

Facies interpretation and geochronology of diverse Eocene floras and faunas, northwest Chubut Province, Patagonia, Argentina

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ABSTRACT

The Eocene Huitrera Formation of northwestern Patagonia, Argentina, is renowned for its diverse, informative, and outstandingly preserved fossil biotas. In northwest Chubut Province, at the Laguna del Hunco locality, this unit includes one of the most diverse fossil floras known from the Eocene, as well as significant fossil insects and vertebrates. It also includes rich fossil vertebrate faunas at the Laguna Fría and La Barda localities. Previous studies of these important occurrences have provided relatively little sedimentological detail, and radioisotopic age constraints are relatively sparse and in some cases obsolete. Here, we describe five fossiliferous lithofacies deposited in four terrestrial depositional environments: lacustrine basin floor, subaerial pyroclastic plain, vegetated, waterlogged pyroclastic lake margin, and extracaldera incised valley. We also report several new ⁴⁰Ar/³⁹Ar age determinations. Among these, the uppermost unit of the caldera-forming Ignimbrita Barda Colorada yielded a ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ age of 52.54 ± 0.17 Ma, ~6 m.y. younger than previous estimates, which demonstrates that deposition of overlying fossiliferous lacustrine strata (previously constrained to older than 52.22 ± 0.22 Ma) must have begun almost immediately on the subsiding ignimbrite surface. A minimum age for Laguna del Hunco fossils is established by an overlying ignimbrite with an age of 49.19 ± 0.24 Ma, confirming that deposition took place during the early Eocene climatic optimum. The Laguna Fría mammalian fauna is younger, constrained between a valley-filling ignimbrite and a capping basalt with ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ ages of 49.26 ± 0.30 Ma and 43.50 ± 1.14 Ma, respectively. The latter age is ~4 m.y. younger than previously reported. These new ages more precisely define the age range of the Laguna Fría and La Barda faunas, allowing greatly improved understanding of their positions with respect to South American mammal evolution, climate change, and geographic isolation.

INTRODUCTION

The Patagonian region of Argentina holds historic and still rapidly expanding significance for understanding the evolution and biogeography of terrestrial life in the Southern Hemisphere (e.g., Ameghino, 1906; Gaudry, 1906; Simpson, 1980; Archangelsky, 2005; Pascual, 2006; Salgado, 2007). In recent years, there has been a marked increase in investigations of early Paleogene strata, which hold vital and still littlestudied records of recovery from the end-Cretaceous extinction, biotic responses to climate changes, and biogeographic events related to the final breakup of Gondwana and the beginning of South American isolation (e.g., see summaries by Goin et al., 2012a; Wilf et al., 2013).

A fundamental factor in the rising significance of Patagonia's outstanding fossils is the increase in stratigraphic and sedimentological studies that give the fossiliferous strata geologic context, including high-precision radioisotopic ages and paleomagnetic data. In just the past few years, a high-resolution temporal and general geologic framework has emerged for the classic, extremely fossiliferous Paleocene to Miocene continental sequence of southern Chubut Province (Bellosi, 2010; Dunn et al., 2013; Clyde et al., 2014; Woodburne et al., 2014a and 2014b; Comer et al., 2015; Krause et al., 2017). These data constrain interpretations for a large variety of studies, from those on individual fossil sites and taxa to reinterpretations of mammalian evolutionary faunas and their biozonations, known as South American Land Mammal "Ages" (SALMAs; Flynn and Swisher, 1995; Gelfo et al., 2009; Woodburne et al., 2014a, 2014b).

Our focus here is on another highly fossiliferous area, in northwest Chubut Province, known as the Middle Chubut River pyroclastic and volcanic complex of the Huitrera Formation (Fig. 1; Aragón and Romero, 1984; Mazzoni et al., 1991; Aragón and Mazzoni, 1997; Aragón et al., 2001, 2004, 2018). The Piedra Parada caldera preserves diverse Eocene volcanic rocks, including the caldera-floor Ignimbrita Barda Colorada, a caldera-filling lacustrine sequence known as the Tufolitas Laguna del Hunco, at least two younger ignimbrite units, and a succession of capping volcanic rocks of the Andesitas Huancache (Figs. 1 and 2; Archangelsky, 1974; Mazzoni et al., 1989, 1991; Aragón and Mazzoni, 1997).

The fossil richness and significance of the Tufolitas Laguna del Hunco have been well known since Berry's (1925) first report of the fossil flora from the principal section at Laguna del Hunco in the northeasternmost exposures of the Tufolitas (Fig. 1). This was followed over several decades by publications on fossil plants (e.g., Frenguelli, 1943; Romero and Hickey, 1976; Romero et al., 1988), insects (Fidalgo and Smith, 1987), catfish (Dolgopol de Sáez, 1941; Azpelicueta and Cione, 2011), and pipoid frogs (Casamiquela, 1961; Báez and Trueb, 1997). Over the past 15 yr, there has been a marked increase in research activity on these strata, fueled by renewed, stratigraphically controlled collecting efforts that have recovered many thousands of specimens (Wilf et al., 2003, 2005a). Initial phases of this work revealed that the Laguna del Hunco flora is among the most diverse from the Eocene worldwide, currently

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Figure 1. Simplified geologic map of the study area, modified from Aragón and Mazzoni (1997), and sampling localities. La Barda locality is off the map, ~6 km distant from the Laguna Fría locality on a 192° bearing (Tejedor et al., 2009). Solid lines represent observed boundaries from field work and satellite imagery. Dashed lines represent inferred boundaries. The resurgent dome area has not yet been mapped in detail but contains pyroclastic deposits of the Tufolitas del Hunco; intracaldera volcanic flows and dikes; and capping Miocene to Pleistocene basalt flows.



Figure 2. Cross-sectional diagram across southern portion of Middle Chubut River pyroclastic volcanic complex. Key fossil sites and rock units with age determinations are emphasized. Figure is not to scale. See Figure 1 for correct spatial distances between localities. Age determinations cited from Wilf et al. (2003, 2005) have been adjusted to more recent standard of Kuiper et al. (2008).

containing more than 200 species (Wilf et al., 2003, 2005a, 2005b). Systematic studies have detailed numerous novel records of diverse plant genera that live today only in Old World rain forests of Australasia and SE Asia; many of these taxa were previously only known as fossils, if at all, in Australia and New Zealand. These records, and accompanying reports of new fossil insects (e.g., Petrulevičius and Nel, 2013; Petrulevičius, 2016), are far too numerous to cite completely here (for summaries, see Wilf et al., 2009, 2013; Kooyman et al., 2014). However, among the most remarkable discoveries are the outstanding fossils of kauris (Agathis, Araucariaceae), gums (Eucalyptus, Myrtaceae), tomatillos (Physalis, Solanaceae), and beech relatives (Castanopsis, Fagaceae) (Gandolfo et al., 2011; Wilf et al., 2014, 2017, 2019). The fossil plants from Laguna del Hunco have revealed Eocene Patagonia as the western end of a trans-Antarctic rain-forest biome that harbored elevated biodiversity that was largely lost to extinction following Antarctic separation and climate change (e.g., Kooyman et al., 2014). In addition, the ages of many fossil plant lineages from Laguna del Hunco are significantly older than comparable molecular-clock estimates, challenging that widely used methodology (Wilf and Escapa, 2015; Wilf et al., 2017).

The fossil richness of the study area also includes a pair of rich Eocene mammalian faunas that occur within valley-fill deposits, the Laguna Fría and La Barda assemblages (Fig. 1). These faunas were first collected by R. Pascual in the 1950s and have been the topic of intense study (Goin et al., 2000, 2001; Tejedor et al., 2005, 2009; Lorente et al., 2016). Together, these sites have produced more than 50 mammalian species, including the oldest South American bats (Tejedor et al., 2005), the last occurrence of South American gondwanatheres (Goin et al., 2012b), and a diverse array of other marsupial and placental taxa, especially xenarthrans and ungulates (Tejedor et al., 2009; Lorente, 2016; Lorente et al., 2016). These faunas, often referred to collectively as the Paso del Sapo fauna (after the nearby village of the same name; Fig. 1), are noted for their familial affinities with middle Eocene Antarctic Peninsula faunas of the La Meseta Formation (e.g., Goin et al., 1999; Reguero et al., 2013, 2014; Goin et al., 2018). In addition, some marsupial remains have been assigned to the australidelphid clade (Lorente et al., 2016), which includes all living Australian marsupials and one South American species. Thus, along with the celebrated Danian monotremes from southern Chubut (Pascual et al., 1992), the Laguna Fría and La Barda faunas provide some of the firmest evidence for a Gondwanic biogeographic signal in South America's

early Paleogene mammals. These discoveries parallel abundant data from nonmammalian vertebrate groups and plants (e.g., for summary, Wilf et al., 2013) and modern paleogeographic data (e.g., Lawver et al., 2013) and contrast with the classic portrayal of South America as an isolated "island continent" for most of the Cenozoic (Simpson, 1950, 1980).

