

# A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs

Ari Iglesias\* Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 1900, La Plata, Argentina

Peter Wilf Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802, USA

Kirk R. Johnson Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado 80205, USA

Alba B. Zamuner Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 1900, La Plata, Argentina

N. Rubén Cúneo Museo Paleontológico Egidio Feruglio, Trelew 9100, Chubut, Argentina

Sergio D. Matheos Centro de Investigaciones Geológicas, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de La Plata, 1900, La Plata, Argentina

Bradley S. Singer Department of Geology and Geophysics, University of Wisconsin, Madison, Wisconsin 53706, USA

## ABSTRACT

Few South American macrofloras of Paleocene age are known, and this limits our knowledge of diversity and composition between the end-Cretaceous event and the Eocene appearance of high floral diversity. We report new, unbiased collections of 2516 compression specimens from the Paleocene Salamanca Formation (ca. 61.7 Ma) from two localities in the Palacio de los Loros exposures in southern Chubut, Patagonia, Argentina. Our samples reveal considerably greater richness than was previously known from the Paleocene of Patagonia, including 36 species of angiosperm leaves as well as angiosperm fruits, flowers, and seeds; ferns; and conifer leaves, cones, and seeds. The floras, which are from siltstone and sandstone channel-fills deposited on low-relief floodplain landscapes in a humid, warm temperate climate, are climatically and paleoenvironmentally comparable to many quantitatively collected Paleocene floras from the Western Interior of North America. Adjusted for sample size, there are >50% more species at each Palacio de los Loros quarry than in any comparable U.S. Paleocene sample. These results indicate more vibrant terrestrial ecosystems in Patagonian than in North American floodplain environments ~4 m.y. after the end-Cretaceous extinction, and they push back the time line 10 m.y. for the evolution of high floral diversity in South America. The cause of the disparity is unknown but could involve reduced impact effects because of greater distance from the Chicxulub site, higher latest Cretaceous diversity, or faster recovery or immigration rates.

**Keywords:** Paleocene, Salamanca Formation, plant diversity, Patagonia, South America.

## INTRODUCTION

Paleocene macrofloras provide fundamental data regarding ecosystem diversity after the end-Cretaceous extinction (e.g., Wolfe and Upchurch, 1986; Johnson and Ellis, 2002; Barclay et al., 2003; Wilf et al., 2006) and before the major biotic transitions that accompanied global warming across the Paleocene-Eocene boundary (e.g., Wing and Harrington, 2001; Jaramillo, 2002). However, there are virtually no records of confirmed Paleocene macrofloras from South America (Burnham and Johnson, 2004; Wing et al., 2004), which harbored elevated plant diversity in both Patagonia and the Neotropics during the Eocene (Berry, 1938; Wilf et al., 2005; Jaramillo et al., 2006). Today, South America has notably high plant diversity in most of its vegetational zones (e.g., Phillips and Miller, 2002).

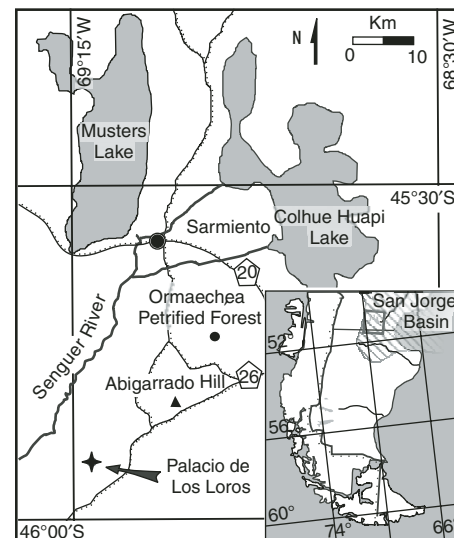
In southern South America, the few floras reported as Paleocene in the literature have either been redated as Eocene (Wilf et al., 2005; Yabe et al., 2006) or have no reliable geochronology. Most floras of possible Paleocene age are known only from small collections that lack stratigraphic context or reliable information about floral diversity. A relatively

well understood example is the Salamanca Formation flora, from central Patagonia (Fig. 1), which is mostly known from palynological and fossil wood studies (Romero, 1968; Archangelsky, 1973; Archangelsky and Romero, 1974; Petriella and Archangelsky, 1975; Archangelsky and Zamalao, 1986; Brea et al., 2005; Matheos et al., 2005). Compression floras from the Salamanca Formation have only been studied by Berry (1937) from a small collection, including 24 figured specimens and 11 species, that has never been revised.

