

Eocene Plant Diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina

Peter Wilf,^{1,*} Kirk R. Johnson,^{2,†} N. Rubén Cúneo,^{3,‡} M. Elliot Smith,^{4,§} Bradley S. Singer,^{4,||} and Maria A. Gandolfo^{5,#}

1. Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802;

2. Department of Earth Sciences, Denver Museum of Nature and Science, Denver, Colorado 80205;

3. Museo Paleontológico Egidio Feruglio, Trelew, Chubut 9100, Argentina;

4. Department of Geology and Geophysics, University of Wisconsin, Madison, Wisconsin 53706;

5. L. H. Bailey Hortorium, Department of Plant Biology, Cornell University, Ithaca, New York 14853

Submitted October 1, 2004; Accepted February 9, 2005;

Electronically published April 7, 2005

Online enhancement: appendix.

ABSTRACT: The origins of South America's exceptional plant diversity are poorly known from the fossil record. We report on unbiased quantitative collections of fossil floras from Laguna del Hunco (LH) and Río Pichileufú (RP) in Patagonia, Argentina. These sites represent a frost-free humid biome in South American middle latitudes of the globally warm Eocene. At LH, from 4,303 identified specimens, we recognize 186 species of plant organs and 152 species of leaves. Adjusted for sample size, the LH flora is more diverse than comparable Eocene floras known from other continents. The RP flora shares several taxa with LH and appears to be as rich, although sampling is preliminary. The two floras were previously considered coeval. However, ⁴⁰Ar/³⁹Ar dating of three ash-fall tuff beds in close stratigraphic association with the RP flora indicates an age of 47.46 ± 0.05 Ma, 4.5 million years younger than LH, for which one tuff is reanalyzed here as 51.91 ± 0.22 Ma. Thus, diverse floral associations in Patagonia evolved by the Eocene, possibly in response to global warming, and were persistent and areally extensive. This suggests

extraordinary richness at low latitudes via the latitudinal diversity gradient, corroborated by published palynological data from the Eocene of Colombia.

Keywords: biodiversity, Eocene, geochronology, paleobotany, paleoclimate, Patagonia.

South American floras today are marked by high diversity and endemism. Most notably, Neotropical plant diversity exceeds other tropical regions by factors of two to three (Gentry 1988b; Davis et al. 1997; Phillips and Miller 2002). Elevated richness exists outside of the main equatorial belt, including the Mata Atlántica region of southeastern Brazil (Mori and Boom 1981). Davis et al. (1997) designated 46 areas of the continent as centers of floral diversity and endemism, including several extratropical locales such as the central Chilean Mediterranean region and the Gran Chaco of Brazil, Bolivia, Argentina, and Paraguay.

Because of a general lack of reliable, quantitative data from plant macrofossils, remarkably little is known about the origins, history, and geologic context of South American floral diversity, especially before the Pleistocene. Modern tropical weathering, vegetative cover, a paucity of investigators, and the obsolescence of historical reports account for the scarcity of information from equatorial latitudes for the Paleogene (Romero 1986; Mello et al. 2002; Burnham and Johnson 2004) and Neogene (Burnham and Graham 1999). Most hypotheses for the Neotropical region have emphasized geologically recent events. Neogene uplift of the Andes is thought to have fostered diversification (Van der Hammen and Hooghiemstra 2000; Colinvaux and De Oliveira 2001), and a palynological study indicates high floral richness during the Miocene in Colombia (Hoorn 1994). The prevailing model for several decades, that Pleistocene rain forest refugia catalyzed current biodiversity as sites of allopatric speciation (Haffer 1969; Haffer and Prance 2001), has been strongly challenged (Nelson et al. 1990; Colinvaux et al. 1996, 2001; Moritz et al. 2000; Kastner and Goñi 2003). Evidence for timing of diversification in various lineages mostly comes

* Corresponding author; e-mail: pwilf@psu.edu.

† E-mail: kjohnson@dmns.org.

‡ E-mail: rcuneo@mef.org.ar.

§ E-mail: msmith@geology.wisc.edu.

|| E-mail: bsinger@geology.wisc.edu.

E-mail: mag4@cornell.edu.

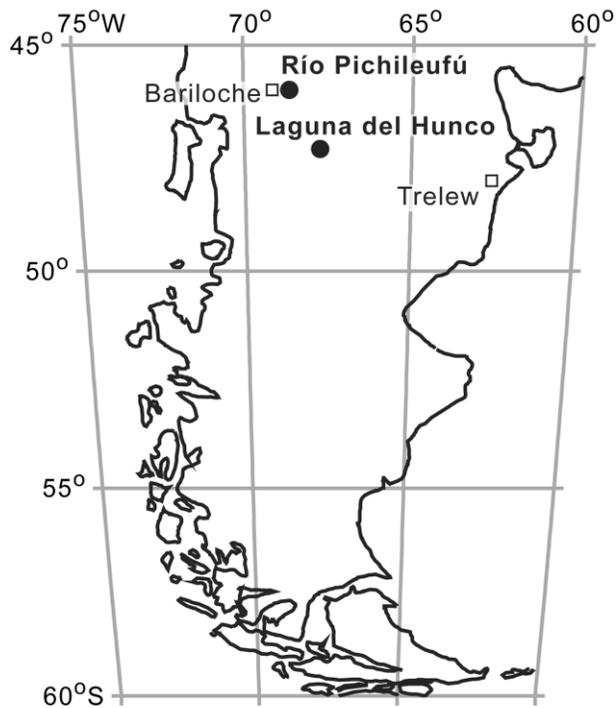


Figure 1: Locations of Laguna del Hunco, Río Pichileufú, and cities mentioned in text, mapped onto 50-Ma positions of modern coastlines, Mollweide Projection. Reconstruction made using the Plate Tectonic Reconstruction Service of the Ocean Drilling Stratigraphic Network, <http://www.odsn.de/odsn/services/paleomap/paleomap.html>, based on data from Hay et al. (1999).

from molecular clock studies, constrained using the few fossil data that are taxonomically reliable (Richardson et al. 2001; Bremer 2002; Davis et al. 2004, 2005).

In contrast to conventional literature, two recent investigations indicate elevated plant diversity in South America during the early Eocene, 30 million years before significant Andean uplift, 50 million years before the Pleistocene, and on a warm and humid continent without Pleistocene analog refugia. First, palynological data from Colombia quantify significant, apparently in situ plant diversification in association with global warming and increasing regional precipitation across the Paleocene/Eocene boundary (Jaramillo and Dilcher 2000; Jaramillo 2002). Second, and antecedent to this article, is a preliminary macrofloral study from Laguna del Hunco (LH) in the northern Patagonian region of Argentina (Wilf et al. 2003; fig. 1). During the globally warm Eocene, when tropical organisms reached middle and high latitudes of both hemispheres (Estes and Hutchison 1980; Greenwood and Wing 1995), LH was located near the southern limit of Neotropical floral influence (Romero 1978, 1986, 1993;

Hinojosa and Villagrán 1997). Today, LH is a desert area with abundant exposures of fossiliferous strata. Analyses of quantitative, stratigraphically controlled, unbiased collections suggested that when adjusted for sample size, LH is the most diverse fossil flora of Eocene age known anywhere in the world (Wilf et al. 2003). However, sample sizes at individual quarries were small compared to North American floras used for comparison (~175–315 specimens vs. typically more than 500 specimens). The report also demonstrated that data from elsewhere in Patagonia are needed to test the pattern of elevated floral richness in time and space.

New results are presented here from significantly expanded collections at Laguna del Hunco and initial collections from Río Pichileufú (RP; fig. 1), a rich Eocene site about 160 km NNW of LH that has received negligible investigation since the 1930s (Berry 1938). We test the observation of elevated floral diversity at Laguna del Hunco using a sample size approximately triple that of the preliminary report (Wilf et al. 2003). We use paleoecological data to ask whether the LH floras are compositionally stable through time, and we refine paleoclimatic estimates and biome interpretation. Using the first quantitative paleobotanical data from Río Pichileufú, we ask whether its flora had diversity comparable to LH. An accurate geochronology for the floras, conventionally assumed to be coeval, is critical for addressing several ecological questions, including persistence. We analyze ashfall tuffs intimately associated with the fossil plants at RP to determine the first high-precision ages for the flora, and we reanalyze a tuff from LH to resolve its age more finely. We conclude by discussing the implications of our results for understanding past and present South American biodiversity.

Laguna del Hunco and Río Pichileufú Floras

Overview and Previous Work

The classic fossil floras from Laguna del Hunco (“Lake of Reeds”) and Río Pichileufú (“Little River”) have a long history of investigation (Berry 1925, 1938), and they feature prominently in phytogeographic and paleoclimatic literature about the continent (Menéndez 1971; Aragón and Romero 1984; Romero 1986, 1993; Hinojosa and Villagrán 1997) and the Southern Hemisphere in general (Christophel 1980; Hill 1994). However, these assemblages are historically understudied and are mostly represented by small museum collections made from limited numbers of quarries collected near the surface without reliable stratigraphic or relative abundance data.

The two floras feature very good (RP) to outstanding

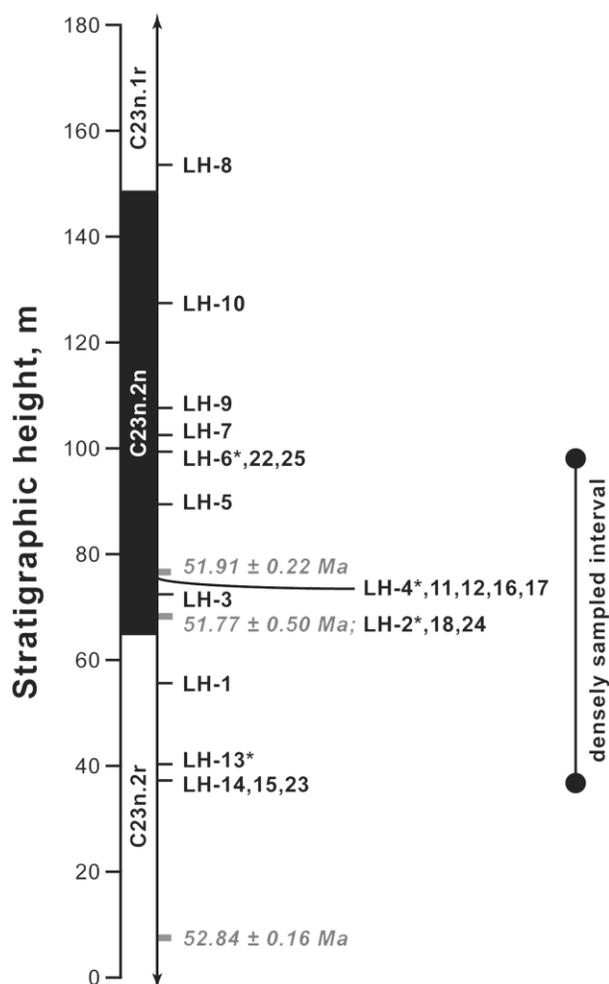


Figure 2: Stratigraphic section of the Tufolitas Laguna del Hunco, revised and simplified from Wilf et al. (2003). Shown are the stratigraphic positions of fossil plant localities (LH-1 to LH-25), the samples yielding radiometric ages (*numbers in gray*), including the reanalyzed age reported here for the uppermost sample, and the paleomagnetic interpretation. Asterisks indicate the four major sampling localities. Only 10 identifiable fossils were found above the labeled densely sampled interval. Localities 19, 20, and 21 are stratigraphically isolated and not included in the figure. See Wilf et al. (2003) for details of stratigraphy, lithology, and paleomagnetic and previous radioisotopic analyses.