Despite the broad significance of the Laguna Fría and La Barda faunas, three issues surround the interpretation of their age, hindering a precise understanding of their position in the evolutionary sequence represented in the SALMA scheme. First, Tejedor et al. (2009; also Woodburne et al., 2014a, 2014b; Goin et al., 2018) proposed that the Laguna Fría and La Barda faunas are, collectively, compositionally and temporally distinct, falling in an otherwise undocumented "Sapoan" provisional SALMA between putatively older Río Chican and younger Vacan faunas. The "Sapoan" concept is widely used, having been followed by all the subsequent workers treating these faunas (citations above). However, the assessment of geologic age of the faunas (Tejedor et al., 2009) was based on a set of unpublished 40Ar/39Ar dates from a conference abstract reporting the M.S. thesis results of the present lead author (Gosses, 2006; Gosses et al., 2006), as well as uncertain correlations to now-obsolete, whole-rock K-Ar dates on basalts exposed elsewhere (e.g., Mazzoni et al., 1991). We, like Krause et al. (2017), emphasize that the critical 40Ar/39Ar ages (Gosses et al., 2006) used by Tejedor et al. (2009) and subsequent workers have not, until now, been vetted, revised, or reanalyzed. Second, the Laguna Fría and La Barda assemblages could be separated enough in time that at least one assemblage temporally overlaps previously defined SALMAs (Krause et al., 2017). Third, and beyond the scope of the present study, the temporal bounds of the Río Chican SALMA used for comparison are not well established because the type Río Chican mammal sites (Simpson, 1935) have not been placed in a modern chronostratigraphic framework (Krause et al., 2017). Further, based on a series of new high-precision U-Pb ages from the Koluel Kaike Formation of southern Chubut Province, which is traditionally but perhaps incorrectly correlated with the type Río Chican section, the Río Chican SALMA is likely to temporally overlap both the Vacan and the La Barda faunas (Krause et al., 2017).

Throughout the study area, reliable stratigraphy that directly constrains the ages of closely associated fossils is, so far, only established at Laguna del Hunco itself (see "Previous Geochronology"). The Laguna Fría and La Barda faunas are only loosely constrained by a set of obsolete K-Ar age determinations of associated volcanic rocks (Archangelsky, 1974; Mazzoni et al., 1991), excepting the use by Tejedor et al. (2005, 2009) of then-unpublished initial geochronologic data, including those of Gosses (2006), which are revised and formally presented here. Several whole-rock K-Ar ages for other units in the volcanic complex were also pioneering for their time but, likewise, used now-obsolete techniques with very large uncertainties (Mazzoni et al., 1991). Similarly, important earlier work on the depositional environments and processes that preserved the fossils (Petersen, 1946; Feruglio, 1949; Aragón and Romero, 1984; Aragón and Mazzoni, 1997) requires updating using new methods and field observations.

In this study, the depositional histories of five fossil-bearing lithofacies were examined to gain insights into the volcano-sedimentary evolution across the study area (Fig. 1). New ⁴⁰Ar/³⁹Ar geochronology was used to improve chronostratigraphic resolution of the uppermost Ignimbrita Barda Colorada, the strata holding the Laguna Fría fauna, and other localities. New age determinations for the Ignimbrita Barda Colorada helped to establish the duration of time between the cessation of primary caldera eruption and fossiliferous lacustrine deposition of the Tufolitas Laguna del Hunco. Other ages permitted improved understanding of the temporal and geographic evolution of the globally significant caldera fossil-lake system and established reliable constraints for the Laguna Fría fauna that will allow it to be placed correctly in the SALMA biozonation.

GEOLOGIC SETTING

The Tufolitas Laguna del Hunco infill the Piedra Parada caldera within the Eocene Middle Chubut River pyroclastic and volcanic complex of the La Huitrera Formation (Aragón and Romero, 1984; Aragón and Mazzoni, 1997; Aragón et al., 2004). The complex occurs along a line of Eocene volcanic centers, referred to as the Pilcaniyeu belt, which stretch in a northsouth direction and lie ~150 km east of modern arc volcanism (Rapela et al., 1984; Dalla Salda and Franzese, 1987; Rapela et al., 1988; Iannelli et al., 2017). Many outstanding fossil sites are located elsewhere in the Pilcaniyeu belt, especially in the western exposures near San Carlos de Bariloche in Río Negro (Berry, 1938; Aragón and Romero, 1984; Báez and Pugener, 2003; Melendi et al., 2003; Barreda et al., 2010; Wilf et al., 2010; Petrulevičius, 2015). The Piedra Parada caldera is trapdoor style (cf. Lipman, 1997), extends 25-30 km N-S, and is located in northwestern Chubut Province, Argentina (Fig. 1). The caldera-forming ignimbrite, known as the Ignimbrita Barda Colorada, is overlain by the Tufolitas Laguna del Hunco, which consists mainly of subaerial and lacustrine ash and lapilli that are variably reworked with a smaller amount of interbedded lava flows and glass domes (Aragón and Mazzoni, 1997). Outcropping strata are as thick as 400 m, with the basal contact often not exposed. Nearly all published fossils from the Tufolitas Laguna del Hunco (cited earlier) come from the principal section at Laguna del Hunco, in the northeasternmost exposures (Fig. 1), but recent discoveries are emerging from the southern outcrops as well (Bippus et al., 2016, 2019; Bomfleur and Escapa, 2019).

Above the Tufolitas Laguna del Hunco, capping deposits extend past the caldera edge and consist of lava flows and dikes but few pyroclastic or sedimentary deposits. The Huancache and Cerro Mirador Formations are some of the capping units. The Laguna Fría fauna (Figs. 1 and 2; citations above) is found within a paleovalley that was incised into the caldera-forming ignimbrite external to the caldera itself and filled with original and reworked pyroclastic deposits (Tejedor et al., 2009). These lithologies are grossly similar in appearance to the later phases of the Tufolitas Laguna del Hunco as seen inside the caldera, but our geochronologic data presented here indicate that they are not correlative. The La Barda fauna comes from another incisedvalley outcrop ~6 km southwest of Laguna Fría (Fig. 1). It occurs within tuff units that are interbedded with basalt flows of the Huancache Formation (Tejedor et al., 2009).

PREVIOUS GEOCHRONOLOGY

Several ⁴⁰Ar/³⁹Ar and K-Ar studies have generated age determinations for portions of the Middle Chubut River pyroclastic and volcanic complex. Archangelsky (1974) used wholerock K-Ar methods to determine the age of a single sample of the Ignimbrita Barda Colorada at Cañadón de Loro, adjacent to Laguna del Hunco (Fig. 1), as 58.6 ± 3.0 Ma ($\pm 1\sigma$; corrected with modern decay constants using Dalrymple, 1979). Mazzoni et al. (1991) reported 12 whole-rock K-Ar age determinations from three different laboratories for lava flows, dikes, and ignimbrites within the complex. Of these, three samples (VH1, 32-5, 54, and 86-107) appear too young, given reported and observed stratigraphic relationships, while sample 87-44 appears too old. A possible cause for some of these discrepancies is low-temperature alteration, which was detected in this study using the ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ incremental-heating technique, but which would not have easily been recognizable using older K-Ar methods.

At Laguna del Hunco, two paleomagnetic reversals are recorded along with three ca. 52 Ma ⁴⁰Ar/³⁹Ar ages from tuffs recovered from the 170 m local section of the Tufolitas Laguna del Hunco (Wilf et al., 2003, 2005a). One of the 40Ar/39Ar ages, from the middle of the densely fossiliferous interval (ash 2211A), was determined from single-crystal fusion analyses of sanidine and is thus considered to be the most reliable; its age was recalibrated to 52.22 ± 0.22 Ma (Wilf, 2012) relative to a Fish Canyon standard age of 28.201 ± 0.046 Ma (Kuiper et al., 2008) and a value for λ^{40} K of $5.463 \pm 0.107 \times 10^{-10} \text{ yr}^{-1}$ (Min et al., 2000). The 52.22 ± 0.22 Ma age is widely applied to the rich Laguna del Hunco fossil assemblage and is not revised here. Finally, the previously mentioned, initial results for three samples in this study (Gosses, 2006; Gosses et al., 2006) used an age of 28.02 Ma for the Fish Canyon standard (Renne et al., 1998).

The Laguna Fría and La Barda faunas are found above the Ignimbrita Barda Colorada (Tejedor et al., 2009). The only previously published lower age constraint for the faunas is the outdated ⁴⁰K-⁴⁰Ar age determination discussed above $(58.6 \pm 3.0 \text{ Ma})$ for the calderaforming Ignimbrita Barda Colorada (Archangelsky, 1974; Mazzoni et al., 1991), which is separated from the fossil-bearing outcrops by an erosional unconformity of uncertain duration. The upper age constraint is the Mazzoni et al. (1991) set of ca. 43 Ma 40K/40Ar ages for flows of the Andesitas Huancache from areas to the west of the fossil exposures; those beds were considered to be stratigraphically higher than the La Barda assemblage by Tejedor et al. (2009).

METHODS

Field Localities and Lithofacies

Fossil-bearing lithofacies were examined in thin section, hand sample, and outcrop in order to interpret the burial processes and depositional environments associated with fossil preservation. Observations within the caldera were concentrated at the Laguna del Hunco site, and at three other sites with lesser plant-fossil preservation (Central caldera, Escuela Piedra Parada, and Zeballos Oeste; Fig. 1). Our observations also included the Laguna Fría site, which lies outside of the caldera.