Here, we report the first quantitative estimates of plant megafossil diversity for the Paleocene of southern South America, using large, unbiased collections of the Salamanca Formation compression flora. We review the stratigraphy and age of the flora, analyze floral richness, contrast the results with comparable Paleocene floras from similar absolute latitudes of the Western Interior of North America, and place these results in the context of early Cenozoic floral diversification in South America.

## GEOLOGICAL SETTING AND AGE

The new collections come from two localities in the Palacio de los Loros ("Parrot Palace") exposures of the Salamanca Formation. These



**Figure 1.** Regional map of the San Jorge Basin and modern location of the fossiliferous Palacio de los Loros outcrops (arrow) in the west-central basin (see also Appendix DR1 [see text footnote 1]). Inset: 62 Ma positions (using Ocean Drilling Stratigraphic Network [2004] online plate reconstruction service, with modern coastlines); box shows study area.

crop out in the western San Jorge Basin, 36 km south of Sarmiento in southern Chubut Province, Argentina (Fig. 1).

In the local section at Palacio de los Loros (GSA Data Repository Appendix DR1<sup>1</sup>), the Salamanca Formation, which is extensively exposed in an old valley of the Senguer River, lies unconformably upon the Late Cretaceous Bajo Barrial Formation of the Chubut Group and conformably beneath the continental,

<sup>1</sup>GSA Data Repository item 2007233, Appendix DR1 (section of the Salamanca Formation at Palacio de los Loros locality), Appendix DR2 (distinguishing features of angiosperm leaf morphotypes from Palacio de los Loros), and Appendix DR3 (relative abundance of dicot leaf morphotypes for rarefaction analysis), is available online at [www.geosociety.org/pubs/ft2007.htm](http://www.geosociety.org/pubs/ft2007.htm), or on request from [editing@geosociety.org](mailto:editing@geosociety.org) or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

\*E-mail: [aiglesias@museo.fcnym.unlp.edu.ar](mailto:aiglesias@museo.fcnym.unlp.edu.ar).

middle and late Paleocene Río Chico Formation. The bulk of the Salamanca Formation is a transgressive marine package, corresponding to the middle and lower Salamanca, but the uppermost Salamanca in the western part of the basin contains mudstone and fine-grained sandstone beds that represent channels and oxbow fills from a meandering, low-relief fluvial environment. The mudstone and some of the sandstone beds contain well-preserved plant compression fossils throughout the exposure area. The two sites reported here, PL1, a channel siltstone, and PL2, a channel siltstone topped by mudstone fill at approximately the same stratigraphic level as PL1, had the best preservation of plant remains.

The Salamanca Formation is generally assigned to the Danian stage, based on foraminifera and ostracoda from the northern and eastern parts of the basin (Méndez, 1966; Bertels, 1975).

Specifically, the foraminifera species present, including *Globanomalina (Turborotalia) compressa* and *Globoconusa daubjergensis*, reliably indicate an upper Danian age (zone P1c) for the marine Salamanca (following Olsson et al., 1999). There are three less reliable but consistent radiometric ages, all from whole-rock K-Ar analyses. First, a tuff reported as being from the uppermost Salamanca Formation, 70 km north-east of Palacio de los Loros, rendered an age of  $62.6 \pm 5.0$  Ma (Andreis, 1977; adjusted using Dalrymple, 1979). Second, two basalt units at or just under the base of the formation yielded ages of  $64.0 \pm 0.8$  Ma and  $62.8 \pm 0.8$  (Marshall et al., 1981). Marshall et al. (1981, 1997) used these ages and paleomagnetic data to assign the overlying Banco Negro Inferior (a massive, black, tabular bed conventionally used to identify the Salamanca–Río Chico contact throughout the basin) at several localities to polarity

subchron C26r. We also sampled a tuff horizon immediately below the Banco Negro Superior (Feruglio, 1949), 41.5 m above correlative plant-bearing levels, for  $^{40}\text{Ar}/^{39}\text{Ar}$  analyses. The sanidines we retrieved were clearly altered, and the resulting isochron age of  $57.80 \pm 6.00$  Ma has little interpretive value.

