

Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest

Scott L. Wing^{a,1}, Fabiany Herrera^{b,c}, Carlos A. Jaramillo^b, Carolina Gómez-Navarro^{b,d}, Peter Wilfe^e, and Conrad C. Labandeira^a

^aDepartment of Paleobiology, P.O. Box 37012, Smithsonian Institution, National Museum of Natural History, Washington, DC 20013; ^bSmithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panamá, República de Panamá; ^cFlorida Museum of Natural History and Department of Biology, University of Florida, P.O. Box 117800, Gainesville, FL 32611-7800; ^dDepartment of Plant and Microbial Biology, University of California, Berkeley, CA 94720; and ^eDepartment of Geosciences, Pennsylvania State University, University Park, PA 16802

Edited by Peter H. Raven, Missouri Botanical Garden, St. Louis, MO, and approved September 4, 2009 (received for review May 11, 2009)

Neotropical rainforests have a very poor fossil record, making hypotheses concerning their origins difficult to evaluate. Nevertheless, some of their most important characteristics can be preserved in the fossil record: high plant diversity, dominance by a distinctive combination of angiosperm families, a preponderance of plant species with large, smooth-margined leaves, and evidence for a high diversity of herbivorous insects. Here, we report on an ≈ 58 -my-old flora from the Cerrejón Formation of Colombia (paleolatitude $\approx 5^\circ \text{N}$) that is the earliest megafossil record of Neotropical rainforest. The flora has abundant, diverse palms and legumes and similar family composition to extant Neotropical rainforest. Three-quarters of the leaf types are large and entire-margined, indicating rainfall $>2,500$ mm/year and mean annual temperature $>25^\circ \text{C}$. Despite modern family composition and tropical paleoclimate, the diversity of fossil pollen and leaf samples is 60–80% that of comparable samples from extant and Quaternary Neotropical rainforest from similar climates. Insect feeding damage on Cerrejón fossil leaves, representing primary consumers, is abundant, but also of low diversity, and overwhelmingly made by generalist feeders rather than specialized herbivores. Cerrejón megafossils provide strong evidence that the same Neotropical rainforest families have characterized the biome since the Paleocene, maintaining their importance through climatic phases warmer and cooler than present. The low diversity of both plants and herbivorous insects in this Paleocene Neotropical rainforest may reflect an early stage in the diversification of the lineages that inhabit this biome, and/or a long recovery period from the terminal Cretaceous extinction.

diversity | stability | paleoclimate | paleobotany | Fabaceae

The earliest modern writings on tropical rainforests attributed their diversity and ecologically specialized species to evolution occurring in a stable, unchanging habitat (1). Over the last few decades, in contrast, it has been proposed that Quaternary glacial cycles and environmental changes have caused repeated fluctuations in the area and species composition of tropical rainforests, leading many to discard the idea of long-term stability (2) and to propose that the diversity of Amazonian rainforests was achieved through geologically recent speciation in a variable environment (3). More recently, work on fossil pollen and spore records from northern South America has shown that changes in rainforest diversity through the Cenozoic were directly correlated with global temperature change, possibly because higher temperatures increased the areal extent of tropical rainforest (4).

Although studies of diversity and climatic fluctuations are important, they do not speak directly to the age of the Neotropical rainforest as defined by its characteristic taxonomic composition, diversity, and leaf physiognomy (5). Identification of a limited number of modern tropical forest families in the Late

Cretaceous, mostly from palynological data, has been used to argue that rainforest of modern composition has existed since that time (6–8), but several of these identifications have been questioned or overturned on more detailed examination (9–11) [*SI Appendix* (see Table S11)]. Other studies have inferred the existence of tropical rainforest from age-calibrated phylogenies of living angiosperm groups, such as Malpighiales, that are today widespread in this biome (12); however, these conclusions depend on accurate inference of the ages of nodes in the phylogeny from few fossil calibration points, and on untested assumptions about relative rates of diversification and extinction in different habitats. Furthermore, neither fossil pollen nor phylogenetic inference provide information about species level diversity, vegetational structure, plant physiognomy, or the type and abundance of insect folivory. The scarcity of Cretaceous and Paleogene tropical megafossils (5) has left the age of the Neotropical rainforest biome a key unanswered question.

Fossils from the Cerrejón Fm. of northern Colombia, reported here, show a relative abundance and diversity of plant families at approximately 58 Ma similar to modern Neotropical rainforest; like living rainforest, it was dominated in biomass and diversity by palms, legumes, laurales, malvales, menisperms, aroids, and zingiberaleans, among others (13–15). The similar composition of Paleocene and modern Neotropical rainforests suggests that these plant groups have managed to control a major portion of the ecological resources in this environment for a geologically long period, retaining dominance through times both warmer and cooler than today, and through major changes in the physiography of the continent (16).