Four samples from lavas or tuffs were collected and analyzed using the 40Ar/39Ar method to constrain age ranges of several fossil localities within the caldera complex (Table 1).1 The Ignimbrita Barda Colorada (Sample QL-9807) records the principal caldera-forming event (Fig. 2), and it establishes a maximum age for the initial formation of the fossiliferous caldera-lake deposits of the Tufolitas Laguna del Hunco (Fig. 1). The lower member of the Ignimbrita Barda Colorada is calc-alkaline and high in sodium (Aragón et al., 1987), and the upper member is calc-alkaline with a medium- to high-K rhyolitic composition (SiO₂ = 72–79 wt%; Aragón et al., 1987). The sample dated in this study was collected from the uppermost Ignimbrita Barda Colorada at the extracaldera Laguna Fría locality, where a paleovalley is incised into the Ignimbrita Barda Colorada (Figs. 3K and 4). The Ignimbrita Barda Colorada at this locality contains multiple cooling units and is at least 100 m thick (Mazzoni and Aragón, 1987; Aragón et al., 1987).

The southern ignimbrite (Sample IDEPP-04) establishes a minimum age for fossils described from the underlying, southernmost exposures of the Tufolitas Laguna del Hunco at Piedra Parada (Fig. 2; Bippus et al., 2016, 2019;

TABLE 1. SUMMARY OF RADIOISOTOPIC AGES

Sample	Unit	Latitude (°S)	Longitude (°W)	Mineral	N	% ³⁹ Ar	MSWD	K/Ca	Plateau age (Ma)	±2σ	Isochron age (Ma)	±2σ	(⁴⁰ Ar/ ³⁶ Ar) _i	±2σ
Incremental h VC-1-04	<u>leating results</u> Laguna Fria Basalt	42.7245	69.8454	Plag	15/24	86.6	1.08	0.0	43.50	1.14	43.50	2.22	298.54	7.05
Single-crystal VC-20-04 IDEPP-1-04 QL-9807	<u>I laser-fusion results</u> Orange ignimbrite Southern ignimbrite Upper Ignimbrita Barda Colorada	42.7245 42.6819 42.7245	69.8454 70.1680 69.8454	Plag Plag San	9/19 18/18 2/16		1.17 1.42 0.09	0.3 0.3 27.3	49.00 49.38 52.54	0.16 0.10 0.17	49.26 49.19 N.D.	0.30 0.24 N.D.	290.5 310.7 N.D.	3.3 3.7 N.D.

Note: Bold font indicates preferred ages. Ages were calculated relative to Fish Canyon sanidine interlaboratory standard at 28.201 Ma (Kuiper et al., 2008). Age uncertainty includes analytical uncertainty + J uncertainty. Decay constants and isotopic abundances are after Min et al. (2000). Plag—plagioclase; San—sanidine; MSWD—mean square of weighted deviates; N.D.—not determined.

¹Supplemental Material. Table S1. Full documentation of ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ geochronology. Please visit https://doi.org/10.1130/GSAB.S.12640676 to access the supplemental material, and contact editing@geosociety.org with any questions.



Bomfleur and Escapa, 2019). It is a 6-m-thick, red, erosion-resistant ignimbrite that comprises the uppermost strata in the hills in the far southeastern part of the caldera. The sample was collected ~2.5 km southeast of Escuela Piedra Parada (Fig. 1). It overlies ash-fall tuffs and fans of reworked pyroclastic material, and it lies stratigraphically several hundred meters above the gray ashy mudstone facies described at the Escuela Piedra Parada locality.

The Laguna Fría orange ignimbrite (Sample VC-20-04) occurs within this locality and establishes a maximum age for the Laguna Fría fauna (Fig. 2). It is a prominent, 14-m-thick welded ignimbrite that lies within a paleovalley eroded into the Upper Ignimbrita Barda Colorada at Figure 3. Field photographs of fossil-bearing lithofacies. (A) Overview of the Tufolitas Laguna del Hunco (Laguna del Hunco locality). (B) Laminated mudstone facies (Laguna del Hunco locality). (C) Photomicrograph of organic-rich laminated mudstone facies (Laguna del Hunco locality). (D) Gray ashy mudstone overlain by sediment gravity flow (resistant bed; Laguna del Hunco locality). (E) Photomicrograph showing microcrystalline nature of the gray ashy mudstone facies (Laguna del Hunco locality). (F) Leaf fossil preserved in gray ashy mudstone (Laguna del Hunco locality). (G) Volcaniclastic turbidite showing all five Bouma subdivisions (Laguna del Hunco locality). (H) Glass dome intruding gray ashy mudstone facies (Central Caldera locality). (I) Petrified tree trunk preserved in a clastrich ash-flow tuff (Escuela Piedra Parada locality). (J) Root cast and cross-bedding in a crystal-rich reworked pyroclastic facies (Laguna Fría locality). (K) Field relationships among the Ignimbrita Barda Colorada, valley-filling volcaniclastic facies, orange ignimbrite, and Laguna Fría capping basalt (Laguna Fría locality). Fossil locality lies stratigraphically above the orange ignimbrite and below the basalt. (L) Oblique composite satellite image looking east at the area between the Laguna Fría and La Barda faunal localities (3× vertical exaggeration. Image used with permission; Image © 2019 Centre National d'Etudes Spatiales [CNES]/Airbus, © 2018 Google, Image © 2019 Maxar Technologies).

the Laguna Fría locality (Fig. 1). The orange ignimbrite thus postdates the Ignimbrita Barda Colorada, but it predates the Laguna Fría fauna.

The Laguna Fría basalt (Sample VC-1-04) is an alkali basalt flow of the Andesitas Huancache that caps the paleovalley where the Laguna Fría faunas are found (Figs. 1, 2, and 3K). It thus establishes a minimum age for the







Figure 3. (Continued)

fauna (Goin et al., 2000, 2001; Tejedor et al., 2005, 2009). At Laguna Fría, the basalt has an exposed thickness of 40 m and is one of many basalt flows that intertongue with and cover the ignimbrite plateau south and west of this area (Figs. 1 and 3L; Aragón and Mazzoni, 1997; Mazzoni et al., 1991).

Geochronology

The ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ age determinations were made from one alkali basalt (Sample VC-1-04) and

three felsic ignimbrites (Spls. VC-20-04, IDEPP-04, QL-9807). Groundmass was separated from basalt, and feldspar (plagioclase and sanidine) crystals were separated from ignimbrites via crushing, sieving to 250–500 μ m, magnetic sorting, density separation using methylene iodide, and ultimately handpicking under a binocular microscope.

Sanidine and plagioclase separates were wrapped in aluminum foil, placed in 2.5 cm aluminum disks, and irradiated along with the 28.201 Ma Fish Canyon sanidine standard (Kuiper et al., 2008) at the Oregon State University TRIGA reactor in the Cadmium-Lined In-Core Irradiation Tube (CLICIT). Two milligrams of plagioclase from sample VC-1-04 were incrementally heated in 24 steps, whereas singlecrystal fusion experiments were performed on the other three samples. Incremental heating is the method of choice when dating basaltic lavas because it permits interrogation of whether alteration or inheritance has biased the age of the flow (Singer et al., 2019). All experiments were conducted in the WiscAr laboratory at the University

A Laguna del Hunco

B Escuela Piedra Parada, Central Caldera



C Zeballos Oeste

D Laguna Fria



Figure 4. Schematic block diagrams of depositional environments interpreted in this study. Scale bars are approximate horizontal distances. Vertical scale is exaggerated. Localities are in bold. Flora/fauna and facies names are (in brackets).

of Wisconsin–Madison using a 50 W CO₂ laser and a Noblesse multicollector mass spectrometer following the procedures in Jicha et al. (2016). Weighted mean ages were calculated with the decay constants of Min et al. (2000) and are reported with $\pm 2\sigma$ analytical uncertainties (95% confidence level). The atmospheric argon value used was that of Lee et al. (2006).

RESULTS

Five different fossil-bearing lithofacies were described for this study. Laminated mudstone and green tuff are interpreted to record deposition in a lacustrine basin-floor environment. Gray ashy mudstone is interpreted to have been deposited both in a lacustrine basin-floor environment and on a subaerial pyroclastic plain. The coal lithofacies is interpreted to record deposition on a vegetated, waterlogged pyroclastic plain. The valley-filling pyroclastic lithofacies is interpreted to record deposition within an incised valley outside of the caldera. An additional fossilbearing siltstone facies described in Wilf et al. (2003) was not included during this study.

Laminated Mudstone Lithofacies

The laminated mudstone facies occurs only at the Laguna del Hunco locality (Figs. 1 and 3A), interbedded with several other lacustrine facies. Beds are several centimeters to a few decimeters thick. The laminae constitute either black and white couplets or black and dark-gray couplets (Fig. 3B), but these two patterns are not observed within the same bed. Thin-section images show that both the black and the white laminations contain mud- to silt-sized crystals and altered glass particles. The black laminations also have elongate, fibrous, brown organic matter (Fig. 3C). The outcrop surface appears to be an off-white or beige color, but a freshly broken surface is medium-brown to black and has a sulfurous odor. Fractures are either conchoidal or follow laminae. Black fragments of leaves and stems are found parallel to laminations. Delicate leaf structures are less common.