Based on this evidence and the lack of significant hiatuses observed between the relevant units, the Palacio de los Loros megaflores, which locally overlie the marine Salamanca and underlie the Banco Negro Inferior, can be well constrained to an age near the Danian-Selandian boundary. This is equivalent to the magnetic polarity chron 26–27 boundary at  $61.7 \pm 0.2$  Ma (Gradstein et al., 2004). However, a more precise age assignment for the Palacio de los Loros floras requires additional work, with particular attention to western strata of the San Jorge Basin.

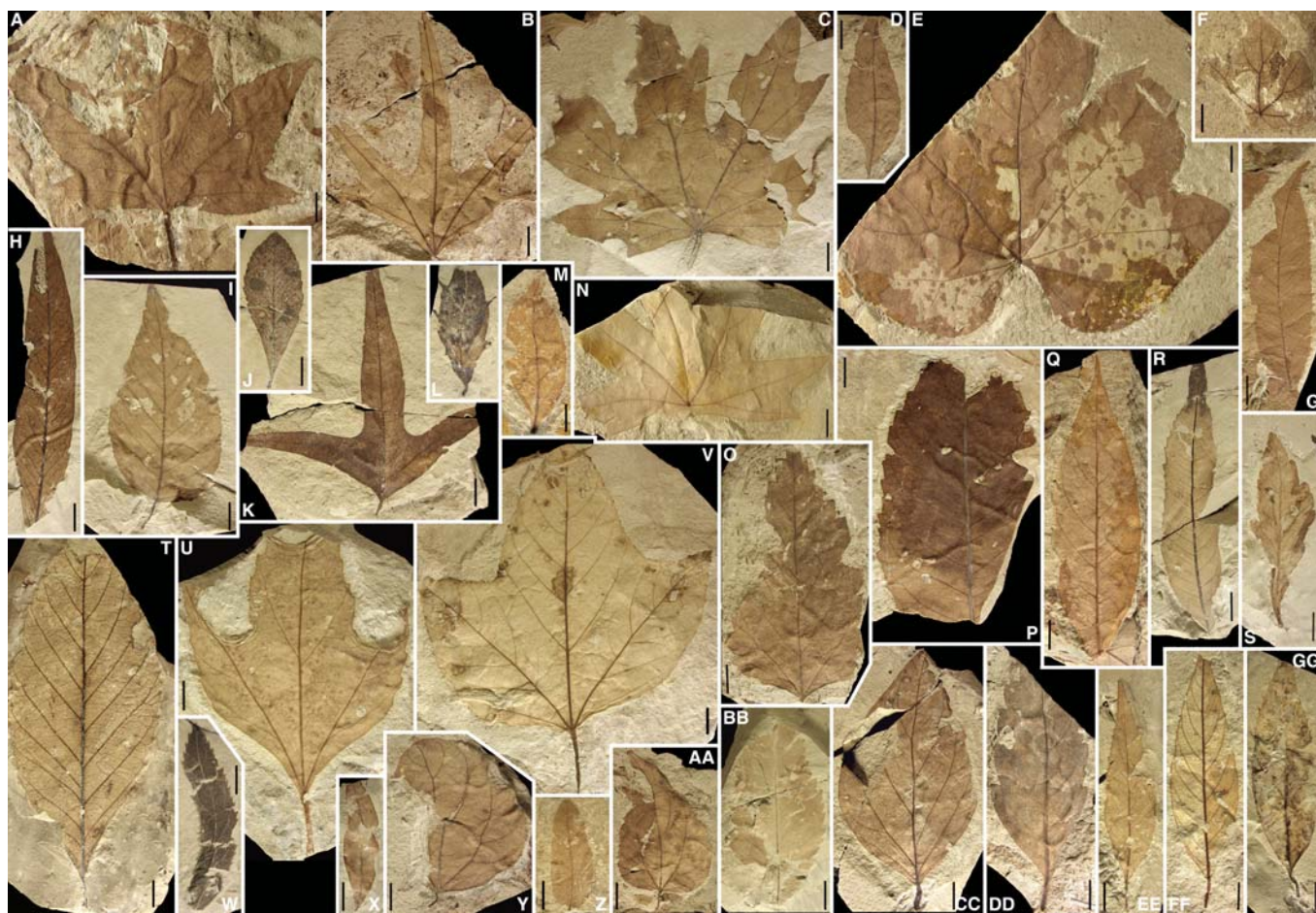


Figure 2. The 33 dicot leaf species found at Palacio de los Loros (see also Appendix DR2 [text footnote 1]). A: Morphotype SA035 (specimen MPEF-Pb-2031 [Museo Paleontológico Egidio Feruglio]). B: “*Sterculia*” *acuminataloba* (MPEF-Pb-2027). C: SA019 (MPEF-Pb-2029). D: SA044 (MPEF-Pb-2037). E: *Paranymphea aristolochiaformis* (MPEF-Pb-2032). F: SA040 (MPEF-Pb-2033). G: SA052 (MPEF-Pb-2045). H: SA016 (MPEF-Pb-2028). I: *Dryophyllum australis* (MPEF-Pb-2022). J: “*Myrica*” *premira* (MPEF-Pb-2042). K: SA058 (MPEF-Pb-2050). L: SA057 (MPEF-Pb-2049). M: *Laurophyllum chubutensis* (MPEF-Pb-2039). N: SA055 (MPEF-Pb-2047). O: SA008 (MPEF-Pb-2024). P: SA054 (MPEF-Pb-2046). Q: SA056 (MPEF-Pb-2048). R: SA020 (MPEF-Pb-2030). S: SA059 (MPEF-Pb-2051). T: SA002 (MPEF-Pb-2021). U: SA047 (MPEF-Pb-2040). V: *Cissites patagonica* (MPEF-Pb-2025). W: SA051 (MPEF-Pb-2044). X: SA050 (MPEF-Pb-2043). Y: SA060 (MPEF-Pb-2052). Z: SA045 (MPEF-Pb-2038). AA: *Banaraphyllum ovatum* (MPEF-Pb-2041). BB: SA043 (MPEF-Pb-2036). CC: *Laurophyllum piatnitzkyi* (MPEF-Pb-2026). DD: *Fagophyllum duseni* (MPEF-Pb-2035). EE: SA005 (MPEF-Pb-2023). FF: SA041 (MPEF-Pb-2034). GG: *Akania* sp. (MPEF-Pb-2020). Scale bar = 1 cm.

