

**PALYNOLOGICAL COMPOSITION OF A LOWER CRETACEOUS SOUTH
AMERICAN TROPICAL SEQUENCE: CLIMATIC IMPLICATIONS AND
DIVERSITY COMPARISONS WITH OTHER LATITUDES**

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- *Premise of the study:* Reconstruction of floristic patterns during the early diversification of angiosperms is impeded by the scarce fossil record, especially in tropical latitudes. Here we collected quantitative palynological data from a stratigraphic sequence in tropical South America to provide floristic and climatic insights into such tropical environments during the Early Cretaceous.
- *Methods:* We reconstructed the floristic composition of an Aptian-Albian tropical sequence from central Colombia using quantitative palynology (rarefied species richness and abundance) and used it to infer its predominant climatic conditions. Additionally, we compared our results with available quantitative data from three other sequences encompassing 70 floristic assemblages to determine latitudinal diversity patterns.
- *Key results:* Abundance of humidity indicators was higher than that of aridity indicators (61% vs. 10%). Additionally, we found an angiosperm latitudinal diversity gradient (LDG) for the Aptian, but not for the Albian, and an inverted LDG of the overall diversity for the Albian. Angiosperm species turnover during the Albian, however, was higher in humid tropics.
- *Conclusions:* There were humid climates in northwestern South America during the Aptian-Albian interval contrary to the widespread aridity expected for the tropical belt. The Albian inverted overall LDG is produced by a faster increase in per-sample angiosperm and pteridophyte diversity in temperate latitudes. However, humid tropical sequences had higher rates of floristic turnover suggesting a higher degree of morphological variation than in temperate regions.

Key words: angiosperm evolution; Colombia; floristic patterns; global warming; latitudinal diversity gradients; quantitative palynology; species turnover; tropical floras.

Flowering plants (angiosperms) originated during the Early Cretaceous, approximately 140–135 million years ago (Ma) (Brenner, 1974; Gübeli et al., 1984; Hughes and McDougall, 1987; Thusu et al., 1988), and rapidly diversified and radiated worldwide (Wang et al., 2009; Moore et al., 2010). Analyses of Cretaceous palynofloras by Crane and Lidgard (1989) and Lupia et al. (1999) suggested that angiosperms increased in abundance and diversity through the Early Cretaceous and that by the Late Cretaceous (Cenomanian to Campanian, 99–70 Ma) they were floristically

dominant in middle and high latitudes of the northern hemisphere. However, the patterns of angiosperm radiation and diversification in low, tropical latitudes are not well understood, mainly because of the few studies from tropical latitudes in Cretaceous successions, compared to the numerous fossil localities studied at higher latitudes (see Crane and Lidgard, 1989; Lupia et al., 1999). Given the scarcity of plant megafossil records in tropical latitudes, the use of palynology has proven crucial in understanding plant distribution and evolution for this age. Besides, palynological data provides high stratigraphic resolution, as well as large sample sizes, offering the opportunity of analyzing the fossil record using quantitative analytical techniques. The focus of many of the existing tropical palynological studies from the Early Cretaceous has been mainly taxonomic and biostratigraphic, providing mostly qualitative (e.g., presence/absence) or semiquantitative data. While we acknowledge that such qualitative data provide important information about floristic assemblages and the initial background for proposing of hypotheses, only quantitative data can be used in more robust statistical analyses, and therefore they are preferred in testing hypotheses and reconstructing floristic patterns through time and space (e.g., latitudinal diversity gradients, changes in floras due to climatic changes, evolutionary changes).

One of the main objectives of this study is to reconstruct the floristic composition of a tropical sequence, in Colombia, of

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Aptian (125–112 Ma) to Albian (112–99 Ma) age, the time of early angiosperm diversification, using quantitative palynological data. We then compare the floristic composition of our Colombian sequence with existing quantitative data from other localities ranging from tropical to temperate latitudes to test the hypothesis of the existence of a latitudinal diversity gradient for flowering plants in the Aptian and Albian (fig. 2 in Crane and Lidgard, 1989). The latitudinal diversity gradient (LDG) is one of the oldest and most widely recognized patterns in ecology (Lomolino et al., 2005; Rosenzweig, 1995), and it predicts higher species richness in the tropics than in high latitudes for most plant groups (e.g., angiosperms). However the strength of the LDG for angiosperms has varied through time, increasing dramatically through the Cretaceous and Cenozoic as angiosperms diversified and as climate cooled (Crame, 2001). Because angiosperms were undergoing their initial diversification process during the Early Cretaceous, we expect to find a LDG much weaker than the modern one.

Furthermore, we provide information on the climatic conditions of northwestern tropical South America, inferred from floristic components to test whether these tropical areas were arid or humid. The Albian-Aptian interval is characterized by both high tropical temperatures (~31°C; Schouten et al., 2003) and high levels of CO₂ (~1000 ppm; Breecker et al., 2010). It has been proposed that tropical low latitudes in northern Gondwana were arid during the Albian-Aptian interval (Ziegler et al., 1987; Herngreen et al., 1996). However, others have proposed humid conditions for the tropics, with models and data from oxygen isotopes of pedogenic carbonates that show an intensification of the hydrological cycle during the Albian, almost doubling modern precipitation values at low latitudes (Ufnar et al., 2004; Suarez et al., 2010). Understanding the nature and behavior of tropical climates during global warming intervals is crucial, since this is one of the most uncertain elements of global circulation climatic models (Chiang, 2009).