The laminated mudstone facies is interpreted as suspension fallout of detrital sediment and organic matter onto a lacustrine basin floor during lulls in volcanic activity, based its grain size, preservation fine laminae, organic matter content, and absence of scour, graded beds, or other evidence for tractive currents (Fig. 4A). The occasionally conchoidal fractures may reflect high silica content. The laminations could be explained through variability in finegrained sediment influx, organic matter influx, organic matter preservation, or some combination of these three. Examinations of thin sections revealed that the amount of organic material varies between laminations, while the detrital component is present throughout. This suggests that the laminations may be primarily due to seasonal variation in the production or preservation of organic material, whereas fine-grained inorganic sediment accumulated more uniformly through time.

Green Tuff Lithofacies

The green tuff facies occurs at the Laguna del Hunco locality (Fig. 1), interbedded with the gray ashy mudstone facies and laminated mudstone facies. This facies consists of pale-green, very fine- to medium-grained tuff with fine- to medium-grained plagioclase and biotite crystals that are often visible with the naked eye. The tuff has a mottled texture in hand sample but does not display other sedimentary structure. Fossils in this facies have a light-brown stain, but less so than in the gray ashy mudstone facies. Fossils are generally preserved on planes parallel to or at a low angle to bedding. These fossils typically do not feature as much detail as those in the gray ashy mudstone beds.

The green tuff facies is interpreted as an ashfall tuff deposited in a lacustrine basin-floor depositional environment, based on its intercalation with laminated mudstone, coarser grain size, and lack of sedimentary structures indicative of tractive transport. Accumulation of these types of deposits typically spans hours to days (Miller and Casadevall, 2000).

Gray Ashy Mudstone Lithofacies

The gray ashy mudstone facies, found at the Laguna del Hunco, Escuela Piedra Parada, and Central Caldera localities (Fig. 1), has a porcellanitic or cryptocrystalline appearance but lacks crystals visible with the naked eye or hand lens. It weathers to an off-white color, but it is gray to brown on a fresh break. Beds are typically a few centimeters to decimeters in thickness and laterally extensive for hundreds of meters (Fig. 3D). Thin sections revealed that 95% of the grains are <5 µm (Fig. 3E). Orange staining is commonly observed on fracture surfaces and fossils, making them more visible. Fossils occur on planes parallel and subparallel to bedding surfaces. Fracture is moderately conchoidal. Swaley cross-stratification has recently been observed in this facies, suggesting episodes of high-energy wave and combined-flow events in a lake (J.M. Krause and E.A. Hajek, 2019, personal commun.).

At the Laguna del Hunco locality, this facies contains well-preserved fossil plants, frogs, fish, and insects. Many whole leaves are preserved (Fig. 3F) with well-preserved venation and insect damage, along with delicate flowers, fruits, and insect body fossils, as reported extensively elsewhere (see Introduction). Bed geometries include sheets, lenses, lobes, and drapes. Gray ashy mudstone beds at the Laguna del Hunco locality are typically intercalated with turbidite, debris-flow, green tuff, laminated mudstone, and green-brown mudstone beds (Figs. 3D and 3G). The sediment gravity-flow deposits exhibit flame structures and meter-scale soft-sediment folds, which together with current ripples indicate a depositional gradient that sloped toward the east or northeast, away from the resurgent caldera dome (see Fig. 1).

Orange staining and fossils are less common at the Escuela Piedra Parada and Central Caldera localities (Fig. 1). In contrast to the Laguna del Hunco locality, the gray ashy mudstone beds are frequently stacked on top of one another with few interbedded strata, and they are associated with extrusive glass domes (Fig. 3H). The only interbedded units are volcaniclastic sandstone beds rich in angular to subangular crystals and tuff clasts. However, the sections above and below the gray ashy mudstone intervals do contain debris flows, ash-fall tuffs, ash-flow tuffs, and double-graded pyroclastic debris flows. Five silicified tree trunks up to 11 m long were observed within the ash-flow tuffs at Escuela Piedra Parada (Fig. 3I), in the same general area that preserved a permineralized fossil fern trunk (Fig. 1, localities 3 and 5; Bomfleur and Escapa, 2019). In two cases, the tree roots are preserved in life orientation, whereas the trunks are oriented subparallel to bedding and aligned parallel to each other.

This facies is interpreted to have been deposited in two different environments. At the Laguna del Hunco locality, it is interbedded with turbidites and other facies indicating a lacustrine basin-floor depositional environment (Fig. 4A). The presence of swaley cross-stratification in the gray ashy mudstone implies at least partial reworking by waves, possibly in combination with unidirectional flow (cf. Dumas and Arnott, 2006). At the Central Caldera and Escuela Piedra Parada localities, it was deposited on a subaerial pyroclastic plain. Associated ash flows knocked down trees and covered the ground surface. Sheetflood transport processes, shallow channelization, and air-fall pyroclastic events deposited centimeter- to decimeter-thick beds of varying geometries and levels of immaturity (Fig. 4B). Meter-scale welded ignimbrites filled in and reorganized the topography above and below the strata containing the gray ashy mudstone facies.

Coal Lithofacies

The coal facies occurs at the Zeballos Oeste locality (Fig. 1). A single centimeter-thick coal seam was observed in place, encased by browngray tuff. Fragmented plant material is preserved on distorted, subparallel surfaces, but leaves are less well preserved than in other facies. Directly below the coal seam, there are decimeter-scale, compensationally stacked beds with a lenticular geometry. The coal is overlain by a massive, several-meter-thick bed that contains coaly intraclasts.

The coal facies is interpreted as a leaf mat deposited under reducing conditions on a vegetated, waterlogged pyroclastic lake margin (Fig. 4C). Coal intraclasts in the overlying beds suggest erosion of updip coal-forming environments.

Valley-Filling Pyroclastic Lithofacies

The valley-filling pyroclastic facies examined for this study is confined to a NW-SE-oriented paleovalley incised into the Ignimbrita Barda Colorada southeast of the caldera (the Laguna Fría locality; Figs. 1 and 2). A modern valley that is oriented NE-SW exposes multiple paleovalleys in this area. The valley-filling pyroclastic facies is broadly defined to include nonwelded tuffaceous deposits and reworked pyroclastic deposits (Fig. 3J). Decimeter-thick beds can have erosive bases, are generally matrix-supported, fine upward, and contain lapilli. In contrast, centimeter-thick beds are more likely to be grain supported and contain cross-bedding and root casts. Some of these beds are dominated by crystal grains or ash lapilli of multiple compositions, with a marked reduction in fine-grained matrix. A few beds have subangular tuff clasts up to 1 cm. Most beds continue across the entire outcrop. Small numbers of the grain-supported beds have very broad U-shaped geometries up to 2 m across. This facies contains abundant vertebrate specimens described as the Laguna Fría fauna (Tejedor et al., 2005, 2009). Silicified trunk material was also found as float at this locality, but no leaves or other plant compressions were found. The Laguna Fría vertebrate assemblage occurs predominantly above the prominent Laguna Fría orange ignimbrite and below the Laguna Fría capping basalt (Fig. 3K).

The valley-filling pyroclastic facies is interpreted as a combination of primary and reworked pyroclastic deposits within an extracaldera paleovalley incised into the Ignimbrita Barda Colorada (Fig. 4D). Composition, grain distribution, and fluid escape tubes suggest some of the pyroclastic material was deposited by ash-fall and other ash-cloud mechanisms. Some beds were buried intact by later pyroclastic eruptions. Others were partially or fully reworked by a combination of fluvial and sheetflood processes. This is especially apparent in the tops of some decimeterscale pyroclastic beds, where centimeter-scale cross-bedded intervals, ripples, and well-sorted volcaniclastic sands suggest partial reworking of the tops of the beds only. Channels of only a few meters width were observed, suggesting an environment controlled by small-scale fluvial and sheetflood processes. The depositional environment was akin to a partially filled alluvial canyon.

40Ar/39Ar Ages1

Upper Ignimbrita Barda Colorada

Laser-fusion experiments were performed on 16 individual crystals. Of these, only two yielded K/Ca ratios consistent with sanidine, whereas the remainder were plagioclase and thus were excluded from analysis. The weighted mean age of the two sanidine dates is 52.54 ± 0.17 Ma (Fig. 5).

Southern Ignimbrite

Plagioclase was separated from this ignimbrite because no sanidine was present. Eighteen laser-fusion experiments on individual plagioclase crystals gave a weighted mean age of 49.38 \pm 0.12 Ma (Fig. 5). However, the isochron calculated from these 18 crystals gave an intercept of 310.7 \pm 3.7 Ma, which is significantly higher than the atmospheric value. Hence, the isochron age of 49.19 \pm 0.24 Ma is preferred.

Laguna Fría orange ignimbrite

Plagioclase crystals were separated from this ignimbrite because no sanidine was present. Single-crystal laser-fusion experiments were performed on 19 plagioclase crystals. Eleven of these experiments produced radiogenic ⁴⁰Ar* concentrations lower than 70%, which may represent postdepositional loss of ⁴⁰Ar*. Excluding these from the results yielded a distribution of dates with a weighted mean age of 49.00 ± 0.16 Ma (Fig. 5). However, the isochron calculated from these 19 crystals gave an intercept of 290.5 ± 3.3 Ma, which is lower than the atmospheric value. Hence, the isochron age of 49.26 ± 0.30 Ma is preferred.