(LH) preservation and are located at similar middle paleolatitudes in the Patagonian region of Argentina (fig. 1). Laguna del Hunco is a desert pond in Chubut Province, located in the midst of the major fossil exposures. The floras from LH are the major focus of this article because of our extensive, recent collections; they are well exposed and feature exceptional preservation equal to that of well-known Eocene floras from North America such as Florissant (MacGinitie 1953) and Republic (Wolfe and Wehr 1987). The Río Pichileufú flora is located near the epon-

ymous stream in Río Negro Province, 160 km northwest of LH, and we report preliminary data based on initial collections.

No significant uplift of the Southern Central Andes occurred before the Miocene (Marshall and Salinas 1990); Eocene Laguna del Hunco lay at a low elevation, and a significant maritime influence moderated its climate. The LH flora was deposited in tuffaceous mudstones and sandstones of the Tufolitas Laguna del Hunco, a lacustrine unit of the middle Chubut River volcanic-pyroclastic complex (Aragón and Romero 1984; Aragón and Mazzoni 1997) and is inferred to represent lakeshore vegetation (Wilf et al. 2003). The RP flora comes from volcanic lake beds of the Ventana Formation and is probably similar in depositional setting to LH (fig. 1; González Díaz 1979; Aragón and Romero 1984). The LH tuffs are well exposed over an area of more than 25 km in diameter (Aragón and Mazzoni 1997), but fossiliferous horizons at Río Pichileufú are restricted to a single small drainage (<300 m of map distance separates the fossil quarries). Compressions of flowers, fruits, seeds, and especially leaves are abundant at both sites. At LH, fossil fish, insects (Fidalgo and Smith 1987; Petrulovicus and Nel 2003), caddis-fly cases (Genise and Petrulovicus 2001), and pipoid frogs (Casamiquela 1961; Báez and Trueb 1997) are present on the same bedding planes as the plants. At RP, large-bodied ants, probably referable to *Archimymex piaznitzkyi* (Viana and Haedo-Rossi 1957; Dlussky and Perfilieva 2003), co-occur with plants, as do frogs (P. Wilf and K. R. Johnson, personal observation).

Fossil plants at Laguna del Hunco were discovered during the 1920s (Clark 1923; Berry 1925), and occasional new descriptions and taxonomic revisions have since been published (Berry 1938; Frenguelli and Parodi 1941; Frenguelli 1943*a*, 1943*b*; Traverso 1964; Romero and Hickey 1976; Durango de Cabrera and Romero 1986; Gandolfo et al. 1988; Romero et al. 1988; González et al. 2002). The total number of formally described entities referable to surviving voucher specimens is about 44 species of leaves, fruits, and seeds, nearly all in need of taxonomic revision: only six species have been described or revised since 1945. The age of the flora was originally reported as Miocene (Berry 1925) and later, from $^{40}\text{K}/^{40}\text{Ar}$ analyses of associated volcanic rocks, was assigned ages ranging from late Paleocene to middle Eocene (Archangelsky 1974; Mazzoni et al. 1991).

The Río Pichileufú flora is the most diverse from Cenozoic South America, with more than 130 formally described entities (Berry 1935*a*, 1935*b*, 1935*c*, 1938); this figure remains a useful starting estimate of richness. However, despite its diversity, very good to excellent preservation, and accessibility from San Carlos de Bariloche (fig. 1), the flora has been little studied since Berry's historic

Table 1: Sampling and taphonomic data for the four principal quarries at Laguna del Hunco (LH)

	LH-13	LH-2	LH-4	LH-6
Meter level (fig. 2)	40.30	68.18	75.63	99.28
Excavated fossiliferous volume (m ³)	1.4	2.0	1.8	1.9
Plant fossil density (specimens/m ³)	1,008	710	929	535
Plant specimens:				
Total	1,451	1,406	1,672	995
Identifiable	1,123 (77%)	647 (46%)	1,268 (76%)	685 (69%)
Leaves, ID'd	1036	626	1260	642
Dicot leaves, ID'd	806	609	1248	530
Dicot reproductive	30	18	7	34
Conifer leaves	218	10	6	86
Conifer reproductive	57	3	0	7
Fern leaves	5	3	5	3
Dicot leaf specimens toothed (%)	38.3	56.7	76.3	47.4
Mean area of all dicot leaves, ln (mm ²)	6.78 ± .92	6.83 ± .91	7.05 ± .85	6.91 ± .95
Helicopter fruits, abundance/species	0/0	0/0	1/1	4/2
Fish fossils	Absent	Absent	Absent	Articulated
Insect accumulations	Present	Absent	Absent	Present
Insect abundance ^a	15%	5%	5%	76%
Interpretation: rank distance from shoreline	2	3	4	1

^a Number of body fossils in 2002 collections divided by the number from all four major localities combined.

efforts. It has been considered approximately coeval to LH on the basis of shared plant species (Berry 1938; Petersen 1946; Arguijo and Romero 1981; Aragón and Romero 1984; Markgraf et al. 1996; Hinojosa and Villagrán 1997), but until recently, neither flora had been reliably dated. Biostratigraphic and ⁴⁰K/⁴⁰Ar analyses of the Ventana Formation from sites with uncertain stratigraphic relationships to the RP flora have suggested ages ranging from late Paleocene to early Oligocene (González Díaz 1979; Rapela et al. 1988).

In November of 1999, our group completed the first stratigraphically controlled, quantitative collection of the LH floras (Wilf et al. 2003). From a 170-m stratigraphic section (fig. 2), we excavated 25 quarries and collected or systematically tallied 1,583 identifiable macrofossil specimens without collection bias (totals and analyses for 1999 collections revised slightly in this article for recently identified material). Plant diversity at LH was compared to and exceeded seven North American midlatitude assemblages that have been collected using similar methods. Of these, a collection of the lacustrine Republic flora from Washington, made by K. R. Johnson and colleagues from Denver Museum of Nature and Science locality 2130 and preliminarily analyzed (Passmore et al. 2002), was the most diverse. Three ⁴⁰Ar/³⁹Ar analyses from tuffs discovered within the LH fossiliferous sequence, coupled with six paleomagnetic reversals, calibrated the fossiliferous strata to ages near 52 Ma and near the base of magnetic polarity Chron 23 (Wilf et al. 2003; fig. 2). These results date the LH flora to the early Eocene climatic optimum, a 1–2-million-year

interval that featured the warmest sustained high temperatures of the Cenozoic (Zachos et al. 2001).

Biome Characterization and Biogeography

Several reconstructions of the warm early Eocene place the RP and LH floras within tropical rain forest areas. According to Morley (2000), tropical rain forest usually requires a minimum mean monthly temperature above 18°C, annual precipitation above 200 cm, and a dry season with no more than 4 months below 10 cm of rainfall per month. In early global reconstructions, tropical rain forests cover most lowland areas up to about 50° north and south paleolatitude (Wolfe 1985; Frakes et al. 1992). Morley (2000) refined the mapping of past rain forest distributions, primarily from palynological data and inference from modern climate systems, and included desert and grassland belts centered on latitudes 30° north and south resulting from Hadley cell circulation. His early Eocene reconstruction shows American tropical rain forests expressed in three latitudinal bands, separated by the dry belts. These are the Neotropical equatorial rain forest; the Boreotropical rain forest, located at middle Northern latitudes; and the Southern Megathermal rain forest at Southern middle latitudes, containing the Patagonian floras discussed here. The eastern margins of continents typically receive significant rainfall from warm offshore currents even in the desert latitudes, and Morley shows his Neo-

Table 2: Diversity and paleoclimatic data, Laguna del Hunco (LH) flora

	LH-13	LH-13 level	LH-2	LH-2 level	LH-4	LH-4 level	LH-6	LH-6 level	All
Meter level (fig. 2)	40.30	37.00, 40.30	68.18	68.18	75.63	75.63	99.28	99.28	All
Plant species:									
All	81	88	75	75	64	72	74	83	186
Leaves	67	74	69	69	59	65	58	66	152 ^a
Dicot leaves	55	61	61	61	53	56	45	52	132
Nonleaves	14	14	6	6	5	7	16	17	34
Paleotemperature:									
Species used	55	61	61	61	53	56	44	51	131
<i>P</i>	.436	.426	.557	.557	.509	.482	.545	.569	.504
MAT (°C)	14.5	14.2	18.2	18.2	16.7	15.9	17.8	18.6	16.6 ^a
σ(MAT) (°C)	2.0	1.9	1.9	1.9	2.1	2.0	2.3	2.1	1.3
Paleoprecipitation:									
Species used	51	57	59	59	48	51	43	49	119
MlnA, ln (mm ²)	7.17	7.15	7.09	7.09	7.38	7.40	7.24	7.20	7.24
MAP (cm)	110	109	104.8	105	123	125	114	112	114 ^a
SE + (MAP) (cm)	47.3	46.9	45.2	45.2	53.3	53.9	49.2	48.2	49.1
SE - (MAP) (cm)	-33.1	-32.8	-31.6	-31.6	-37.2	-37.6	-34.3	-33.6	-34.3

Note: Levels are the minor localities grouped with major localities at the same stratigraphic levels (see fig. 2; LH-13 was grouped with LH-14, 15, and 23, all 3.3 m below LH-13). Dicot leaf species used for mean annual temperature (MAT) and precipitation (MAP) estimates differ slightly because some species suitable for leaf-margin analysis were too fragmentary for reliable measurement of leaf area. *Gymnostoma* was not used for climate estimates because of unusual leaf morphology; σ(MAT) = binomial sampling error, used as a minimum error estimate for MAT when >2.0°C; when σ(MAT) < 2°C, ±2°C is the recommended minimum error estimate (Wilf 1997). *P* = proportion of dicot leaf species with untoothed margins; MlnA = mean natural log of species leaf areas (Wilf et al. 1998). SE = standard error.

^a We consider these values to be the best single estimates for the flora.

tropical and Southern Megathermal Patagonian tropical rain forests connected by a narrow strip of moist climatic conditions along the Atlantic Coast. Morley did not present direct evidence for Eocene tropical rain forests in middle latitude South America, save for the presence of diverse fossil floras with tropical affinities such as Río Pichileufú. A dry or semiarid biome north of the LH and RP floras is supported by evaporite occurrences (Ziegler et al. 2003) and diverse evidence from the early Eocene Gran Salitral Formation (Melchor et al. 2002).