MATERIALS AND METHODS

Geologic setting—Rock core samples were taken from the Alpujarra, Ocal, and Caballos Formations in the Upper Magdalena Valley, southwestern central Colombia (Fig. 1). The Upper Magdalena Valley is a basin located between the Central and Eastern Cordilleras of Colombia (Barrio and Coffield, 1992; Prössl and Vergara, 1993). The combined thickness of the three Formations varies from 100 to 400 m (Vergara et al., 1995), bounded at the top by the marls, mudstones, and calcareous rocks of the Villeta Formation (Ramon and Fajardo, 2004) and either lying conformably on top of the Yaví Formation (Vergara, 1992) or unconformably overlapping pre-Cretaceous rocks (Corrigan, 1967). The age of the Alpujarra-Caballos sequence is middle Aptian to middle Albian (118 to 106 Ma), based on ammonites, inoceramid bivalves, and dinoflagellates (Corrigan, 1967; Beltran and Gallo, 1968; Etayo, 1993; Villamil, 1998).

The Alpujarra, Ocal, and Caballos Formations are mainly composed of sandstones (80–90%) and shales (10–20%; Florez and Carrillo, 1993). The Alpujarra Formation (the lowest in the sequence) is mainly sandy and accumulated in floodplains (Ramon and Fajardo, 2004) and tidal-flats environments (Vergara et al., 1995). The overlying Ocal Formation is composed of intercalated shales and sands that accumulated in fluvial channels, coastal and interior floodplains, low energy bays, and distal bay deposits (Ramon and Fajardo, 2004). The Caballos Formation (highest in the sequence) is predominantly sandy, interbedded with dark gray shales and thin coal laminations interpreted as accumulating in estuarine deposits (Florez and Carrillo, 1993).

Sampling, processing, and analyses—Thirty-three samples were taken from a 145.7 m section of the Los Mangos 31 core (–75°32'W, 2°37'14.56"N), which covers the uppermost portion of the Alpujarra Formation, the Ocal Formation, and the Caballos Formation, extending from the Aptian to the Albian.

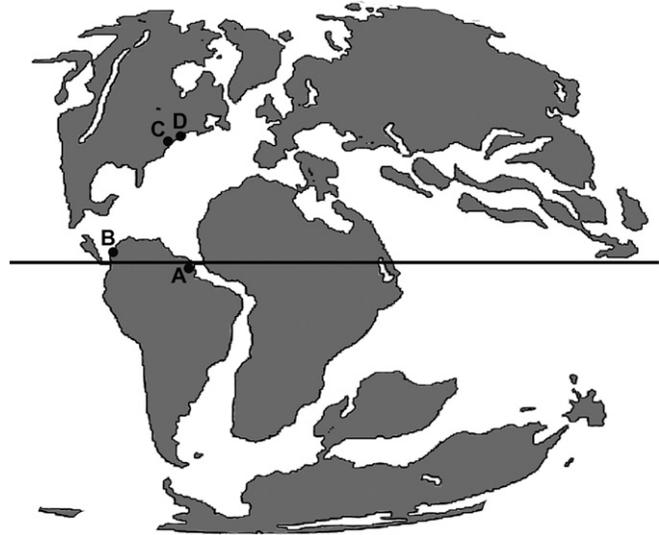


Fig. 1. Location of Aptian and Albian sequences used in this study. (A) Brazil, Barrerinhas Basin (paleolatitude: 0.2°S; Herngreen, 1973, 1975); (B) Colombia, Alpujarra, Ocal, and Caballos Formations in the Upper Magdalena Valley (paleolatitude: 6.9°N; present study); (C) USA₁, Potomac group in Maryland (paleolatitude: 37.9°N; Doyle, 1968); (D) USA₂, Potomac group in Maryland (paleolatitude: 38.4°N; Brenner, 1963). Base map modified from Scotese (2004).

Six additional samples from nearby cores (within the same petroleum field), including five from Los Mangos 7 (–75°32'47.93"W, 2°37'11.39"N) and one from Los Mangos 4 (–75°32'33"W, 2°37'29"N), were used to fill sampling gaps in the stratigraphic section of Los Mangos 31, for a total of 39 samples (Fig. 2). Those additional cores were correlated to Los Mangos 31 using gamma ray logs. Each sample, consisting of ~30–50 g of sediment, was prepared following standard palynological techniques described by Traverse (2007). Three hundred palynomorphs were counted per slide (when possible) to allow for a good statistical approximation of the real proportion of species in a population (Hayek and Buzas, 1997). Pollen and spores were identified to species level or assigned to morphospecies if the species had not been formally named in the literature. The repository of the palynological slides is the Colombian National Rock Library (Litoteca Nacional) in the Colombian Institute of Petroleum (ICP) in Bucaramanga, Colombia.

Palynomorphs were grouped into four plant groups to facilitate the description of the floristic composition: angiosperm pollen, non-gnetalean gymnosperm pollen, gnetalean pollen, and spores. Gymnosperms were divided into non-gnetalean gymnosperms and gnetales because the latter are important climate indicators and an important component of equatorial Cretaceous floras. The non-gnetalean gymnosperm pollen in our samples includes those of conifers, and monosulcate pollen grains such as those of Cycadales and Bennettitales. The floristic composition of the Alpujarra, Ocal, and Caballos Formations was determined from palynomorph abundance and rarefied species richness. Rarefaction is a technique that allows comparing richness at equal counting levels (Simberloff, 1972). All samples were rarefied to 200 specimens, and mean abundance and rarefied species richness were calculated per floristic group for each sample (Fig. 3 and Table 1). Raw counts and England Finder coordinates are recorded in online Appendix S1 (see Supplemental Data with the online version of this paper).

