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To cite this article: Paula J. Mejia-Velasquez, Steven R. Manchester, Carlos A. Jaramillo, Luis Quiroz & Lucas Fortini (2018) Floristic and climatic reconstructions of two Lower Cretaceous successions from Peru, *Palynology*, 42:3, 420-433, DOI: [10.1080/01916122.2017.1373310](https://doi.org/10.1080/01916122.2017.1373310)

To link to this article: <https://doi.org/10.1080/01916122.2017.1373310>

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Floristic and climatic reconstructions of two Lower Cretaceous successions from Peru

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ABSTRACT

Climate during the Early Cretaceous in tropical South America has often been reconstructed as arid. However, some areas seem to have been humid. We reconstructed the floristic composition of two tropical stratigraphic successions in Peru using quantitative palynology (rarefied species richness and abundance), and used the abundance of aridity vs. humidity indicator species to infer the predominant climate conditions of this region. The Berriasian to Hauterivian La Merced succession was dominated by fern spores and was predominantly humid. The Albian Aguas Frias succession yielded rich palynofloras, with 127 species, and also indicates predominantly humid conditions. These results support the hypothesis that the west margin of South America was humid during the Early Cretaceous, thus improving the tropical climate reconstructions during the Cretaceous severe global warming episodes.

KEYWORDS

Cretaceous; quantitative palynology; Oriente Group; global warming; tropical floras; palynofloras; South American pollen

1. Introduction

One of the warmest episodes in Earth's history was the Cretaceous Period (Hay & Floegel 2012). Some of the Early Cretaceous ages, e.g. Aptian–Albian, were characterised by elevated worldwide temperatures and very high mean annual tropical temperatures, which reached $\sim 31^{\circ}\text{C}$ (Schouten et al. 2003), elevated levels of CO_2 up to ~ 1000 ppm (Breecker et al. 2010) and the initial diversification of flowering plants (Wang et al. 2009; Moore et al. 2010). Whether the hot tropical belt of the Early Cretaceous was arid or humid remains controversial (Mejia-Velasquez et al. 2012). This question is essential to the understanding of tropical ecosystem functioning during global warming times, as water availability is as important as temperature for plant performance (Cernusak 2013; Cheesman & Winter 2013).

Most climate reconstructions of terrestrial environments during the Early Cretaceous depict tropical latitudes as arid (Ziegler et al. 1987; Chumakov et al. 1995). These reconstructions are mainly based on lithologic evidence, such as the presence of evaporites and the distribution of climate-sensitive fossils (Chumakov et al. 1995). Some palynological studies also suggest that the tropical latitudes were arid (Herngreen et al. 1996). In contrast, global circulation climatic models suggest that tropical latitudes were humid (Fluteau et al. 2007), as do some palynological studies (de Lima 1983; Thusu et al. 1988; Herngreen & Dueñas Jimenez 1990; Schrank 1992; Mejia-Velasquez et al. 2012). Pollen and spores can be excellent sources of data for floristic reconstructions and climate inference (Traverse 2007). Well-preserved pollen and spores of Early Cretaceous age are abundant in tropical latitudes, and a few grams of sediment can potentially provide large sample sizes suitable for

accurate floristic reconstructions with strong statistical support. However, most previous palynological studies of Cretaceous tropical floras focused on biostratigraphy dealing only with a selected set of taxa rather than complete floras. Therefore, there is a need for quantitative analyses of tropical floras to determine whether climate in the tropical latitudes during the Early Cretaceous was arid or humid.

Here, we present a quantitative analysis of the palynological content of two Early Cretaceous successions from Peru, with the goals of (i) reconstructing the floristic composition using pollen and spores and (ii) assessing whether the climate was humid or arid.

2. Materials and methods

2.1. Geologic setting

Samples were collected from two outcrop successions, La Merced Succession in central Peru (Figures 1 and 2) and the Aguas Frias Succession in eastern Peru (Figures 1 and 3). The Lower Cretaceous sediments sampled belong to the Oriente Group, which spans from 1000 m in the east to 1700 m towards the west (Kummel 1948). The Oriente Group represents mainly fluvial deposition and it is composed primarily of cross-bedded sandstones with interbedding shales. The Oriente Group is underlain unconformably by the Sarayaquillo Formation (Upper Jurassic), and overlain by the Upper Cretaceous Chonta Formation (Kummel 1948). In the Contamana region, the Oriente Group is composed of three formations: (i) Cushabatay, (ii) Raya and (iii) Agua Caliente (Kummel 1948; Hermoza et al. 2005).

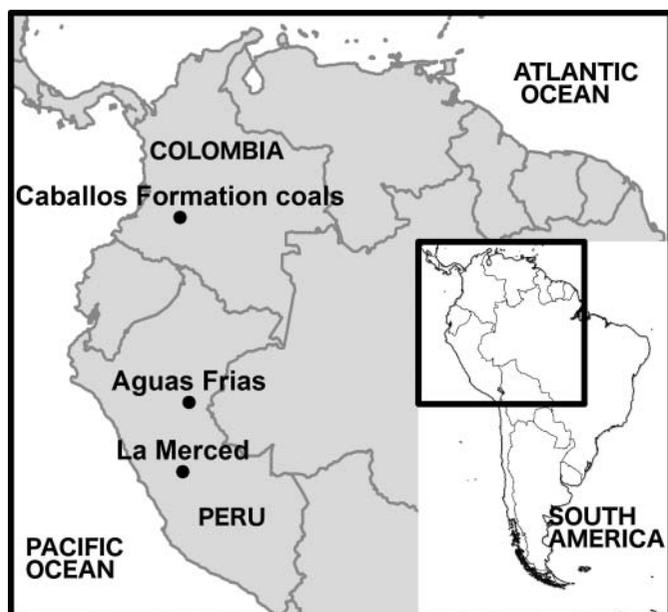


Figure 1. Geographic location of the La Merced and Aguas Frias successions in Peru and the coals from the Caballos Formation in Colombia.

2.1.1. La Merced succession

This succession was sampled in the Ucayali Basin, Junin, Peru, along the Puacartambo River, near Oxapampa Road, $-10^{\circ}50'28.1900''$, $-075^{\circ}17'13.2299''$ (Figure 1). Cretaceous deposition started in the Marañón/Ucayali basin during the Neocomian–Aptian and was characterised by fluvial to marginal-marine clastics occasionally punctuated by carbonate sedimentation (PARSEP-Perupetro S.A. 2000). The succession is 540 m thick and spans from the Jurassic Sarallaquiyo Formation to the Aptian–Albian Raya Formation. The succession starts with a Lower Cretaceous unit that overlies the red and green mudstone of the Sarallaquiyo Formation. This unit is 67 m thick and is mainly composed of sandstone with carbonaceous laminae and tuffaceous mudstone at the base followed by thin- to medium-bedded, lenticular to tabular, fine- to medium-grained ripple-cross laminated sandstones, with abundant carbonaceous debris, interbedded with organic-rich mudstone, which is interpreted to have been deposited in a deltaic to coastal plain environment. The Cushabatay Formation is 320 m thick and erosively overlies the Lower Cretaceous unit. It is composed of medium to thick beds of coarse-grained and conglomeratic cross-bedded sandstone, grading upward to intercalations of mottled mudstone and thin-bedded sandstones, interpreted as a braided fluvial system (Figure 2).

2.1.2. Aguas Frias succession

The Oriente Group was sampled in the Contamana Mountains, Loreto, Peru (Figure 1), about 400 km north of the Merced succession. We sampled the Raya and Agua Caliente formations, along the Aguas Frias Creek ($-07^{\circ}11'40.8901''$, $-074^{\circ}57'37.8698''$), a tributary of the Ucayali River. The Raya Formation is 138 m thick and it is mainly composed of white to yellow-brown ripple-cross laminated and bioturbated sandstones interbedded with mudstone beds, containing plant fragments and mica flakes. The Agua Caliente Formation is 159 m

thick and composed of white, yellow-brown cross-bedded sandstones, and thin intercalations of mudstone beds with plant fragments (Figure 3). The environments of deposition range from shallow to marginal-marine environments in the Raya Formation to estuarine and tide-influenced channels in the Agua Caliente Formation.

2.2. Floristic composition

Twenty-five samples were analysed: 13 from the La Merced succession and 12 from the Aguas Frias succession (Figures 2 and 3). Samples were prepared following standard palynological techniques by Paleoflora Ltd. The procedure included the digestion of 10 grams of rock in hydrochloric acid (HCl) for 12 hours to remove the calcareous material, after which water was added and the solution was decanted. Hydrofluoric acid (HF) was then added to remove the silicates. Water was added and the acid solution was decanted after 24 hours. The resulting residue was passed initially through a 250- μm -mesh sieve to eliminate the coarse fraction, followed by sieving through a 10- μm -mesh sieve. The organic residue was cleaned using ultrasonic equipment for some seconds, and then concentrated by centrifugation, followed by mounting of a first cover slide in a solution of polyvinyl alcohol. A second cover slide was mounted after oxidation of the residue with nitric acid (HNO_3). Canadian balsam was used to seal both mounted slides. Each sample was labelled using three letters from their sampling outcrop (MER for La Merced and CTA for Contamana mountains, where the Aguas Frias succession was sampled) followed by a number (e.g. CTA 15-2).

