Fossil ferns from the Eocene of Argentina and the deep-time links between Southern Hemisphere rainforests

Carvalho, M. R., P. Wilf, M. A. Gandolfo, N. R. Cúneo, and K. R. Johnson

In recent years, paleobotanical explorations in southern South America have recovered an increasing number of taxa currently restricted to Australasian rainforests, highlighting biotic connectivity between these areas in the geologic past and suggesting a complex biogeographic history. The Eocene deposits of Laguna del Hunco (51.9 Ma), Patagonia, Argentina, bear remains of the oldest known *Eucalyptus* (Myrtaceae), as well as many rainforest-associated gymnosperm taxa including *Papuacedrus* (Cupressaceae), *Agathis* (Araucariaceae), and *Dacrycarpus* (Podocarpaceae) and several angiosperm taxa such as *Gymnostoma* (Casuarinaceae), Proteaceae, Atherospermataceae and Cunoniaceae. Herein, we show that the pattern of widespread Gondwanan distribution observed for angiosperms and gymnosperms is also evident for the pteridophyte component of this flora. Three fern species have been recently recovered and identified based on the preservation of fertile fronds and sporangial remains. One fossil species bears acrosticoid sporangia on pinnatifid frond fragments typical of Osmundaceae. Dicksoniaceae is recognized based on remains of fronds with marginal sori covered by a bivalved indusium, while the presence of Gleicheniaceae is confirmed by fertile fronds that have naked, round sori composed of 3-5 sporangia restricted to the upper branch of bifurcating secondary veins. Total evidence approaches based on morphology and previously sequenced chloroplast (*rbc*L, *atp*B, *rps*4) and nuclear genes (18S rDNA) were used for testing the natural affinities of these fossils. Each fossil species was scored for 25–35 characters of frond and reproductive structure morphology, rendering hypotheses of relationships of the fossils to each of the three mentioned families. The results suggest intrafamilial affinities to *Todea* (Osmundaceae), *Dicksonia* (Dicksoniaceae), and *Sticherus* (Gleicheniaceae). These genera include species native to Australia and have varying number of endemic species in montane and lowland rainforests. *Todea* is now restricted to montane, humid subtropical and tropical Australasia and South Africa, and has been reported for the Jurassic of Argentina. *Dicksonia* is present in the wet subtropics and tropics of Australasia and South America, while *Sticherus* is pantropical and austral, and mostly humid montane. Although the fossil record for *Dicksonia* and *Sticherus* is sparse; both genera are known from Oligocene deposits of Tasmania, and the former was previously reported from the middle Eocene of Argentina. The records from the Eocene of Patagonia show a wider distribution for these three genera in the past, and the same long-term patterns of shared lineages between Australasia and South America observed before in angiosperms and conifers. Whether the extant distribution of fern lineages shared between Australia and South America is a product of independent colonization events, or evidence of a shared, widespread ancestral biota remains unknown. However, the warmer climate that predominated the Eocene, and the closer proximity of both South America and Australia to Antarctica support the hypothesis of a nearly continuous forest cover throughout these landmasses. The widespread-Gondwana biogeographical pattern shared by multiple lineages in this Eocene flora suggests that an important

portion of the biogeography of the Southern Hemisphere biotas is related to processes of range expansion and local/regional extinctions of taxa in the geological past.

Early Eocene winged fruits of the walnut family (Juglandaceae) from Patagonia, Argentina.

Hermsen, E. J. and M. A. Gandolfo

The early Eocene (ca. 51.9 Ma) Laguna del Hunco flora of Chubut Province, Argentina, is a diverse paleoflora that includes abundant plant remains, including ferns, conifers, and angiosperms. Although the flora has been known since the early twentienth century, the majority of angiosperm taxa described from it are based on vegetative remains. A wealth of angiosperm reproductive material has also been collected from the fossil localities, but very little of it (only five genera and six species) has been formally described. In this paper, we present undescribed fossil fruits that can be confidently assigned to Juglandaceae. Each fruit consists of a nutlet attached to a trilobed wing; although the wing venation is not preserved, the wing has parallel ridges. A prophyllum is highly reduced or absent. The nutlet has a single locule with two to four compartments (one to two septa) and a single, highly lobed seed. The single-seeded nutlet with partitioned locule, lobed seed, and lobed wing is characteristic of the family Juglandaceae. The trilobed wing is further characteristic of Engelhardiodeae, which includes three living and several extinct genera. The living genera are distributed in Central America and southeast Asia, south to New Guinea. To date, the macrofossil record ofJuglandaceae has been restricted to the Northern Hemisphere. Thus, evidence of Engelhardioideae in Paleogene South Amerlca is surprising. In addition to the morphological evidence supportingthe affinities of the fossilwith Juglandaceae subfamily Engelhardiodeae, the presence of Engelhardioideae in Paleogene South America is further supported by early Paleocene and early Eocene occurrences of the dispersed pollen taxon *Plicatopollis wodehousei* (also known from the Paleocene of North America) in Patagonia. The phylogenetic affinities of the fossil fruits will be explored through cladistic analyses.