Climatic inference—The degree of aridity vs. humidity was established by using indicator species that have been identified to prefer a given environment based on known climatic preferences of their extant relatives (e.g., *Ephedra*). Indicators of arid climates include *Classopollis*, ephedroid pollen grains, and elater-bearing species, while the indicators of humid climates include fern spores (Herngreen et al., 1996). This assignment treats all spores collectively as humidity indicators, but we recognize that a few species might have belonged to arid-adapted ferns (i.e., *Onychiopsis* and *Ruffordia*; Friis et al., 2011). The abundance of dry and humid indicators was calculated for each sample and plotted to determine changes in predominant climatic conditions through the chronostratigraphic sequence (Fig. 2C).

Selection of quantitative data from other sequences—To determine latitudinal diversity patterns, we compared the floristic composition of 70 floristic assemblages (i.e., pollen and spores present in a sample) from four stratigraphic sequences representing different latitudes (Fig. 1, Table 1). We used new data from the Colombian sequence (data set identified as Colombia) and published quantitative data sets from other Aptian and/or Albian sequences. To perform quantitative analyses, the published data sets were filtered based on the following criteria: (1) raw counts reported for all species (i.e., not only for certain plant groups or selected species); (2) at least 200 grains counted per sample, in at least five samples per sequence; (3) an absolute count for each species could be derived from the study (i.e., no semiquantitative classes such as common, rare or presence/absence). For tropical latitudes we reviewed nearly 100 palynological publications (online Appendices S2 and S3). Only two Albian publications from the Barrerinhas Basin in Brazil met these three criteria, as they provided a sufficient number of samples when combined (online Appendix S4; Hengreen, 1973, 1975). The data from these two publications were combined into a single Brazilian data set (identified as Brazil), because they are from the same age, sedimentary basin and are geographically close to each other (~86.5 km; Giel, 1996). For temperate latitudes, we reviewed 63 palynological studies (online Appendices S2 and S5). For North America, we only reviewed the palynological studies already catalogued as having quantitative data by Lupia et al., (1999). Only two publications meet our three criteria, including Doyle (1968), which contains Aptian assemblages, and Brenner (1963), which contains Aptian and Albian assemblages. These two temperate data sets, both from the Potomac Group of Maryland, are identified as USA₁ (Doyle, 1968) and USA₂ (Brenner, 1963; online Appendices S6 and S7, respectively). The paleolatitude for all the sequences compared are 37.9°N for USA₁, 38.4°N for USA₂ (Lupia et al., 1999), 6.9°N for Colombia and 0.2°S for Brazil (Tauxe, 2011; Fig. 1). In total, we selected 70 floristic assemblages for our latitudinal comparisons (including 33 from our Colombian sequence), which contained ~240 species, and ~18 800 individuals (Table 1).

Comparison of within-sample diversity—We use the term diversity, also called species richness, to indicate the number of species (sensu Rosenzweig, 1995). We rarefied all the samples to a common count level of 200 specimens and performed independent comparisons for the Aptian and Albian floristic assemblages. Differences in rarefied species richness (within-sample diversity) and in the abundance of each palynomorph group (i.e., angiosperms, gymnosperms, non-gnetalean gymnosperms, gnetales and spores) were determined among the three sequences of Aptian age (Colombia, USA₁, and USA₂), and the three sequences of Albian age (Brazil, Colombia, and USA₂) using ANOVA tests and post hoc Tukey tests. First, a goodness of fit test was made to evaluate normality of data distribution. If data failed the test, we sequentially applied data transformations (ln+1, square root, cube root) until normality was achieved. If the previous set of transformations failed, these data were ranked prior to conducting the ANOVA, which is equivalent to performing equivalent nonparametric tests. ANOVA comparisons that resulted in significant differences among groups were subjected to a Tukey test to determine which groups were statistically different from each other. Matlab (Matwork Inc., 2000) and

R (R Development Core Team, 2011) were used in calculating rarefied species and statistical comparisons; all codes used in our analyses are presented in online Appendix S8.

Comparison of among-sample diversity—To compare the rate at which new species were found with increased sampling effort along the stratigraphic column, we calculated the bootstrapped species accumulation curves for all species in the assemblages and then for angiosperms alone for each Aptian and Albian assemblage, according to the method described by Willott (2001). To test whether the rate of species accumulation was different among sequences during both stages, we statistically compared the slope of the species accumulation curves using Monte Carlo-based permutation tests. We tested differences in the slopes at the ends of the curves as these values may indicate how close a curve is to reaching an asymptotic plateau. Since all sequences had different number of samples that collectively spanned similar temporal ranges (Table 1), we only compared curves that had similar numbers of samples to avoid biased comparisons. Hence, for the Aptian, we compared the species accumulation curves from Colombia and USA₁, and for the Albian, we compared the curves for Colombia and USA₂. Despite avoiding the use of frequentist statistics that are heavily influenced by sample size, preliminary results showed that the number of slope values (generated by shuffling all samples at each sequence) still influenced the significance of the permutation test results. Therefore, we performed our tests using a conservative approach by which we used the total number of samples per sequence (i.e., the number of independent measures for each sequence, ranging from 5 to 21) as the number of slopes to be compared for each sequence. Last, since Monte Carlo permutation tests give increasingly variable results with smaller sample sizes, we performed each slope comparison thousands of times to derive a stable, average *P* value. Bootstrapped species accumulation curves were calculated using R (R Development Core Team, 2011; see code in online Appendix S8).