Pollen and spores were identified to species level or assigned to an informal species if it had not been formally described. Informal species were named using a formal genus and an epithet enclosed in quotation marks, e.g. *Retitricolpites 'colpoverrucatus'*. Palynomorphs were grouped into four groups: angiosperm pollen, non-gnetalean gymnosperm pollen, gnetalean pollen, and spores, to facilitate the description of the floristic composition. Gnetales were placed in their own category rather than lumped with all other gymnosperms, as they are an important component of equatorial Cretaceous floras (Herngreen et al. 1996) as well as climate indicators. Non-gnetalean gymnosperms include conifers, cycads and Bennettitales.

Three hundred palynomorphs were counted per sample when possible. The floristic composition was determined from palynomorph abundance and rarefied species richness. Rarefaction is a technique that allows the comparison of richness between samples of different counts by recalculating the richness of each sample (i.e. rarefied richness) at the same counting level (Simberloff 1972). All counts per sample were rarefied to 250 and statistical comparisons among groups were performed using analysis of variance (ANOVA) and post hoc Tukey tests, to determine the significance of differences among the floristic components. ANOVA tests were used to determine whether there is a significant difference among several groups ($p < 0.05$), while the complementary post hoc Tukey test shows specifically which of the groups compared with the ANOVA test are significantly different from each other (Zar 2010). Results of the post hoc Tukey test are usually noted with letters: if two groups have the same letter (e.g. a-a) this indicates that there is not a

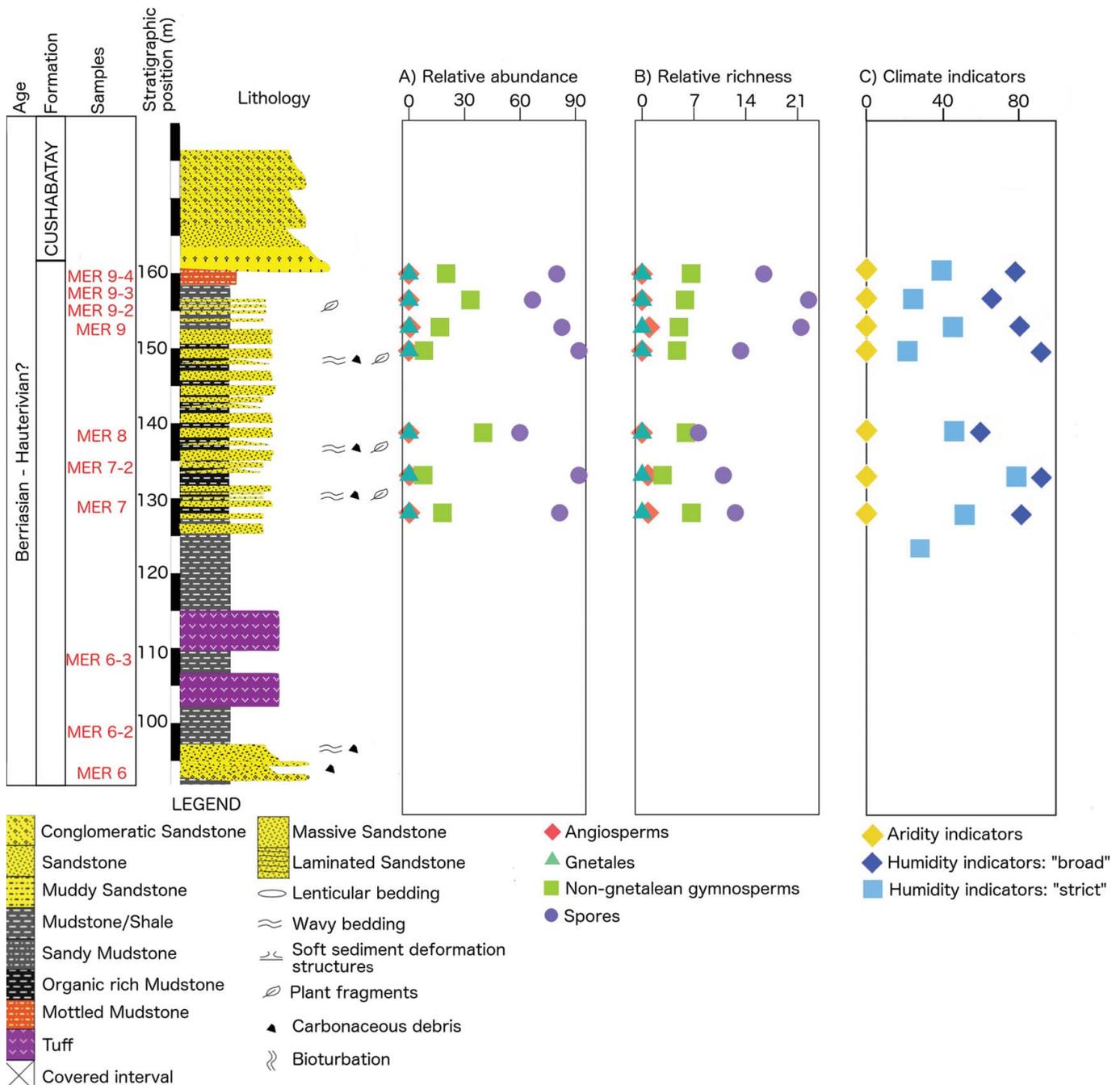


Figure 2. Lithostratigraphic column of La Merced succession showing sample locations. Samples MER 11 (507 m), MER12 (524 m) and MER 13 (540 m) are not shown in the column and were not included in the statistical analyses. A, Relative abundance of palynomorphs; B, rarefied richness; C, abundance of aridity, 'broad' and 'strict' humidity indicators.

significant difference between them ($p > 0.05$), while different letters (e.g. a-b) indicate that there is a significant difference between the groups ($p < 0.05$). Additionally, comparisons were made between the two successions to determine any significant differences in the abundance and rarefied richness of each floristic group using a t-test (Zar 2010). Finally, to compare the difference in species accumulation between the two successions, a bootstrapped species accumulation curve was calculated for each succession, according to the method described by Willott (2001). All the aforementioned statistical tests were performed using R (R Foundation for Statistical Computing 2013). All microplankton (i.e. algae and dinoflagellates) and

fungi were removed from the sample count prior to rarefaction, excluding them from any statistical analysis. Samples with counts < 250 grains were also excluded from the statistical analyses. All samples are permanently archived and accessible at the Tropical Smithsonian Research Institute (STRI) in Panama City, Panama.

2.3. Climatic inferences

The most common approach to reconstruct humid vs. arid climates using pollen and spores is the abundance of indicator species (Schrank & Nesterova 1993; Mejia-Velasquez et al.