Figure 5. Summary of ⁴⁰Ar/³⁹Ar dates from sanidine and plagioclase in Laguna Fría orange ignimbrite, southern ignimbrite, and upper Ignimbrita Barda Colorada. Inverse isochron diagrams for the southern ignimbrite and Laguna Fría orange ignimbrite display intercepts that diverge from atmospheric values, and so the isochron age is preferred in both cases. Open points indicate analyses excluded from weighted mean age calculations. Weighted mean ages are shown with 2σ uncertainties, whereas individual analyses are shown with 1σ uncertainties. The isochron age of the Laguna Fría capping basalt is denoted by a dashed line, with 2σ uncertainties indicated by a gray band. MSWD—mean square of weighted deviates.

Laguna Fría Capping Basalt

A 24 step incremental heating experiment on a 2 mg groundmass separate yielded an age spectrum with low-temperature steps characterized by younger apparent ages. We interpret this discordance to reflect argon loss due to weathering and excluded the younger steps in the calculation of a plateau age. Notwithstanding this issue, an age plateau defined by 87% of the ³⁹Ar released signifies that the basalt has a largely homogeneous distribution of radiogenic argon, and it yielded an apparent age of 43.50 ± 1.14 Ma, which is indistinguishable from the inverse isochron age of 43.50 ± 2.22 Ma (Fig. 6).

DISCUSSION

The ⁴⁰Ar/³⁹Ar ages reported here represent new, fully documented constraints on the timing of the Laguna del Hunco flora and Laguna Fría fauna (Fig. 7). The age of the Ignimbrita Barda Colorada was previously reported as 58.6 ± 3.0 Ma ($\pm 1\sigma$) based on older 40 K/ 40 Ar techniques (Archangelsky, 1974), but it can now be revised to 52.54 ± 0.17 Ma ($\pm 2\sigma$), a difference of ~6 m.y. The new age is not distinguishable from the ⁴⁰Ar/³⁹Ar ages of tuffs at the Laguna del Hunco locality (52.22 ± 0.22 Ma; Wilf, 2012) given the 2σ uncertainties, a finding that is consistent with rapid initial deposition (Figs. 2 and 7) following the formation of a topographic depression during or shortly after the initial caldera eruption.

The southern ignimbrite occurs hundreds of meters stratigraphically above the gray ashy mudstone facies at Escuela Piedra Parada. Its 49.19 ± 0.24 Ma age therefore establishes a minimum age for the gray ashy mudstone facies at this locality. The same constraint may also extend to the gray ashy mudstone facies at the Laguna del Hunco locality, if deposition of this facies in both areas occurred in response to a common eruptive history. The southern ignimbrite may also constrain the age of fossil fern trunks located ~5 km to the west (Fig. 1; Bippus et al., 2019; Bomfleur and Escapa, 2019).

Maximum and minimum age constraints for the Laguna Fría fauna are defined by the underlying 49.26 ± 0.30 Ma Laguna Fría orange ignimbrite, and the overlying 43.50 ± 1.14 Ma Laguna Fría capping basalt. The relationship of these ages to the nearby La Barda fauna remains unclear, however. Tejedor et al. (2009) inferred that the Laguna Fría capping basalt represents a basal basalt flow of the Andesitas Huancache, and that the La Barda fauna lies stratigraphically above this basal flow and therefore must be younger. They assumed a 47-45 Ma age range for the La Barda fauna, based on a preliminary ⁴⁰Ar/³⁹Ar age determination for the Laguna Fría basalt of 47.89 ± 1.21 Ma (Gosses et al., 2006) and on 40K/40Ar ages of ca. 43 Ma for an overlying lava flow (Mazzoni et al., 1991). If the stratigraphic relationships inferred by Tejedor et al. (2009) are correct, our revised age for the Laguna Fría capping basalt requires that the La Barda fauna is in fact younger than ca. 43.50 Ma. It must be noted, however, that these localities lie ~6 km apart in an area that experienced a spatially complex history of basaltic eruptions. The detailed stratigraphy of these flows has not been mapped, making precise correlation between sites problematic. Examination of satellite imagery (Fig. 3L) suggests that both localities lie stratigraphically below a prominent mesa-forming basalt, which approximately corresponds to the Laguna Fría capping basalt sampled in this study. Tejedor et al. (2009) reported faunistic similarities between the two fossil assemblages. Based on the data presented here, we cannot conclusively determine the age relationship between the La Barda and Laguna Fría faunas; it appears possible that they are the same age. A more detailed investigation of field relationships and basalt ages is needed to resolve this ambiguity. More broadly, the available age constraints on these faunas overlap with the age ranges proposed by Krause et al. (2017) for the Riochican and Vacan faunas and therefore do not

directly support the existence of a temporally distinct "Sapoan" SALMA.

Tejedor et al. (2009) considered the vegetation and paleoclimate for the Laguna Fría and La Barda mammals to be best represented by the ca. 52.2 Ma Laguna del Hunco and ca. 47.7 Ma Río Pichileufú (Río Negro) rain-forest floras (Berry, 1938; Wilf et al., 2005a; Wilf, 2012). These sites show that generally similar floral composition, elevated floral richness, and a mesic rain-forest environment persisted in the region for an extended period of time, which encompassed the existence of these faunas. Our new geochronologic results show that this argument remains plausible, but only in the older part of its possible age range. The younger end of the permissible age range, extending to 43.50 ± 1.14 Ma, corresponds with substantially cooler and drier conditions and major vegetation changes, both regionally and globally (Palazzesi and Barreda, 2007; Zachos et al., 2008; Dunn et al., 2015).

CONCLUSIONS

The Middle Chubut River pyroclastic and volcanic complex preserves fossil assemblages associated with multiple terrestrial, volcaniclastic lithofacies that lie stratigraphically above the caldera-forming Ignimbrita Barda Colorada. A new ⁴⁰Ar/³⁹Ar age for the caldera-forming Ignimbrita Barda Colorada of 52.54 ± 0.17 Ma is preferred over previous age determinations. This age is indistinguishable, given the 2σ uncertainties, from a 52.22 \pm 0.22 Ma ⁴⁰Ar/³⁹Ar age previously reported for a tuff at the Laguna del Hunco fossil locality (Wilf, 2012), demonstrating rapid onset of lacustrine deposition and prolific fossil preservation following caldera subsidence. An ignimbrite deposited above the fossil strata gives an age of 49.19 ± 0.24 Ma, collectively indicating that the Laguna del Hunco flora broadly coincided with the early Eocene climatic optimum (ca. 53-50 Ma; Zachos et al., 2008).



Figure 6. Age spectrum and inverse isochron diagrams illustrating results of a ⁴⁰Ar/³⁹Ar incremental heating experiment on groundmass from the Laguna Fría capping basalt. Steps excluded from analysis are shown as open boxes. MSWD—mean square of weighted deviates.

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Figure 7. Summary of Eocene age relationships and terrestrial fauna and flora, modified from Krause et al. (2017) and Wilf (2012) based on new results from the Piedra Parada caldera (reported in this study). Age determinations are based on ⁴⁰Ar/³⁹Ar and have been adjusted to decay constants of Kuiper et al. (2008). Shaded boxes indicate potential age range for each fossil assemblage, taking into account 2σ errors.

The Laguna Fría fauna is younger, constrained between the 49.26 ± 0.30 Ma Laguna Fría orange ignimbrite and the 43.50 ± 1.14 Ma Laguna Fría capping basalt. The age of the nearby La Barda fauna is more difficult to confidently determine. If previous stratigraphic relations inferred by Tejedor et al. (2009) are correct, then the La Barda fauna is at least 2 m.y. younger than its previously assumed age range of 47-45 Ma. The detailed stratigraphy of basaltic eruptions is poorly known however, and it is therefore possible that the La Barda and Laguna Fría faunas are similar in age. Finally, the Laguna Fría age range overlaps with the age ranges proposed by Krause et al. (2017) for the Riochican and Vacan faunas and therefore does not directly support the existence of a temporally distinct "Sapoan" SALMA.

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REFERENCES CITED

- Ameghino, F., 1906, Les formations sédimentaires du Crétacé Superieur et du Tertiaire de Patagonie avec un paralléle entre leurs faunes mammalogiques et celles de l'ancien continent: Anales del Museo Nacional de Historia Natural de Buenos Aires, v. 15, no. 8, p. 1–568.
- Aragón, E., and Mazzoni, M.M., 1997, Geología y estratigrafía del complejo volcánico piroclástico del Río

Chubut medio (Eoceno), Chubut, Argentina: Revista de la Asociación Geológica Argentina, v. 52, no. 3, p. 243–256.