Previous paleoclimatic analyses based specifically on the paleobotany of the LH and RP floras have suggested some type of moist to seasonally dry tropical or subtropical climate (Berry 1925, 1938; Aragón and Romero 1984; Romero 1986; Markgraf et al. 1996; Wilf et al. 2003). However, none has indicated a tropical rain forest biome matching the reconstructions discussed above.

Living relatives of taxa from the LH and RP floras are dispersed widely, for the most part in tropical and temperate areas of South America and Australasia; current biogeographic knowledge of individual taxa is summarized in the appendix in the online edition of the *American Naturalist*. Gondwanic affinities of the floras are much better understood than Neotropical relationships (e.g., Hill and Carpenter 1991; Hill 1994). Although diverse tropical elements are present in the fossil floras, including many lineages that are diverse and abundant in today's Neo-

tropics, few of these are confirmed to be Neotropical endemics (Durango de Cabrera and Romero 1986). Nevertheless, the proximity of the American tropics and the presumed existence of direct interchange corridors (i.e., the Atlantic coast) support the argument for Neotropical interchange with Patagonia. The warm Paleogene climate presumably furthered the southward dispersal of Neotropical elements, in concert with poleward migrations of numerous tropical elements worldwide (e.g., Pole and MacPhail 1996; Harrington 2004). The extant Chilean and Argentine floras contain significant numbers of genera with disjunct distributions in the Neotropics that may be Paleogene relicts (Davis et al. 1997; Villagrán and Hinojosa 1997).

The combined presence of taxa with tropical and Gondwanic/Antarctic affinities at LH, RP, and other Paleogene floras in Patagonia led Romero (1978, 1986) to coin the descriptive term "mixed paleoflora" for these associations, which he considered to be stable vegetational units without direct modern analog. Because both the LH and RP macrofloras lack the cold-tolerant genus *Nothofagus*, Romero considered them among the warmest type of mixed paleoflora. However, *Nothofagus fusca*-type pollen was recently discovered at RP, occurring at low abundance (W. Volkheimer, personal communication, 2004; palynological preparations from LH so far have been unproductive).

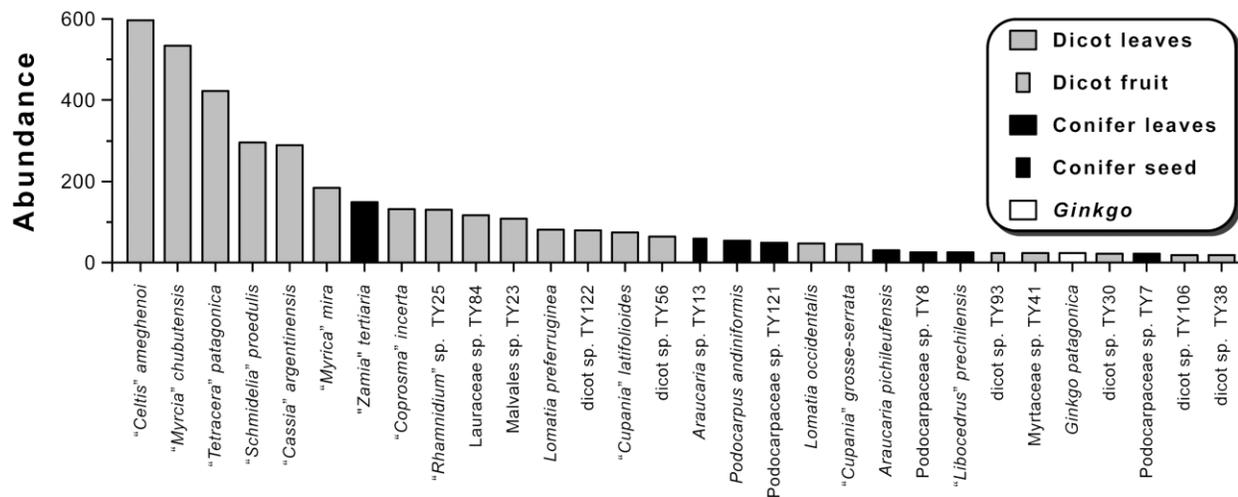


Figure 3: The 30 most abundant plant species at Laguna del Hunco; all localities grouped

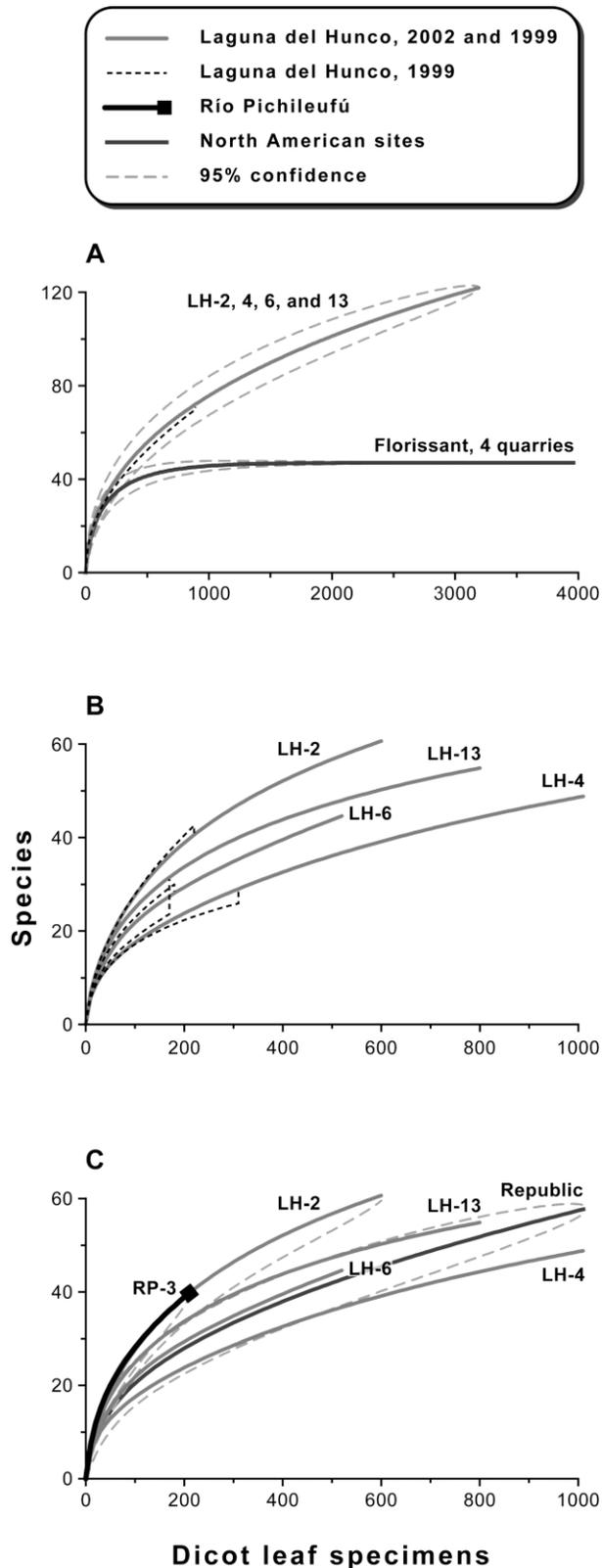
Collections and Methods

Major new collections from LH reported here were made in December of 2002 and are combined with the material reported by Wilf et al. (2003; collected in 1999); all were acquired using identical procedures, as was the RP sample. All LH voucher specimens, more than 3,500 in total, are housed in the Paleobotanical Collections of the Museo Paleontológico Egidio Feruglio, in Trelew, Chubut Province. The repository for the RP fossils is the Museo Paleontológico Asociación Paleontológica Bariloche in Bariloche, Río Negro Province. Historic collections from LH and RP are not included in our analyses because previous researchers did not use an unbiased, quantitative, stratigraphic methodology. To improve the comparison to North American plant diversity, we have also reanalyzed the sample from Republic, mentioned earlier, and have incorporated additional specimens. Although an exact analog to LH does not exist in North America, the Republic flora has the most similar combination of age (49–50 Ma) and paleoenvironmental setting to the Patagonian floras, and it is extremely diverse (Wolfe and Wehr 1987; Pigg et al. 2001; Wilf et al. 2003).

At LH, our major effort was intensive sampling of the four most productive quarries identified in 1999. These sites (LH-2, LH-4, LH-6, and LH-13; table 1; fig. 2) are hereafter referred to as the principal or major quarries and the remaining sites as the minor quarries. The total for all unbiased, identifiable material is 4,303 plant specimens, of which 3,723 (87%) come from the four major quarries (table 1). We also collected 57 float specimens, mostly not assignable to specific horizons; these are not included in analyses except where mentioned specifically below.

At Río Pichileufú, we found two sites, RP-1 and RP-3, with very good preservation and diverse floras, occupying approximately the same stratigraphic position (we could not correlate them precisely because of covered and locally slumped bedding). We made a preliminary, unbiased collection of 341 specimens from RP-3, the most productive quarry, of which 252 were identifiable and 213 were identifiable dicot leaves assigned to 39 species. Three tuffs were found in close stratigraphic proximity to the fossil floras; tuff RP1 lies immediately on top of the RP-1 fossil layer, tuff 2 occurs approximately 6 m below RP-1 (although its position may be slumped), and tuff RP3 is located about 6 m above RP-3. In addition, as an independent laboratory test, we reanalyzed a tuff from LH, 2211A, which previously yielded an age from U.S. Geological Survey laboratories of 52.13 ± 0.32 Ma (Wilf et al. 2003). More than $140^{40}\text{Ar}/^{39}\text{Ar}$ laser fusion and incremental heating analyses of sanidine crystals from the four tuffs, using the methodology of Smith et al. (2003), were undertaken at the University of Wisconsin–Madison Rare Gas Geochronology Laboratory. Details of radioisotopic analyses are provided in the appendix.

From our inspection of the type and referred material, many of Berry's identifications are clearly incorrect, are based on poorly preserved specimens that would not merit formal nomenclature today, or are not supported with sufficient diagnostic characters by modern standards (see also Dilcher 1973; Hill and Brodrick 1999). For these reasons, most of Berry's generic names are enclosed here in quotations. Both Berry's taxa and the large numbers of new species found in our collections will require a major effort toward systematic analysis and revision, now un-



derway and led by M. A. Gandolfo (Gandolfo et al. 1988, 2004; Romero et al. 1988; González et al. 2002).

Lack of a comprehensive reliable taxonomy is a typical problem in floras dominated by angiosperm leaves, which tend to be very diverse; even in floras that are relatively well understood, it is not unusual for a significant fraction of species to remain undiagnosed even to the family level (e.g., Johnson 2002). However, a standard procedure exists, which relies on detailed leaf architectural analyses to discriminate distinct leaf morphotypes that represent probable biological species (Hickey 1979; Johnson et al. 1989; Ash et al. 1999). This approach, which we use here, and others like it have been applied successfully to many fossil floras to analyze ecological, diversity-related, and paleoclimatic variables that require presence-absence or relative abundance data for all species in a flora (Hill 1982; Johnson et al. 1989; Burnham 1994; Wing 1998; Smith et al. 1998; Jacobs and Herendeen 2004; Wilf and Johnson 2004) and to provide an initial framework for systematic descriptions (Crane et al. 1990; Johnson 1996).

