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Journal of Mammalian Evolution

ISSN 1064-7554
Volume 21
Number 1

J Mammal Evol (2014) 21:1-73
DOI 10.1007/s10914-012-9222-1

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ORIGINAL PAPER

Paleogene Land Mammal Faunas of South America; a Response to Global Climatic Changes and Indigenous Floral Diversity

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Abstract An appraisal of Paleogene floral and land mammal faunal dynamics in South America suggests that both biotic elements responded at rate and extent generally comparable to that portrayed by the global climate pattern of the interval. A major difference in the South American record is the initial as well as subsequent much greater diversity of both Neotropical and Austral floras relative to North American counterparts. Conversely, the concurrent mammal faunas in South America did not match, much less exceed, the diversity seen to the north. It appears unlikely that this difference is solely due to the virtual absence of immigrants subsequent to the initial dispersal of mammals to South America, and cannot be explained solely by the different collecting histories of the two regions. Possible roles played by non-mammalian vertebrates in niche exploitation remain to be explored.

The Paleogene floras of Patagonia and Chile show a climatic pattern that approximates that of North America, with an increase in both Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) from the Paleocene into the Early Eocene Climatic Optimum (EECO), although the Paleocene-Eocene Thermal Maximum (PETM) is not recognized in the available data set. Post-EECO temperatures declined in both regions, but more so in the north than the south, which also retained a higher rate of precipitation.

The South American Paleogene mammal faunas developed gradual, but distinct, changes in composition and diversity as the EECO was approached, but actually declined somewhat during its peak, contrary to the record in North America. At about 40 Ma, a post-EECO decline was recovered in both hemispheres, but the South American record achieved its greatest diversity then, rather than at the peak of the EECO as in the north. This post-EECO faunal turnover apparently was a response to the changing conditions when global climate was deteriorating toward the Oligocene. Under the progressively more temperate to seasonally arid conditions in South America, this turnover reflected a major change from the more archaic, and more tropical to subtropical-adapted mammals, to the beginning of the ultimately modern South American fauna, achieved completely by the Eocene-Oligocene transition. Interestingly, hypsodonty was achieved by South American cursorial mammals about 15–20 m.y. earlier than in North America. In addition to being composed of essentially different groups of mammals, those of the South American continent seem to have responded to the climatic changes associated with the ECCO

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and subsequent conditions in a pattern that was initially comparable to, but subsequently different from, their North American counterparts.

Keywords South America · Biotic change · Evolution · Paleontology · Early Cenozoic

Introduction

The Paleogene Period witnessed major global changes in climate and ocean temperatures (Zachos et al. 2001), with the Early Eocene Climatic Optimum (EECO) having been the warmest interval of the Cenozoic Era and a very low thermal gradient between the poles and the equator (Keating-Bitonti et al. 2011). This report investigates the evolution of land mammal faunas of South America in terms of the paleoclimatic setting of that interval based on terrestrial floras. The project began as part of an appraisal of Paleocene and Eocene floral and land mammal biotic patterns during a time of global temperature fluctuation, culminating in the EECO and its aftermath. The project first focused on the record in North America (Woodburne et al. 2009a, b), and detailed numerous changes in faunal diversity and composition in response to a number of fluctuations in the plant record response to the ebb and flow of subtropical, tropical, and more arid conditions.

The plants and land mammals of South America are and were substantially different from their North American counterparts. As regards the Paleogene plants, and although much effort has been taken to compare plant species between both hemispheres in recent years, only one taxon (the menispermacean podocarp *Palaeoluna*; Herrera et al. 2011) was found in common between North and South America. In contrast, several plant families recognized in the fossil record of southern South America are shared, both as fossil and recent taxa, with the Australasian region. Examples are Araucariaceae, Podocarpaceae, Proteaceae, Nothofagaceae, as well as Eocene records of the genera *Papuacedrus*, *Gymnostoma*, and *Ecualyptus* (Zamaloa et al. 2006; González et al. 2007; Wilf et al. 2009; Gandolfo et al. 2011). All of these records suggest a strong southern Gondwana floral belt during the Late Cretaceous and early Paleogene (Iglesias et al. 2011), distinct from floras in the northern part of South America (e.g., Crisci et al. 1991; Moreira-Muñoz 2007).

For the mammals, the two hemispheres experienced dramatically different evolutionary histories, and were provided with substantially different groups of mammals. As summarized in Woodburne et al. (2009a, b), North American Paleogene therian mammals had a long history that extended well into the Cretaceous, and developed a relatively complex pattern of endemic evolution energized by immigrations from elsewhere in Holarctica, as well as by climate changes. In addition to a relatively small component of metatherians, the North American biota enjoyed a diversity of small-sized insectivorous to omnivorous mammals (‘insectivores,’ primates) as well as a variety of non-therian multituberculates. Larger-sized mammals included a host of placental carnivorans as well as the various and diverse ungulates.