## SALAMANCA FLORA AND PALEOCENE PLANT DIVERSITY

Fossil plants at Palacio de los Loros were discovered by A. Piatnitzky (Feruglio, 1949), who collected the 24 type specimens (Berry, 1937) from an unknown stratigraphic level. Prospecting in this area, we discovered the PL1 and PL2 sites and sampled them using standard bench-quarrying techniques (e.g., Barclay et al., 2003). All identifiable material, including 1119 specimens from PL1 and 1397 from PL2, was prepared and deposited at the Museo Paleontológico Egidio Feruglio (MPEF), Trelew, Argentina. The 2417 leaf specimens were segregated into discrete morphotypes using distinct leaf architectural features (Johnson et al., 1989; Ash et al., 1999; Fig. 2; Appendix DR2 [see text footnote 1]) to allow for paleoecological and paleoclimatic analyses.

From these morphotypes, we estimate the presence of 36 angiosperm leaf species, including 33 dicots (Fig. 2; Appendix DR2) and three monocots. Recognizable angiosperm groups include: a large-leaved *Nothofagus* (Southern Beech, Fig. 2D); Menispermaceae (moonseed family, Fig. 2Y); *Akania* (an Australian rain-forest endemic also known from early Eocene Patagonia; Romero and Hickey, 1976; Fig. 2GG); a variable species of Lauraceae (laurel family, Fig. 2CC); at least one species of Urticaceae (nettle family, Fig. 2W); legume leaflets that represent one of the oldest records of the family (Fabaceae, Fig. 2Z); at least one species of Sapindaceae (litchie family, Figs. 2G and 2BB); palmately lobed Malvaceae of the “*Sterculia*” type (Figs. 2B and 2K); and Rosaceae (Fig. 2O). Well-preserved angiosperm flowers, fruits, and seeds are also present. Also, the flora contain conifers, including Araucariaceae cone scales and Podocarpaceae leaves and cones, and at least two fern species including *Lygodium*. These are the first occurrences of reproductive and foliar organs of gymnosperms and the first fern foliage found in the Salamanca Formation, corroborating data from wood and palynomorphs (Archangelsky, 1973; Romero, 1968; Matheos et al., 2005). The recognizable elements, especially *Nothofagus*, *Akania*, and the conifer groups, indicate a Gondwanan affinity for the flora.