We followed a conservative “lumping” approach where a well-preserved, vouchered exemplar specimen with a unique, reproducible suite of diagnostic architectural characters and accompanying description must represent each morphotype. The common preservation of nearly complete leaves and fine venation features, especially at LH, facilitated this methodology: the morphotypes established from the 1999 collections, even when based on single specimens, proved reliable for identifying 2002 collections in the field and laboratory. For convenience, we will use “species” here to indicate both formally described species and morphotypes; comprehensive descriptions of these entities are in separate preparation. Existing paleobotanical nomenclature, abundance data, and voucher specimen numbers are provided in tables A2 and A3 in the appendix. Mean annual temperature (MAT) and precipitation

Figure 4: Rarefaction results for identified dicot leaves, with comparisons to the most diverse Eocene floras known from North America collected using similar techniques. *A*, Four major quarries at Laguna del Hunco combined, showing the effect of increased sampling from 1999 (reported in Wilf et al. 2003) to 2002 collections, compared to the four census sites from Florissant, 34 Ma (Evanoff et al. 2001), Colorado, reported by MacGinitie (1953). *B*, Effect of increased sampling at each of the Laguna del Hunco major quarries. Vertical dotted lines connect the maximum values of the 1999 data to the current rarefaction curves for each locality. *C*, Single-quarry comparisons, including selected 95% confidence intervals, for comparison to the Republic flora (49–50 Ma, Washington, Denver Museum of Nature and Science locality 2130). Republic data are reanalyzed and updated for new specimens from Wilf et al. (2003), with a resulting increase in rarefied diversity (the previous curve was nearly identical to the present curve for LH-4). Rarefactions and confidence intervals computed from the formulas of Tipper (1979). LH = Laguna del Hunco; RP = Río Pichileufú.

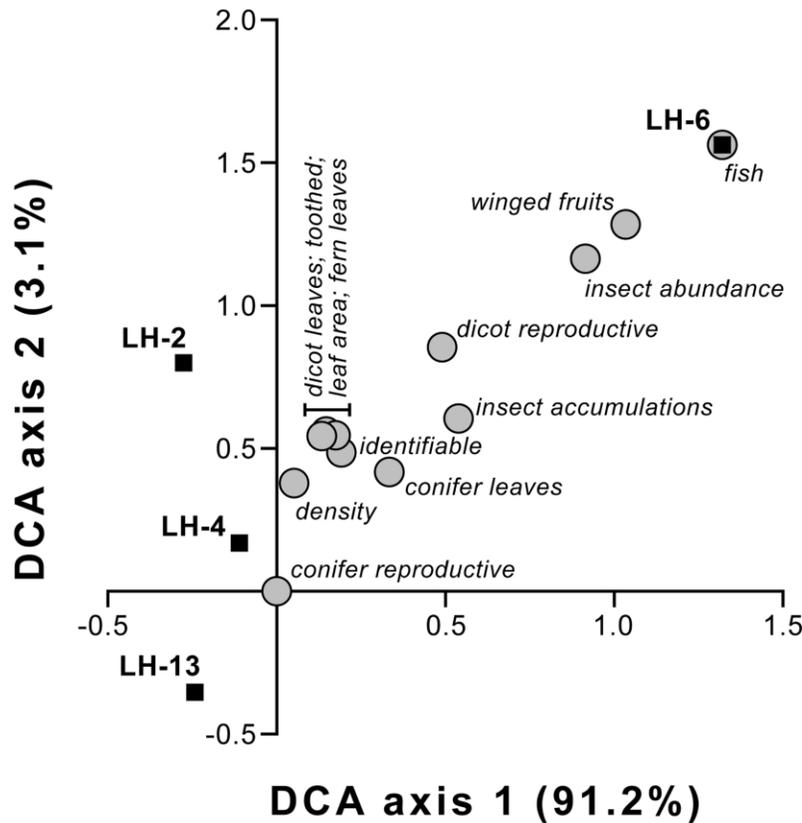


Figure 5: Detrended correspondence analysis of major quarries and taphonomic variables of the Laguna del Hunco (*LH*) flora (from table 1; most values entered as proportions). Axes are labeled with their percentages of total variance explained. Computed using MVSP 3.1 (Kovach 2000).

(MAP) were estimated for LH, the better-sampled flora, using the standard techniques of leaf-margin (Wolfe 1979; Wing and Greenwood 1993; Wilf 1997) and leaf-area analysis (Wilf et al. 1998), respectively.

Ages of the Floras

All three tuff beds collected at Río Pichileufú produced abundant sanidine phenocrysts that yielded $^{40}\text{Ar}/^{39}\text{Ar}$ ages with low analytical uncertainties of 4748 ± 0.10 Ma for tuff RP1, 4748 ± 0.47 Ma for tuff 2, and 4745 ± 0.06 Ma for tuff RP3 ($\pm 95\%$ confidence about the mean). These ages were calculated relative to 28.34 Ma for the Taylor Creek rhyolite sanidine (Renne et al. 1998) using the decay constants of Steiger and Jäger (1977). Given the uncertainties, the three $^{40}\text{Ar}/^{39}\text{Ar}$ ages for RP are indistinguishable from one another, thereby indicating a common depositional age for these sediments of 4746 ± 0.05 Ma, the weighted mean age from all three tuffs (middle Eocene, Lutetian). In terms of global climate, this age places the

RP flora within the initial phase of cooling subsequent to the early Eocene climatic optimum, although temperatures were high at this time compared to the remainder of the Cenozoic (Zachos et al. 2001). Results from the reanalyzed Laguna del Hunco 2211A ash gave a weighted mean age of 51.91 ± 0.22 Ma, indistinguishable from the 52.13 ± 0.32 Ma age reported by Wilf et al. (2003). Therefore, both floras are securely dated at high precision, and the RP flora is about 4.5 million years younger than the Laguna del Hunco flora, previously considered as nearly coeval. These results demonstrate for the first time longevity of the diverse Patagonian paleofloras, discussed in more detail below.

Floral Diversity

The total count of plant organ species from our Laguna del Hunco collections is 186, including 152 leaves and 132 dicot leaves (table 2); these totals are more than four times the sum of historic data. The nondicotyledonous foliar

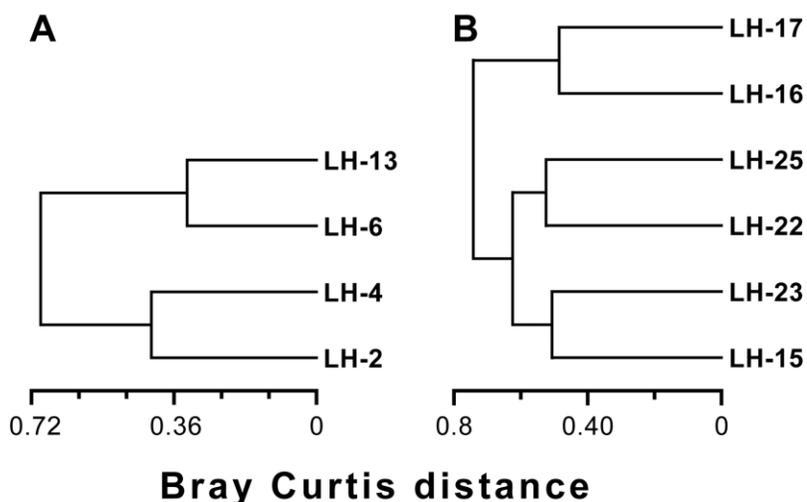


Figure 6: Cluster analyses, derived from Bray-Curtis distances, of relative abundance data from Laguna del Hunco (LH) plant species. *A*, Major quarries, proportional data. *B*, Minor quarries with at least 40 specimens, raw data (sample size is insufficient for reliable proportional data, although a similar clustering results). Note the stratigraphic correspondence of clusters to the major localities in *A* (cf. fig. 2). Computed using MVSP 3.1 (Kovach 2000).

species are eight conifers, one cycad, one *Ginkgo*, three monocots, and seven ferns. The remaining species include 27 angiosperm fruits, seeds, and flowers; four or possibly five types of coniferous cone scales, seeds, and pollen cones; and one bryophyte. The total richness increases slightly with float specimens, which include three additional species each of dicot leaves and dicot fruits. All four principal localities produced comparable raw values for plant richness, for example, 58–69 leaf species (table 2), and the maximum occurred at LH-2. The most abundant species at all sites combined are shown in rank order in figure 3; thermophilic families are abundant, such as Myrtaceae (“*Myrcia*”), Sapindaceae (“*Schmidelia*,” “*Cupania*”), Fabaceae (“*Cassia*”), Lauraceae, and Araucariaceae. Although *Lomatia* is common, the prevalence of “temperate” or tropical montane groups is hard to assess because many common species are poorly understood taxonomically.

Rarefaction analyses of dicot leaf data demonstrate high plant diversity at LH at robust sample sizes (fig. 4). In general, increased sampling led to dramatic increases in species recovered, and individual rarefaction trajectories remained the same or increased. The four principal quarries combined show increasing diversity past 3,000 specimens, along the trajectory of the 1999 collections (fig. 4A). In contrast, MacGinitie’s (1953) classic collections from Florissant, Colorado, the most comparable data set available for quarries from several stratigraphic levels within a short-lived lacustrine sequence, do not produce new species after about 1,000 specimens (fig. 4A). At the principal localities, numerous additional species accu-

mulated, mostly along the previous rarefaction trajectories (fig. 4B). The most significant change occurred at LH-13, which showed a dramatic jump in rarefied richness and a total increase in dicot leaves from 24 to 55 species. The maximum raw richness occurred at LH-2, which increased from 43 to 61 dicot leaf species.

All four principal quarries have a rarefied richness comparable to the extremely diverse Republic flora, and two, LH-2 and LH-13, are more rich (fig. 4C). The difference is significant for LH-2, based on separation of 95% confidence intervals, and at 600 specimens, LH-2 has one-third more species than Republic (61 vs. 46). This is the case even though the reanalyzed Republic sample has higher rarefied diversity than reported earlier (Wilf et al. 2003). Although rarefaction curves are beginning to flatten at the four principal quarries, there is great potential for a significant number of additional plant species to be found at LH, considering the large area of exposure available.

The preliminary sample from RP is as diverse on a rarefied basis as the most diverse LH locality, LH-2 (fig. 4C), supporting the richness described in the historic monograph (Berry 1938) and our observations of corresponding type material. This, along with our geochronologic results, shows exceptional plant diversity at a different time and location in Eocene Patagonia from LH. Moreover, the high diversity recovered at RP, despite having a distinctly lower quality of preservation than LH, diminishes the possible importance of preservation bias on rarefaction results for both floras.