Results

From coal strip-mine exposures of the Cerrejón Formation, we recovered 2,191 foliar fossils from 16 localities [Fig. 1, Table 1, and *SI Appendix* (see Fig. S1 and Table S1)] and segregated them into 65 morphotypes using leaf architectural characters [Fig. 2, Table 1, *SI Appendix* (see Figs. S2–S98 and Tables S1, S2, S10, and S11)]. The fossils include leaves of 46 nonmonocot angiosperms, 13 monocots, five ferns, and one conifer; we also recovered 33 types of compressed fruits and seeds [*SI Appendix* (see Figs. S65–S98)]. Between 19 (conservative) and 32 (best guess) of the leaf morphotypes could be assigned to families or

Author contributions: S.L.W., F.H., and C.A.J. designed research; S.L.W., F.H., C.A.J., C.G.-N., P.W., and C.C.L. performed research; S.L.W., C.A.J., P.W., and C.C.L. analyzed data; and S.L.W., F.H., C.A.J., and P.W. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

¹To whom correspondence should be addressed. E-mail: wings@si.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0905130106/DCSupplemental.

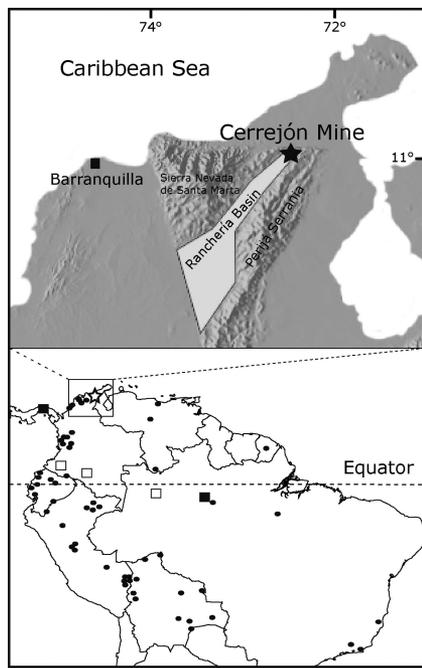


Fig. 1. Location of Cerrejón fossil flora and comparative modern samples. (Upper) Cerrejón fossil flora location (*). (Lower) Comparative modern samples are indicated by: □, Quaternary pollen cores; ■, modern leaf litter samples; ●, modern forest transects. See *SI Appendix* (Tables S1–S4) for details on comparative samples. Base map of Cerrejón region courtesy of National Aeronautics and Space Administration Jet Propulsion Laboratory, California Institute of Technology.

orders, the most diverse and abundant being: Araceae (six to seven leaf types), Arecaceae (two leaf types, three fruit types), Fabaceae (five to seven leaf types, seven fruit types), Lauraceae (two leaf types), Malvaceae (two to four leaf types), Menispermaceae [four leaf types (17), one fruit type], and Zingiberales

(two leaf types) [*SI Appendix* (see Table S10)]. Angiosperms so far identified to extant taxa below the family level include the Neotropical aroid *Montrichardia* (18) and a member of the palm subtribe Euterpeinae (19). The four, rare ferns belong to distinctive genera: the pantropical, floating-aquatic *Salvinia*; *Stenochlaena*, a common climbing fern in Old World tropical swamps; the cosmopolitan *Lygodium*; and *Acrostichum*, a pantropical fern common in freshwater and mangrove swamps.

To compare the familial/ordinal taxonomic composition of the Cerrejón megaf flora with that of extant lowland Neotropical forests, we selected 72 of Gentry's 0.1 hectare transects (20) as a comparative modern dataset [Fig. 1 and *SI Appendix* (see Table S5)]. The small size of the modern plots is a good match for the spatial scale of the parautochthonous Cerrejón fossil assemblages (21) and the minimum stem diameter of 2.5 cm at 1.5 m above the ground also simulates the dominance of woody plant remains in leaf litter and fossil leaf deposits (22). We excluded Gentry's sites from higher elevations and different climatic zones. For each modern site, we tabulated the proportions of species and individuals belonging to each family/order. For the fossils, we tabulated the proportion of leaf morphotypes in each family/order for the whole flora and the number of leaves in each family/order for random samples collected at two sites, 0307 and 0705 [*SI Appendix* (see Tables S2, S5, and S10)].