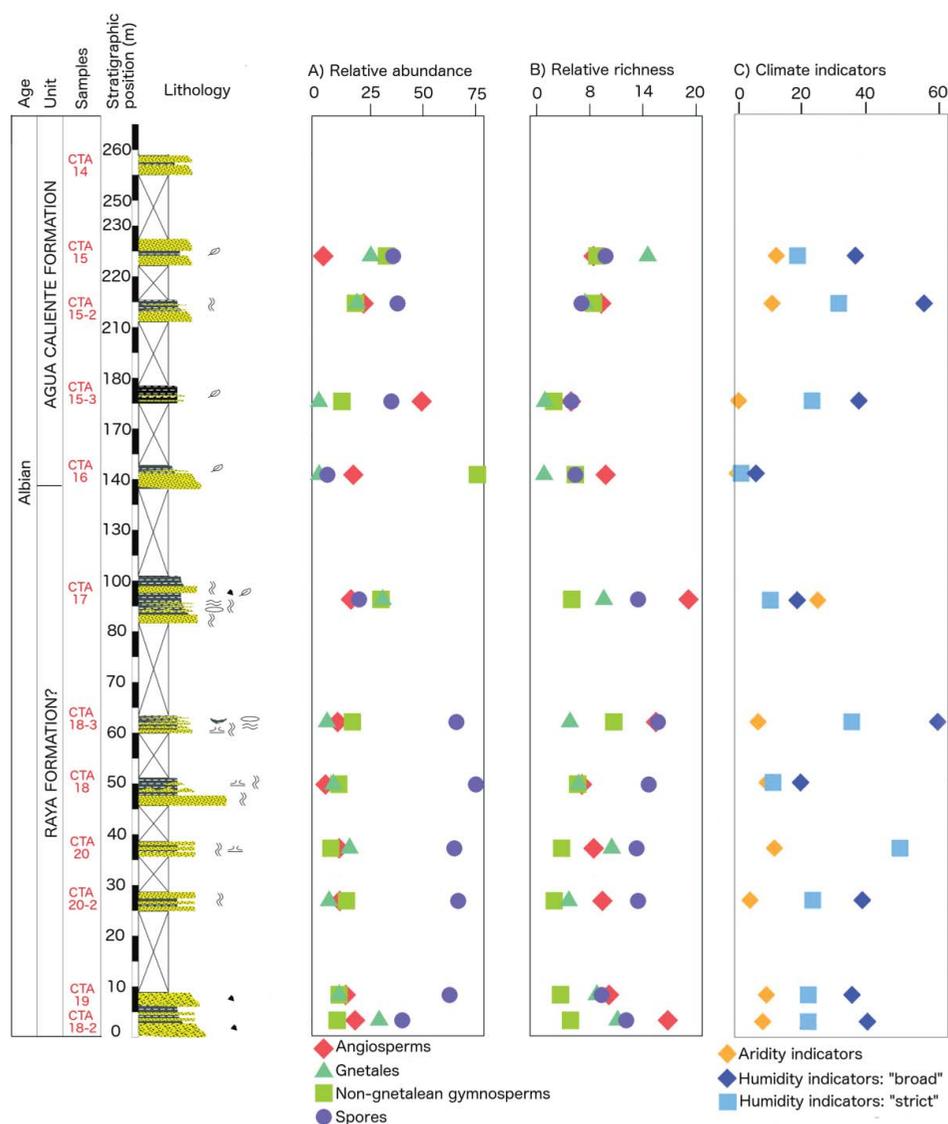


Figure 3. Lithostratigraphic column of the Aguas Frias succession showing sample locations. A, Abundance of palynomorphs; B, species richness; C, abundance of aridity, 'broad' and 'strict' humidity indicators. See legend on Figure 2.

2012). Cretaceous indicator species that suggest arid climates include both ephedroid pollen grains and *Classopollis*. Ephedroid pollen grains are used as aridity indicators because of their inferred affinities to modern *Ephedra* (Rydin et al. 2004) and *Welwitschia* (Dilcher et al. 2005). *Classopollis* are the pollen grains of the extinct gymnosperm family Cheirolepidiaceae. They have been inferred to indicate dry climates because their associated megafossils have reduced leaves, thick cuticles and sunken stomata (Watson & Alvin 1996).

Cretaceous indicators that suggest humid climate include fern spores (Schrank & Nesterova 1993; Mejia-Velasquez et al. 2012). However, some species of modern ferns (e.g. *Cheilantes*), as well as a few Cretaceous ferns (e.g. *Onychiopsis* and *Weichselia*), are known to have xerophytic characters such as reduced pinnules and sporangia embedded in protective tissue (Friis & Pedersen 1990; Friis et al. 2011). To assess which spore species were indicators of humid climates in the tropical latitudes of South America during the Lower Cretaceous, we analysed the palynological content of several tropical coal deposits. These analyses are independent from the floristic analyses performed

for the La Merced and Aguas Frias successions, and are only intended to refine the method of climatic inferences using palynomorphs. The coals analysed are from core samples of the Caballos Formation in the Upper Magdalena Valley, in central Colombia (Figure 1). The Caballos Formation is predominantly sandy, interbedded with shales and thin coals, interpreted to have been deposited in estuarine systems (Florez & Carrillo 1993). Its age ranges from mid Aptian to mid Albian (Corrigan 1967; Beltran & Gallo 1968; Etayo 1993; Villamil 1998).

Eleven coal samples were obtained from eight different rock cores of the Caballos Formation from wells in the Huila region of Colombia: Quebrada la Barniza (01°43'57.72", -75°56'22.92"), Quebrada El Pescador (02°31'27.84", -75°25'54.84"), Mina El Castel (03°15'29.88", -75°30'21.24"), Quebrada La Puerta (03°19'58.08", -75°20'15"), Quebrada Paredes (03°18'28.80", -75°14'36.96"), Vereda El Chorrillo (02°17'07.44", -75°49'39.72"), Quebrada Tafura (02°59'17.16", -75°03'36.72") and Vereda El Espejo (02°59'35.88", -75°03'33.84"); Figure 1). All samples from the Caballos Formation coals were prepared and analysed following the same

procedures described for La Merced and Aguas Frias successions in section 2.2, 'Floristic composition'.

We chose coals because they are thought to accumulate under humid conditions (Parrish et al. 1982) and rarely develop and become preserved in dry environments. Hence, the total abundances of the most common fern species in the coal samples were used as 'strict' humidity indicators. Alternatively, the total spore abundance is considered as 'broad' humidity indicators (Schrank & Nesterova 1993; Mejia-Velasquez et al. 2012). To determine whether it was more accurate to use 'strict' or 'broad' humidity indicators, we compared the differences of 'strict' (abundance of most common spores species) vs. 'broad' (total spore abundance) indicators using floristic data from three successions of Lower Cretaceous age: Aguas Frias (this study), Caballos Formation (Mejia-Velasquez et al. 2012) and Potomac Formation (Brenner 1963). We then correlated the 'broad' and 'strict' humidity indicators with the aridity indicators (ephedralean Gnetales and *Classopollis*) present in the same successions. Using this ad hoc approach, we would expect the indicator with higher negative correlation with aridity indicators to be the most reliable indicator of humid conditions. Because of the highly variable species counts across samples, including many absences, we calculated the correlation of aridity vs. 'broad' and 'strict' humidity indicators using three metrics. The first approach summed the abundance of all indicator species present in each group in a given sample (Schrank & Nesterova 1993; Mejia-Velasquez et al. 2012). This approach, however, can be influenced by outlier values, by sparse non-zero values and by the number of species chosen as indicator taxa. Hence, we also calculated a NonZeroMean metric, which is the mean number of individuals/indicator species present in each group in a given sample. Lastly, we calculated a NonZeroMedian metric, which is the median number of individuals/indicator species present in each group in a given sample. Because neither of those two metrics is based on total counts, they are not influenced by the number of chosen indicator species.

3. Results

3.1. Spores as indicators of humid climate

A total of 16 pollen and spores species were found in the 11 tropical Lower Cretaceous coal samples from the Caballos Formation, of which five were angiosperm pollen, one was non-gnetalean gymnosperm pollen, one was a gnetalean pollen and nine were spores (Supplemental online material 1: Plate S1). Spores were the most abundant palynomorphs with 99.5% of the abundance on average per sample (Supplemental material 1: Figures S1 and S2; Table S1). The most abundant spore species were *Cyathidites minor*, *Cyathidites australis* and *Todisporites minor*, which were selected as the 'strict' humidity indicators (Supplemental material 1: Figure S2).

Analyses undertaken to refine a selection of spore species for climate reconstructions were inconclusive, as they show that the three 'strict' humidity indicator species were not more strongly negatively correlated with their counterpart aridity indicators than were all spores ('broad' indicators), suggesting that the abundance of 'strict' indicators is not better at identifying humid conditions than are the total number of spores, or

Table 1. Correlation among aridity and multiple humidity indicators using all spores as 'broad' humidity indicators and selected spores or 'strict' humidity indicators from the Caballos Formation (Mejia-Velasquez et al. 2012), the Aguas Frias succession in this study and the Potomac sequence (Brenner 1963).

Variable	Type of humidity indicator (spores)	Caballos Formation	Aguas Frias	Potomac
NonZeroMedian	Broad	0.11	-0.39	0.17
	Strict	-0.35	-0.25	0.02
NonZeroMean	Broad	0.18	-0.18	-0.21
	Strict	-0.09	-0.05	-0.12
Abundance	Broad	-0.21	0.19	-0.39
	Strict	-0.13	0.2	-0.28

'broad' humidity indicators (Table 1). Based on these results, in further analyses we used the abundance of all spores as indicators of humidity (Figures 2 and 3).

3.2. Floristic composition of the La Merced succession

Sixty-six species of pollen and spores were found in the La Merced succession, including five species of angiosperm pollen, 12 of non-gnetalean gymnosperm pollen, two of gnetalean pollen and 49 of spores (Supplemental materials 2 and 3: Plates S1–S12). Total abundance and number of species per sample are shown in Table 2. Spores were significantly the most abundant and diverse palynomorphs, with an average of 79.2% of the abundance and 15 species (73.7%) on average per sample (Abundance $F_{3, 20} = 134.26$, $p < 0.01$; richness $F_{3, 20} = 44.9$, $p < 0.01$; Table 3 and Figure 5A). The most abundant spores (Figure 4) in this succession are *Todisporites minor* (41% on

Table 2. Raw data summary for the La Merced and Aguas Frias successions. A, Total abundance of terrestrial palynomorphs. B, Number of species per sample. C, Sum of 'broad' humidity indicators per sample. D, Sum of aridity indicators per sample.