Using standard techniques of leaf-margin (updated in Wilf, 1997, their equations 2 and 4) and leaf-area (Wilf et al., 1998, p. 204) analyses from the 33 dicot leaves at both Palacio de los Loros outcrops combined (Appendix DR2, see footnote 1), we estimated a mean annual temperature of  $14.1 \pm 2.6$  °C (57.6% of species toothed) and mean annual precipitation of at least 115 cm (+50/–35 cm), consistent with the lack of Andean rain shadow at this time.

The paleoclimate estimates are supported by the presence of diverse thermophilic groups, such as palm organs, which are found throughout the basin (Romero, 1968; Archangelsky, 1973), and alligatorids from the eastern basin, which require a

minimum winter isotherm of 10 °C (Bona, 2005). Podocarps nearly exclusively inhabit high-rainfall environments (e.g., Brodribb and Hill, 1999), and *Akania* today only survives in eastern Australian tropical and subtropical rain forest. Growth-ring studies of petrified wood also suggest a frost-free environment (Brea et al., 2005).

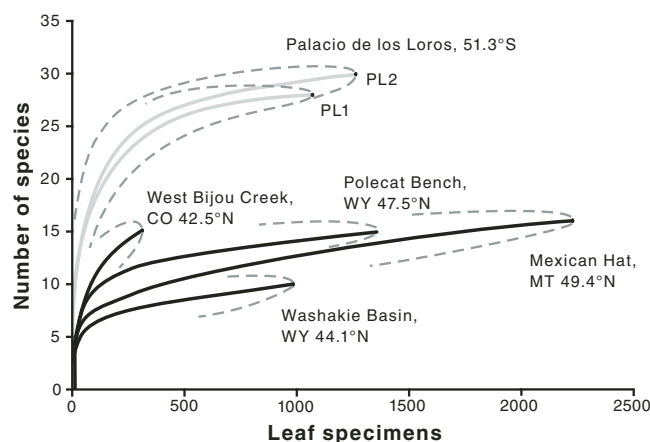
Alpha diversity of dicot leaves was adjusted for sample size using rarefaction (Fig. 3; Appendix DR3) and compared with well-sampled Paleocene floras that represent the maximum Paleocene alpha diversity conventionally known (see below) from hundreds of sites in the Western Interior of North America (e.g., Wing et al., 1995; Wilf, 2000; Barclay et al., 2003). These samples come from similar paleolatitudes and paleotemperatures and from comparable low-relief, floodplain paleoenvironments (e.g., Wing et al., 1995); they all were collected using similar, unbiased methods. Our results (Fig. 3) show that diversity at both PL1 and PL2 is more than 50% higher than comparable U.S. floras. We note that a suite of diverse Paleocene floras, including the Castle Rock flora, has been discovered in the Denver Basin of Colorado, proximal to the elevated Laramide Front Range (Johnson and Ellis, 2002; Ellis et al., 2003; Johnson et al., 2003). However, these floras clearly are not analogs for Palacio de los Loros because they represent premontane, high-rainfall environments, whereas the samples in Figure 3 come from basin centers or other low-relief settings. The foliar physiognomy of the Castle Rock flora indicates higher temperatures by 8 °C and twice the annual rainfall of the Palacio de los Loros floras, indicating benign conditions associated with very high biodiversity today.

Eocene floras from Patagonia are known for high diversity far exceeding the Paleocene Sala-

manca floras (Berry, 1938; Wilf et al., 2005). Although observed here at a much coarser temporal scale, this pattern is consistent with Paleocene-Eocene diversification seen in Neotropical palynofloras (Jaramillo, 2002; Jaramillo et al., 2006) and in Northern Hemisphere macrofloras and palynofloras (e.g., Wing and Harrington, 2001). The species composition of the Palacio de los Loros floras is dissimilar to that of the extremely diverse Laguna del Hunco flora, from early Eocene (51.9 Ma) tuffaceous lake beds in northwest Chubut Province (Wilf et al., 2005), although there is taxonomic overlap at the generic and familial level (Appendix DR3; Wilf et al., 2005). Therefore, a number of turnover events occurred between the Paleocene and early Eocene that remain to be documented; globally increasing temperatures during the early Eocene would have facilitated immigration and evolutionary diversification that increased floral diversity in Patagonia, as seen in other areas of the Americas (Wilf, 2000; Wing and Harrington, 2001; Jaramillo, 2002; Jaramillo et al., 2006).