We quantified the similarities between all pairs of living and fossil samples by converting proportional diversity and proportional abundance values to rank orders and calculating Spearman's rank order correlation coefficient [Fig. 3 and *SI Appendix* (see Table S5)]. We used both the conservative and best guess taxonomic assignments for the fossil flora. In living forest plots, leaf abundance and stem basal area per species are strongly positively correlated (22), so we compared the rank order abundance of leaves (fossil samples) with stems (living forests) per family. The mean Spearman correlation coefficient between the Cerrejón and all extant sites was 0.20 (best guess taxonomy) or 0.22 (conservative taxonomy). These values did not differ significantly from the mean Spearman coefficient of 0.35 obtained by comparing rank order abundance of families among all

Table 1. Diversity and evenness of Cerrejón leaf and pollen floras compared with Paleogene fossils and Quaternary–Recent tropical samples

	Leaves										Pollen			
	Modern tropical litter			Paleogene temperate sites							Tropical Quaternary cores			
	Cerrejón	BCI	Rio Negro	W. Bijou	S. WY Ti	S. WY Cf	S. WY Eoc	N. WY Eoc	Castle Rock	Palacio de Loros	Cerrejón	Lagoa das Patas	Monica	Piusbi
No. sites	16	3	7	4	13	10	5	22	5	2	74	49	17	57
No. specimens	2,191	672	1,048	1,548	8,695	4,216	3,295	6,633	1,015	2,298	10,925	18,750	5,777	19,006
S_{total}	65	79	110	26	37	16	32	68	90	33	148	169	146	187
Mean S_{100}	18	24	21	9	6	4	7	9	30	18	17	24	31	27
Mean S_{alpha}	23	32	26	12	10	5	11	23	48	28	21	41	54	50
S_{beta}	34	47	84	14	27	11	21	56	42	5	127	128	92	137
Proportion S_{alpha}	0.40	0.40	0.23	0.47	0.26	0.32	0.34	0.18	0.46	0.85	0.14	0.24	0.37	0.27
Proportion S_{beta}	0.60	0.60	0.77	0.53	0.74	0.68	0.66	0.82	0.54	0.15	0.86	0.76	0.63	0.73
D_{total}	0.94	0.95	0.95	0.85	0.81	0.55	0.80	0.87	0.95	0.90	0.85	0.92	0.88	0.88
Mean PIE	0.83	0.86	0.88	0.76	0.60	0.25	0.46	0.73	0.91	0.88	0.75	0.89	0.86	0.87
Mean D_{alpha}	0.82	0.85	0.85	0.76	0.60	0.27	0.45	0.73	0.91	0.88	0.74	0.88	0.86	0.86
D_{beta}	0.13	0.09	0.10	0.09	0.21	0.28	0.34	0.14	0.04	0.02	0.11	0.04	0.02	0.02
Proportion D_{alpha}	0.87	0.90	0.89	0.90	0.74	0.48	0.57	0.84	0.96	0.98	0.87	0.96	0.98	0.98
Proportion D_{beta}	0.13	0.10	0.11	0.10	0.26	0.52	0.43	0.16	0.04	0.02	0.13	0.04	0.02	0.02

Information on sites is given in *SI Appendix* (Tables S1–S4); details of analysis are given in *SI Appendix* (Table S6). S_{total} , number of species in all samples; S_{alpha} , number of species within samples; S_{100} , number of species in sample rarefied to 100 specimens; S_{beta} , among sample diversity calculated using formula of Lande (38); D_{total} , Simpson's diversity index for all samples; D_{alpha} , Simpson's diversity index within samples; D_{beta} , among sample Simpson's diversity index calculated using the formula of Lande (38); PIE , Hurlbert's probability of interspecific encounter.