Succession/sample	Height (m)	(A) Abundance of terrestrial palynomorphs	(B) Total number of species	(C) Sum of 'broad' humidity indicators	(D) Sum of aridity indicators
La Merced					
MER 5	65	3	2	2	2
MER 6	93	252	21	232	0
MER 6-2	97	7	3	2	0
MER 6-3	108	0	0	0	0
MER 7	129	302	19	246	0
MER 7-2	134	321	16	295	0
MER 8	139	305	14	182	0
MER 9	153	342	20	314	0
MER 9-2	155	315	29	256	0
MER 9-3	157	318	30	212	0
MER 9-4	159	313	23	248	0
MER 11	507	4	9	3	0
MER 12	524	46	10	20	0
MER 13	540	5	1	1	0
Aguas Frias					
CTA 18-2	0	363	49	118	29
CTA19	6	320	35	183	29
CTA 20-2	26	328	34	189	14
CTA 20	36	325	39	189	37
CTA 18	46	346	38	233	32
CTA 18-3	60	348	48	173	23
CTA 17	85	354	52	66	85
CTA 16	142	357	20	12	2
CTA 15-2	175	322	19	93	3
CTA 15-3	211	365	35	124	39
CTA 15	222	386	43	101	46
CTA 14	255	8	2	8	0

Table 3. Quantitative data for the floristic composition and comparisons of La Merced and Aguas Frias successions. All species richness data are rarefied to 250 individuals per sample. Rarefied richness and relative abundances are the means (standard deviation – SD) of all samples per succession.

Variable	La Merced	Aguas Frias	F-value	p-value
No. individuals	2468	3814		
No. samples (counts > 250)	8	11		
Total no. of species	66	128		
Average no. species per sample	23.5	37.2		
Average rarefied richness (SD) at 250 count	20.7 (5.8)	35.6 (10.13)	12.31	0.003
Average rarefied angiosperm richness	0.25 (0.43)	10.83 (4.31)	43.31	6.32E-06
Average rarefied non-gnetalean gymnosperm richness	5.36 (1.35)	6.26 (2.2)	0.92	0.352
Average rarefied Gnetales richness	0 (0)	7.63 (3.86)	26.8	9.18E-06
Average rarefied spore richness	15.12 (5.4)	10.88 (3.7)	3.93	0.065
Average angiosperm abundance	0.14% (0.25)	16.75% (12.17)	8.01	0.000026
Average non-gnetalean gymnosperm abundance	20.64% (12.13)	22.58 (20.09)	0.002	0.967
Average Gnetales abundance	0% (0)	14.52 (12.17)	11.95	0.003
Average spore abundance	79.22 (12.04)	46.14 (21.98)	13.13	0.002

average per sample; Plate 1, figure 5), *Cyathidites minor* (19% on average per sample; Plate 1, figure 3) and *Ruffordiaspora australiensis* (12.4% on average per sample; Plate 1, figure 4).

Non-gnetalean gymnosperms were the second most abundant and diverse palynomorph in this succession, with a 20.6% mean abundance and 5.1 (25.1%) species on average per sample (Table 3 and Figure 5A). The most common non-gnetalean gymnosperms (Figure 4) include *Araucariacites australis* (11.8% grains on average per sample), *Inaperturopollenites dubius* (4.7%

on average per sample) and *Callialasporites dampieri* (3% on average per sample; Plate 1, figure 19). The abundance and rarefied richness of angiosperm and gnetalean pollen were significantly lower compared to those of spores (post hoc Tukey test $p > 0.01$ for both; Table 3 and Figure 5A). Only five species of angiosperm pollen were found (Supplemental materials 2 and 3: Plate S1, figures 5, 13 and 21; Plate S2, figure 9; Plate S3, figure 1). The most abundant angiosperm species was *Retimonocolpites 'colpomaculosus'* (two grains on average per sample;

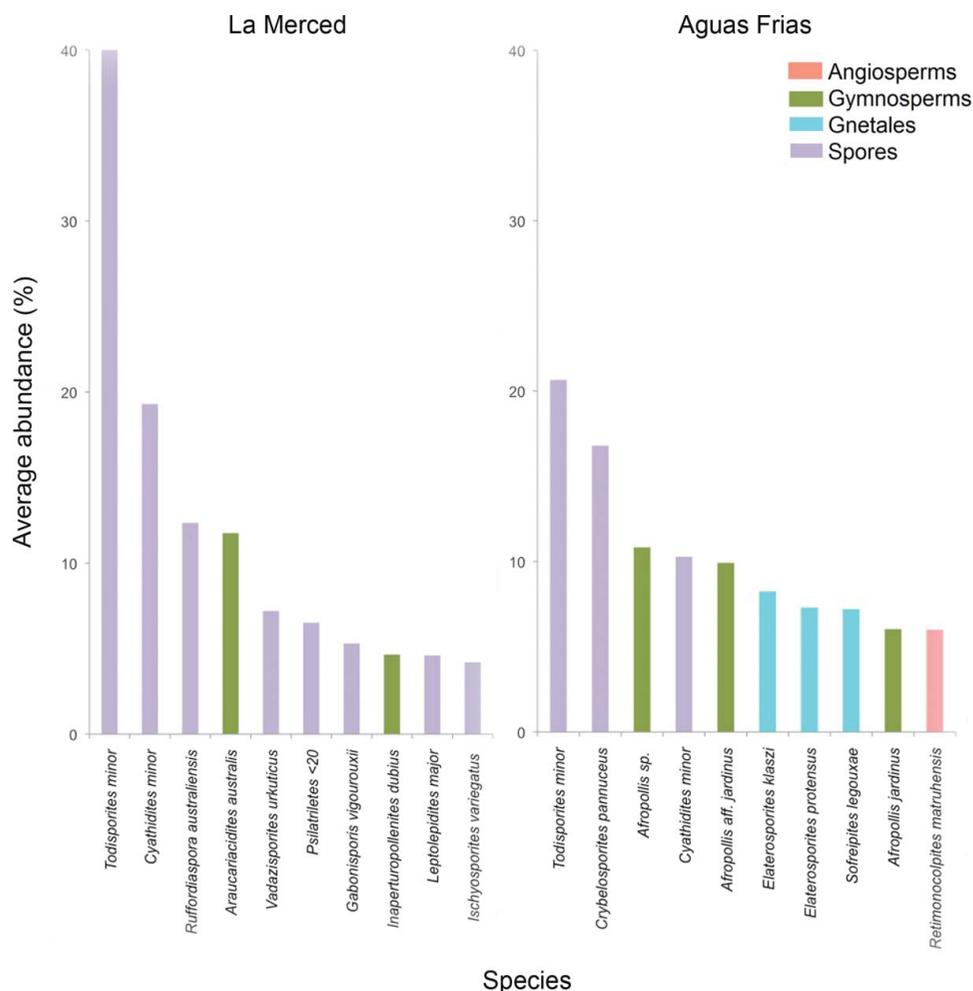


Figure 4. Most abundant palynomorph species in the La Merced and Aguas Frias successions.