The elevated richness of Patagonian Paleocene floras adds a new dimension to the history of South American biodiversity. Shortly after the end-Cretaceous event, Patagonia already harbored considerably richer Paleocene plant communities than comparable environments in the Western Interior of North America. This high baseline presumably anchored the evolution of the floral diversity seen 10 m.y. later at Laguna del Hunco, apparently mirrored in diverse Eocene Neotropical palynofloras (Jaramillo et al., 2006). The cause of the Paleocene diversity pattern is not known but may be related to greater distance from the Chicxulub impact, differences in Cretaceous plant diversity, and/or higher immigration or speciation rates.

**Figure 3. Rarefied richness of dicot leaf species, with selected 95% confidence intervals (Tipper, 1979) and paleolatitudes (using Ocean Drilling Stratigraphic Network [2004] online plate reconstruction service) at Palacio de los Loros (localities PL1 and PL2; Appendix DR3 [see text footnote 1]) and representative and identically collected Paleocene floras from single localities in the Western Interior of North America. The West Bijou Creek sample is from Denver Museum of Nature and Science loc. 2379, in the D1 unit (ca. 65.5 Ma), eastern Denver Basin (Barclay et al., 2003). The 64.4 Ma Mexican Hat sample is from Smithsonian National Museum of Natural History (USNM) loc. 42090, from the Lebo Member of the Fort Union Formation, Powder River Basin, south-eastern Montana (Wilf et al., 2006). The Polecat Bench sample is the 57.5 Ma Lur'd Leaves site (USNM loc. 42042; Wilf et al., 2006) from the Fort Union Formation, Bighorn Basin, Wyoming. The ca. 56.5 Ma Washakie Basin, Wyoming, sample is USNM loc. 41270 (Wilf, 2000) from the uppermost Fort Union Formation. For West Bijou Creek and the Washakie Basin, which each had multiple published localities, we selected the most diverse localities for this analysis.**



## ACKNOWLEDGMENTS

For generous support, we thank the National Science Foundation (grant DEB-0345750). We also thank the Agencia Nacional de Promoción Científica y Tecnológica (Project PICT 07-08671); Consejo Nacional de Investigaciones Científicas y Técnicas; B. Huber for biostratigraphic assistance; M. Caffa, L. Canessa, B. Carigliño, I. Escapa, C. González, R. Horwitt, P. Puerta, and E. Ruigomez for exceptional assistance in the field and laboratory; Secretaría de Cultura de la Provincia de Chubut for permits; and the landowners at Palacio de los Loros, Hugo Visser, Edna de Galáz, and Clara Salazar, for access. This work is part of the Ph.D. thesis of Iglesias at Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