***Eucalyptus* from the early Eocene of Patagonia, Argentina: phylogenetic, biogeographic, and ecological implications for understanding eucalypt evolution**

Hermsen, E. J., M. A. Gandolfo, K. R. Johnson, M. C. Zamaloa, K. C. Nixon, P. Wilf, and N. R. Cúneo,

The early Eocene Laguna del Hunco beds of Patagonia, Argentina contain a diverse fossil assemblage of angiosperms, gymnosperms, ferns, insects, fish, and frogs. 40Ar/39Ar radioisotopic analyses of tuffs interbedded with the fossiliferous, caldera-lake sediments indicate that the assemblage is ca. 51.9 Ma. Some of the most significant fossils from this site are abundant leaves, several buds, a flower, and numerous infructescences and isolated capsules with features characteristic of the extant genus *Eucalyptus*. The leaves are falcate with numerous, closely-spaced secondary veins and

oil glands. Each bud displays a transverse scar separating the hypanthium from an apical operculum. The scar is interpreted as having been left by loss of a caducous calyx, while the operculum is interpreted as corolline. The margins of the individual petals comprising the corolline operculum are visible, indicating that the petals were coherent rather than connate. The single specimen representing an open flower lacks a perianth, has a single style and stigma, and likely had numerous stamens (only some of which are preserved). Infructescences are composed of several umbellasters with 3–7 capsules each; capsules display valvate dehiscence and have perianth and staminophore scars as well as a prominent disc. Phylogenetic analyses indicate that the fossils belong within the *Eucalyptus* clade. The presence of a calycine scar on the flower buds is characteristic of species within and closely allied to *Eucalyptus* subgenus *Symphyomyrtus*, indicating that the fossils have affinities to this subgenus. These fossils are currently the oldest record of *Eucalyptus* in the world, as previously the only reliably dated and diagnosed *Eucalyptus* fossils were from Neogene sediments. The fossils also represent the only known natural occurrence of the genus outside Australasia. Given the derived phylogenetic position of the fossils, however, they do not provide direct evidence that *Eucalyptus* arose or underwent early diversification in South America. They instead provide the first reliable evidence for a more complicated, partially extra-Australasian scenario for the biogeographic history of the genus. The presence of *Eucalyptus* at Laguna del Hunco is part of a broader pattern indicating biogeographic links between Eocene floras of Patagonia and modern floras of Australasia exemplified by other taxa from the flora, such as *Akania* (Akaniaceae), *Gymnostoma* (Casuarinaceae), and *Papuacedrus* (Cupressaceae). Seedlings of modern *Eucalyptus* subgenus *Symphyomyrtus* that occur in caldera habitats of Papua New Guinea today make use of volcanic destruction of standing rainforest to establish themselves, thus suggesting a possible ecological analog for *Eucalyptus* at Laguna del Hunco.

Fossil and modern phylogenetic components of Patagonian seed plant diversity

Nixon, K. C., M. A. Gandolfo, E. J. Hermsen, and M. C. Zamaloa

Analysis of turnover in paleofloras suggest four distinct floristic intervals during the Tertiary of Patagonia in southern South America (Paleocene–Early Eocene, Middle Eocene–Early Oligocene, Late Oligocene–Early Miocene, and Middle–Late Miocene). These turnovers are significant and provide a basis for understanding the origin and evolution of modern Patagonian floras. We use the palynological and paleobotanical data summarized by Barreda and Palazzesi to analyze 33 Patagonian Tertiary formations (10 Paleocene–Early Eocene sites, 9 Middle Eocene–Early Oligocene sites, 12 Late Oligocene–Early Miocene sites and 2 Mi dle–Late Miocene sites). We augmented these data with recent additions to the paleofloras of sites in Patagonia, including Salamanca, Laguna del Hunco, Rio Pichileufu, Rio Nirihuau and Cullen Formations among others. Modern floristic data from extant floras of Patagonia, northern Argentina, Australia, South Africa, New Caledonia, New Zealand and selected Northern Hemisphere sites including the arid west of North America were then combined into a comprehensive matrix that was analyzed for clade correspondence