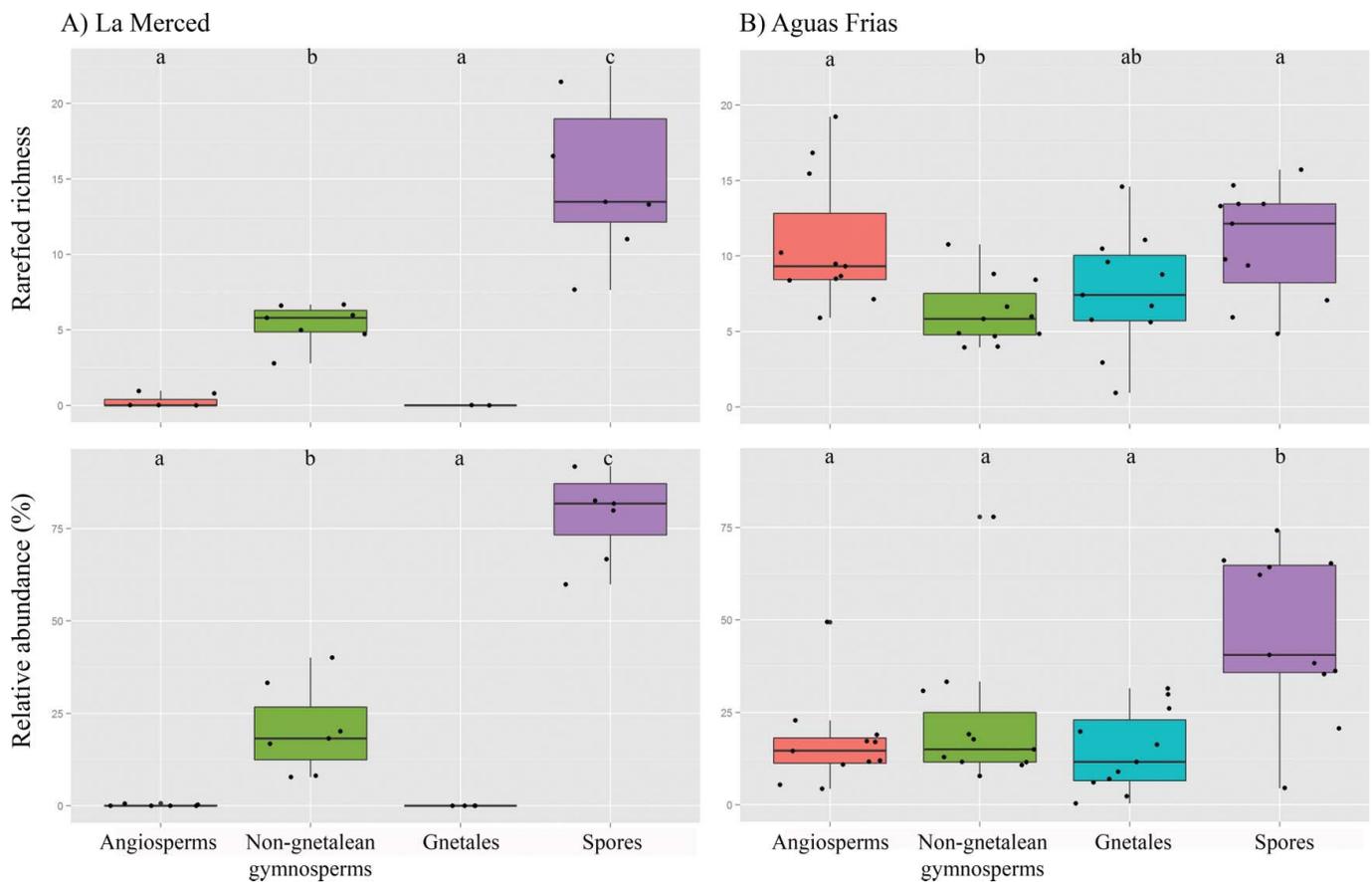


Figure 5. Floristic composition of the La Merced and Aguas Frias successions. A, Relative abundance and richness comparisons of angiosperms, non-gnetalean gymnosperms, Gnetales and spores in the La Merced succession; B, relative abundance and richness comparisons of angiosperms, non-gnetalean gymnosperms, gnetales and spores in the Aguas Frias succession. Results of the post hoc Tukey test are noted with letters: if two groups have the same letter (e.g. a-a), that indicates that there is not a significant difference between them ($p > 0.05$), while different letters (e.g. a-b) indicate that there is a significant difference between the groups ($p < 0.05$).

Plate 1, figure 12). Only one triaperturate species of angiosperm pollen (?*Periretisyncolpites* aff. *giganteus*; Plate 1, figure 10) was found towards the top of the succession (sample MER-12), but this sample was not included in the statistical analyses because the number of taxa on the slide that included this taxon was <250 grains (46 grains). Only two pollen grains of gnetalean affinity were found in this succession, *Ephedripites costaliferus* and *Gnetaceapollenites barghoornii*, but they were also found in samples for which the prepared slides contained <250 individuals and were therefore excluded from our quantitative analyses.

The sum of 'broad' humidity indicators represented a mean of $80.5 \pm 12.1\%$ per sample, while the 'strict' humidity indicators accounted for $49.6 \pm 20.5\%$ on average per sample. Aridity indicators were tallied at zero since, as mentioned above, the two ephedroid grains found in this succession were present in samples with <250 count that were not included in the statistical analyses (Table 2 and Figure 2).

3.3. Floristic composition of the Aguas Frias succession

A terrestrial palynoflora of 127 species was identified in Aguas Frias, including 46 species of angiosperms, 15 of non-gnetalean gymnosperms, 25 of gnetaleans and 41 of spores (Supplemental materials 2 and 3: Plates S1–S12). Total abundance and number of species per sample are shown in Table 2. Spores were

significantly the most abundant palynomorph in this succession (average: $46.15 \pm 21.98\%$, $F_{3,40} = 8.01$, $p < 0.01$; Table 3 and Figure 5B), while the relative abundances from the three remaining groups were not significantly different from one another (angiosperms 16.75%, gnetales 14.52% and non-gnetalean gymnosperms 22.58%; post hoc Tukey test $p > 0.05$ for all of them; Table 3 and Figure 5B).

Angiosperms and spores had similar species richness, averaging 10.8 (30.9%) and 10.8 (30.8%) species per sample, respectively, in rarefied counts of 250 (post hoc Tukey test $p > 0.05$; Table 3 and Figure 5B). The most abundant spores (Figure 4) were *Todisporites minor* (14.9% spores on average per sample), *Crybelosporites pannuceus* (9.9% spores on average per sample; Plate 1, figure 1), and *Cyathidites minor* (6.7% spores on average per sample; Plate 1, figure 3). The most abundant angiosperms include *Retimonocolpites matruhensis* (4.3% on average per sample; Plate 1, figure 14), *Retimonocolpites 'definitus'* (2.7% on average per sample; Plate 1, figure 13) and *Psilatricolpites tetradus* (1.1% on average per sample; Plate 1, figure 11). Non-gnetalean gymnosperms were also common in the Aguas Frias succession (Figure 4), with *Afropollis* aff. *jardinus* (6.5% on average per sample), *Afropollis jardinus* (4.4% on average per sample; Plate 1, figure 18) and *Araucariacites australis* (2.4% on average per sample) being the most abundant species. Finally, the most abundant gnetalean species found in the succession were *Elaterosporites klaszi* (2.7% on average per sample; Plate 1,

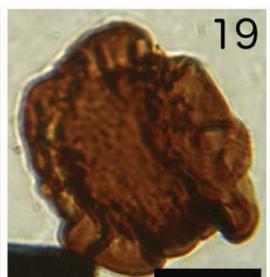
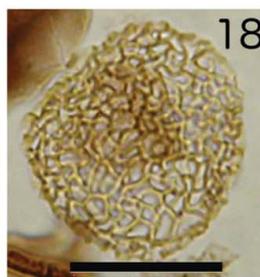
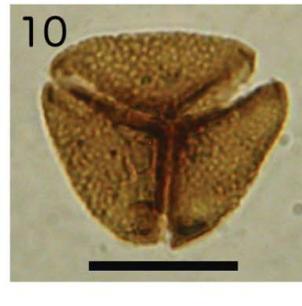
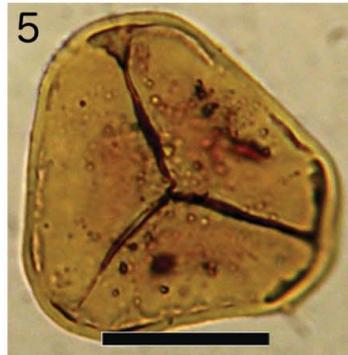
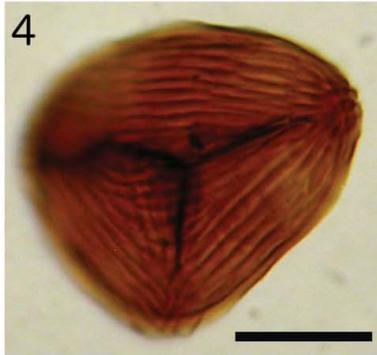
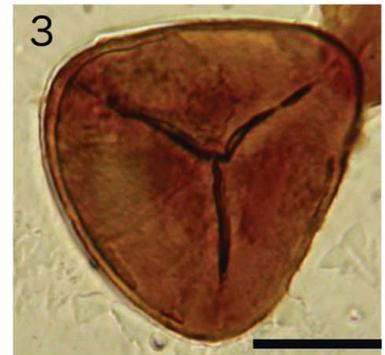
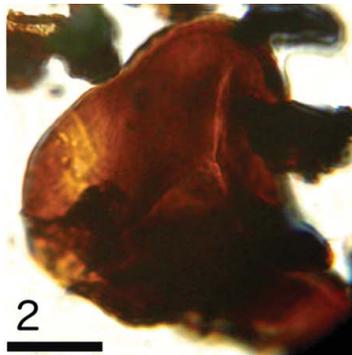
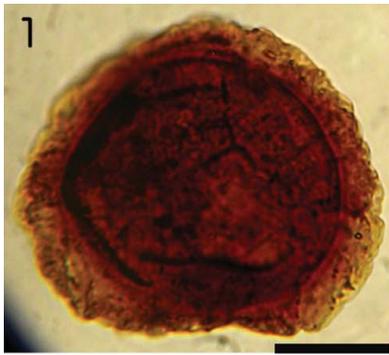


figure 16), *Elaterosporites protensus* (1.9% on average per sample; Plate 1, figure 17) and *Alaticolpites limai* (0.6% on average per sample; Plate 1, figure 15).

The average sum of broad humidity indicators ($39.4 \pm 20\%$ on average per sample) and the 'strict' humidity indicators ($21.85 \pm 12.5\%$) were significantly higher than the sum of aridity indicators ($8.8 \pm 6.4\%$ on average per sample; $t_{10} = 4.8$, $p < 0.01$ for all spores and $t_{10} = 3.11$, $p < 0.05$ for 'strict' humidity spores; Table 2 and Figure 3).