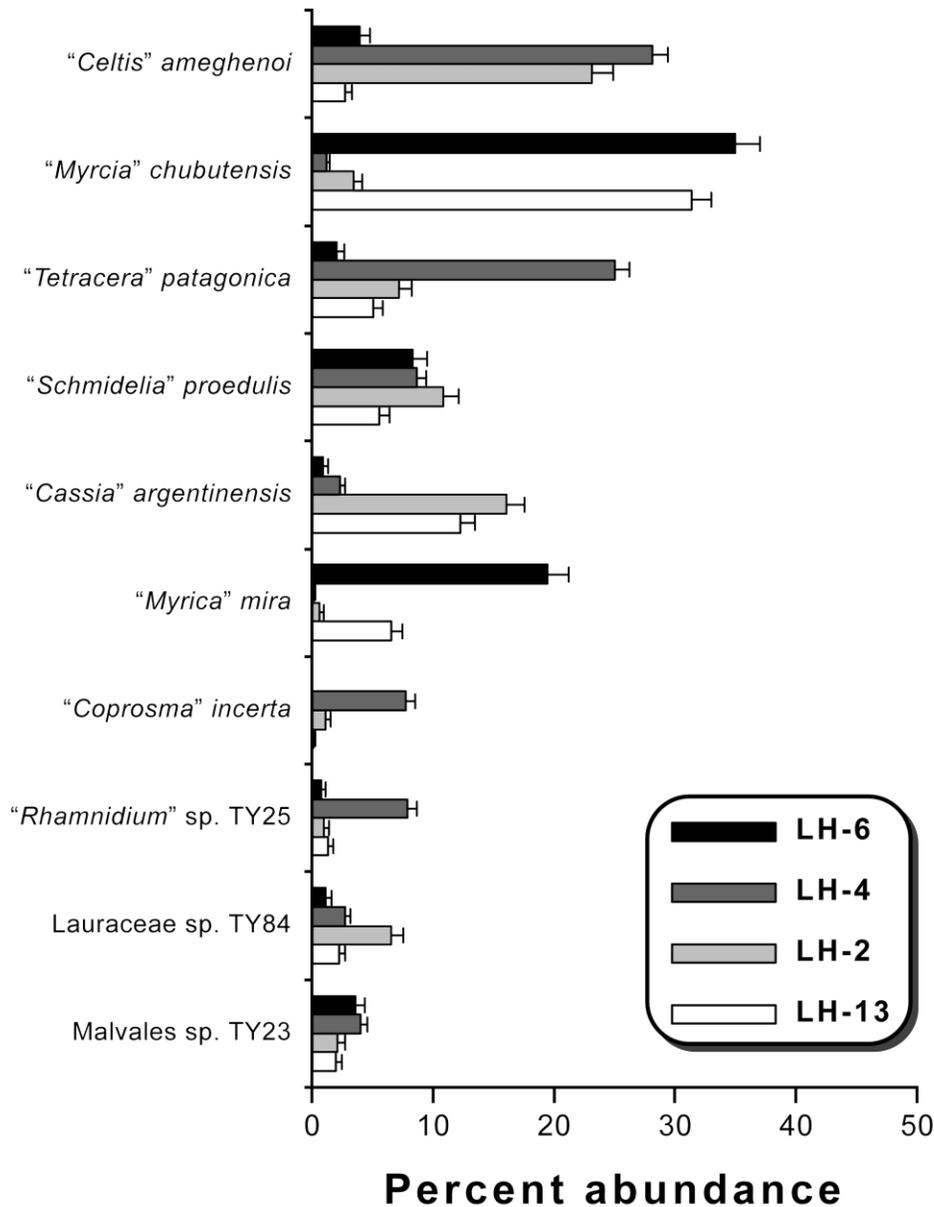
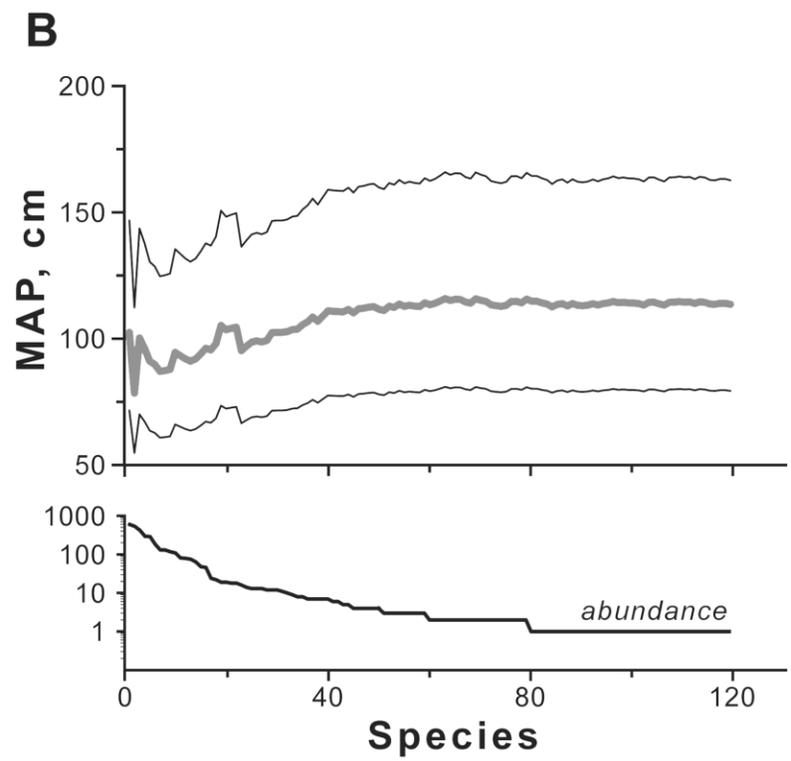
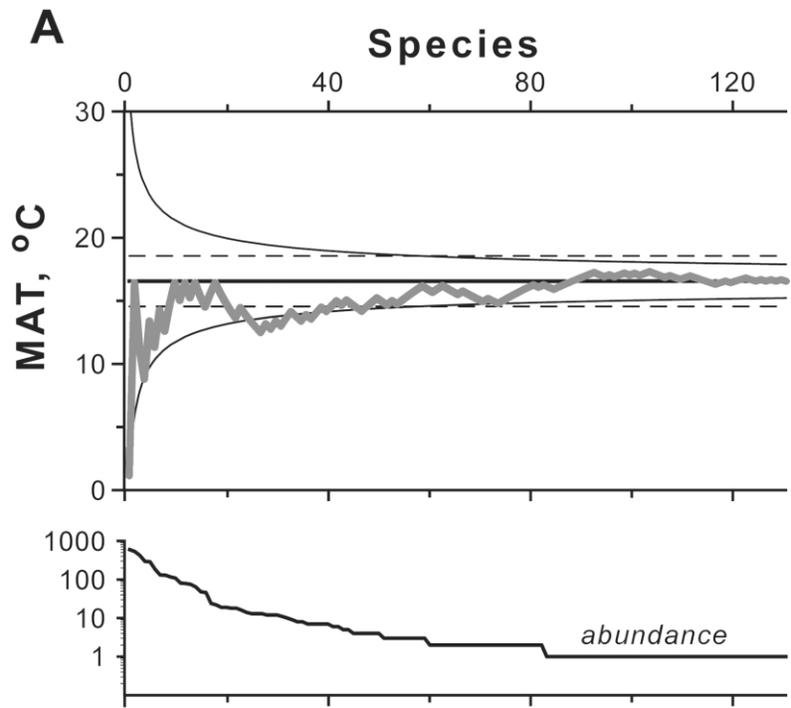


Figure 7: Percent abundance at each major quarry for the 10 most abundant species of dicot leaves at Laguna del Hunco (LH), calculated relative to all dicot leaves from the quarry.

Stability of Floral Associations

To what extent do the LH and RP floras represent a broadly coherent, persistent floral association versus a suite of mostly unrelated floras that share only high richness as a common characteristic? Abundant evidence indicates the former at LH, where the major source of variation in the floras appears to be environment of deposition. The four principal quarries show differences in taphonomic characteristics that apparently reflect distance from shoreline

(table 1); LH-6 has the most distinct offshore signature, seen especially in its thin, well-laminated bedding and the presence of articulated fossil fish, symmetrically winged ("helicopter") dicot fruits, and relatively abundant insect fossils (the latter two also at LH-13). Helicopter fruits and insects are likely to be entrained in prevailing winds and deposited far from their source, where they become better represented in fossil deposits than material deposited solely by gravity and water (Wilson 1980; Augspurger 1986). In



a detrended correspondence analysis (DCA) of quarries and taphonomic variables (fig. 5), LH-6 is alone in its position on the first axis, and its most strongly associated variables, in decreasing order, are the presence of fish, winged fruits, and insects.

Clustering based on Bray-Curtis distance, which is computed using relative abundance data, grouped locality LH-6 with LH-13 and locality LH-2 with LH-4 (fig. 6A). A similar grouping of LH-6 and LH-13 along the first axis results from a DCA of species relative abundance and quarries (not shown). Although data from minor localities are preliminary because of their small sample sizes, cluster analysis based on Bray-Curtis distance also resolved the stratigraphic groupings of six minor localities with at least 40 specimens each (fig. 6B).

The clustering of the stratigraphically lowest (LH-13) and highest (LH-6) major and corresponding minor localities (fig. 6), combined with the prevalence of the same dominant taxa at all localities (fig. 7), suggests that floral differences within the LH sequence reflect paleoenvironment of deposition more than compositional change through time. These differences are mostly expressed in varying relative abundance (figs. 6, 7) and not in composition. We therefore consider the LH floras to represent a single major association that is preserved in a variety of lacustrine environments.

The Laguna del Hunco and Río Pichileufú floras have been considered to be similar in species composition since Berry's original treatments (Berry 1925, 1938; Arguijo and Romero 1981; Markgraf et al. 1996; Hinojosa and Villagrán 1997). Notably, Petersen (1946) listed 50 species shared between the floras, but no surviving voucher specimens are known that could be used to evaluate his identifications. Because the floras are shown here to be separated by 4.5 million years, the assumption of species-level similarity deserves a critical reevaluation, although significant overlap of angiosperm families is indisputable (appendix). A reevaluation of shared leaf species (table A4 in the appendix) produces a list of 10 angiosperms that is short in comparison to the prodigious angiosperm diversity of the two sites already discussed, although it is likely to grow with increased collecting at RP. Significantly, only one of

the 10 most abundant dicot species at RP, "*Cassia*" *argentinensis*, is among the top 10 at LH (fig. 7). Thus, the best current support for close species similarity among the floras is in the less diverse gymnosperm fraction (table A4).