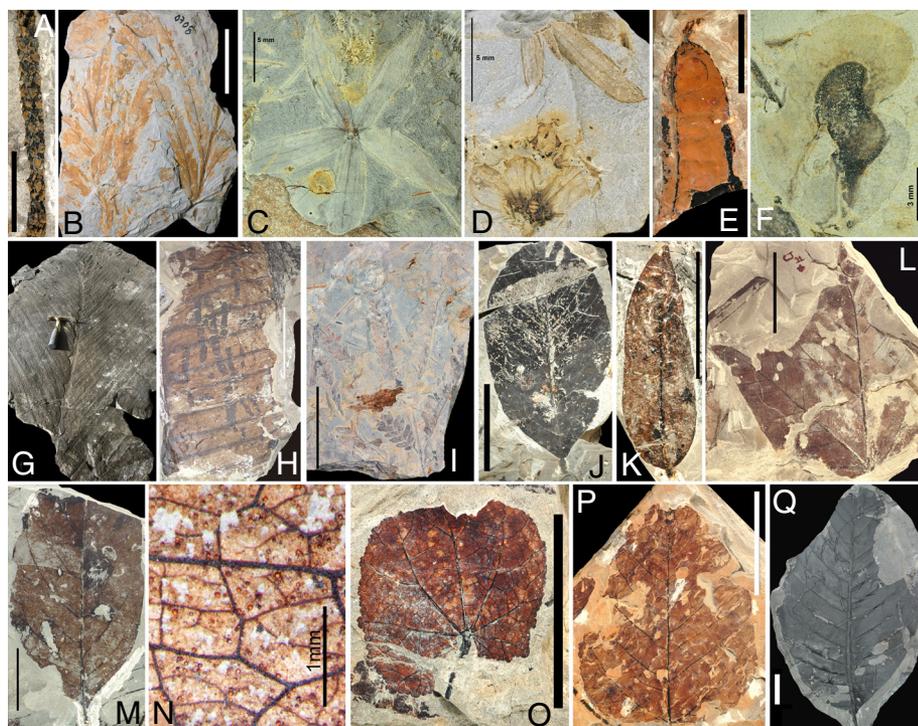


Fig. 2. Cerrejón megafossils identifiable to various higher taxa. (Scale bar: 5 cm, except where noted in parentheses after taxon.) (A) Coniferales (CJ60, 3 cm); (B) *Stenochlaena* (CJ81); (C and D) undetermined flowers (CJ77, CJ78); (E) fruit of Fabaceae (CJ100); (F) winged seed of Fabaceae (CJ79); (G) Arecaceae, possibly *Nypa* (CJ68, hammer \approx 30 cm); (H) Zingiberales (CJ65, 10 cm); (I–K) leaves and leaflets of Fabaceae (CJ76, CJ1, and CJ19); (L) Malvales with hole feeding (CJ11); (M) Lauraceae (CJ22); (N) closeup of M showing laminar resin glands (1 mm); (O) Malvaceae (CJ26); (P) Euphorbiaceae (CJ24); (Q) Sapotaceae with margin and hole feeding (CJ8). See *SI Appendix* (Table S10 and Figs. S2–S98) for descriptions and photographs of all morphotypes.

pairs of modern sites [*SI Appendix* (see Table S5)]. Calculating Spearman coefficients using rank order diversity (species or leaf morphotypes per family) showed even higher congruence between Cerrejón and the modern sites. The mean Spearman coefficient of Cerrejón with the modern sites was 0.30 (best guess) or 0.41 (conservative), whereas the mean Spearman coefficient among the modern sites was 0.38 [*SI Appendix* (see

Table S5)]. Thus, in terms of the rank-order diversity and abundance of plant families, the Cerrejón flora is within the range of living Neotropical lowland forest plots. Legumes and palms especially, the modern forest dominants in the region (14), were already established as diverse and abundant families during the late Paleocene. The diversity and abundance of legume megafossils at Cerrejón is particularly intriguing, because the Cerrejón legumes are among the earliest reliable records of the family (23, 24) (all from South America), which is thought to have diversified rapidly in the Paleocene (25).

We estimated the temperature under which the Cerrejón flora grew using the positive correlation observed in living floras between mean annual temperature (MAT) and the proportion of dicot species with untoothed leaves (*P*) (26, 27). Thirty-five of 45 dicot leaf types from Cerrejón are untoothed ($P = 0.78$), yielding estimates of MAT ranging from 24 °C (28) to 31 °C (29) depending on the regression used. The 95% confidence intervals of the MAT estimates are 2.1–2.7 °C using the method of Miller et al. (28). Like other wetland fossil assemblages, Cerrejón leaves likely overrepresent toothed leaf types in the regional vegetation and therefore underestimate MAT (30, 31). We thus favor an MAT estimate of ≥ 28 °C, which is consistent with oxygen isotopic estimates of late Paleocene tropical sea surface temperature from pristine foraminifer tests (28 °C at 58.5 Ma, 29.5 °C at 56.6 Ma) (32), and the MAT estimate of 32–33 °C derived from the exceptionally large-bodied fossil snakes recovered from the Cerrejón Formation (33). After deposition of the Cerrejón flora in the late Paleocene, global and tropical temperatures rose several degrees into the early Eocene (32, 34), almost certainly subjecting Neotropical rainforests to MATs higher than 30 °C.

We estimated precipitation for Cerrejón using correlations of leaf size and precipitation observed in living vegetation (35, 36). More than 50% of the dicot leaves in the Cerrejón flora are mesophyll or larger in size ($>1,900$ mm²), which is striking given the preservational biases against large leaves (37). We infer mean annual precipitation (MAP) of 3,240 mm (range 2,260–4,640 mm), which is probably an underestimate (35). Surpris-

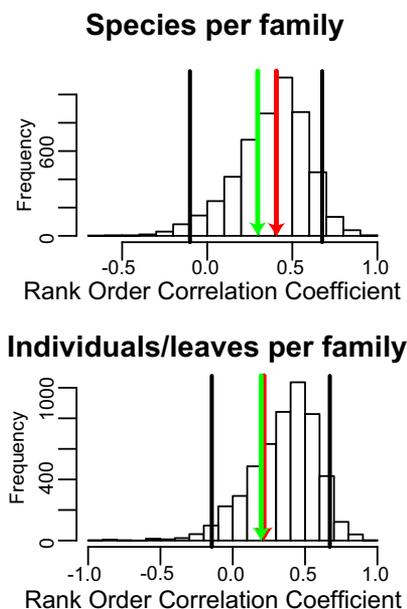


Fig. 3. Similarity of the Cerrejón megafauna to living Neotropical forests. Histograms are the frequency distributions of Spearman rank order correlation coefficients derived from all pairwise comparisons of 72 living forest sites [*SI Appendix* (see Table S5)]. Arrows show the mean similarity of the Cerrejón flora to all living sites (red, conservative identifications of fossils; green, best-guess identifications). Black lines represent 95% confidence intervals. See *SI Appendix* (Table S5) for additional information.