RESULTS

Floristic composition of Alpujarra, Ocal, and Caballos Formations and climatic indicators—A total of 110 species of pollen and spores were recovered in the sediments of the uppermost Alpujarra, Ocal, and Caballos Formations, including 51 species of spores, 31 of angiosperm pollen, 16 of non-gnetalean gymnosperm pollen, and 12 of gnetalean pollen (online Appendix S1, Table 1). The relative abundance and rarefied species richness of the palynomorphs are shown in Fig. 2A, B and Table 1. Spores were the most abundant palynomorph in nearly all samples, with a mean abundance of 61% (SD = 22.1), while the least abundant were the gnetales (mean = 1.4%, SD = 2). Species richness (at a 200 count cut-off) was also higher for spores

TABLE 1. Quantitative data for the floristic composition of all Aptian and Albian sequences compared. All species richness data are rarefied to 200 individuals. Richness and relative abundances are the means (SD) of all the samples per sequence.

Variable	Aptian			Albian		
	Colombia	USA ₁	USA ₂	Brazil	Colombia	USA ₂
No. individuals	1444	1843	3583	1386	4895	5665
No. samples (counts >200)	5	8	14	5	17	21
No. of species	66	16	91	43	85	121
No. species per sample	28.2	19.1	38.1	20.8	25.8	54.5
Rarefied richness	24.5 (12.4)	16.4 (3.2)	28.1 (8.3)	18.2 (4.4)	22.3 (6.3)	37.5 (6.1)
Rarefied angiosperm richness	3.7 (2.1)	2 (0.7)	1.2 (0.8)	3.3 (0.7)	3.3 (3.7)	4.2 (1.8)
Rarefied non-gnetalean gymnosperm richness	3.4 (1.4)	6.9 (1.1)	9.8 (4.1)	4 (1.3)	6.8 (1.5)	12.9 (2.1)
Rarefied gnetales richness	3.5 (2.5)	0.63 (0.4)	0.24 (0.5)	7 (2.8)	0.9 (0.8)	0.5 (0.5)
Rarefied spores richness	14 (8.5)	6.9 (2.1)	16.8 (5.6)	4 (1.3)	11.2 (2.5)	20 (6.6)
Angiosperm abundance	7.2% (9.9)	4.2% (7.5)	2.1% (3.9)	9% (5.5)	5.3% (10.7)	15% (14.2)
Non-gnetalean gymnosperm abundance	23.5% (26.5)	66.3% (11.5)	35% (34.4)	53% (17.7)	34.3% (16.3)	48% (17.4)
Gnetales abundance	4% (2.3)	0.6% (0.7)	0.23% (0.6)	30.8% (18.1)	0.6% (0.5)	0.3% (0.4)
Spores abundance	65.4% (32.9)	28.9% (10.7)	62.8% (23.4)	7.2% (4.6)	59.8% (19)	36.7% (17.1)