In the Late Cretaceous, South America began with its own component of non-therian mammals. These were mostly comprised of dryolestoids, but also included ‘triconodonts,’ ‘symmetrodonts,’ substantially specialized gondwanatheres, and a single multituberculate (Kielan-Jaworowska et al. 2007; Rougier et al. 2009a). In the early Paleocene, first metatherian, and then placental mammals, were introduced via as yet undocumented immigration events that likely began in the Late Cretaceous, at least for metatherians (Pascual and Ortiz-Jaureguizar 1991, 1992; Case et al. 2005). As far as is known, no other small-sized insectivorous to omnivorous, or even carnivorous eutherian mammals accompanied the first metatherians. The first placental mammals were mostly kollpaniine ‘condylarths’ and a few other archaic groups, such as pantodonts. The net effect was that therian mammals of South America began the Paleogene with a set of taxa that was substantially less diverse both phyletically and ecologically-adaptively than seen in North America. How this unique group of mammals reacted to the same global temperature changes as seen in North America is the focus of the present study.

Cenozoic South American mammalian dynamics have been the subject of research since Ameghino’s contributions in the late XIX Century (see Patterson and Pascual 1972; Pascual 1996; and literature cited therein). In recent decades, the contributions by Rosendo Pascual and Edgardo Ortiz-Jaureguizar (Pascual 2006; Pascual and Ortiz-Jaureguizar 1990, 2007; Ortiz-Jaureguizar and Cladera 2006) stand out, with North and South American Late Cretaceous-Paleocene mammalian faunas having been compared by Ortiz-Jaureguizar and Pascual (1989) and Pascual and Ortiz-Jaureguizar (1992). The following presentation benefitted from these and many other outstanding publications.

Our presentation is organized in three parts. The first documents and summarizes the paleofloral record of South America from the Late Cretaceous to early Oligocene in order to set the vegetational and climatic context in which the evolution of the mammalian faunas can be viewed. The first mammalian section sets out the fundamental chronologic, geographic, and taxonomic data by which the individual SALMAs can be recognized and characterized, with information on their ecological structure. The second mammalian section integrates the first two sections in order to place the faunal succession and its structural changes into a climatic and ecological framework. The final portion of the treatment summarizes that synthesis and compares it to the patterns seen in coeval record of North America. The Appenedix documents the bases for the ages of the SALMAs.

Methods

Definitions and Abbreviations

brachydont	A descriptor of the height of crown above the roots in mammalian teeth generally referred to as being low-crowned. Damuth and Janis (2011) and Janis (1988) utilized an index based on the m3 height/width of <1.7 to define brachydont.
CIE	Carbon Isotope Excursion; sharp decrease in δ^{13}C recorded at the beginning of the Sparnacian Stage/Age and the Wasatchian NALMA (Thiry et al. 2006); CIE lasted about 113,000 years, with a recovery interval of about 83,000 years (Murphy et al. 2010).
EECO	Early Eocene Climatic Optimum (Fig. 1; see text). This signifies the interval that experienced the highest mean ocean temperature of the Cenozoic Era (Wolfe 1978; Zachos et al. 2001, 2008). It began about 53 Ma and persisted to about 50 Ma (Tsukui and Clyde 2012) and occurred in the context of the overall relatively warm conditions that characterized the early Cenozoic from the Paleocene to about medial Eocene.
euhypsodont	A term used by Mones (1982) for hypselodont of Damuth and Janis (2011) and Janis (1988).
FAD	First Appearance Datum; first stratigraphic occurrence of a taxon, considered to have been synchronous over a specified geographic region (Woodburne 1996).
GPTS	Geomagnetic Polarity Time Scale (Gradstein et al. 2004).
hypsodont	A descriptor of the height of crown above the roots in mammalian teeth generally referred to as being high-crowned. Damuth and Janis (2011) and Janis (1988) utilized an index based on the m3 height/width of 3.5–5.0 to define hypsodont.
hypselodont	Teeth in mammals that are not only hypsodont but also ever-growing (Janis 1988; Damuth and Janis 2011), with an hypsodonty index >5.01.
k.y.	A segment of geologic time one thousand years in duration or the age of an event (e.g., ten thousand years ago), without reference to a point or set of points on the radioisotopic time scale.
LAD	Last Appearance Datum; last stratigraphic occurrence of a taxon, considered to have been synchronous over a specified geographic region (Woodburne 1996).
Ma	Megannum. One million years in the radioisotopic time scale (e.g., 10 Ma refers to the ten million year point on the time scale).
MAP	Mean Annual Precipitation (as inferred from paleobotanical leaf margin data; Wilf et al. 1998).
MAT	Mean Annual Temperature (as inferred from paleobotanical leaf margin data).
MECO	Mid-Eocene Climatic Optimum; a hyperthermal warming event at about 41.6 Ma (Zachos et al. 2008; Figueirido et al. 2012).
MPBE	Mid-Paleocene Biotic Event; biotic response to the short-term hyperthermal pulse at the latest Selandian or the beginning of the Thanetian, ca 58.7 Ma (Bernaola et al. 2007). Westerhold et al. (2011) referred to the thermal event as the Early Late Paleocene Event (ELPE) and considered its age as about 58.2 Ma (Fig. 1).
m.y.	A segment of geologic time one million years in duration or the age of an event (e.g., ten million years ago) without reference to a point or a set of points on the radioisotopic time scale.
NALMA	North American Land Mammal Age (Woodburne 2004a); an interval of time based on mammalian biochronology. Tiffanian, Clarkforkian, Wasatchian, Bridgerian, and Uintan NALMAs are discussed in this report (see Fig. 1).
NPHP	North Patagonian High Plateau (Aragón et al. 2011).
PETM	Paleocene-Eocene Thermal Maximum; short-term hyperthermal pulse of global warming at the Paleocene-Eocene boundary (Zachos et al. 2008; McInerney