## REFERENCES CITED

- Andrés, R.R., 1977, Geología de Cañadón Hondo, Departamento Escalante, Provincia del Chubut, República Argentina: Revista del Museo de La Plata Obra del Centenario, Geología, v. 4, p. 77–102.
- Archangelsky, S., 1973, Palinología del Paleoceno de Chubut. I. Descripciones sistemáticas: Ameghiniana, v. 10, p. 339–399.
- Archangelsky, S., and Romero, E.J., 1974, Polen de gimnospermas del Cretácico y Paleoceno de Patagonia: Ameghiniana, v. 11, p. 217–236.
- Archangelsky, S., and Zamaló, M.C., 1986, Nuevas descripciones palinológicas de las formaciones Salamanca y Bororó (Paleoceno de Chubut, República Argentina): Ameghiniana, v. 23, p. 35–46.
- Ash, A.W., Ellis, B., Hickey, L.J., Johnson, K.R., Wilf, P., and Wing, S.L., 1999, Manual of Leaf Architecture: Morphological Description and Categorization of Dicotyledonous and Net-Veined Monocotyledonous Angiosperms: Washington, D.C., Smithsonian Institution, 65 p.
- Barclay, R.S., Johnson, K.R., Betterton, W.J., and Dilcher, D.L., 2003, Stratigraphy, megafloora, and the K-T boundary in the eastern Denver Basin, Colorado: Rocky Mountain Geology, v. 38, p. 45–71, doi: 10.2113/gsrocky.38.1.45.
- Berry, E.W., 1937, A Paleocene flora from Patagonia: Johns Hopkins University Studies in Geology, v. 12, p. 33–50.
- Berry, E.W., 1938, Tertiary Flora from the Río Pichileufú, Argentina: Geological Society of America Special Paper 12, 149 p.
- Bertels, A., 1975, Bioestratigrafía del Paleógeno en la República Argentina: Revista Española de Micropaleontología, v. 7, p. 429–450.
- Bona, P., 2005, Sistemática y biogeografía de las tortugas y los cocodrilos Paleocenos de la Formación Salamanca, provincia de Chubut, Argentina [Ph.D. thesis]: La Plata, Argentina, Universidad Nacional de La Plata, 186 p.
- Brea, M., Matheos, S., Zamuner, A.B., and Ganuza, D., 2005, Análisis de los anillos de crecimiento del bosque fósil de Víctor Szlápelis, Terciario inferior del Chubut, Argentina: Ameghiniana, v. 42, p. 407–418.
- Brodrick, T.J., and Hill, R.S., 1999, Southern conifers in time and space: Australian Journal of Botany, v. 47, p. 639–696, doi: 10.1071/BT98093.
- Burnham, R.J., and Johnson, K.R., 2004, South American paleobotany and the origins of Neotropical rainforests: Philosophical Transactions of the Royal Society of London, ser. B, v. 359, p. 1595–1610.
- Dalrymple, G.B., 1979, Critical tables for conversion of K-Ar ages from old to new constants: Geology, v. 7, p. 558–560, doi: 10.1130/0091-7613(1979)7<558:CTFCOK>2.0.CO;2.
- Ellis, B., Johnson, K.R., and Dunn, R.E., 2003, Evidence for an in situ early Paleocene rainforest from Castle Rock, Colorado: Rocky Mountain Geology, v. 38, p. 73–100, doi: 10.2113/gsrocky.38.1.173.
- Feruglio, E., 1949, Descripción Geológica de la Patagonia, Vol. II: Buenos Aires, Ministerio de Industria y Comercio de la Nación, Dirección General de Yacimientos Petrolíferos Fiscales, 349 p.
- Gradstein, F.M., Ogg, J., and Smith, A., 2004, A Geologic Time Scale 2004: Cambridge, Cambridge University Press, 589 p.
- Jaramillo, C.A., 2002, Response of tropical vegetation to Paleogene warming: Paleobiology, v. 28, p. 222–243, doi: 10.1666/0094-8373(2002)028<0222:ROTVTP>2.0.CO;2.
- Jaramillo, C.A., Rueda, M.J., and Mora, G., 2006, Cenozoic plant diversity in the Neotropics: Science, v. 311, p. 1893–1896, doi: 10.1126/science.1121380.
- Johnson, K.R., and Ellis, B., 2002, A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary boundary: Science, v. 296, p. 2379–2383, doi: 10.1126/science.1072102.
- Johnson, K.R., Nichols, D.J., Attrep, M., Jr., and Orth, C.J., 1989, High-resolution leaf-fossil record spanning the Cretaceous-Tertiary boundary: Nature, v. 340, p. 708–711, doi: 10.1038/340708a0.
- Johnson, K.R., Reynolds, M.L., Werth, K.W., and Thomasson, J.R., 2003, Overview of the Late Cretaceous, early Paleocene, and early Eocene megaflooras of the Denver Basin, Colorado: Rocky Mountain Geology, v. 38, p. 101–120, doi: 10.2113/gsrocky.38.1.101.
- Marshall, L.G., Butler, R.F., Drake, R.E., and Curtis, G.H., 1981, Calibration of the beginning of the age of mammals in Patagonia: Science, v. 212, p. 43–45, doi: 10.1126/science.212.4490.43.