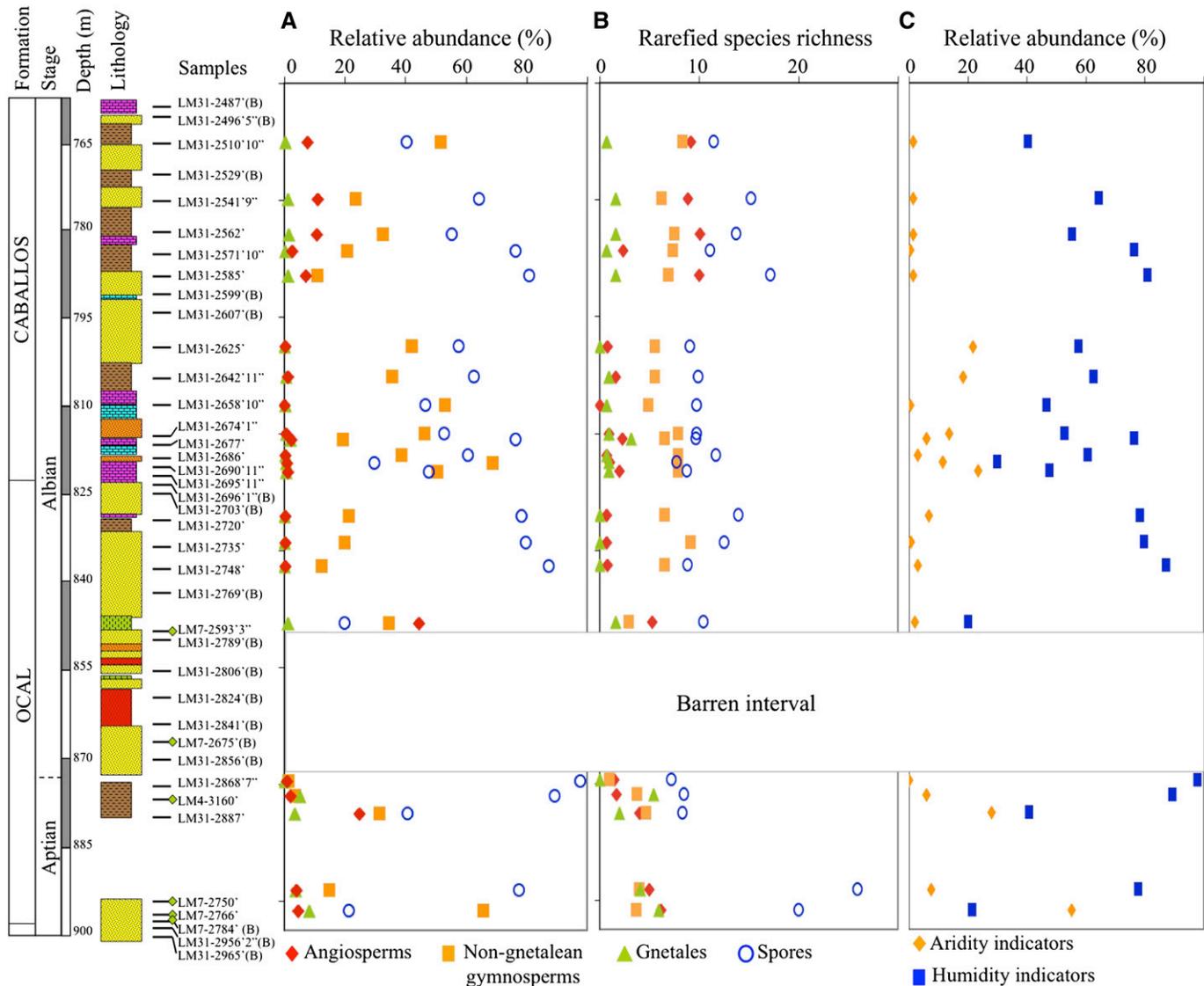


Fig. 2. Quantitative distribution of major palynomorph groups in the Alpujarra, Ocal, and Caballos Formations from Los Mangos 31 section. Samples from the Los Mangos 4 and 7 cores are indicated by a green dot next to the sample's location, and barren samples are indicated by a "B" next to the sample's name. (A) Relative abundance of palynomorphs per sample after rarefaction. (B) Rarefied species richness of palynomorphs per sample. (C) Percentage of aridity vs. humidity indicators. Aridity indicators include *Classopollis* and ephedralean pollen grains; humidity indicators include fern spores.

(mean = 11.8, SD = 4.5), and lowest for gnetales (mean = 1.5; SD = 1.7). The mean abundance and species richness for every plant group can be found in Table 1.

The amount of humidity indicators was on average 61% (SD = 22.1) per sample, compared to only 10% (SD = 13.2) of aridity indicators (Fig. 2C). The most abundant spore species in the sequence were *Cyathidites minor* and *Cyathidites australis*, related to the family Cyatheaceae, which represent 46% of the total palynomorphs counted (online Appendix S1). The most common species of non-gnetalean gymnosperm pollen was *Classopollis classoides*, which is related to the extinct family Cheirolepidiaceae (7.6% of the total count). The most abundant angiosperm pollen species was *Pennipollis reticulatus* (1.9% of the total count), which has been related to *Anacostia*, an inferred sister taxon of Chloranthaceae (Doyle and Endress, 2010; Friis et al., 2000). Finally, the most abundant species of gnetalean

pollen in the sequence studied was *Equisetosporites "medius"* (0.3% of the total count), which is related to Ephedraceae.

Differences in diversity among sequences—Quantitative comparisons of rarefied species richness (diversity) per sequence of Aptian age show no significant difference in the overall number of species among the tropical and temperate sequences (post hoc Tukey test, $P = 0.65$ for Colombia and USA₁; post hoc Tukey test, $P = 0.14$ for Colombia and USA₂; Table 1, Fig. 3). Fern spores were the most diverse group of palynomorphs in both Colombia and USA₂, while gnetalean pollen was the least diverse in the three sequences compared (Table 1, Fig. 3). Angiosperms had a significantly higher number of species in the tropical Colombian sequence than in the temperate sequences USA₁ (post hoc Tukey test, $P < 0.05$) and USA₂ (post hoc Tukey test, $P < 0.001$; Table 1, Fig. 3). In contrast, non-gnetalean

gymnosperms were more diverse in the temperate sequences than in the tropics ($F_{2,24} = 8.23$, $P < 0.01$; Table 1, Fig. 3).

In Albian assemblages, the overall number of species was higher in the temperate USA₂ sequence compared to the tropical sequences in Brazil (post hoc Tukey test, $P < 0.001$) and Colombia (post hoc Tukey test, $P < 0.001$; Table 1, Fig. 3). Spores and non-gnetalean gymnosperm pollen were also more diverse in the temperate USA₂ sequence, than in the tropical Brazilian (post hoc Tukey test, $P < 0.001$), and Colombian sequences (post hoc Tukey test, $P < 0.005$ for spores; $P < 0.01$ for non-gnetalean gymnosperm pollen), but gnetales were more diverse in Brazil ($F_{2,40} = 11.95$, $P < 0.001$; Table 1, Fig. 3). In the case of the angiosperms, there were no significant differences in the number of angiosperm species among the tropical and temperate assemblages compared ($F_{2,40} = 2.63$, $P = 0.08$; Fig. 3, Table 1).

Rate of species accumulation—The species accumulation curves show a nearly constant rate of increase in the overall number of species and angiosperm species for tropical latitudes, while in the temperate latitudes the increase is fast at first but quickly levels to form a plateau (Fig. 4). Permutation tests comparing the rate of species accumulation between our Colombian tropical sequence and temperate sequences for angiosperms and for all species combined confirm these results (Permutation tests, P values ranging from $P < 0.05$ to $P < 0.001$ depending on comparison; Fig. 4). In all cases, by comparing curves from Colombia with USA₁ for the Aptian and curves from Colombia and USA₂ for the Albian, the rate of species accumulation was higher for the tropical Colombian sequence than for the temperate sequences (Permutation test, $P < 0.001$; $P < 0.025$, respectively; Fig. 4).