	and Wing 2011). This is the earliest Eocene hyperthermal event, calibrated at 56.33 Ma (Westerhold et al. 2009). It had a duration of 120–220 k.y. (Murphy et al. 2010), with an initial pulse of about 10 k.y., during which global sea surface temperatures rose 5–9 °C.
protohypsodont	A term used by Mones (1982) for hypsodont of Damuth and Janis (2011) and Janis (1988).
SALMA	South American Land Mammal Age; comparable to NALMA; see Pascual et al. (1965), Simpson (1971), Patterson and Pascual (1972), Marshall et al. (1983).

The classification of non-therians follows Kielan-Jaworowska et al. (2004). Metatherian classification follows Goin et al. (2012a), while that for eutherian mammals follows Gelfo et al. (2009: table S1).

Floral Terms

Vegetation classification follows Graham (1999); natural life zones are from Holdridge (1967); information on modern plants is taken from Heywood (1993)

Tropical Forest (paratropical to tropical): MAT ca. 25 °C; subhumid, MAP ca 165 cm/year; little seasonality; growth rings absent to weak; broad-leaved evergreen, single-tiered, open canopy vegetation; leaves mostly entire-margined; thick textured; few drip tips.

Tropical rain forest: mean temperature of coldest month not below ca. 18 °C; MAT above 25 °C; MAP above 165 cm/year; no pronounced dry season; broad leaved, evergreen, multistratal; drip tips, lianas (high-climbing woody vines), and buttressing common (supporting of trees or vines by each other); leaves sclerophyllous, mostly mesophyllous (megaphyllous in substratum), entire-margined leaves majority (above 75 %).

Subtropical rain forest (= paratropical of authors): may experience some frost; MAT 20–25 °C; no extended dry season; precipitation may be seasonal; floristically like tropical rain forest, mostly broad-leaved evergreens with a few deciduous plants; woody lianas diverse; buttressing present; mostly entire-margined leaves (57–75 %).

Subtropical forest: frost present but not severe; MAT between 13 °C and 18 °C; mean of coldest month between 0 °C and 18 °C; more seasonal rainfall; sclerophylls abundant; few lianas; no buttressing; mostly broad-leaved evergreen forest with some conifers; entire-margined leaves 39–55 %.

Megathermal rain forest: Such a forest requires a minimum mean monthly temperature above 18 °C, an annual precipitation above 200 cm, and a dry season in which no more than 4 months have less than 10 cm of rainfall per month (Morley 2000).

Notophyllous broad-leaved evergreen forest (ecotonal; oak-laurel forest of eastern Asia): mean of coldest month about 1 °C; MAT about 13 °C; some broad-leaved deciduous trees present; conifers not common; woody climbers abundant; buttressing absent; sclerophyllous; no drip tips; entire-margined leaves 40 %–60 %.

Cool-temperate forest: temperatures fall below 0 °C for several months (mean coldest month between −3 °C and 2 °C); pronounced seasonality in climate; MAT between 6 °C and 12 °C; broad-leaved deciduous forest, with conifers; broad-leaved evergreens present but not dominant; entire-margined leaves about 30–38 %.

Megathermal: MAT above 20 °C.

Mesothermal: MAT between 20 °C and 13 °C.

Microthermal: MAT less than 13 °C.

Modern counterparts of plant families and other groups referred to in the text are from Stevens (2007) and Heywood (1993).

