samples are separated according to systems tracts. Thus, the Eocene transgressive systems tract is more diverse than the Paleocene transgressive systems tract (SI: 2.47 vs. 1.90), and the Eocene highstand systems tract is more diverse than the Paleocene highstand systems tract (SI: 2.58 vs. 2.28). ANOVA results indicate

TABLE 1. DIVERSITY DATA

S	G	Sp	R1	R2	SI	DC	St	F	L
5.4	172	20	16	18	1.80	6.51	14	0.86	0.00
30.6	114	29	23	29	2.10	4.55	26	0.46	0.08
37	170	25	17	21	1.60	4.90	31	0.19	0.13
46.8	75	27	27		2.49	4.12	35	0.11	0.00
79.2	336	21	13	15	1.87	5.59	38	0.11	0.08
81	80	18	18		2.24	4.34	39	0.08	0.00
105.3	500	24	12	14	1.23	5.37	42	0.07	0.07
131.4	89	32	31		3.06	3.35	45	0.13	0.02
154.8	100	21	18		2.10	3.37	44	0.00	0.02
196.2	387	33	17	21	1.42	3.16	47	0.09	0.02
203.4	36	13			2.42	3.66	46	0.00	0.04
214.2	318	31	20	23	2.31	4.45	45	0.02	0.07
266.4	254	36	21	25	2.51	3.21	43	0.00	0.33
311.4	91	24	22		2.16	3.09	30	0.00	0.23
475.2	409	13	5	6	0.71		26	0.12	0.08
636.6	112	33	26		2.72	2.80	38	0.37	0.03
660.6	212	46	28	35	2.81	2.23	57	0.35	0.00
673.8	30	21			3.44	2.44	60	0.05	0.02
682.2	21	9			2.25	2.92	60	0.02	0.00
689.4	113	60	46		3.86	0.00	76	0.20	0.00
696.6	355	41	22	27	2.69	2.38	80	0.04	0.03
702.9	387	42	21	25	1.97	1.65	83	0.05	0.00
710.8	379	40	19	24	1.51	1.98	83	0.00	0.00
715.6	424	66	26	33	1.59	1.52	85	0.06	0.01
724.9	199	34	21	27	2.20	1.81	84	0.01	0.02
733.7	410	74	28	37	2.48	1.54	91	0.04	0.08
738.3	315	64	33	41	3.04	1.37	85	0.01	0.05
752.6	339	40	21	26	2.06	0.16	80	0.01	0.04
758.6	269	44	24	30	2.21	0.46	80	0.04	0.04
766.8	250	50	30	37	2.96	0.43	76	0.00	0.07
775.6	378	51	25	31	2.31	0.83	72	0.01	0.22
784.8	410	68	32	40	3.06	-0.48	57	0.18	0.00

S: sample (in stratigraphic meters from base Arcillas de El Limbo Formation); G: grains count; Sp: species count; R1: rarefaction 75 grains cutoff; R2: rarefaction 115 grains cutoff; SI: (-log[unbiased Simpon Index]); DC: first axis DCA; St: standing diversity after range through; F: first occurrences/standing diversity; L: last occurrences/standing diversity

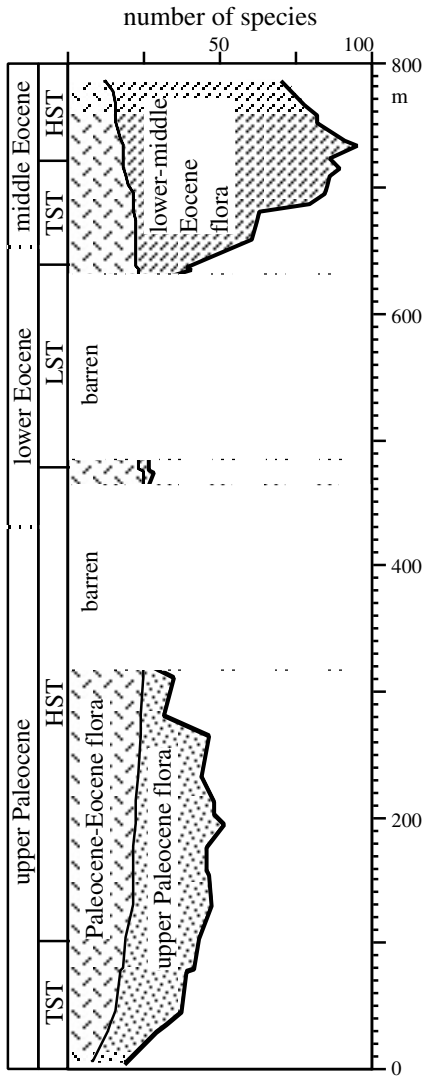

Figure 3. Standing diversity of range-through sporomorphs divided into those restricted to Paleocene, those restricted to Eocene, and those in both Paleocene and Eocene strata. Taxa with occurrences in only one sample were excluded. LST—lowstand systems tract; TST—transgressive systems tract; HST—highstand systems tract.