3.4. Floristic comparisons

The Aguas Frias succession had more total species at a rarefied count of 250 grains per sample than the La Merced succession ($F_{1,16} = 12.31$, $p < 0.01$; Table 3 and Figure 6). Aguas Frias also had both a higher number of angiosperm species ($F_{1,16} = 43.31$, $p < 0.01$; Table 3; Figure 7A) and a higher abundance of angiosperm pollen than La Merced ($F_{1,16} = 8.01$, $p < 0.01$; Table 3 and Figure 7B). There were no significant differences in richness and abundance of non-gnetalean gymnosperm species (richness: $F_{1,16} = 0.92$, $p > 0.05$; abundance: $F_{1,16} = 0.002$, $p > 0.05$; Table 3 and Figure 7). The abundance of spores was higher in La Merced ($F_{1,16} = 13.13$, $p < 0.01$; Table 3 and Figure 7B), whereas there was no significant difference in spore richness ($F_{1,16} = 3.93$, $p > 0.05$; Table 3 and Figure 7A). The species accumulation curves show that the Aguas Frias succession has a higher among-sample diversity, thus accumulating species faster as more samples are analysed, but neither of them reached a plateau, indicating that additional effort would be required to reach the maximum of the diversity of both successions (Figure 8).

4. Discussion

4.1. Age of the successions

4.1.1. La Merced

The palynological content of the Lower Cretaceous La Merced succession indicates a pre-Aptian age. We used publications from Brazil as baselines for assigning ages to the succession, as there is no published biostratigraphic zonation for the Early Cretaceous of Peru. The most complete Lower Cretaceous biostratigraphic work in tropical latitudes of South America was conducted in Brazil (Regali et al. 1974; Regali & Viana 1989). The Berriasian to Barremian interval comprises a single biostratigraphic superzone in the tropical latitudes of South America, the *Cedridites?* sp. superzone, defined by the appearance of *Dicheiropollis etruscus* and *Cedridites?* sp. (Regali & Viana 1989; Regali et al. 1974), which are not present in our samples. The lower *Cedridites?* sp. superzone has three zones; from oldest to youngest: *Alisporites?* sp. 1, *Leptolepidites major* and

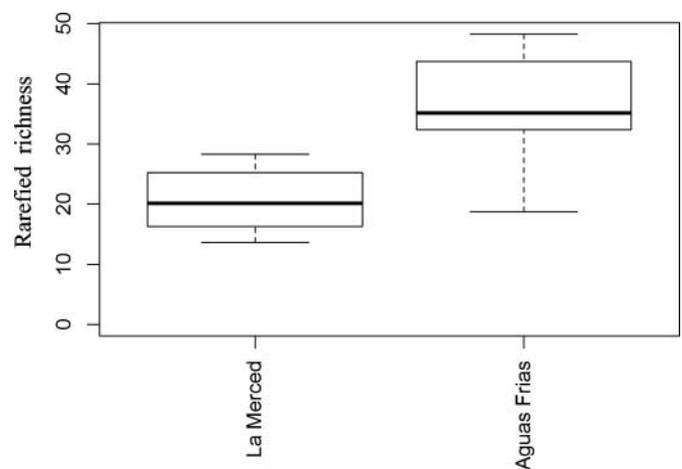


Figure 6. Comparison of mean rarefied richness per sample (rarefied sample count = 250) between the La Merced and Aguas Frias successions.

Vitreisporites pallidus. The disappearance of *Alisporites?* sp. 1 defines the upper boundary of the *Alisporites?* sp. 1 zone. The disappearance of *Leptolepidites major* defines the upper boundary of the *L. major* zone, while the disappearance of *V. pallidus* defines the upper boundary of the *V. pallidus* zone (Regali et al. 1974; Regali & Viana 1989). *L. major* and *V. pallidus* co-occur in the La Merced succession, suggesting that its age corresponds to the *Alisporites?* sp. 1 to *L. major* zones. Both zones correspond to the Rio da Serra Brazilian chronology that has been calibrated as Berriasian to Hauterivian (Regali & Viana 1989).

Typical tropical latitude palynofloras of Early Cretaceous pre-Aptian age in northern Gondwana (the *Dicheiropollis etruscus* / *Afropollis* Province) are characterized by abundant *Classopollis*, as well as gymnospermous species like *Araucariacites*, *Inaperturopollenites* and *Exesipollenites*, ephedroid pollen grains, and low abundances of angiosperm pollen (Herngreen et al. 1996). The La Merced succession has both *Araucariacites* and *Inaperturopollenites*, but lacks *Classopollis*, which can account for up to 80% abundance in other tropical latitude successions of this age (Herngreen et al. 1996). As discussed below, the absence of this taxon in the La Merced succession could be related to climate.

4.1.2. Aguas Frias

We found the co-occurrence of several taxa that suggest an Albian age for this succession, including *Elaterosporites protensus* that has its complete range within the Albian (Regali et al. 1974), *Afropollis jardinus* that extends from the late Aptian to the early Cenomanian but is more commonly found within the Albian (Regali et al. 1974), and *Cretaceiporites polygonalis* that extends from the early Albian to Campanian (Regali et al. 1974; Regali & Viana 1989). Albian palynofloras from tropical South

Plate 1. Selected palynomorphs from the La Merced and Aguas Frias successions. Each sample is identified by its sampling outcrop (CTA for Contamana and MER for La Merced) and a number (e.g. CTA 15-2), followed by the England Finder coordinate. Humidity indicators: Figure 1. *Crybelosporites pannuceus*, CTA 18, R42/2. Figure 2. *Cyathidites australis*, CTA 7-2, F57. Figure 3. *Cyathidites minor*, CTA 18-2, X57. Figure 4. *Ruffordiaspora australiensis*, CTA 15-2, F52. Figure 5. *Todisporites minor*, MER 7, M46/2. Aridity indicators: Figure 6. *Classopollis classoides*, CTA 17, X45/1. Figure 7. *Ephedripites costaliferus*, CTA 20-02, X53. Figure 8. *Ephedripites* sp. A Brenner 1968, CTA 19, X59/2. Figure 9. *Ephedripites strigatus var minor*, CTA 17, U49. Most common angiosperm pollen grains: Figure 10. *Periretisyncolpites aff. giganteus*, MER 12, U50/2. Figure 11. *Psilatricolpites tetradus*, CTA 20, T58/1. Figure 12. *Retimonocolpites 'colpomaculosus'*, MER 9-2, T64/1. Figure 13. *Retimonocolpites 'definitus'*, CTA 15-2, Q52/1. Figure 14. *Retimonocolpites matruhensis*, CTA 15-2, U65/3. Most common gnetalean pollen grains: Figure 15. *Alatisporites limai*, CTA 17, S51/3. Figure 16. *Elaterosporites klaszi*, CTA 15-2, S47/4. Figure 17. *Elaterosporites protensus*, CTA 18-2, X53/1. Most common non-gnetalean gymnosperms pollen grains: Figure 18. *Afropollis jardinus*, CTA 17, V56. Figure 19. *Callialasporites dampieri*, MER 7, S47. Scale bars = 20 μm .