- Marshall, L.G., Sempere, T., and Butler, R.F., 1997, Chronostratigraphy of the mammal-bearing Paleocene of South America: Journal of South American Earth Sciences, v. 10, p. 49–70, doi: 10.1016/S0895-9811(97)00005-9.
- Matheos, S., Brea, M., Zucol, A.F., Prámparo, M., Raigemborn, M.S., Iglesias, A., and Fisher, A., 2005, Análisis paleoambiental de las sedimentitas del Daniano del sector sur de los lagos Musters y Colhué Huapi (Chubut, Argentina): Actas XVI Congreso Geológico Argentino, T. III, p. 83–90.
- Méndez, I., 1966, Foraminíferos, edad y correlación estratigráfica del Salamanquense de Punta Peligro (45°30'S; 67°11'W), provincia del Chubut: Revista de la Asociación Geológica Argentina, v. 21, p. 127–157.
- Ocean Drilling Stratigraphic Network, 2004, ODSN Plate Tectonic Reconstruction Service: GEOMAR (Research Center for Marine Geosciences-Kiel), and the Geological Institute, University of Bremen: www.odsn.de/odsn (March 2007).
- Olsson, R.K., Berggren, W.A., Hemleben, C., and Huber, B.T., 1999, Atlas of Paleocene planktonic foraminifera: Smithsonian Contributions to Paleobiology, v. 85, p. 1–252.
- Petriella, B.T.P., and Archangelsky, S., 1975, Vegetación y ambientes en el Paleoceno de Chubut: Actas I Congreso Argentino de Paleontología y Bioestratigrafía, Tucumán, v. 2, p. 257–270.
- Phillips, O.L., and Miller, J.S., 2002, Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set: St. Louis, Missouri Botanical Garden Press, 319 p.
- Romero, E.J., 1968, *Palmoxylon patagonicum* n. sp. del Terciario Inferior de la Provincia del Chubut, Argentina: Ameghiniana, v. 5, p. 417–432.
- Romero, E.J., and Hickey, L.J., 1976, Fossil leaf of Akaniaceae from Paleocene beds in Argentina: Bulletin of the Torrey Botanical Club, v. 103, p. 126–131, doi: 10.2307/2484888.
- Tipper, J.C., 1979, Rarefaction and rarefaction—The use and abuse of a method in paleontology: Paleobiology, v. 5, p. 423–434.
- Wilf, P., 1997, When are leaves good thermometers? A new case for leaf margin analysis: Paleobiology, v. 23, p. 373–390.
- Wilf, P., 2000, Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis: Geological Society of America Bulletin, v. 112, p. 292–307, doi: 10.1130/0016-7606(2000)112<0292:LPEECC>2.3.CO;2.
- Wilf, P., Wing, S.L., Greenwood, D.R., and Greenwood, C.L., 1998, Using fossil leaves as paleoprecipitation indicators, an Eocene example: Geology, v. 26, p. 203–206, doi: 10.1130/0091-7613(1998)026<0203:UFLAPI>2.3.CO;2.
- Wilf, P., Johnson, K.R., Cúneo, N.R., Smith, M.E., Singer, B.S., and Gandolfo, M.A., 2005, Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina: American Naturalist, v. 165, p. 634–650, doi: 10.1086/430055.
- Wilf, P., Labandeira, C.C., Johnson, K.R., and Ellis, B., 2006, Decoupled plant and insect diversity after the end-Cretaceous extinction: Science, v. 313, p. 1112–1115, doi: 10.1126/science.1129569.
- Wing, S.L., and Harrington, G.J., 2001, Floral response to rapid warming in the earliest Eocene and implications for concurrent faunal change: Paleobiology, v. 27, p. 539–563, doi: 10.1666/0094-8373(2001)027<0539:FRTRWI>2.0.CO;2.
- Wing, S.L., Alroy, J., and Hickey, L.J., 1995, Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 115, p. 117–155, doi: 10.1016/0031-0182(94)00109-L.
- Wing, S.L., Herrera, F., and Jaramillo, C.A., 2004, A Paleocene flora from the Cerrejón Formation, Guajira Peninsula, northeastern Colombia, in VII Quadrennial Conference Abstracts: Bariloche, Argentina, International Organization of Paleobotany, p. 146–147.
- Wolfe, J.A., and Upchurch, G.R., 1986, Vegetation, climatic and floral changes at the Cretaceous-Tertiary boundary: Nature, v. 324, p. 148–152, doi: 10.1038/324148a0.
- Yabe, A., Uemura, K., and Nishida, H., 2006, Geological notes on plant fossil localities of the Ligorio Márquez Formation, central Patagonia, Chile, in Nishida, H., ed., Post-Cretaceous Floristic Changes in Southern Patagonia, Chile: Tokyo, Chuo University, p. 29–35.

Manuscript received 15 March 2007  
Revised manuscript received 29 May 2007  
Manuscript accepted 4 June 2007

Printed in USA