ingly, given the large size of Cerrejón fossil dicot leaves, only three of 27 morphotypes (11%) with preserved apices have drip tips, whereas modern tropical forests typically have 25–75% of species with drip tips (5). The low proportion of drip tips among Cerrejón fossil leaves may result from a taphonomic bias against their preservation or a real difference in optimal leaf shape reflecting Paleocene climatic and/or atmospheric conditions different from present. Using petiole widths and areas of the fossil leaves combined with the scaling relationship observed in living plants between petiole width squared and leaf mass (38), we estimate a mean leaf mass per area of 92 g/m² (95% prediction interval \pm 9 g/m²) from 24 morphotypes that have preserved petioles and estimable leaf areas [SI Appendix (see Table S7)]. The low mean and narrow range (44–125 g/m²) in leaf mass per area are typical of evergreen tropical forests with >3,000 mm MAP (39). The abundant, thick beds of low-ash, low-sulfur coal in the Cerrejón Fm. also indicate a wet climate (40).

We compared the diversity of palynomorph and leaf fossil samples from Cerrejón with taphonomically similar samples from the Quaternary–Recent Neotropics and midlatitude Paleogene leaf sites [Fig. 1, Table 1, and SI Appendix (see Tables S1–S4 and S6)]. For diversity analyses, we used all leaf morphotypes, not just those assigned to higher taxa. For each sample, we calculated rarefied richness at 100 specimens (S_{100}) to standardize for sample size differences (41) and also Hurlbert's probability of interspecific encounter (PIE) as a measure of the evenness of relative abundance distribution independent of sample size (42). We also examined richness and evenness at the spatial scale of samples (alpha) and sites (beta) through additive partitioning (43) (Table 1).

The mean rarefied richness of Cerrejón leaf samples (derived from small fluvial channels) is 2–4.5 \times that of similar parautochthonous leaf assemblages from the Paleocene and Eocene midlatitudes of North America ($P < 0.0001$) [Table 1 and SI Appendix (see Table S6)], equivalent to that of the Palacio de los Loros compression flora from the Paleocene (\approx 62 Ma) of central Patagonia (23), but only 80% of that of the modern tropical litter samples, and 60% of the highly diverse Castle Rock flora from the Paleocene of Colorado (44) ($P < 0.003$). Values of PIE for Cerrejón samples are not statistically different from those of modern tropical forest litter, Palacio de los Loros, or Castle Rock, but they are significantly higher ($P < 0.002$) than those of most Paleocene–Eocene North American sites. Beta richness at Cerrejón is high compared with many of the North American Paleogene fossil sites but much lower than that seen in tropical litter and at Castle Rock (Table 1). Cerrejón plant diversity is lower than modern tropical floras but higher than most contemporary midlatitude samples at both the spatial scale of individual leaf samples (1–3 m² derived from a local area of forest) and of sites (groups of samples derived from a few km² or less). We note that the Cerrejón leaf samples were collected from a stratigraphic interval several hundred meters thick, therefore certainly spanning more time than any of the other fossil sites. Given the larger temporal range at Cerrejón, its beta diversity would be expected to be much higher.

Palynomorphs generally permit taxonomic discrimination at the generic or family rather than at the species level, but because they are more easily transported, they represent a larger area of vegetation than do leaves (45). We compared 74 Cerrejón pollen samples (excluding those from coal- or marine-influenced rocks that might be depauperate because of edaphic conditions or transport) with tropical rainforest palynofloras sampled from Quaternary cores (Table 1 and SI Appendix (see Tables S1 and S6)). The mean rarefied richness of Cerrejón pollen samples is approximately two-thirds that of the Quaternary Amazonian samples ($P \ll 0.001$) [Table 1 and SI Appendix (see Table S6)]. Mean evenness of Cerrejón pollen samples is 85% that of the Quaternary tropical samples, also highly significant ($P \ll 0.001$).

Although alpha richness and evenness are substantially lower at Cerrejón, beta richness is similar to that seen in the Quaternary cores, and the beta component of evenness is higher at Cerrejón. Relatively high beta richness and evenness at Cerrejón suggests heterogeneity in the composition of Paleocene Neotropical vegetation at larger scales, although again the Cerrejón samples represent far more time than the Quaternary cores, so this heterogeneity may record temporal more than spatial variation.