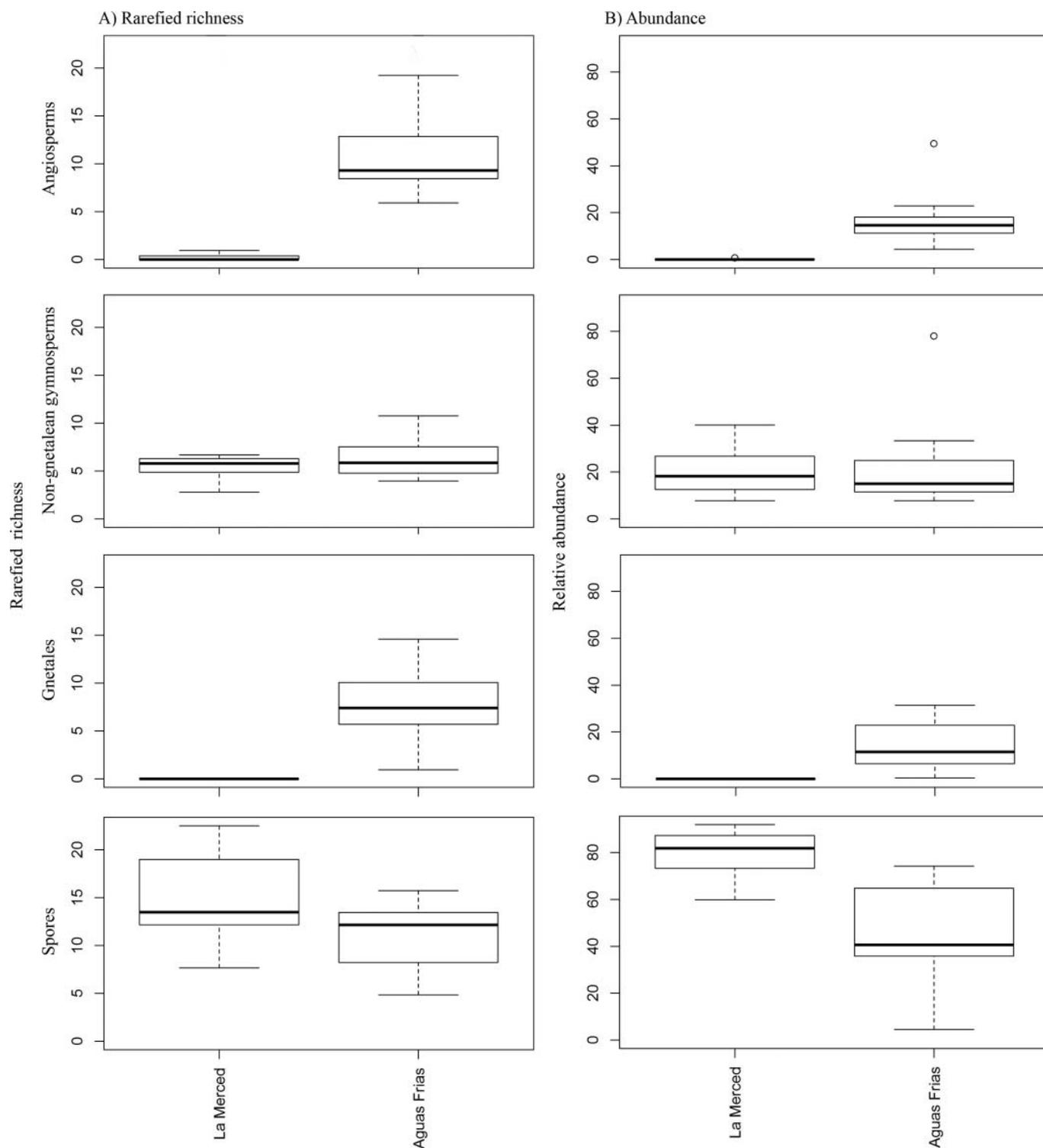


Figure 7. Floristic comparisons between the La Merced and Aguas Frias successions. A, Comparison of per-sample rarefied richness between the La Merced and Aguas Frias successions for angiosperm, non-gnetalean gymnosperms, gnetales and spores; B, comparison of per-sample relative abundance between the Aguas Frias and La Merced successions for angiosperm, non-gnetalean gymnosperms, gnetales and spores.

America have been described from Peru (Brenner 1968), Brazil (Herngreen 1973; Herngreen 1974; Herngreen 1975) and Colombia (Mejia-Velasquez et al. 2012). In Africa, there are numerous sequences of this age, including in Egypt (Abdel-Kir-eem et al. 1996; Ibrahim 1996), Morocco (Bettar & Méon 2001), Libya (Batten & Uwins 1985), Ghana (Atta-Peters & Salami 2006) and Ivory Coast (Jardine & Magloire 1965). Typical Albanian

palynofloras in northern Gondwana, or the Elaterates Province, contain elater-bearing species (gnetales), common ephedroid pollen grains, *Classopollis*, *Araucariacites*, high abundance and diversity of angiosperm pollen, and usually scarce spores (Herngreen et al. 1996). All these components are found in our Aguas Frias samples, except for scarcity of spores, which in contrast were abundant and diverse (Figures 2, 4 and 5B).

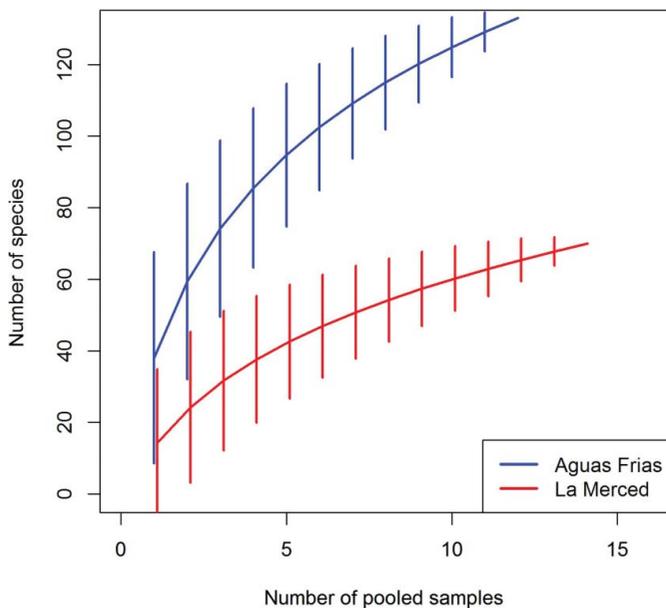


Figure 8. Species accumulation curves with 95% confidence intervals for the overall number of species in the La Merced (lower curve, Berriasian–Hauterivian) and the Aguas Frias (upper curve, Albian) successions.

4.2. Change in floristic composition

We found 164 species of palynomorphs in the Aguas Frias and La Merced successions: 49 angiosperms, 25 gnetaleans, 20 non-gnetalean gymnosperms and 70 spores (Supplemental materials 2 and 3). The two successions had large floristic differences, with only 29 species (17% of the overall assemblage) in common. The Albian Aguas Frias succession had a higher number of species than the Berriasian–Hauterivian La Merced succession (35.6 vs. 20.7 sp. per sample on a 250 rarefied count per sample; Figures 6 and 8). This pattern has also been found in macrofloras and palynofloras of middle and high latitudes, where there is a gradual increase in the total number of plant species through the entire Cretaceous (Lidgard & Crane 1990). This increase is mostly due to the increasing diversity of both angiosperms and gnetales. In our analyses angiosperms show a significant increase in abundance (0.14% vs. 16.75% per sample; Table 3 and Figure 7) and richness (0.25 vs. 10.83 species on a 250 rarefied count per sample; Figure 7), as well as gnetales (richness 0 vs. 7.63 species, abundance 0% vs. 14.52%; Table 3 and Figure 7). These increases indicate a rapid diversification of both groups during the Early Cretaceous.

Angiosperms first appeared in the fossil record during the Hauterivian (Brenner 1974; Hughes & McDougall 1987), and soon after their appearance they started a rapid diversification (Wang et al. 2009; Moore et al. 2010). The increase in angiosperm abundance and diversity has also been recorded at middle and high latitudes (Crane & Lidgard 1989; Lupia et al. 1999), and by the Albian angiosperms were already an abundant and diverse component of palynofloras worldwide (Herngreen et al. 1996; Lupia et al. 1999). This rapid early Cretaceous diversification of angiosperms was paralleled by gnetales in tropical latitudes (Crane & Lidgard 1989). In contrast, the abundance and richness of non-gnetalean gymnosperms (e.g. araucarians and Cheirolepidiaceae) did not change from the Berriasian–

Hauterivian to the Albian in the tropical latitude successions analysed (richness 5.36 vs. 6.26 species, abundance 20.64% vs. 22.58%; Table 3 and Figure 7). This pattern is similar to that reported in mid and high latitudes of North America, where the abundance and diversity of non-gnetalean gymnosperms, especially conifers, remained stable through the Cretaceous (Lupia et al. 1999).

Spores decreased in relative abundance from the Berriasian–Hauterivian (79.22%) to the Albian (46.14%), although their species richness remained stable (15.12 vs. 10.88 species in a 250 rarefied count per sample; Table 3 and Figure 7). This apparent decrease in abundance could be a statistical artifact called ‘the closer effect’, i.e. as the abundances of both gnetales and angiosperms increased, the relative abundance of spores must decrease. Even with a decrease in abundance, our results demonstrate spores were still a very diverse and abundant group in the tropics during the Albian, even as angiosperms and gnetales were diversifying. It has been suggested that ferns also diversified during the Cretaceous, as new niches emerged as a consequence of the explosive angiosperm and gnetalean diversification (Schneider et al. 2004). Although we did not find evidence of a higher spore diversity to directly support this hypothesis of Cretaceous fern diversification, the fact that spores remained highly diverse in spite of their significant decrease in abundance could be an indication of high origination rates in the group.

4.3. Climate

We found higher abundance of humidity indicators than of aridity indicators for both the La Merced and Aguas Frias successions (Table 2; Figures 2 and 3), indicating that a humid climate prevailed in northwestern South America during the Berriasian–Hauterivian and the Albian intervals. Most climatic reconstructions based on climate-sensitive sediments imply the prevalence of arid climate in most of western Gondwana during the pre-Aptian interval of the Early Cretaceous (Chumakov et al. 1995). However, palaeoclimatic reconstructions based on pollen and spores of northern Gondwana indicate that the Berriasian–Hauterivian interval was potentially more humid, as inferred from the predominance of spores and bisaccate pollen species (Herngreen et al. 1996). Results from our climatic analyses also suggest that the Berriasian to Hauterivian La Merced succession had a predominantly humid climate, supporting the climatic interpretations made by Herngreen et al. (1996).