- Aragón, E., and Romero, E.J., 1984, Geología, paleoambientes y paleobotánica de yacimientos Terciarios del occidente de Río Negro, Neuquén y Chubut, *in* Actas del IX Congreso Geológico Argentino, Volumen 4: San Carlos de Bariloche, Argentina, Asociación Geológica Argentina, p. 475–507.
- Aragón, E., Mazzoni, M.M., and Merodio, J., 1987, Caracterización geoquímica de Ignimbrita Barda Colorada en el Río Chubut medio, Argentina, *in* Actas del Décimo Congreso Geológico Argentino: Buenos Aires, Asociación Geológica Argentina, v. 10, p. 171–173.
- Aragón, E., Aguilera, Y.D., González, P.D., Gómez Peral, L., Cavarozzi, C.E., and Ribot, A., 2001, El Intrusivo Florentina del complejo volcánico piroclástico del Río Chubut medio (Paleocene-Eoceno medio): Un ejemplo de etmolito o embudo: Revista de la Asociación Geológica Argentina, v. 56, no. 2, p. 161–172.
- Aragón, E., González, P.D., Aguilera, Y., Marquett, C., Cavarozzi, C., and Ribot, A., 2004, El domo vitrofírico Escuela Piedra Parada del Complejo Volcanico Piroclastico del Río Chubut Medio: Revista de la Asociación Geológica Argentina, v. 59, no. 4, p. 634–642.

- Aragón, E., Castro, A., Diaz-Alvarado, J., Pinotti, L., D'eramo, F., Demartis, M., Coniglio, J., Hernando, I., and Rodriguez, C., 2018, Mantle derived crystal-poor rhyolitic ignimbrites: Eruptive mechanism from geochemical and geochronological data of the Piedra Parada caldera, southern Argentina: Geoscience Frontiers, v. 9, no. 5, p. 1529– 1553, https://doi.org/10.1016/j.gsf.2017.09.004.
- Archangelsky, S., 1974, Sobre la edad de la tafoflora de la Laguna del Hunco, Province de Chubut: Ameghiniana, v. 11, p. 413–417.
- Archangelsky, S., 2005, La paleobotánica en Argentina y su desarrollo durante los últimos 50 años: Buenos Aires, Asociación Paleontolológica Argentina Publicación Especial 10, p. 37–49.
- Azpelicueta, M.M., and Cione, A.L., 2011, Re-description of the Eocene catfish *Bachmannia chubutensis* (Teleostei: Bachmanniidae) of southern South America: Journal of Vertebrate Paleontology, v. 31, p. 258–269, https://doi .org/10.1080/02724634.2011.550351.
- Báez, A.M., and Pugener, L.A., 2003, Ontogeny of a new Palaeogene pipid frog from southern South America and xenopodinomorph evolution: Zoological Journal of the Linnean Society, v. 139, no. 3, p. 439–476, https://doi .org/10.1046/j.1096-3642.2003.00085.x.
- Báez, A.M., and Trueb, L., 1997, Redescription of the Paleogene Shelania pascuali from Patagonia and its bearing on the relationships of fossil and Recent pipoid frogs: The University of Kansas Natural History Museum: Scientific Papers, v. 4, p. 1–41.
- Barreda, V.D., Palazzesi, L., Tellería, M.C., Katinas, L., Crisci, J.V., Bremer, K., Passalia, M.G., Corsolini, R., Rodríguez Brizuela, R., and Bechis, F., 2010, Eocene Patagonia fossils of the daisy family: Science, v. 329, no. 5999, p. 1621, https://doi.org/10.1126/science.1193108.
- Bellosi, E.S., 2010, Physical stratigraphy of the Sarmiento Formation (middle Eocene–lower Miocene) at Gran Barranca, central Patagonia, *in* Madden, R.H., Carlini, A.A., Vucetich, M.G., and Kay, R.F., eds., The Paleontology of Gran Barranca: Cambridge, UK, Cambridge University Press, p. 19–31.
 Berry, E.W., 1925, A Miocene flora from Patagonia:
- Berry, E.W., 1925, A Miocene flora from Patagonia: Johns Hopkins University: Studies in Geology (Tulsa), v. 6, p. 183–251.
- Berry, E.W., 1938, Tertiary Flora from the Río Pichileufú, Argentina: Geological Society of America Special Paper 12, 198 p., https://doi.org/10.1130/SPE12-p1.
- Bippus, A.C., Escapa, I.H., and Tomescu, A., 2016, Tiny ecosystems: Bryophytes and other biotic interactions around an osmundaceous fern from the Eocene of Patagonia, *in* Botany 2016, Abstracts: Savannah, Georgia, Botanical Society of America.
- Bippus, A.C., Escapa, I.H., Wilf, P., and Tomescu, A.M.F., 2019, Fossil fern rhizomes as a model system for exploring epiphyte community structure across geologic time: Evidence from Patagonia: PeerJ, v. 7, p. e8244, https:// doi.org/10.7717/peerj.8244.
- Bomfleur, B., and Escapa, I., 2019, A silicified *Todea* trunk (Osmundaceae) from the Eocene of Patagonia: Paläontologische Zeitschrift, v. 93, p. 543–548, https://doi .org/10.1007/s12542-019-00479-6.
- Casamiquela, R.M., 1961, Un pipoideo fósil de Patagonia: Revista del Museo de La Plata: Sección Paleontología, v. 4, no. 22, p. 71–123.
- Clyde, W.C., Wilf, P., Iglesias, A., Slingerland, R.L., Barnum, T., Bijl, P.K., Bralower, T.J., Brinkhuis, H., Comer, E.E., Huber, B.T., Ibañez-Mejia, M., Jicha, B.R., Krause, J.M., Schueth, J.D., Singer, B.S., Raigemborn, M.S., Schmitz, M.D., Sluijs, A., and Zamaloa, M.C., 2014, New age constraints for the Salamanca Formation and lower Río Chico Group in the western San Jorge Basin, Patagonia, Argentina: Geological Society of America Bulletin, v. 126, no. 3–4, p. 289–306, https:// doi.org/10.1130/B30915.1.
- Comer, E.E., Slingerland, R.L., Krause, J.M., Iglesias, A., Clyde, W.C., Raigemborn, M.S., and Wilf, P., 2015, Sedimentary facies and depositional environments of diverse early Paleocene floras, north-central San Jorge Basin, Patagonia, Argentina: Palaios, v. 30, p. 553–573, https://doi.org/10.2110/palo.2014.064.
- Dalla Salda, L.H., and Franzese, J., 1987, Las Megaestructuras de macizo y cordillera Norpatagónica Argentina y la

génesis de las cuencas volcano-sedimentarias terciarias: Revista Geológica de Chile, v. 31, p. 3–13.

- Dalrymple, G., 1979, Critical tables for conversion of K-Ar ages from old to new constraints: Geology, v. 7, p. 558–560, https://doi.org/10.1130/0091-7613(1979)7<558:CTFCOK>2.0.CO;2.
- Dolgopol de Sáez, M., 1941, Noticias sobre peces fósiles Argentinos: Siluroideos Terciarios de Chubut: Notas del Museo de La Plata, v. 35, p. 451–457.
- Dumas, S., and Arnott, R.W.C., 2006, Origin of hummocky and swaley cross-stratification—The controlling influence of unidirectional current strength and aggradation rate: Geology, v. 34, p. 1073–1076, https://doi .org/10.1130/G22930A.1.
- Dunn, R.E., Madden, R.H., Kohn, M.J., Schmitz, M.D., Strömberg, C.A.E., Carlini, A.A., Ré, G.H., and Crowley, J., 2013, A new chronology for middle Eocene– early Miocene South American Land Mammal Ages: Geological Society of America Bulletin, v. 125, no. 3-4, p. 539–555, https://doi.org/10.1130/B30660.1.
- Dunn, R.E., Strömberg, C.A.E., Madden, R.H., Kohn, M.J., and Carlini, A.A., 2015, Linked canopy, climate, and faunal change in the Cenozoic of Patagonia: Science, v. 347, no. 6219, p. 258–261, https://doi .org/10.1126/science.1260947.
- Feruglio, E., 1949, Descripción Geológica de la Patagonia, Volumen II: Buenos Aires, Argentina, Ministerio de Industria y Comercio de la Nación, Dirección General de Yacimientos Petroliferos Fiscales, 349 p.
- Fidalgo, P., and Smith, D.R., 1987, A fossil Siricidae (Hymenoptera) from Argentina: Entomological News, v. 98, no. 2, p. 63–66.
- Flynn, J.J., and Swisher, C.C., III, 1995, Cenozoic South American Land Mammal Ages: Correlation to global geochronologies, *in* Berggren, W.A., Kent, D.V., Aubry, M.-P., and Hardenbol, J., eds., Time Scales and Global Stratigraphic Correlation: Society of Economic Paleontologists and Mineralogists (SEPM) Special Publication 54, p. 317–333, https://doi.org/10.2110/pec.95.04.0317.
- Frenguelli, J., 1943, Restos de Casuarina en el Micceno de El Mirador, Patagonia central: Notas del Museo de La Plata, v. 8, no. 56, p. 349–354.
- Gandolfo, M.A., Hermsen, E.J., Zamaloa, M.C., Nixon, K.C., González, C.C., Wilf, P., Cúneo, N.R., and Johnson, K.R., 2011, Oldest known *Eucalyptus* macrofossils are from South America: PLoS One, v. 6, no. 6, p. e21084, https://doi.org/10.1371/journal.pone.0021084.
- Gaudry, M.A., 1906, Fossiles de Patagonie: Étude sur une portion du monde Antarctique: Annales de Paléontologie, v. 1, p. 101–143.
- Gelfo, J.N., Goin, F.J., Woodburne, M.O., and de Muizon, C., 2009, Biochronological relationships of the earliest South American Paleogene mammalian faunas: Palaeontology, v. 52, no. 1, p. 251–269, https://doi .org/10.1111/j.1475-4983.2008.00835.x.
- Goin, F.J., Case, J.A., Woodburne, M.O., Vizcaíno, S.F., and Reguero, M.A., 1999, New discoveries of "opossum-like" marsupials from Antarctica (Seymour Island, medial Eocene): Journal of Mammalian Evolution, v. 6, no. 4, p. 335–365, https://doi.org/10.102 3/A:1027357927460.
- Goin, F.J., Tejedor, B.M., Lopez, G., and Reguero, M., 2000, Mamíferos Eocenos de Paso del Sapo, Chubut, Argentina: Ameghiniana, v. 37, p. 25R–26R.
- Goin, F.J., Tejedor, M., and Abello, A., 2001, Conclusiones preliminares sobre la asociación de marsupiales Paleogenos de Laguna Giordanella, Paso del Sapo, Chubut, Argentina: Eoceno Medio: Ameghiniana, v. 38, p. 9R-10R.
- Goin, F.J., Gelfo, J.N., Chornogubsky, L., Woodburne, M.O., and Martin, T., 2012a, Origins, radiations, and distribution of South American mammals: From greenhouse to icehouse worlds, *in* Patterson, B.D., and Costa, L.P., eds., Bones, Clones, and Biomes: The History and Geography of Recent Neotropical Mammals: Chicago, Illinois, University of Chicago Press, p. 20–50, https:// doi.org/10.7208/chicago/9780226649214.003.0003.
- Goin, F.J., Tejedor, M., Chornogubsky, L., López, G.M., Gelfo, J.N., Bond, M., Woodburne, M.O., Gurovich, Y., and Reguero, M., 2012b, Persistence of a Mesozoic, non-therian mammalian lineage (Gondwanatheria) in the mid-Paleogene of Patagonia: Natur-