An inspection of 507 well-preserved fossil leaves from Cerrejón showed that 50% of the specimens had been attacked by herbivorous insects, significantly more than any midlatitude Paleocene flora. However, considering the elevated incidence of insect damage both on the bulk sample and on individual host species, the diversity of damage types is not high (46) [SI Appendix (see Tables S8 and S9)]. Insect damage at Cerrejón is overwhelmingly external foliage feeding that could have been made by relatively few species of insects (47). Specialized feeding, particularly mining, galling, and piercing-sucking, is also rare, a pattern seen in nearly all but the latest Paleocene floras of North America (46). Thus, the Cerrejón flora records high herbivore pressure, as is seen in modern Neotropical rainforests (48), but without the characteristic elevated insect-feeding diversity and host-specialized feeding associations (49).

Discussion and Conclusions

Cerrejón pollen, leaves, and insect-feeding damage consistently demonstrate local diversity in the Paleocene that is low compared with extant Neotropical rainforest, but we cannot yet be sure if this low diversity characterizes the Paleocene Neotropical biome or is a more local phenomenon. Fossil leaf assemblages, particularly those from low-energy depositional environments like Cerrejón, are dominated by local plants (21). The low diversity of the Cerrejón leaf assemblages could thus reflect their source in tropical wetland vegetation, which even today can be somewhat less diverse on a per-area basis than surrounding better-drained areas (50). Palynomorph samples record a larger area of vegetation than do leaves, but are still local enough to show some compositional differences among different fluvial subenvironments at the same stratigraphic level (51); therefore Cerrejón pollen samples could be dominated by wetland vegetation of lower diversity than typical terra firme forest. Other evidence, however, suggests that Cerrejón fossil assemblages are representative of the broader Neotropical region. Paleocene pollen samples from across much of northern South America have similar composition to those from Cerrejón (4), and recent collections of leaf fossils from Paleocene deposits near Bogotá, Colombia share many taxa with the Cerrejón flora. If Paleocene Neotropical rainforests were less diverse than extant ones, despite existing in a warm, wet climate and being composed of the same plant families, this low diversity would be consistent with ecosystems in an early stage of diversification, and/or a long recovery period after the end-Cretaceous mass extinction. Preliminary pollen data suggest a 70% extinction at the end of the Cretaceous in tropical South America (52), and a recently found flora from the Maastrichtian Guaduas Fm. of Colombia lacks the most abundant families present at Cerrejón, consistent with major floral turnover at the end of the Cretaceous. The low diversity and generalized nature of insect feeding damage on Cerrejón leaves also is consistent with the idea that Neotropical terrestrial ecosystems were still recovering from the end-Cretaceous extinction in the late Paleocene.

The approximately 58 million-year-old Cerrejón flora, which matches extant Neotropical rainforest in family composition, demonstrates that despite fluctuations in climate and forest area, the same families have dominated this biome since the Paleocene. Evidently, major long-term environmental changes, such as high equatorial temperatures during the Eocene, Neogene uplift of the Andes, and Quaternary cycles of cooling and drying,

have not dislodged palms, legumes, aroids, malvaceans, and other groups from their important roles in Neotropical rainforest. However, the low diversity of the Cerrejón flora and its herbivores is consistent with the idea of a major extinction and change in floral composition of Neotropical vegetation at the end-Cretaceous extinction.

Materials and Methods

Geological and Collecting Information. The Cerrejón Formation consists of approximately 800 m of sandstone, mudstone, and coal that were deposited in a mosaic of fluvial, lacustrine, and estuarine environments on a coastal plain facing the Tethys Sea during the middle-late Paleocene (53). Sediments were probably derived from early uplift in the Sierra Nevada de Santa Marta to the west (53). The formation is now exposed in coal strip mines near the base of the Guajira Peninsula at $\approx 11.1^\circ\text{N}$, 72.5°W (paleolatitude $\approx 5.5^\circ\text{N}$) (Fig. 1). Early reports on the Cerrejón flora showed that leaf cuticle was preserved (54), but there has been little additional work on the fossils until the last few years.

We collected fossil leaves and fruits from six lens-shaped, siltstone/sandstone bodies with inclined heterolithic strata that suggest deposition in low-energy channels. Ten other localities preserve leaves in thin but tabular beds of flat-laminated siltstone that indicate deposition in small lakes. The megafossil localities occur from 100–750 m above the base of the formation [SI Appendix (see Fig. S1)]. We also collected 91 samples for palynological analysis from two cores spanning the interval from 400–795 m (coal beds 100–156) and averaging one sample per 4.3 m. The palynological assemblages belong to the *Foveotricolpites*

perforatus zone and zone Cu-02, indicating a middle-to-late Paleocene age based on stable carbon isotope stratigraphy and cooccurrence of these pollen zones with marine microfossils in other areas (54).