DISCUSSION

Humid climates in northwestern South America—The humidity indicators were dominant in most of the samples studied (61% average abundance throughout the chronostratigraphic sequence; Fig. 2C), indicating humid climates on this area of northwestern South America during the Aptian-Albian interval. These results are unexpected because the most widespread characterization of the Cretaceous palynological provinces predicts aridity for tropical latitudes during this time (Herngreen et al., 1996).

The sequence studied was deposited during the upper Aptian and lower-middle Albian, belonging to two different palynological provinces, both interpreted to have been arid. The lower sequence corresponds to the pre-Albian Early Cretaceous *Dicheiropollis etruscus* / *Afropollis* equatorial Palynoprovince (Herngreen et al., 1996). This province, initially defined based on palynological data from the paleoequatorial area of western Africa and eastern South America, is dominated by Cheirolepidiaceae (*Classopollis*) pollen and has a high abundance of ephedralean pollen and few pteridophyte spores (Herngreen et al., 1996). The upper portion of the sequence was deposited during the lower to mid Albian, corresponding to the Elaterates Province (Herngreen et al., 1996). This province is characterized by abundant ephedroid pollen, elater-bearing taxa, high percentage and variety of angiosperm pollen, scarcity of fern spores, and the absence of bi- and trisaccate gymnospermous pollen (Herngreen et al., 1996). Both of these provinces in northern Gondwana had been assumed to represent arid climatic conditions given their common xerophytic elements like *Classopollis* and ephedralean pollen (Herngreen et al., 1996; Wood et al.,

1997). Cheirolepidiaceae gymnosperm and ephedralean pollen grains have been assumed to represent xerophytic plants (Doyle et al., 1982; Vakhrameev, 1991) as the former have sunken stomata and both are commonly associated with salt deposits in the South Atlantic rift.

In contrast to the typical arid components described in these provinces, our results suggest that at least the western region of tropical Gondwana was much more humid than it has been assumed. Other tropical palynological studies from northeastern Africa (Thusu et al., 1988; Schrank, 1992), Colombia (Herngreen and Duenas Jimenez, 1990) and Brazil (de Lima, 1983) have also found assemblages with high abundance and species richness of spores in tropical sediments of similar age. It could be that sites closer to the equatorial tropics, as our Colombian sequence (6.9°N), had a higher rainfall compared to sites closer to subtropics (Doyle et al., 1982; Schrank, 1990; Brenner, 1996). However, this fails to explain the floristic composition of the Brazilian sequence, which despite being closer to the equator (0.2°S) had a dominance of gnetalean pollen grains and a scarcity of fern spores, suggesting dry conditions, as the Elaterates province predicted (Fig. 3). De Lima (1983) proposed that, as in modern ecosystems, during the Lower and Mid Cretaceous coastal ecosystems were probably more humid than those in the continental interior because of oceanic influences. Our Colombian sequence was located near the coastline at the northwestern corner of South America (Fig. 1), where it had the influence of the Pacific Ocean and the Tethys Sea and thus probably a higher humidity compared to inland sites. In contrast, the Brazilian sequence was located near the eastern coast of South America, possibly cut off from extensive oceanic circulation because Africa and South America had started to spread apart and there was just a very weak connection between the North and South Atlantic basins (Pitman et al., 1993). Climate model simulations suggest that the northern South Atlantic was extremely warm and saline (Poulsen et al., 2001) at that time, which could create very dry conditions in the Brazilian and nearby West African coastlines.

Additional lines of evidence also support the presence of humid tropical conditions during the Mid Cretaceous in northwestern Gondwana. First, isotopic composition of pedogenic carbonates in the Caballos Formation show mean annual precipitation values slightly higher than the ones occurring today in tropical latitudes (Suarez et al., 2010). Second, coal beds found at several localities in the tropical belt (McCabe and Parrish, 1992), including the Caballos Formation (Florez and Carrillo, 1993), suggest the presence of wet environments. Moreover, some climatic models indicate higher precipitation at tropical latitudes as a result of increased intensity of the hydrological cycle during global warming episodes (Ufnar et al., 2004). It seems plausible that during the Aptian-Albian interval, precipitation varied across the tropics, with humid conditions both at the northwestern margin of South America and the eastern margin of Africa, while drier conditions developed both in tropical Brazil and tropical West Africa. These contrasting climatic variations across the tropics during the Aptian-Albian interval could have played an important role in early angiosperm diversification (e.g., Did early angiosperms prefer dry or wet environments?).