[1]GSA Data Repository item 200086, Full pollen and spore biostratigraphic range chart, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, editing@geosociety.org, or at www.geosociety.org/pubs/ft2000.htm.

also that lithofacies does not influence the diversity differences between Paleocene and Eocene samples.

Standing diversity, using the range-through method that tends to eliminate lithofacies and sample-size effects, shows that the upper Paleocene is less diverse (38 species per sample) than the late early-middle Eocene (73 species per sample). The lowermost Eocene sample (475.2 m) has a very low standing diversity (26 species). This sample was not included in any of the Eocene diversity calculations because it is isolated in a stratigraphic interval that has a long barren interval above and below. This sample could have a strong biofacies control (it is dominated by palm pollen *Longapertites*), that may be producing this low diversity value, although the possibility of a real decrease in diversity could not be fully ruled out.

A floral change trend through the late Paleocene to early-middle Eocene interval is evident from the detrended correspondence analysis, first and last occurrence rates (Table 1), and the composition of the floras (Fig. 3). It is clear that a very distinct Paleocene flora (taxa restricted to the Paleocene) declined toward the end of the Paleocene and was replaced by a much more diverse and distinct Eocene flora. The topology of this change is unknown because the stratigraphic interval containing those changes was barren. Only two lower Eocene samples could be analyzed; the lowermost Eocene sample (475. 2 m) and an uppermost Eocene sample (636.6 m). Therefore, it is still unknown if the decline of the late Paleocene flora or the high diversity observed in mostly middle Eocene samples originated in a single event or was a gradual change. Rull (1999) showed a gradual and significant palynofloral change from late Paleocene to early Eocene strata in Venezuela, suggesting that the early Eocene could be a time of high speciation rate, a hypothesis that needs to be tested. Unfortunately, most palynological studies (e.g., Germeraad et al., 1968) from tropical regions focus exclusively on biostratigraphic key taxa precluding any conclusion on diversity changes. However, some pollen groups such as *Bombacacidites* (similar to that of extant *Bombax* and relatives) are twice as diverse in the Eocene as in the Paleocene, and several of their Paleocene species have regional extinctions at the end of the Paleocene (e.g., *Bombacacidites annae*), suggesting that the overall pattern may not be the product of regional migrations but of in situ evolution.

This overall pattern of latest Paleocene plant extinction followed by increase in diversity was observed in the Bighorn basin in Wyoming (Wing, 1998). Wing suggested that warming at the latest Paleocene thermal maximum followed by cooling and then warming again in early Eocene and intercontinental migration were the principal causes that explain the pattern observed. The similarity with the pattern found here may suggest that the observed vegetational change could be correlated with tropical climate changes during the late Paleocene–middle Eocene interval. However, sampling of the critical latest Paleocene–earliest Paleocene interval, coupled with a more refined calibration of the biostratigraphic framework than that used for this study (e.g., carbon isotopes, magnetic stratigraphy), are necessary to evaluate the timing of these floristic changes in relation to the latest Paleocene thermal maximum and the Eocene thermal maximum.

CONCLUSIONS

Analysis of pollen and spore diversity in the Piñalerita section indicates that the uppermost lower to middle Eocene record contains a statistically significant higher diversity than the associated upper Paleocene strata. This pattern is maintained after sample size, number of samples per time unit, lithofacies, and depositional systems are accounted for. Another clear signal of the pollen and spore record is the decline of a late Paleocene flora toward the end of the Paleocene and its subsequent replacement by a more diverse upper-early to middle Eocene flora (Fig. 3). The correlation of these palynoflora patterns with climatic conditions during the latest Paleocene and subsequent Eocene thermal maximum is still uncertain. However, the data may suggest that tropical climates during the late Paleocene to middle Eocene fluctuated and exerted pressure on patterns of neotropical plant distribution and diversification.

ACKNOWLEDGMENTS

We thank three anonymous reviewers, A. Traverse, D. Fastovsky, S. Wing, M. Barreto, G. Bayona, and R. Holdo for their useful comments. This study was funded by the National Science Foundation (INT-9724122), Colciencias, Banco de la República, Geological Society of America, American Association of Petroleum Geologists, American Association of Stratigraphic Palynologists, Gerson Fellowship, Becker-Dilcher Paleobotany Endowment, and University of Florida Geology Department.

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Manuscript received March 27, 2000
Revised manuscript received June 5, 2000
Manuscript accepted June 20, 2000