ACKNOWLEDGMENTS. This research was made possible through the collaboration and assistance of Leon Teicher, Fernando Chavez, and the geology team at Minas Cerrejón. We thank Hernan Antolinez, German Bayona, Jon Bloch, Edwin Cadena, Edwin Correa, David Dilcher, Gabriela Doria, Regan Dunn, Beth Ellis, Paola Florez, Ivan Gutierrez, Kirk Johnson, Camilo Montes, Felipe de la Parra, Angelo Plata, Monica Ramirez, Aldo Rincon, Carlos Sanchez, Carolina Vargas, and Erik Wing for help with field work in Colombia and Brazil. Hermann Behling shared unpublished data from the Piusbi1 and Monica1 cores; Lagoa das Patas data were downloaded from the Latin American Pollen Database, <http://www.ncdc.noaa.gov/paleo/lapd.html>. Beth Ellis provided updated information on the Castle Rock flora. Walton Green collaborated in writing R scripts for the additive diversity analysis, available at <http://www.bricol.net/stratigraph/>. Daniel Peppe shared an unpublished compilation of leaf margin data that influenced our thinking about leaf physiognomic analyses. C.J. thanks the Biostratigraphic Team at the Colombian Petroleum Institute, Universidad Industrial de Santander of Colombia, and M. I. Barreto for her support and ideas. This work was funded by Carbones del Cerrejón, The Explorers Club (Youth Activity Fund grant) (F.H. and C.G.), Corporación Geológica Ares, the Colombian Petroleum Institute, Fondo para la Investigación de la Ciencia y Tecnología del Banco de la República of Colombia, United States National Science Foundation grants (C.J. and P.W.), the Ryan Family Foundation (P.W.), and the Smithsonian Institution. This paper is contribution 177 of the Evolution of Terrestrial Ecosystems Program at the National Museum of Natural History in Washington, D.C.