using a 'supertree' generated from the most recent molecular analyses for all clades represented in the fossil floras of Patagonia. A comparison of results using different phylogenetically-based approaches will be presented. This provides both an understanding of the biogeographic affinities of the southern cone Tertiary paleofloras as well as the ability to generate phylogenetic indices for shared clades among fossil and modern floras.

Eocene caldera floras of Patagonia, Argentina: the peak of Australasian rainforest signal in South America

Wilf, P., M. R. Carvalho, E. J. Hermsen, M. A. Gandolfo, N. R. Cúneo, and K. R. Johnson

We report ongoing investigations of the classic caldera lake floras from Laguna del Hunco (LH) and Río Pichileufú (RP) in Patagonia. 40Ar–39Ar analyses on sanidine from tuffs intercalated with the fossiliferous horizons give high-precision ages of 51.91 ± 0.22 Ma from LH (early Eocene) and 47.46 ± 0.05 Ma from RP (middle Eocene). Stratigraphically controlled bench quarrying of >10,000 plant specimens from multiple horizons reveals hundreds of species at both sites, comprising a floral diversity among the highest known from the Eocene, and many important occurrences of fossil insects, insect-feeding damage, and vertebrates. The biogeographic and paleoenvironmental signals from these assemblages have previously remained enigmatic due to undersampling, historical misidentifications, and lack of sustained taxonomic study. We find that the strongest affinity, now clear among conifers, angiosperms, and ferns, is to very humid, usually montane forests of tropical and subtropical Australasia. All of the taxa listed below are present at LH, and most are also present at RP. The conifer assemblages include attached foliage and seed cone of *Papuacedrus* (Cupressaceae); foliage, cone scales, and probable pollen cones of *Agathis* and *Araucaria* Sec. *Eutacta* (Araucariaceae); and diverse Podocarpaceae, including foliage attached to seed and pollen cones of *Dacrycarpus*, and foliage of *Acmopyle*, *Retrophyllum*, and *Podocarpus*. These conifer taxa today demonstrate physiological intolerance to drought (especially *Acmopyle* and *Dacrycarpus*) and are entirely confined to rainforest; nearly all only occur in Australasia. The fern floras display a similar, though more cosmopolitan pattern, and include fertile fronds of *Todea* (Osmundaceae), *Dicksonia* (Dicksoniaceae), and *Sticherus* (Gleicheniaceae). Among angiosperms, the Australasian connection is strongly represented by fruits and male inflorescences attached to branches of *Gymnostoma* (Casuarinaceae); compound leaves of *Akania* (Akaniaceae); flower buds, infructescences, and leaves of *Eucalyptus* subgenus *Symphyomyrtus* (Myrtaceae); fruits of *Orites* and diverse leaves of other Proteaceae, and leaves and fruits of Atherospermataceae, Monimiaceae, Lauraceae, and Cunoniaceae. The presence of abundant *Eucalyptus* subgenus *Symphyomyrtus* in the ancient volcanic environment strongly suggests a vegetational mosaic of diverse rainforest alongside recent lava flows dominated by *Eucalyptus*, exemplified by the modern analog *E. deglupta* (also subgenus *Symphyomyrtus*) in calderas of New Britain. Most of the taxa listed have Paleogene fossil records in southeastern Australia, and a few have been found in Antarctica; they document a long and complex history of retreat and survival in the face

of severe climate change, regional extinction, and the movement of northern Australia into the tropics. Neotropical affinities of the floras remain few and mostly montane, and affinities to Andean temperate rainforest are scarce. The extensive taxonomic similarity of ancient Patagonian to modern Australasian, and to fossil southeast Australian, floras at the generic level is characteristic only during the Eocene. It is reduced in Late Cretaceous, Paleocene, or younger Patagonian floras and appears to indicate extensive lineage mobility across warm high latitudes, followed by migrations into lower latitudes in response to cooling and drying. This scenario is analogous to well-documented distributional shifts of coeval Northern Hemisphere floras and faunas but was not previously observed on this scale in the Southern Hemisphere.