Besides palynology, the presence of humid areas during this time interval in the tropical latitudes of western Gondwana is also supported by other sources of evidence. The climatic interpretations of aridity come from the wide distribution of evaporites and calcretes in northern South America and northern Africa (Figure 9; modified from Chumakov et al. 1995; Scotese et al. 1999). However, the presence of several coal deposits in northwestern South America and northern Africa (Scotese et al. 1999) indicates a humid climate, as do climate models, which predict that tropical areas were only seasonally dry but humid during the summer (Rees et al. 2000). These inferences coincide with our findings of humid climate in the coastal area of northwestern South America during the Berriasian to Hauterivian interval.

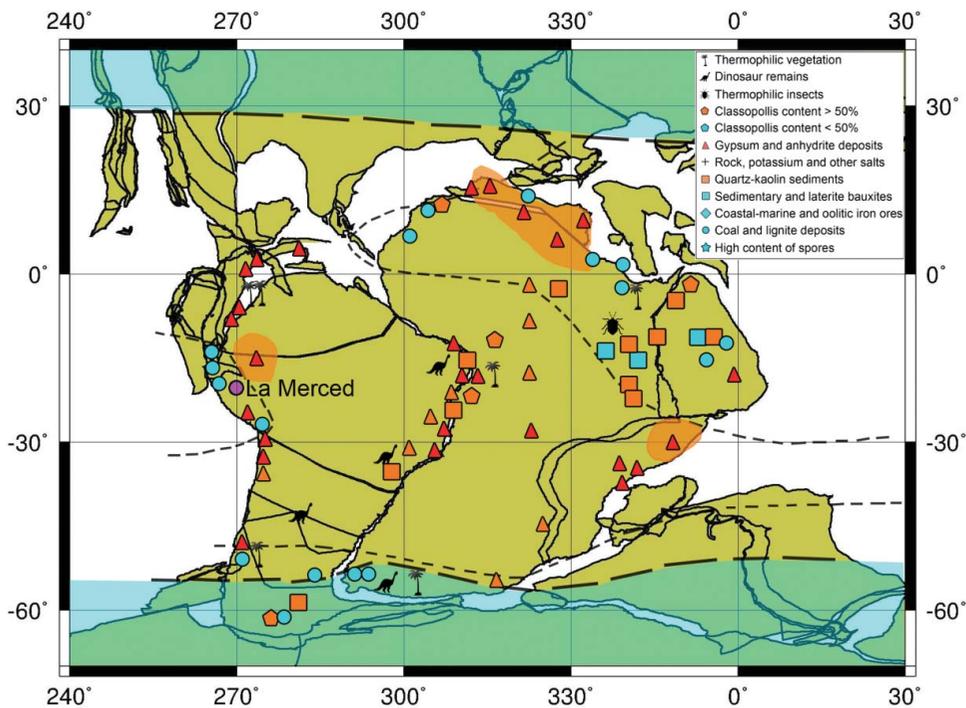


Figure 9. Palaeogeographic location of the La Merced succession in Peru (145 Ma). Location of climate-sensitive sediments in western Gondwana from Scotese et al. (1999) and Chumakov et al. (1995). Palaeomap created using Advanced Plate Tectonic Reconstruction Service (ODSN). Short dashed lines indicate the climatic interpretation of humidity by Scotese et al. (1999). Poleward-shaded areas are interpreted as mid-latitude warm humid belts, highlighted continental areas are interpreted as evaporite belts and remaining continental areas are interpreted as arid by Chumakov et al. (1995).

The Albian stage has been reconstructed as semi-arid or arid based on pollen and spores: the scarcity of spores and bisaccate pollen grains, and the high abundance of the arid-related ephedroid pollen grains and *Classopollis* (Hengreen et al. 1996). In

contrast, the Albian Aguas Frias succession is dominated by spores, which suggests a humid climate (Figure 3). Other palynological studies in the tropical latitudes of South America have also led to inferences of humid climates during the Albian

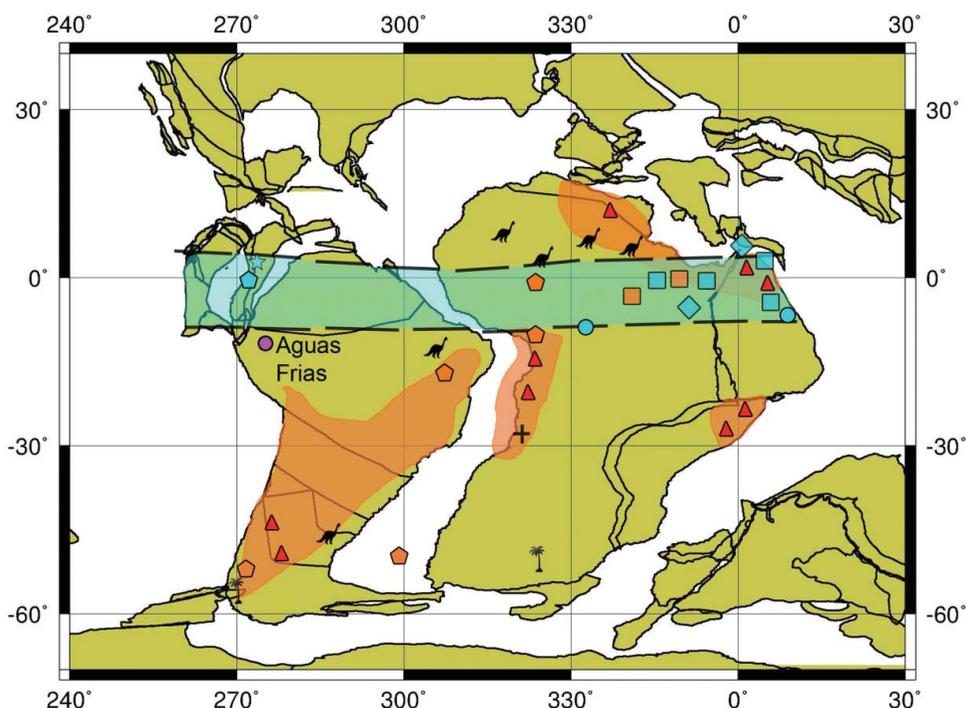


Figure 10. Palaeogeographic location of the Aguas Frias succession in Peru (110 Ma). Location of climate-sensitive sediments in western Gondwana from Chumakov et al. (1995). Palaeomap created using Advanced Plate Tectonic Reconstruction Service (ODSN). Tropical-shaded area between dashed lines is interpreted as a humid belt, highlighted continental areas are interpreted as evaporite belts and remaining continental areas are interpreted as arid by Chumakov et al. (1995). See legend on Figure 9.

stage, indicating that the northwestern margin of South America was humid during that time interval (Herngreen & Dueñas Jimenez 1990; Mejia-Velasquez et al. 2012). Other sources of evidence also support the presence of humid climate in the tropical latitudes of western South America during the Albian. First, distributions of climate-sensitive sediments and fossils suggest the presence of a small humid tropical latitude belt during the Albian (Chumakov et al. 1995; Figure 10; modified from Chumakov et al. 1995). Additional lithological evidence supporting this hypothesis, not included in Chumakov et al. (1995), includes the numerous coal layers found in the Albian deposits from the Caballos Formation in Colombia (Florez & Carrillo 1993). Second, the isotopic composition of palaeosols from the Albian Caballos Formation in Colombia also indicates the presence of humid conditions (Suarez et al. 2010). Finally, climate models for the mid Cretaceous show increasing humidity and an enhanced hydrological cycle (Sellwood & Valdes 2006) and predict the presence of at least seasonal humidity at tropical latitudes for the middle Cretaceous (Fluteau et al. 2007). All these sources of evidence cast doubt on the existence of a continuous tropical arid belt during the greenhouse event of the middle Cretaceous, as suggested by palynological interpretations (Herngreen et al. 1996), indicating instead humid conditions in several tropical latitude regions.

The presence of humid climates in northwestern South America during the Early Cretaceous could be a consequence of a 'supercontinent effect', when the coastal areas of Gondwana were probably more humid than areas in its vast interior. On large continents, like Gondwana, moisture cannot be easily carried from the coast, creating interior deserts at any latitude (Scotese et al. 1999). Under this scenario, tropical areas of South America near the Pacific Ocean would have been more humid than areas in the interior of Gondwana.

In conclusion, the floristic and climate reconstructions presented here show an increase of angiosperm abundance and diversity from the Berriasian–Hauterivian to the Albian in tropical latitudes, and demonstrate the presence of humid climates in northwestern South America during the Berriasian–Hauterivian and Albian ages.

Acknowledgements

Financial support for this project came from the Smithsonian Tropical Research Institute, the Anders Foundation, 1923 Fund and Gregory D. and Jennifer Walston Johnson, and a Geological Society of America (GSA) research grant. Thanks to Pierre-Olivier Antoine and his team in Montpellier for field support. The authors thank Dr Mohamed Zobaa and two anonymous reviewers for comments and suggestions. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Smithsonian Tropical Research Institute; Andersen Corporate Foundation; 1923 Fund; Gregory D. and Jennifer Walston Johnson; Geological Society of America [grant number 9209-03].

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