Paleoclimate

Our paleoclimatic results indicate that Eocene Laguna del Hunco was neither warm nor humid enough to be a tropical rain forest as suggested in previous global reconstructions (Wolfe 1985; Frakes et al. 1992; Morley 2000), although moisture was abundant and the maritime climate limited seasonality to a narrow range of temperatures that precluded frost. Results for major localities and associated sampling levels at LH are shown in table 2, along with notes on methodology. The high numbers of species used in the estimates help to counteract well-known biases from undersampling, paleoenvironment, and taphonomy (Burnham 1994; Wilf 1997; Burnham et al. 2001). For MAT at individual sampling levels, there is less than 5°C spread between the minimum estimate of $14.2^\circ \pm 2.0^\circ\text{C}$ at the LH-13 level and the maximum estimate of $18.6^\circ \pm 2.1^\circ\text{C}$ at the LH-6 level (table 2). Because there is no evidence for significant change in floral composition or available moisture, major shifts in temperature do not seem likely. Accordingly, we place the greatest confidence in the lumped estimate from all localities, $16.6^\circ \pm 2.0^\circ\text{C}$, based on 131 dicot leaf species. This result is within the range ($16^\circ\text{--}17^\circ\text{C}$) of coeval sea surface temperatures analyzed from several cores at bounding paleolatitudes of the South Atlantic (Zachos et al. 1994).

Paleoprecipitation estimates for LH are nearly identical at the various sampling levels (table 2). The 119 species that were measurable for leaf size produce a lumped estimate of about 1.1 m/year. We consider this a minimum estimate because transport into lakes generally selects against larger leaves (Roth and Dilcher 1978). Although several species are represented by very large leaves (area $>10,000\text{ mm}^2$), their signal is diluted by numerous rare species assumed to be undersampled for leaf size.

Sensitivity of climate estimates to sample size is tested using the method of Burnham et al. (2001), where suc-

Figure 8: Paleoclimatic results from (A) leaf-margin and (B) leaf-area analysis, Laguna del Hunco bulk flora (see table 2), plotted using the method of Burnham et al. (2001), where successive estimates are graphed from left to right as species are added in decreasing rank abundance order. Abundances of the species as they are added are shown in the small accessory graphs; the two abundance graphs differ slightly because some specimens suitable for leaf-margin analysis were too fragmentary for reliable measurement of leaf area. In A, the central horizontal line shows the best value for the sample based on all species. Symmetrical curves show 1 SD (standard deviation) about the best value based on number of species and a binomial probability model (Wilf 1997). Temperature estimates above or below these curves indicate leaf-margin percentages that deviate significantly from a random order of margin types taken from the entire sample. The accessory horizontal lines show $\pm 2^\circ\text{C}$ from the best value, considered to be a minimum error for leaf-margin analysis when the binomial error is less than $\pm 2^\circ\text{C}$ (Wilf 1997). B includes estimated mean annual precipitation and the standard error of the estimate using the regression of Wilf et al. (1998); errors are asymmetrical because they are transformed from logarithmic data. MAT = mean annual temperature; MAP = mean annual precipitation.

cessive estimates are graphed as species are added in decreasing rank abundance order (fig. 8A). For the LH bulk flora, MAT estimates begin to converge near 60 species, which suggests that the estimated paleotemperature is very unlikely to change significantly with additional sampling, although increased resolution of climate from individual horizons may be possible. A similar plot of MAP estimates shows instability below about 40 species but little variation past about 60 species (fig. 8B).

The modern climatic ranges of several higher taxa in the LH flora are well studied, helping to define climatic seasonality using nearest living relatives. The combined presence of palms, cycads, at least two species of araucarian conifers, at least five species of podocarps, and possibly three species of *Gymnostoma* (Gandolfo et al. 2004), along with numerous additional tropical elements (appendix) and the apparent absence of *Nothofagus*, provides strong evidence for an equable climate with winter mean temperatures warmer than 10°C and abundant rainfall (Christopher 1980; Romero 1986; Hill 1994; Greenwood and Wing 1995; Hill and Brodribb 1999; Kershaw and Wagstaff 2001).

From the RP-3 locality, 23 of the 39 dicot species were untoothed, yielding a preliminary MAT estimate of $19.2^\circ \pm 2.4^\circ\text{C}$. However, greater species sampling at RP will probably change this estimate (see fig. 8). Global marine data indicate cooling in the interval from 52 to 47 Ma (Zachos et al. 2001), which can be tested in Patagonia with increased sampling at RP.

The nontropical but moist and equable climates may explain the long-observed “mixing” (sensu Romero 1978, 1993) of temperate and tropical elements; the absence of drought and frost fostered the growth of tropical lineages, while the lack of high temperatures allowed the simultaneous presence of Gondwanic elements (see Axelrod et al. 1991). Except for moist corridors that probably existed to the Neotropical region, the biome containing the LH and RP floras was bounded by cooler winters to the south and aridity to the north. This biome could be considered an ancient biodiversity “hot spot,” although much better documentation of floral endemism than may ever be available from fossils would be required to test a hot spot hypothesis by comparison to modern definitions (e.g., Mittermeier et al. 1998).

Discussion

The Laguna del Hunco and Río Pichileufú floras represent a highly biodiverse, floristically and climatically distinct region. They provide the best macrofossil evidence for an ancient history of high plant diversity in Cenozoic South America. The 4.5-million-year age difference between them shows that richness was both long-lived and wide-

spread in Patagonia. Their diversity exceeds that of any comparable Eocene flora from the middle latitudes of western North America, the only region with quantitative data derived using equivalent collection strategies, and exceeds on an absolute basis all Eocene leaf floras known to us from outside the Americas. Even without sample size correction, organ type equivalence, or stratigraphic control in the comparisons, they rank among the most diverse fossil macrofloras known from any time period (e.g., Knoll et al. 1979). Eocene floras with equal or greater species richness, such as the Clarno nut beds (Manchester 1994) and the London Clay flora (Reid and Chandler 1933; Collinson 1983), are fruit and seed assemblages, which are produced via fundamentally different taphonomic pathways and increased temporal averaging in comparison to assemblages dominated by leaves (Behrensmeyer et al. 2000). They also have been collected selectively over many decades from unknown numbers of specimens, assumed to be in the tens to hundreds of thousands. The Castle Rock flora, which preserves forest floor litter from the early Paleocene of Colorado (Johnson and Ellis 2002; Ellis et al. 2003), is the only known assemblage, dominated by angiosperm leaves and collected using comparable methods to LH and RP, with similar species diversity. However, it represents a true rain forest with a significantly warmer and wetter environment than the Patagonian floras (Ellis et al. 2003); this climate should allow the presence of elevated plant diversity by analogy to living forests (Phillips and Miller 2002).

Diverse floras at Patagonian middle latitudes imply great richness at tropical latitudes of Eocene South America via the latitudinal diversity gradient, which appears to apply to most present and past vegetation (Crane and Lidgard 1989; Willig et al. 2003; Harrington 2004; Hillebrand 2004). Palynological data from the Paleocene-Eocene interval of Colombia strongly support a hyperdiverse Eocene tropics (Jaramillo 2002), and a latitudinal diversity gradient existed for Eocene vegetation in North America (Harrington 2004). Patagonian diversity was probably driven both by in situ evolution and the “spillover” of tropical taxa from extremely diverse floras of lower latitudes with Eocene warming. Immigrants from low latitudes consequently mixed with resident, temperate, and endemic taxa as well as tropical migrants from other continents. An analogous effect has been observed in Eocene palynofloras from North America (Harrington 2004).

Reliable quantitative paleontological data for plant diversity from other areas of South America remain rare, and diversity fluctuated between the Eocene and Recent (Jaramillo 2003). Any explanation for past diversity or its connection to modern floral richness is speculative, but we make a few general points here. South America has possessed immense areas of low-latitude land surface since

the Early Cretaceous and of tropical rain forest cover, dominated by angiosperms, at low latitudes since at least the late Paleocene (Morley 2000; Schettino and Scotese 2001; Jaramillo 2002; Wing et al. 2004). Accordingly, there has been great potential for diversification through time from populations separated by geography, climate, or ecological selection regime, as supported by studies in modern Amazonia (Gentry 1988a; Schneider et al. 1999; Moritz et al. 2000; Smith et al. 2001; Ogden and Thorpe 2002; Tuomisto et al. 2003; Fine et al. 2004). The association of global warming across the Paleocene-Eocene boundary and significant in situ diversification of palynofloras in northern South America (Rull 1999; Jaramillo 2002) suggests that a major diversity increase occurred in Eocene South America, mediated by climate change. Testing this hypothesis in Patagonia awaits quantitative analyses of suitable Paleocene floras.

Acknowledgments

For generous support, we thank the National Geographic Society (grant 7337-02), the National Science Foundation (grants DEB-0345750, EAR-0230123, and EAR-0114055), the University of Pennsylvania Research Foundation, the Andrew W. Mellon Foundation, and the Petroleum Research Fund (grant 35229-G2). For exceptional assistance in the field and laboratory, we are grateful to M. Caffa, L. Canessa, B. Cariglino, I. Escapa, C. González, R. Horwitt, P. Puerta, E. Ruigomez, H. Smekal, X. Zhang, and the Museo Paleontológico Asociación Paleontológica Bariloche. Comments on drafts and reviews by E. Aragón, R. Horwitt, C. Jaramillo, D. Royer, and two anonymous reviewers greatly improved the manuscript. We are grateful to the Nahueltripay family and INVAP (Instituto de Investigaciones Aplicadas) for land access.