- Wallace AR (1878) *Tropical Nature and Other Essays* (McMillan, New York), p 377.
- Hooghiemstra H, Van der Hammen T (1998) Neogene and Quaternary development of the Neotropical rain forest: The forest refugia hypothesis, and a literature overview. *Earth Sci Rev* 44:147–183.
- Richardson JE, Pennington RT, Pennington TD, Hollingsworth PM (2001) Rapid diversification of a species-rich genus of Neotropical rain forest trees. *Science* 293:2242–2245.
- Jaramillo C, Rueda MJ, Mora G (2006) Cenozoic plant diversity in the Neotropics. *Science* 311:1893–1896.
- Burnham RJ, Johnson KR (2004) South American palaeobotany and the origins of Neotropical rainforests. *Philos Trans R Soc Lond Ser B* 359:1595–1610.
- Germeraad JH, Hopping CA, Muller J (1968) Palynology of Tertiary sediments from tropical areas. *Rev Palaeobot Palynol* 6:189–198.
- Muller J (1981) Fossil pollen records of extant angiosperms. *Bot Rev* 47:1–142.
- Morley RJ (2000) *Origin and Evolution of Tropical Rain Forests* (John Wiley and Sons, Chichester, UK), p 362.
- Herendeen P, Crepet W, Dilcher D (1992) The fossil history of the Leguminosae: Phylogenetic and biogeographic implications. In *Advances in Legume Systematics, Part 4. The Fossil Record*, eds Herendeen P, Dilcher D (Kew Publishing, Surrey, UK), pp 303–316.
- Hesse M, Zetter R (2007) The fossil pollen record of Araceae. *Plant Syst Evol* 263:93–115.
- Zetter R, Hesse M, Frosch-Radivo A (2001) Early Eocene zona-aperturate pollen grains of the *Proxapertites* type with affinity to Araceae. *Rev Palaeobot Palynol* 117:267–279.
- Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ (2005) Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *Am Nat* 165:E36–E65.
- Gentry AH (1988) Tree species richness of upper Amazonian forests. *Proc Natl Acad Sci USA* 85:156–159.
- Terborgh J, Andresen E (1998) The composition of Amazonian forests: Patterns at local and regional scales. *J Trop Ecol* 14:645–664.
- ter Steege H, et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443:444–447.
- Antonelli A, Nylander JAA, Persson C, Sanmartin I (2009) Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proc Natl Acad Sci USA* 106:9749–9754.
- Doria G, Jaramillo C, Herrera F (2008) Menispermaceae from the Cerrejón formation, middle to late Paleocene, Colombia. *Am J Bot* 95:954–973.
- Herrera F, Jaramillo C, Dilcher DL, Wing SL, Gómez-Navarro C (2008) Fossil Araceae from a Paleocene Neotropical rainforest in Colombia. *Am J Bot* 95:1–16.
- Gómez-Navarro C, Jaramillo CA, Herrera FA, Callejas R, Wing SL (2009) Palms (Arecaceae) from a Paleocene rainforest of northern Colombia. *Am J Bot* 96:1300–1312.
- Phillips O, James M, Gentry A (2002) *Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set* (Missouri Botanical Garden Press, St. Louis), p 319.
- Davies-Vollum KS, Wing SL (1998) Sedimentological, taphonomic, and climatic aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, WY). *Palaio* 13:28–40.
- Burnham RJ, Wing SL, Parker GG (1992) The reflection of deciduous forest communities in leaf litter—implications for autochthonous litter assemblages from the fossil record. *Paleobiology* 18:30–49.
- Iglesias A, et al. (2007) A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* 35:947–950.
- Brea M, Zamuner A, Matheos S, Iglesias A, Zucol A (2008) Fossil wood of the Mimosoideae from the early Paleocene of Patagonia, Argentina. *Alcheringa* 32:427–441.
- Lavin M, Herendeen PS, Wojciechowski MF (2005) Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the Tertiary. *Syst Biol* 54:575–594.
- Wolfe JA (1979) Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions in the Northern Hemisphere and Australasia. *US Geological Survey Professional Paper* 1106:1–37.
- Adams JM, Green WA, Zhang Y (2008) Leaf margins and temperature in the North American flora: Recalibrating the paleoclimatic thermometer. *Glob Planet Change* 60:523–534.
- Miller IM, Brandon MT, Hickey LJ (2006) Using leaf margin analysis to estimate the mid-Cretaceous (Albian) paleolatitude of the Baja BC block. *Earth Planet Sci Lett* 245:95–114.
- Kowalski EA, Dilcher DL (2003) Warmer paleotemperatures for terrestrial ecosystems. *Proc Natl Acad Sci USA* 100:167–170.
- Burnham RJ, Pitman NCA, Johnson KR, Wilf P (2001) Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. *Am J Bot* 88:1096–1102.
- Royer DL, Kooymann RM, Little SA, Wilf P (2009) Ecology of leaf teeth: A multi-site analysis from an Australian subtropical rainforest. *Am J Bot* 96:738–750.
- Pearson PN, et al. (2007) Stable warm tropical climate through the Eocene Epoch. *Geology* 35:211–214.
- Head JJ, et al. (2009) Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* 457:715–717.
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–693.
- Wilf P, Wing SL, Greenwood DR, Greenwood CL (1998) Using fossil leaves as paleoprecipitation indicators: An Eocene example. *Geology* 26:203–206.
- Jacobs BF, Herendeen PS (2004) Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania. *Palaeoogeogr Palaeoecol* 213:115–123.
- Roth J, Dilcher DL (1978) Some considerations in leaf size and leaf margin analysis of fossil leaves. *Cool Forschungsinst Senckenb* 30:165–171.
- Royer DL, et al. (2007) Fossil leaf economics quantified: Calibration, Eocene case study, and implications. *Paleobiology* 33:574–589.
- Wright IJ, et al. (2005) Modulation of leaf economic traits and trait relationships by climate. *Glob Ecol Biogeogr* 14:411–421.
- Lottes AL, Ziegler AM (1994) World peat occurrence and the seasonality of climate and vegetation. *Palaeoogeogr Palaeoecol* 106:23–37.
- Hurlbert SH (1971) The nonconcept of species diversity: A critique and alternative parameters. *Ecology* 52:577–586.
- Olszewski TD (2004) A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* 104:377–387.
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Ellis B, Johnson KR, Dunn RE (2003) Evidence for an in situ early Paleocene rainforest from Castle Rock, Colorado. *Rocky Mountain Geology* 38:73–100.
- Traverse A (1988) *Paleopalynology* (Unwin Hyman, Boston).
- Wilf P, Labandeira CC, Johnson KR, Ellis B (2006) Decoupled plant and insect diversity after the end-Cretaceous extinction. *Science* 313:1112–1115.
- Basset Y, Höft R (1994) Can apparent leaf damage in tropical trees be predicted by herbivore load or host-related variables? A case study in Papua New Guinea. *Selbyana* 15:3–13.

48. Coley PD, Aide TM (1991) Comparisons of herbivory and plant defenses in temperate and tropical broad-leaved forests. In *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, eds Price PW, Lewinsohn TM, Fernandes GW, Benson WW (John Wiley and Sons, New York), pp 25–49.
49. Dyer LA, et al. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448:696–699.
50. Macia MJ, Svenning JC (2005) Oligarchic dominance in western Amazonian plant communities. *J Trop Ecol* 21:613–626.
51. Farley MB (1989) Palynological facies fossils in nonmarine environments in the Paleogene of the Bighorn Basin. *Palaios* 4:565–573.
52. De la Parra F, Jaramillo CA, Dilcher DL (2007) Paleocological changes of spore producing plants through the Cretaceous-Paleocene boundary in Colombia. *Palynology* 32:258–259.
53. Jaramillo C, et al. (2007) Palynology of the Upper Paleocene Cerrejón Formation, Northern Colombia. *Palynology* 31:153–189.
54. Doubinger J, Pons D (1970) Les cuticules dispersées du Crétacé et du Tertiaire de Colombie. *Geología Colombiana* 7:79–98.