wissenschaften, v. 99, no. 6, p. 449-463, https://doi .org/10.1007/s00114-012-0919-z.

- Goin, F.J., Vieytes, E.C., Gelfo, J.N., Chornogubsky, L., Zimicz, A.N., and Reguero, M.A., 2018, New metatherian mammal from the early Eocene of Antarctica: Journal of Mammalian Evolution, v. 27, p. 17–36, https:// doi.org/10.1007/s10914-10018-19449-10916.
- Gosses, J., 2006, Stratigraphy and ⁴⁰Ar/³⁹Ar Geochronology of the Laguna del Hunco Formation: A Lacustrine and Sub-aerial Caldera Moat Formation [M.S. thesis]: Madison, Wisconsin, University of Wisconsin, 265 p.
- Gosses, J., Carroll, A., Aragón, E., and Singer, B., 2006, The Laguna del Hunco formation: Lacustrine And Sub-Aerial Caldera Fill, Chubut Province, Argentina: Geological Society of America Abstracts with Programs, v. 38, no. 7, p. 502.
- Iannelli, S.B., Litvak, V.D., Fernández Paz, L., Folguera, A., Ramos, M.E., and Ramos, V.A., 2017, Evolution of Eocene to Oligocene arc-related volcanism in the North Patagonian Andes (39–41°S), prior to the break-up of the Farallon plate: Tectonophysics, v. 696–697, p. 70– 87, https://doi.org/10.1016/j.tecto.2016.12.024.
- Jicha, B.R., Singer, B.S., and Sobol, P., 2016, Re-evaluation of the ages of ⁴⁰Ar/³⁹Ar sanidine standards and supereruptions in the western U.S. using a Noblesse multi-collector mass spectrometer: Chemical Geology, v. 431, p. 54–66, https://doi.org/10.1016/ j.chemgeo.2016.03.024.
- Kooyman, R.M., Wilf, P., Barreda, V.D., Carpenter, R.J., Jordan, G.J., Sniderman, J.M.K., Allen, A., Brodribb, T.J., Crayn, D., Feild, T.S., Laffan, S.W., Lusk, C.H., Rossetto, M., and Weston, P.H., 2014, Paleo-Antarctic rainforest into the modern Old World Tropics: The rich past and threatened future of the "southern wet forest survivors": American Journal of Botany, v. 101, no. 12, p. 2121–2135, https://doi.org/10.3732/ajb.1400340.
- Krause, J.M., Clyde, W.C., Ibañez-Mejía, M., Schmitz, M., Barnum, T., Bellosi, E., and Wilf, P., 2017, New age constraints for early Paleogene strata of central Patagonia, Argentina: Implications for the timing of South America Land Mammal Ages: Geological Society of America Bulletin, v. 129, p. 886–903, https://doi .org/10.1130/B31561.1.
- Kuiper, K.F., Deino, A., Hilgen, F.J., Krijgsman, W., Renne, P.R., and Wijbrans, J.R., 2008, Synchronizing rock clocks of Earth history: Science, v. 320, p. 500–504, https://doi.org/10.1126/science.1154339.
- Lawver, L.A., Gahagan, L.M., and Dalziel, I.W.D., 2013, A different look at gateways: Drake Passage and Australia/Antarctica, *in* Anderson, J.B., and Wellner, J.S., eds., Tectonic, Climatic, and Cryospheric Evolution of the Antarctic Peninsula: American Geophysical Union Special Publication 63, p. 5–33, https://doi .org/10.1029/2010SP001017.
- Lee, J.-Y., Marti, K., Severinghaus, J.P., Kawamura, K., Yoo, H.-S., Lee, J.B., and Kim, J.S., 2006, A redetermination of the isotopic abundance of atmospheric Ar: Geochimica et Cosmochimica Acta, v. 70, p. 4507–4512, https:// doi.org/10.1016/j.gca.2006.06.1563.
- Lipman, P.W., 1997, Subsidence of ash-flow calderas: Relation to caldera size and magma-chamber geometry: Bulletin of Volcanology, v. 59, p. 198–218, https://doi .org/10.1007/s004450050186.
- Lorente, M., 2016, Isolated Litopterna postcranial remains from La Barda Tuff (early Eocene), Paso del Sapo, Chubut, Argentina: Proposed association with dental taxa and their implications: Ameghiniana, v. 53, no. 1, p. 26– 38, https://doi.org/10.5710/AMGH.16.09.2015.2914.
- Lorente, M., Chornogubsky, L., and Goin, F.J., 2016, On the existence of non-microbiotherian Australidelphian marsupials (Diprotodontia) in the Eocene of Patagonia: Palaeontology, v. 59, no. 4, p. 533–547, https://doi .org/10.1111/pala.12241.
- Mazzoni, M.M., and Aragón, E., 1987, La Ignimbrita Barda Colorada del complejo volcánico piroclástico del Río Chubut Medio, *in* Actas 10th Congreso Geólogico Argentino: La Plata, Argentina, Asociación Geológica Argentina, v. 10, p. 168–170.
- Mazzoni, M.M., Aragón, E., and Merodio, J.C., 1989, La Ignimbrita Barda Colorada del complejo volcánico piroclástico del Río Chubut Medio: Revista de la Asociación Geológica Argentina, v. 44, no. 1–4, p. 246–258.

- Mazzoni, M.M., Kawashita, K., Harrison, S., and Aragón, E., 1991, Edades radimétricas Eocenas: Borde occidental del Macizo Norpatagónico: Revista de la Asociación Geológica Argentina, v. 46, no. 1–2, p. 150–158.
- Melendi, D.L., Scafati, L.H., and Volkheimer, W., 2003, Palynostratigraphy of the Paleogene Huitrera Formation in N-W Patagonia, Argentina: Neues Jahrbuch für Geologie und Palaontologie, Abhandlungen, v. 228, no. 2, p. 205–273.
- Miller, T., and Casadevall, T.J., 2000, Volcanic ash hazards to aviation, *in* Sigurdsson, H., ed., Encyclopedia of Volcanoes: San Diego, Academic Press, p. 915–930.
- Min, K., Mundil, R., Renne, P.R., and Ludwig, K.R., 2000, A test for systematic errors in ⁴⁰Arf³⁹Ar geochronology through comparison with U/Pb analysis of a 1.1-Ga rhyolite: Geochimica et Cosmochimica Acta, v. 64, p. 73– 98, https://doi.org/10.1016/S0016-7037(99)00204-5.
- Palazzesi, L., and Barreda, V., 2007, Major vegetation trends in the Tertiary of Patagonia (Argentina): A qualitative paleoclimatic approach based on palynological evidence: Flora, v. 202, p. 328–337, https://doi .org/10.1016/j.flora.2006.07.006.
- Pascual, R., 2006, Evolution and geography: The biogeographic history of South American land mammals: Annals of the Missouri Botanical Garden, v. 93, no. 2, p. 209–230, https://doi.org/10.3417/0026-6493(2006)93[209:EAGTBH]2.0.CO;2.
- Pascual, R., Archer, M., Ortiz-Jaureguizar, E., Prado, J.L., Godthelp, H., and Hand, S.J., 1992, First discovery of monotremes in South America: Nature, v. 356, no. 6371, p. 704–706, https://doi.org/10.1038/356704a0.
- Petersen, C.S., 1946, Estudios Geológicos en la Región del Río Chubut Medio: Boletín de la Dirección Nacional de Geología y Minería 59, 137 p.
- Petrulevičius, J., 2015, A new Synlestidae damselfly (Insecta: Odonata: Zygoptera) from the early Eocene of Nahuel Huapi Este, Patagonia, Argentina: Arquivos Entomolóxicos, v. 14, p. 287–294.
- Petrulevičius, J.F., 2016, A new pentatomoid bug from the Ypresian of Patagonia, Argentina: Acta Palaeontologica Polonica, v. 61, no. 4, p. 863–868, https://doi .org/10.4202/app.00308.2016.
- Petrulevičius, J.F., and Nel, A., 2013, A new Frenguelliidae (Insecta: Odonata) from the early Eocene of Laguna del Hunco, Patagonia, Argentina: Zootaxa, v. 3616, no. 6, p. 597–600, https://doi.org/10.11646/zootaxa.3616.6.6.
- Rapela, C.W., Spalletti, L.A., Merodio, J.C., and Aragón, E., 1984, El vulcanismo Paleoceno–Eoceno de la provincial volcánica Andino–Patagónica, *in* Actas 9th Congreso Geológico Argentino: Buenos Aires, Asociación Geológica Argentina, v. 10, p. 189–213.
- Rapela, C.W., Spalletti, L.A., Merodio, J.C., and Aragón, E., 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, v. 1, p. 75–88, https://doi.org/10.1016/0895-981 1(88)90017-X.
- Reguero, M., Goin, F., Hospitaleche, C.A., Dutra, T., and Marenssi, S., 2013, Late Cretaceous/Paleogene West Antarctica Terrestrial Biota and its Intercontinental Affinities: Dordrecht, Netherlands, Springer, Springer Briefs in Earth System Sciences, 120 p.
- Reguero, M.A., Gelfo, J.N., López, G.M., Bond, M., Abello, A., Santillana, S.N., and Marenssi, S.A., 2014, Final Gondwana breakup: The Paleogene South American