Literature Cited

- Aragón, E., and M. M. Mazzoni. 1997. Geología y estratigrafía del complejo volcánico piroclástico del Río Chubut medio (Eoceno), Chubut, Argentina. *Revista de la Asociación Geológica Argentina* 52:243–256.
- Aragón, E., and E. J. Romero. 1984. Geología, paleoambientes y paleobotánica de yacimientos Terciarios del occidente de Río Negro, Neuquén y Chubut. *Actas del IX Congreso Geológico Argentino*, San Carlos de Bariloche 4:475–507.
- Archangelsky, S. 1974. Sobre la edad de la taoflora de la Laguna del Hunco, Provincia de Chubut. *Ameghiniana* 11:413–417.
- Arguijo, M. H., and E. J. Romero. 1981. Analisis bioestratigrafico de formaciones portadores de taofloras Terciarias. *Actas del VIII Congreso Geológico Argentino* 4:691–717.
- Ash, A. W., B. Ellis, L. J. Hickey, K. R. Johnson, P. Wilf, and S. L. Wing. 1999. *Manual of leaf architecture: morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms*. Smithsonian Institution, Washington, DC.
- Augsburger, C. K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of Neotropical trees. *American Journal of Botany* 73:353–363.
- Axelrod, D. I., M. K. Arroyo, and P. H. Raven. 1991. Historical development of temperate vegetation in the Americas. *Revista Chilena de Historia Natural* 64:413–446.
- Báez, A. M., and L. Trueb. 1997. Redescription of the Paleogene *Shelania pascuali* from Patagonia and its bearing on the relationships of fossil and Recent pipoid frogs. *Scientific Papers, Natural History Museum, The University of Kansas* 4:1–41.
- Behrensmeyer, A. K., S. M. Kidwell, and R. A. Gastaldo. 2000. Taphonomy and paleobiology. *Paleobiology* 26S:103–147.
- Berry, E. W. 1925. A Miocene flora from Patagonia. *Johns Hopkins University Studies in Geology* 6:183–251.
- . 1935a. A fossil *Cochlospermum* from northern Patagonia. *Bulletin of the Torrey Botanical Club* 62:65–67.
- . 1935b. The Monimiaceae and a new *Laurelia*. *Botanical Gazette* 96:751–754.
- . 1935c. A Tertiary *Ginkgo* from Patagonia. *Torreyana* 35:11–13.
- . 1938. Tertiary flora from the Río Pichileufú, Argentina. *Geological Society of America Special Paper* 12:1–149.
- Bremer, K. 2002. Gondwanan evolution of the grass alliance of families (Poales). *Evolution* 56:1374–1387.
- Burnham, R. J. 1994. Paleocological and floristic heterogeneity in the plant-fossil record: an analysis based on the Eocene of Washington. *U.S. Geological Survey Bulletin* 2085-B:1–36.
- Burnham, R. J., and A. Graham. 1999. The history of Neotropical vegetation: new developments and status. *Annals of the Missouri Botanical Garden* 86:546–589.
- Burnham, R. J., and K. R. Johnson. 2004. South American palaeobotany and the origins of Neotropical rainforests. *Philosophical Transactions of the Royal Society of London B* 359:1595–1610.
- Burnham, R. J., N. C. A. Pitman, K. R. Johnson, and P. Wilf. 2001. Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. *American Journal of Botany* 88:1096–1102.
- Casamiquela, R. M. 1961. Un pipoideo fósil de Patagonia. *Revista del Museo de La Plata, Sección Paleontología* 4:71–123.
- Christophel, D. C. 1980. Occurrence of *Casuarina* megafossils in the Tertiary of southeastern Australia. *Australian Journal of Botany* 28:249–259.
- Clark, B. 1923. The economic deduction from an incidental general reconnaissance of Patagonia between east central Santa Cruz and northwestern Chubut. ESSO, Field Office Argentine No. 35, Office Argentine No. 70, New York.
- Colinvaux, P. A., and P. E. De Oliveira. 2001. Amazon plant diversity and climate through the Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166:51–63.
- Colinvaux, P. A., P. E. De Oliveira, J. E. Moreno, M. C. Miller, and M. B. Bush. 1996. A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* 274:85–88.
- Colinvaux, P. A., G. Irion, M. E. Rasanen, M. B. Bush, and J. A. S. N. De Mello. 2001. A paradigm to be discarded: geological and paleoecological data falsify the Haffer and Prance refuge hypothesis of Amazonian speciation. *Amazoniana* 16:609–646.
- Collinson, M. E. 1983. *Fossil plants of the London Clay*. Palaeontological Association, London.
- Crane, P. R., and S. Lidgard. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* 246:675–678.
- Crane, P. R., S. R. Manchester, and D. L. Dilcher. 1990. A preliminary

- survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. *Fieldiana Geology* 20:1–63.
- Davis, C. C., P. W. Fritsch, C. D. Bell, and S. Mathews. 2004. High-latitude Tertiary migrations of an exclusively tropical clade: evidence from Malpighiaceae. *International Journal of Plant Sciences* 165(suppl.):S107–S121.
- Davis, C. C., C. O. Webb, K. J. Wurdack, C. A. Jaramillo, and M. J. Donoghue. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *American Naturalist* 165:E36–E65.
- Davis, S. D., V. H. Heywood, O. Herrera MacBryde, and A. C. Hamilton. 1997. Centres of plant diversity: a guide and strategy for their conservation. Vol. 3. The Americas. World Wide Fund for Nature, London.
- Dilcher, D. L. 1973. A revision of the Eocene flora of southeastern North America. *Palaeobotanist* 20:7–18.
- Dlussky, G. M., and K. S. Perfilieva. 2003. Paleogene ants of the genus *Archimyrmex* Cockerell, 1923. *Paleontological Journal* 37:39–47.
- Durango de Cabrera, J., and E. J. Romero. 1986. *Roupala patagonica* n. sp. de Laguna del Hunco (Paleocene), Provincia Chubut, Argentina. *Actas del V Congreso Argentino de Paleontología y Bioestratigrafía* 3:121–124.
- Ellis, B., K. R. Johnson, and R. E. Dunn. 2003. Evidence for an in situ early Paleocene rainforest from Castle Rock, Colorado. *Rocky Mountain Geology* 38:73–100.
- Estes, R., and J. H. Hutchison. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* 30:325–347.
- Evanoff, E., W. C. McIntosh, and P. C. Murphey. 2001. Stratigraphic summary and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology of the Florissant Formation, Colorado. Pages 1–16 in E. Evanoff, K. M. Gregory-Wodzicki, and K. R. Johnson, eds. *Fossil flora and stratigraphy of the Florissant Formation, Colorado*. Denver Museum of Nature and Science, Denver, CO.
- Fidalgo, P., and D. R. Smith. 1987. A fossil Siricidae Hymenoptera from Argentina. *Entomological News* 98:63–66.
- Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305:663–665.
- Frakes, L. A., J. E. Francis, and J. I. Syktus. 1992. *Climate modes of the Phanerozoic*. Cambridge University Press, Cambridge.
- Frenguelli, J. 1943a. Proteaceas del Cenozoico de Patagonia. *Notas del Museo de La Plata* 8:201–213.
- . 1943b. Restos de *Casuarina* en el Mioceno de El Mirador, Patagonia central. *Notas del Museo de La Plata* 8:349–354.
- Frenguelli, J., and L. R. Parodi. 1941. Una *Chusquea* fósil de El Mirador (Chubut). *Notas del Museo de La Plata* 6:235–238.
- Gandolfo, M. A., M. C. Dibern, and E. J. Romero. 1988. *Akania patagonica* n. sp. and additional material on *Akania americana* Romero and Hickey (Akaniaceae), from Paleocene sediments of Patagonia. *Bulletin of the Torrey Botanical Club* 115:83–88.
- Gandolfo, M. A., M. C. Zamalao, C. C. González, N. R. Cúneo, P. Wilf, and E. J. Romero. 2004. Early history of Casuarinaceae in the Paleogene of Patagonia, Argentina. *International Organization of Paleobotany, Seventh Quadrennial Conference, Bariloche, Argentina, Abstracts*, pp. 36–37.
- Genise, J. F., and J. F. Petrulevicius. 2001. Caddisfly cases from the early Eocene of Chubut, Patagonia, Argentina. *Second International Congress on Paleontomology, September 5–9, 2001, Kraków, Poland, Abstracts*, pp. 12–13.
- Gentry, A. H. 1988a. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1–34.
- . 1988b. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the USA* 85:156–159.
- González, C. C., M. A. Gandolfo, N. R. Cúneo, and P. Wilf. 2002. Revisión de las Myrtaceae de Laguna del Hunco y Río Pichileufú (Eoceno Inferior), Patagonia, Argentina. *Simposio Argentino de Paleobotánica y Palinología, Abstracts*, p. 12.
- González Díaz, E. F. 1979. La edad de la Formación Ventana, en la area al norte y al este del Lago Nahuel Huapi. *Revista de la Asociación Geológica Argentina* 34:113–124.
- Greenwood, D. R., and S. L. Wing. 1995. Eocene continental climates and latitudinal temperature gradients. *Geology* 23:1044–1048.
- Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* 165:131–137.
- Haffer, J., and G. T. Prance. 2001. Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* 16:579–605.
- Harrington, G. J. 2004. Structure of the North American vegetation gradient during the late Paleocene/early Eocene warm climate. *Evolutionary Ecology Research* 6:33–48.
- Hay, W. W., R. DeConto, C. N. Wold, K. M. Wilson, S. Voigt, M. Schulz, A. Wold-Rosby, et al. 1999. Alternative global Cretaceous paleogeography. *Geological Society of America Special Paper* 332:1–47.
- Hickey, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. Pages 25–39 in C. R. Metcalfe and L. Chalk, eds. *Anatomy of the dicotyledons*. 2nd ed. Clarendon, Oxford.
- Hill, R. S. 1982. The Eocene megafossil flora of Nerriga, New South Wales, Australia. *Palaeontographica Abteilung B: Palaeophytologie* 181:44–77.
- . 1994. The history of selected Australian taxa. Pages 390–419 in R. S. Hill, ed. *History of the Australian vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge.
- Hill, R. S., and T. J. Brodribb. 1999. Southern conifers in time and space. *Australian Journal of Botany* 47:639–696.
- Hill, R. S., and R. J. Carpenter. 1991. Extensive past distributions for major Gondwanic floral elements: macrofossil evidence. Pages 239–247 in M. R. Banks, S. J. Smith, A. E. Orchard, and G. Kantvilas, eds. *Aspects of Tasmanian botany*. Royal Society of Tasmania, Hobart.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192–211.
- Hinojosa, L. F., and C. Villagrán. 1997. History of the southern South American forests. I. Paleobotanical, geological and climatical background on Tertiary of southern South America. *Revista Chilena de Historia Natural* 70:225–239.
- Hoorn, C. 1994. Fluvial paleoenvironments in the intracratonic Amazonas Basin (early Miocene–early middle Miocene, Colombia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 109:1–54.
- Jacobs, B. F., and P. S. Herendeen. 2004. Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213:115–123.
- Jaramillo, C. A. 2002. Response of tropical vegetation to Paleogene warming. *Paleobiology* 28:222–243.