P0048 – **ePoster**

Diversity and evolution of Araucariaceae: in pursuit of ghost lineages from South American fossils

Escapa, I., N. R. Cúneo, and P. Wilf

In South America, the family Araucariaceae is represented by two living species of the genus *Araucaria* section *Araucaria*, *A. araucana* and *A. angustifolia*, which along with the Australasian species of *Araucaria*, *Agathis*, and *Wollemi* define a mostly Southern Hemisphere distribution for the family. In addition, the Araucariaceae shows an extended fossil record with occurrences recognized since the early Mesozoic in both hemispheres. Stratigraphic adjustment of phylogenetic hypotheses for the family indicates that divergences leading to the major clades probably occurred as early as the Early Jurassic. Despite the extensive fossil record of the family, the phylogeny indicates ghost lineages for several genera and sections. We discuss the rich record of the family in South America and its implications for understanding the evolutionary relationships and the geographic distributions of past and present species. Several of these taxa fill remarkable temporal and morphological gaps in the record of Araucariaceae and therefore provide a more complete assessment of the evolutionary history of the group. New findings from Jurassic, Cretaceous and Paleogene localities in Argentina and Colombia are highlighted in this evolutionary context.

P0820 – ePoster

Systematics and morphology of selected angiosperm reproductive structures from the Eocene Laguna del Hunco flora, Chubut Province, Argentina

Hermsen, E. J., M. A. Gandolfo, P. Wilf, N. R. Cúneo, and K. R. Johnson

The early Eocene (ca. 51.91 Ma) Laguna del Hunco (LH) flora of Chubut Province, Argentina, is preserved in tuffaceous sediments and was deposited in a caldera-lake environment along with an assemblage of insects and some vertebrates. The paleoflora

is highly diverse, with taxa that today can be characterized as belonging to three different groups of rainforest plants displaying different climatic tolerances and geographical distributions: 1) subtropical to tropical Australasian taxa; 2) neotropical taxa; 3) and Gondwanan temperate taxa. Despite the excellent preservation, diversity, and interesting biogeographic connections of the flora, very little research has been done documenting the abundant angiosperm reproductive material that has been collected from LH. E.W. Berry named and illustrated the taxon *Schmidelia eduliforma* based on a single infructescence in 1925 (he transferred the species to the extant genus *Allophylus* (Sapindaceae) in 1938); he also described four other taxa, three species of *Carpolithus* and one species of *Malvacarpus*, in each case based on one to several specimens of angiosperm fruits or seeds. Only one of these species – the fruit taxon – has since been formally revisited; it has been revised several times, and was most recently included in the extant genus *Orites* (Proteaceae). The only angiosperm reproductive material that has been newly described includes staminate inflorescences and ovulate 'cones' assigned to the extant genus *Gymnostoma* (Casuarinaceae). Work on a large suite of leaves, infructescences, capsules, buds, and a flower of *Eucalyptus* (Myrtaceae) is ongoing. Given that reproductive organs are, in general, the most taxonomically diagnostic and the most phylogenetically informative structures in the flowering plants, it is critical that the LH angiosperm reproductive structures be fully documented so that this information can be incorporated into a more complete understanding of the composition and biogeographic relationships of the LH paleoflora. In this poster, we will introduce selected undescribed angiosperm reproductive material from LH that is currently under investigation, and revisit one previously described taxon. Special attention will be given to inflorescences and infructescences bearing bicarpellate capsules and thought to have affinities to the extant genus *Weinmannia* or other Cunoniaceae; the aforementioned '*Allophylus'* infructescences, which bear multicarpellate fruits; and several types of winged fruits. The latter include specimens with what is interpreted as a robust, persistent calyx reminiscent of the fruits of *Ceratopetalum* (Cunoniaceae), and examples of another type of fruit with a tri-lobed wing and planar grouping of four seeds that resembles the arrangement of seeds in fruits of some extinct Juglandaceae from the Northern Hemisphere, although its affinities require further investigation. Of these reproductive structures, the fruits with likely affinities to *Ceratopetalum* show a clear Australasian rainforest signal. Where the other taxa fit into the emerging concept of the LH flora remains less clear, and will require more precise phylogenetic placement to decipher.