native ungulates and the demise of the South America–Antarctica land connection: Global and Planetary Change, v. 123B, p. 400–413, https://doi.org/10.1016/ j.gloplacha.2014.07.016.

- Renne, P.R., Swisher, C., Deino, A., Karner, D., Owens, T., and DePaola, D., 1998, Intercalibration of standards, absolute ages and uncertainties in ⁴⁰Ar/³⁹Ar dating: Chemical Geology, v. 145, p. 117–152, https://doi .org/10.1016/S0009-2541(97)00159-9.
- Romero, E.J., and Hickey, L.J., 1976, A fossil leaf of Akaniaceae from Paleocene beds in Argentina: Bulletin of the Torrey Botanical Club, v. 103, no. 3, p. 126–131, https://doi.org/10.2307/2484888.
- Romero, E.J., Dibbern, M.C., and Gandolfo, M.A., 1988, Revisión de Lomatia bivascularis (Berry) Frenguelli (Proteaceae) del yacimiento de la Laguna del Hunco (Paleoceno), Provincia del Chubut, in Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía, Volumen 3: Mendoza, Argentina, El Congreso (Mendoza), p. 125–130.
- Salgado, L., 2007, Patagonia and the study of its Mesozoic reptiles: A brief history, *in* Gasparini, Z., Salgado, L., and Coria, R.A., eds., Patagonian Mesozoic Reptiles: Bloomington, Indiana, Indiana University Press, p. 1–28.
- Simpson, G.G., 1935, Occurrence and relationships of the Río Chico fauna of Patagonia: American Museum Novitates, v. 818, p. 1–21.
- Simpson, G.G., 1950, History of the fauna of Latin America: American Scientist, v. 38, no. 3, p. 361–389.
- Simpson, G.G., 1980, Splendid Isolation: The Curious History of South American Mammals: New Haven, Connecticut, Yale University Press, 266 p.
- Singer, B.S., Jicha, B.R., Mochizuki, N., and Coe, R.S., 2019, Synchronizing volcanic, sedimentary, and ice core records of Earth's last magnetic polarity reversal: Science Advances, v. 5, no. 8, p. eaaw4621, https://doi .org/10.1126/sciadv.aaw4621.
- Tejedor, M.F., Czaplewski, N.J., Goin, F.J., and Aragón, E., 2005, The oldest record of South American bats: Journal of Vertebrate Paleontology, v. 25, p. 990–993, https:// doi.org/10.1671/0272-4634(2005)025[0990:TOROSA]2.0.CO;2.
- Tejedor, M.F., Goin, F.J., Gelfo, J.N., López, G., Bond, M., Carlini, A.A., Scillato-Yané, G.J., Woodburne, M.O., Chornogubsky, L., Aragón, E., Reguero, M.A., Czaplewski, N.J., Vincon, S., Martin, G.M., and Ciancio, M.R., 2009, New early Eocene mammalian fauna from western Patagonia, Argentina: American Museum Novitates, v. 3638, p. 1–43, https://doi .org/10.1206/577.1.
- Wilf, P., 2012, Rainforest conifers of Eocene Patagonia: Attached cones and foliage of the extant Southeast Asian and Australasian genus *Dacrycarpus* (Podocarpaceae): American Journal of Botany, v. 99, no. 3, p. 562–584, https://doi.org/10.3732/ajb.1100367.
- Wilf, P., and Escapa, I.H., 2015, Green Web or megabiased clock? Patagonian plant fossils speak on evolutionary radiations: The New Phytologist, v. 207, no. 2, p. 283– 290, https://doi.org/10.1111/nph.13114.
- Wilf, P., Cúneo, N.R., Johnson, K.R., Hicks, J.F., Wing, S.L., and Obradovich, J.D., 2003, High plant diversity in Eocene South America: Evidence from Patagonia: Science, v. 300, no. 5616, p. 122–125, https://doi .org/10.1126/science.1080475.

- Wilf, P., Johnson, K.R., Cúneo, N.R., Smith, M.E., Singer, B.S., and Gandolfo, M.A., 2005a, Eocene plant diversity at Laguna del Hunco and Rio Pichileufu, Patagonia, Argentina: American Naturalist, v. 165, p. 634–650, https://doi.org/10.1086/430055.
- Wilf, P., Labandeira, C.C., Johnson, K.R., and Cúneo, N.R., 2005b, Richness of plant-insect associations in Eocene Patagonia: A legacy for South American biodiversity: Proceedings of the National Academy of Sciences of the United States of America, v. 102, no. 25, p. 8944– 8948, https://doi.org/10.1073/pnas.0500516102.
- Wilf, P., Little, S.A., Iglesias, A., Zamaloa, M.C., Gandolfo, M.A., Cúneo, N.R., and Johnson, K.R., 2009, *Pap-uacedrus* (Cupressaceae) in Eocene Patagonia: A new fossil link to Australasian rainforests: American Journal of Botany, v. 96, no. 11, p. 2031–2047, https://doi .org/10.3732/ajb.0900085.
- Wilf, P., Singer, B.S., Zamaloa, M.C., Johnson, K.R., and Cúneo, N.R., 2010, Early Eocene ⁴⁰Ar/³⁹Ar age for the Pampa de Jones plant, frog, and insect biota (Huitrera Formation, Neuquén Province, Patagonia, Argentina): Ameghiniana, v. 47, no. 2, p. 207–216, https://doi .org/10.5710/AMGH.v47i2.7.
- Wilf, P., Cúneo, N.R., Escapa, I.H., Pol, D., and Woodburne, M.O., 2013, Splendid and seldom isolated: The paleobiogeography of Patagonia: Annual Review of Earth and Planetary Sciences, v. 41, p. 561–603, https://doi .org/10.1146/annurev-earth-050212-124217.
- Wilf, P., Escapa, I.H., Cúneo, N.R., Kooyman, R.M., Johnson, K.R., and Iglesias, A., 2014, First South American *Agathis* (Araucariaceae): Eocene of Patagonia: American Journal of Botany, v. 101, no. 1, p. 156–179.
- Wilf, P., Carvalho, M.R., Gandolfo, M.A., and Cúneo, N.R., 2017, Eocene lantern fruits from Gondwanan Patagonia and the early origins of Solanaceae: Science, v. 355, no. 6320, p. 71–75, https://doi.org/10.1126/science.aag2737.
- Wilf, P., Nixon, K.C., Gandolfo, M.A., and Cúneo, N.R., 2019, Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests: Science, v. 364, no. 6444, p. eaaw5139, https://doi.org/10.1126/science. aaw5139.
- Woodburne, M.O., Goin, F.J., Bond, M., Carlini, A.A., Gelfo, G.M.L., Iglesias, A., and Zimicz, A.N., 2014a, Paleogene land mammal faunas of South America: A response to global climatic changes and indigenous floral diversity: Journal of Mammalian Evolution, v. 21, p. 1–73, https://doi.org/10.1007/s10914-012-9222-1.
- Woodburne, M.O., Goin, F.J., Raigemborn, M.S., Heizler, M., Gelfo, J.N., and Oliveira, E.V., 2014b, Revised timing of the South American early Paleogene land mammal ages: Journal of South American Earth Sciences, v. 54, p. 109–119, https://doi.org/10.1016/ j.jsames.2014.05.003.
- Zachos, J.C., Dickens, G.R., and Zeebe, R.E., 2008, An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics: Nature, v. 451, no. 7176, p. 279– 283, https://doi.org/10.1038/nature06588.

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