- . 2003. Maastrichtian to early Miocene patterns of plant diversification in the Neotropics. *Geological Society of America Abstracts with Programs* 35:58.
- Jaramillo, C. A., and D. L. Dilcher. 2000. Microfloral diversity patterns of the late Paleocene–Eocene interval in Colombia, northern South America. *Geology* 28:815–818.
- Johnson, K. R. 1996. Description of seven common plant megafossils from the Hell Creek Formation (Late Cretaceous: late Maastrichtian), North Dakota, South Dakota, and Montana. *Proceedings of the Denver Museum of Natural History* 3:1–48.
- . 2002. The megafloora of the Hell Creek and lower Fort Union formations in the western Dakotas: vegetational response to climate change, the Cretaceous–Tertiary boundary event, and rapid marine transgression. *Geological Society of America Special Paper* 361:329–391.
- Johnson, K. R., and B. Ellis. 2002. A tropical rainforest in Colorado 1.4 million years after the Cretaceous–Tertiary boundary. *Science* 296:2379–2383.
- Johnson, K. R., D. J. Nichols, M. Attrep Jr., and C. J. Orth. 1989. High-resolution leaf-fossil record spanning the Cretaceous–Tertiary boundary. *Nature* 340:708–711.
- Kastner, T. P., and M. A. Goñi. 2003. Constancy in the vegetation of the Amazon Basin during the late Pleistocene: evidence from the organic matter composition of Amazon deep sea fan sediments. *Geology* 31:291–294.
- Kershaw, P., and B. Wagstaff. 2001. The southern conifer family Araucariaceae: history, status, and value for paleoenvironmental reconstruction. *Annual Review of Ecology and Systematics* 32:397–414.
- Knoll, A. H., K. J. Niklas, and B. H. Tiffney. 1979. Phanerozoic land-plant diversity in North America. *Science* 206:1400–1402.
- Kovach, W. L. 2000. MVSP: a multivariate statistical package for Windows. Version 3.12c. Kovach Computing, Petraeth, Wales.
- MacGinitie, H. D. 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Institution of Washington Publication 599:1–198.
- Manchester, S. R. 1994. Fruits and seeds of the middle Eocene nut beds flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58:1–205.
- Markgraf, V., E. J. Romero, and C. Villagrán. 1996. History and paleoecology of South American *Nothofagus* forest. Pages 354–386 in T. T. Veblen, R. S. Hill, and J. Read, eds. *The ecology and biogeography of Nothofagus forests*. Yale University Press, New Haven, CT.
- Marshall, L. G., and P. Salinas. 1990. Stratigraphy of the Río Frías Formation (Miocene), along the Alto Río Cisnes, Aisén, Chile. *Revista Geológica de Chile* 17:57–87.
- Mazzoni, M. M., K. Kawashita, S. Harrison, and E. Aragón. 1991. Edades radimétricas Eocenas en el borde occidental del Macizo Norpatagónico. *Revista de la Asociación Geológica Argentina* 46:150–158.
- Melchor, R. N., J. F. Genise, and S. E. Miquel. 2002. Ichnology, sedimentology and paleontology of Eocene calcareous paleosols from a palustrine sequence, Argentina. *Palaios* 17:16–35.
- Mello, C. L., L. P. Bergqvist, and L. G. Sant'Anna. 2002. Fonseca, MG: vegetais fósseis do Terciário brasileiro. Pages 73–79 in C. Schobbenhaus, D. A. Campos, E. T. Queiroz, M. Winge, and M. L. C. Berbert-Bron, eds. *Sítios geológicos e paleontológicos do Brasil*. Comissão Brasileira de Sítios Geológicos e Paleobiológicos, Brasília.
- Menéndez, C. A. 1971. Floras Terciarias de la Argentina. *Ameghiniana* 8:357–368.
- Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. da Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12:516–520.
- Mori, S. A., and B. B. Boom. 1981. Final report to the World Wildlife Fund U.S. on the botanical survey of the endangered moist forests of eastern Brazil. New York Botanical Garden, New York.
- Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics* 31:533–563.
- Morley, R. J. 2000. *Origin and evolution of tropical rain forests*. Wiley, New York.
- Nelson, B. W., C. A. C. Ferreira, M. F. da Silva, and M. L. Kawasaki. 1990. Endemism centers, refugia and botanical collection density in Brazilian Amazonia. *Nature* 345:714–716.
- Ogden, R., and R. S. Thorpe. 2002. Molecular evidence for ecological speciation in tropical habitats. *Proceedings of the National Academy of Sciences of the USA* 99:13612–13615.
- Passmore, S. M., K. R. Johnson, M. Reynolds, M. Scott, and D. Meade-Hunter. 2002. Through the Quaternary looking glass: the middle Eocene Republic flora over short timescales. *Geological Society of America Abstracts with Programs* 34:556.
- Petersen, C. S. 1946. Estudios geológicos en la región del Río Chubut medio. Dirección de Minas y Geología Boletín 59:1–137.
- Petrulevicius, J. F., and A. D. Nel. 2003. Frenguelliidae, a new family of dragonflies from the earliest Eocene of Argentina (Insecta: Odonata): phylogenetic relationships within Odonata. *Journal of Natural History* 37:2909–2917.
- Phillips, O. L., and J. S. Miller. 2002. Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set. Missouri Botanical Garden Press, St. Louis.
- Pigg, K. B., W. C. Wehr, and S. M. Ickert-Bond. 2001. *Trochodendron* and *Nordenskiöldia* (Trochodendraceae) from the middle Eocene of Washington State, USA. *International Journal of Plant Sciences* 162:1187–1198.
- Pole, M. S., and M. K. MacPhail. 1996. Eocene *Nypa* from Regatta Point, Tasmania. *Review of Palaeobotany and Palynology* 92:55–67.
- Rapela, C. W., L. A. Spalletti, J. C. Merodio, and E. Aragón. 1988. Temporal evolution and spatial variation of early Tertiary volcanism in the Patagonian Andes (40°S–42°30'S). *Journal of South American Earth Sciences* 1:75–88.
- Reid, E. M., and M. E. J. Chandler. 1933. *The London Clay flora*. British Museum (Natural History), London.
- Renne, P. R., C. C. Swisher, A. L. Deino, D. B. Karner, T. L. Owens, and D. J. DePaolo. 1998. Intercalibration of standards, absolute ages and uncertainties in ⁴⁰Ar/³⁹Ar dating. *Chemical Geology* 145:117–152.
- Richardson, J. E., R. T. Pennington, T. D. Pennington, and P. M. Hollingsworth. 2001. Rapid diversification of a species-rich genus of Neotropical rain forest trees. *Science* 293:2242–2245.
- Romero, E. J. 1978. Paleoecología y paleofitografía de las tafofloras del Cenofítico de Argentina y áreas vecinas. *Ameghiniana* 15:209–227.
- . 1986. Paleogene phytogeography and climatology of South America. *Annals of the Missouri Botanical Garden* 73:449–461.
- . 1993. South American paleofloras. Pages 62–85 in P. Gold-

- blatt, ed. Biological relationships between Africa and South America. Yale University Press, New Haven, CT.
- Romero, E. J., and L. J. Hickey. 1976. Fossil leaf of Akaniaceae from Paleocene beds in Argentina. *Bulletin of the Torrey Botanical Club* 103:126–131.
- Romero, E. J., M. C. Dibbern, and M. A. Gandolfo. 1988. Revisión de *Lomatia bivascularis* (Berry) Frenguelli (Proteaceae) del yacimiento de la Laguna del Hunco (Paleoceno), Pcia. del Chubut. *Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía* 3:125–130.
- Roth, J. L., and D. L. Dilcher. 1978. Some considerations in leaf size and leaf margin analysis of fossil leaves. *Courier Forschungs-Institut Senckenberg* 30:165–171.
- Rull, V. 1999. Palaeofloristic and palaeovegetational changes across the Paleocene/Eocene boundary in northern South America. *Review of Palaeobotany and Palynology* 107:83–95.
- Schettino, A., and C. R. Scotese. 2001. New Internet software aids paleomagnetic analysis and plate tectonic reconstructions. EOS electronic supplement. Vol. 82. http://www.agu.org/eos_elec/010181e.html.
- Schneider, C. J., T. B. Smith, B. Larison, and C. Moritz. 1999. A test of alternative models of diversification in tropical rainforests: ecological gradients vs. rainforest refugia. *Proceedings of the National Academy of Sciences of the USA* 96:13869–13873.
- Smith, G. A., S. R. Manchester, M. Ashwill, W. C. McIntosh, and R. M. Conrey. 1998. Late Eocene–early Oligocene tectonism, volcanism, and floristic change near Gray Butte, central Oregon. *Geological Society of America Bulletin* 110:759–778.
- Smith, M. E., B. Singer, and A. Carroll. 2003. $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology of the Eocene Green River Formation, Wyoming. *Geological Society of America Bulletin* 115:549–565.
- Smith, T. B., C. J. Schneider, and K. Holder. 2001. Refugial isolation versus ecological gradients. *Genetica* 112/113:383–398.
- Steiger, R. H., and E. Jäger. 1977. Subcommission on geochronology: convention on the use of decay constants in geo- and cosmochronology. *Earth and Planetary Science Letters* 36:359–362.
- Tipper, J. C. 1979. Rarefaction and rarefaction: the use and abuse of a method in paleontology. *Paleobiology* 5:423–434.
- Traverso, N. E. 1964. La epidermis de *Ginkgo patagonica* Berry, del Terciario de El Mirador, Provincia del Chubut. *Ameghiniana* 3:163–166.
- Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299:241–244.
- Van der Hammen, T., and H. Hooghiemstra. 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quaternary Science Reviews* 19:725–742.
- Viana, M. J., and J. A. Haedo-Rossi. 1957. Primer hallazgo en el hemisferio sur de Formicidae extinguidos y catálogo mundial de los Formicidae fósiles. Primera parte. *Ameghiniana* 1:108–113.
- Villagrán, C., and L. F. Hinojosa. 1997. History of the forests of southern South America. II. Phytogeographical analysis. *Revista Chilena de Historia Natural* 70:241–267.
- Wilf, P. 1997. When are leaves good thermometers? a new case for leaf margin analysis. *Paleobiology* 23:373–390.
- Wilf, P., and K. R. Johnson. 2004. Land plant extinction at the end of the Cretaceous: a quantitative analysis of the North Dakota megafossil record. *Paleobiology* 30:347–368.
- Wilf, P., S. L. Wing, D. R. Greenwood, and C. L. Greenwood. 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. *Geology* 26:203–206.
- Wilf, P., N. R. Cúneo, K. R. Johnson, J. F. Hicks, S. L. Wing, and J. D. Obradovich. 2003. High plant diversity in Eocene South America: evidence from Patagonia. *Science* 300:122–125.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273–309.
- Wilson, M. V. H. 1980. Eocene lake environments: depth and distance-from-shore variation in fish, insect, and plant assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 32:21–44.
- Wing, S. L. 1998. Late Paleocene–early Eocene floral and climatic change in the Bighorn Basin, Wyoming. Pages 380–400 in M.-P. Aubry, S. Lucas, and W. A. Berggren, eds. *Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records*. Columbia University Press, New York.
- Wing, S. L., and D. R. Greenwood. 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. *Philosophical Transactions of the Royal Society of London B* 341:243–252.
- Wing, S. L., F. Herrera, and C. A. Jaramillo. 2004. A Paleocene flora from the Cerrejon Formation, Guajira Peninsula, northeastern Colombia. *International Organization of Paleobotany, Seventh Quadrennial Conference, Bariloche, Argentina, Abstracts*, pp. 146–147.
- Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions in the Northern Hemisphere and Australasia. U.S. Geological Survey Professional Paper 1106:1–37.
- . 1985. Distribution of major vegetational types during the Tertiary. Pages 357–375 in E. T. Sundquist and W. S. Broecker, eds. *The carbon cycle and atmospheric CO₂: natural variations Archean to present*. Geophysical Monograph 32. American Geophysical Union, Washington, DC.
- Wolfe, J. A., and W. C. Wehr. 1987. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. *U.S. Geological Survey Bulletin* 1597:1–25.
- Zachos, J. C., L. D. Stott, and K. C. Lohmann. 1994. Evolution of early Cenozoic marine temperatures. *Paleoceanography* 9:353–387.
- Zachos, J. C., M. Pagani, L. C. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–693.
- Ziegler, A. M., G. Eshel, P. M. Rees, T. A. Rothfus, D. B. Rowley, and D. Sunderlin. 2003. Tracing the tropics across land and sea: Permian to present. *Lethaia* 36:227–254.

Editor: Jonathan B. Losos
Associate Editor: Mark Westoby