Was there a latitudinal diversity gradient in the Aptian-Albian?—Our results show that there was no latitudinal diversity gradient (LDG) in the overall number of species for Aptian floras, while there was an inverted LDG for the Albian, with floras at high latitudes containing more species per sample than

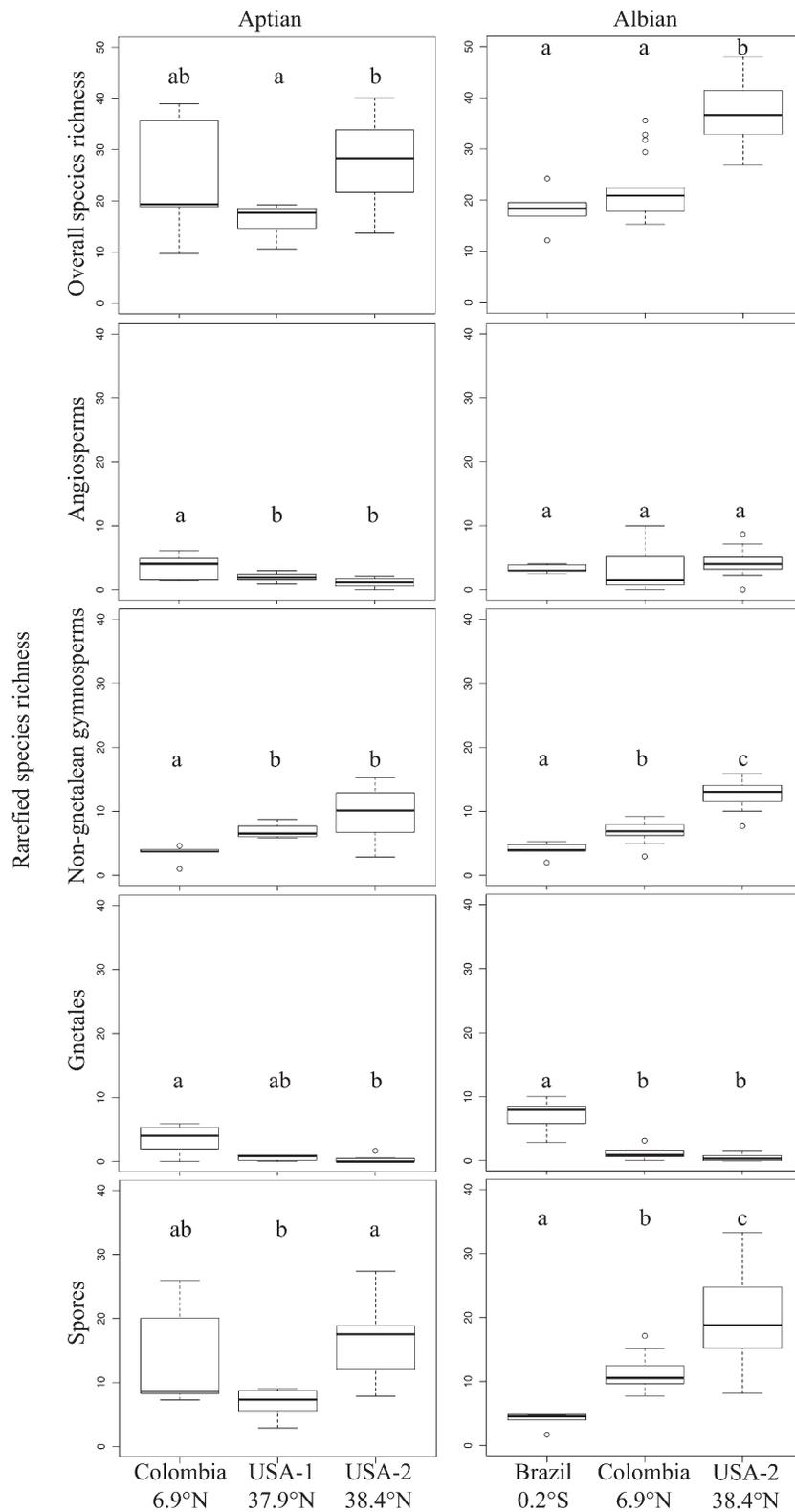


Fig. 3. Rarefied species richness in relation to latitude for the overall number of species, angiosperms, non-gnetalean gymnosperms, gnetales, and spores for Aptian and Albian assemblages. Midlines represent the median, boxes delimit the 25% and 75% quartiles and bars represent the range. Results from the post hoc Tukey test are shown with different letters above each data set. Letters denote groupings based on lack of statistical difference among sequences. (i.e., for a given plot, sequences marked “a” are statistically indistinguishable from each other). Sequences marked “ab” mean that there is no significant difference between this sequence and either the sequence marked with “a” or the one marked as “b”.

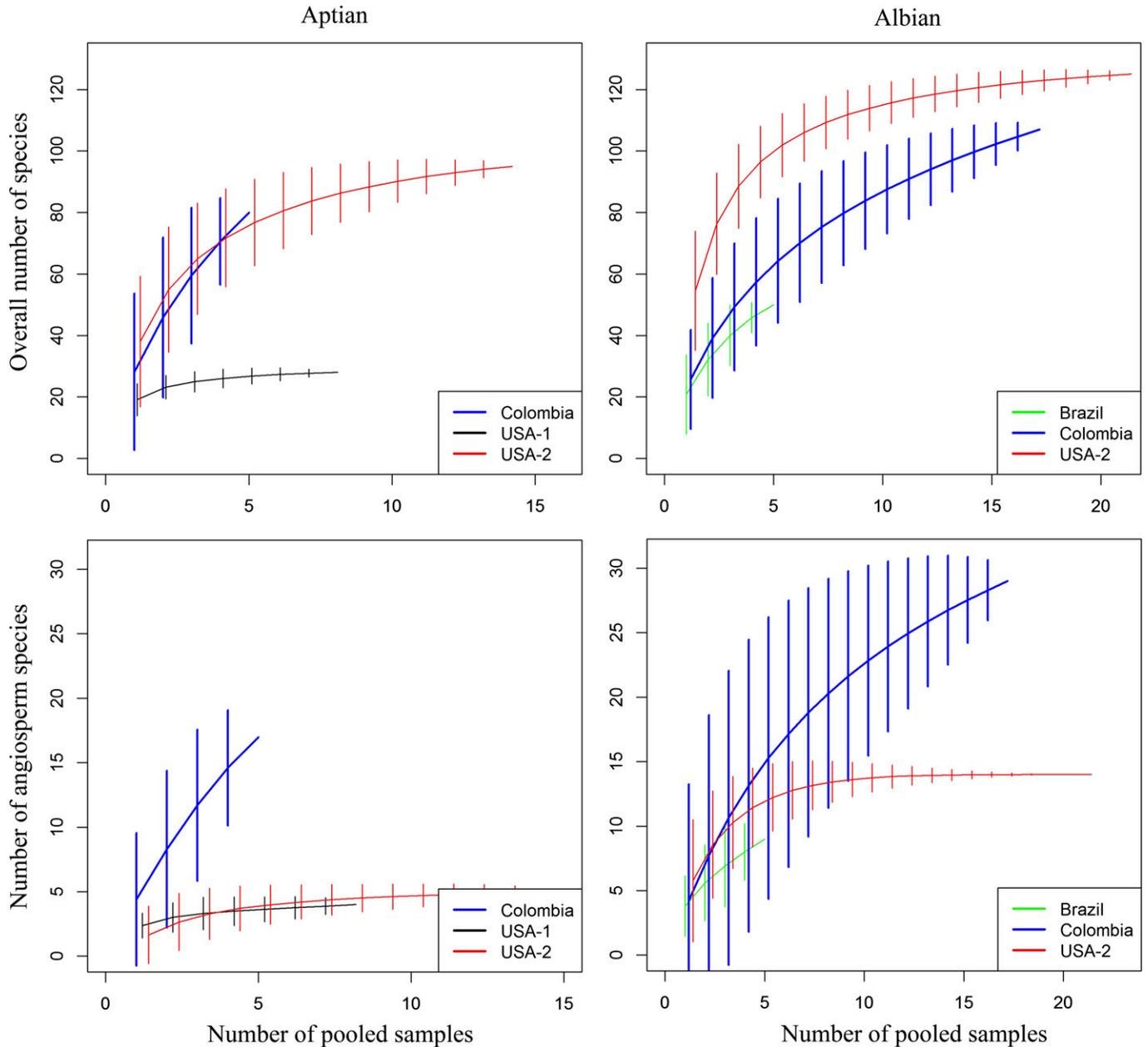


Fig. 4. Species accumulation curves with 95% confidence intervals for the overall number of species and for just angiosperm species for Aptian and Albian samples.

floras in the tropics (Fig. 3). The latitudinal temperature gradient during the Early Cretaceous was much flatter than the modern gradient. The mean annual temperature difference between the tropics and the north pole is inferred to have been $\sim 23^{\circ}\text{C}$ ($31^{\circ}\text{--}32^{\circ}\text{C}$ in the tropics vs. $\sim 9^{\circ}\text{--}10^{\circ}\text{C}$ in the arctic; Norris et al., 2002; Schouten et al., 2003; Herman and Spicer, 2010), while today this difference is $\sim 46^{\circ}\text{C}$ (Rind, 1998). In modern plant ecosystems, there is a strong correlation between the LDG and the latitudinal temperature gradient (Francis and Currie, 2003). If this correlation can be extrapolated to the Aptian-Albian, we would expect a LDG considerably less pronounced than today. This would explain the flat LDG during the Aptian for the overall flora. However, it would not explain the inverted

LDG during the Albian. Spores transitioned from not exhibiting a LDG in the Aptian to having an inverted LDG in the Albian (Fig. 3). Angiosperms transitioned from a positive LDG in the Aptian (i.e., greater tropical diversity) to a flat LDG in the Albian (Fig. 3). The increased diversity of both spores and angiosperm pollen in temperate latitudes, in addition to the higher diversity of non-gnetalean gymnosperms, accounts for the inverted LDG during the Albian. The inverted LDG for spores and non-gnetalean gymnosperms (Fig. 3) agrees with the pattern found in North America (Crane and Lidgard, 1989; Lupia et al., 1999).

The weakening of the angiosperm LDG from the Aptian to the Albian contrasts with the pattern found by Crane and Lidgard

(1989, their fig. 2). It was expected that as angiosperms radiated throughout the Cretaceous, the LDG would intensify over time (fig. 2 in Crane and Lidgard, 1989). However, our results show that the LDG for angiosperms flattened in the Albian because the number of angiosperm species per sample increased significantly in temperate sequences during the Albian while it remained stable in the tropics (Fig. 3, Table 1).

Although per-sample angiosperm diversity was higher in temperate latitudes than in tropical latitudes, our species accumulation curves show a higher species turnover in the tropics than in the temperate ecosystems, suggesting a greater angiosperm morphological variability in humid tropics during early angiosperm radiation, as supported by prior studies that have proposed the tropics as a major source of evolutionary novelty (Jablonski, 1993). Unfortunately, the low number of samples in the Brazilian sequence did not allow for similar intratropical comparisons, a limitation we hope to overcome with additional tropical sequences currently being analyzed.

We are aware, however, that our four latitudinal sequences represent a small and limited geographical representation of paleolatitudes during this crucial time of flowering plant evolution and diversification. Additional tropical and temperate sequences and quantitative analyses similar to those employed in this paper will be useful to understand further the early angiosperm diversification.

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