Biogeographic Terminology

Biogeographic classification and terminology follows Morrone (2002, 2006).

Neotropical Region– Effectively all of South America east of the Andes and north of Patagonia and adjacent Chile, from the latitude of Buenos Aires northwestward to about latitude 28°S. It forms part of the Holotropical Kingdon (sensu Morrone 2002), together with tropical Africa and southern Asia.

Andean Region– Patagonia and adjacent Chile, from the latitude of Bahia Blanca (38°S) northwestward to about latitude 28°S. It forms part of the Austral Kingdom (sensu Morrone 2002) together with Antarctica, the Cape region, and the Australiasian Region.

Australasian Region– Australia, New Zealand, New Guinea, and neighboring islands in the Pacific Ocean.

Mammalian Ecological Categories

Ecological categories after Woodburne et al. (2009b).

Herbivore: utilizing plant resources including both high energy and low energy herbaceous foliage.

Insectivore: utilizing high energy insect or arthropod resources.

Hypercarnivore: utilizing exclusively high-energy vertebrate resources.

Carnivore: diet dominated by high-energy vertebrate resources but may include other high-energy resources (insects, invertebrates).

Omnivore: diet dominated by high-energy fruits, seeds, and insects but may also utilize other invertebrates as well as high-energy vertebrate resources.

Small size: less than 1 kg of body mass.

Medium size: 1 to 10 kg.

Large size: greater than 10 kg.

Long-term Climatic Trends and Transient Hyperthermal Events

The general climatic pattern of the early Cenozoic Era has been updated recently (Zachos et al. 2008, 2010; Westerhold et al. 2011) from previous analyses (e.g., Zachos et al. 2001). The Paleogene Period witnessed the most important long-term warming trend of the Cenozoic. As indicated in Fig. 1, the warmer global climates began in the early Paleocene and achieved their maximum development during the EECO, with subsequent cooling toward the onset of the Icehouse World at the beginning of the Oligocene. Several short-term hyperthermal pulses (on the order of a few tens of k.y.) were superimposed on this pattern, with the most impressive being the PETM at the Paleocene-Eocene boundary. Other hyperthermal pulses have yet to be shown as global in extent. Unfortunately the South American land mammal record appears to not preserve the PETM, but the MPBE, if global, may be generally correlative with the *Carodnia* Zone, and the Itaboraian to Tinguiririican mammals could reflect the warm to cooler climates indicated on Fig. 1. Based on the sharp drop in temperatures and associated impact on indigenous floras, mammal faunas of Tinguiririican and Deseadan age could be expected to show a biofacies that was comparable between them and also different from those of previous intervals.

Mammalian Biochrons

This report employs an updated chronology of fossil mammal-bearing successions in North and South America (Fig. 1) not only in terms of the Cenozoic time scales presented in Gradstein et al. (2004), but also with respect to advances made subsequent to compilations for North America (Woodburne 2004b; Woodburne et al. 2009b) and South America (Flynn and Swisher 1995; Pascual et al. 1996). It is convenient to utilize the Paleogene and Neogene time scales presented in Gradstein et al. (2004) as a template in which to accomplish these aims.

North America

The North American Land Mammal Ages (NALMA) follow Woodburne (2004b) and Woodburne et al. (2009b), but with adjustments made relative to the Luterbacher et al. (2004) time scale.

South America

Historically, the main sequence of Paleogene mammal faunas in South America (Fig. 1) was documented in the Golfo San Jorge Basin of Patagonia (Fig. 2a), as summarized by Bond et al. (1995) and Pascual and Ortiz-Jaureguizar (2007). Beginning about 1990, fossil-bearing sequences in Bolivia, Brazil, Chile, Perú, and Colombia have made important contributions to our understanding of South American Paleogene biochronology and counterparts of some of them (Itaboraian, Tinguiririican) have been recognized in Patagonia as well (Roth 1903; Gayet et al. 1991; Sempere et al. 1997; Marshall et al. 1997; Croft et al. 2008b).

The incorporation of the Tiupampan (early Paleocene) and Peligran (medial Paleocene) SALMAs (Ortiz-Jaureguizar and Pascual 1989; Bonaparte et al. 1993) and the reconsideration of the Casamayoran SALMA from its conventional early Eocene age to the late Eocene (Kay et al. 1999) were the first major temporal revisions of the conventional SALMA biochronological scale (Fig. 1). This was followed by the addition of a new early Oligocene Tinguiririican SALMA (Flynn et al. 2002, 2003), a new earliest Paleocene Grenier Farm metatherian record (Goin et al. 2006a), a new early Eocene Paso del Sapo fauna (Tejedor et al. 2009), and a reinterpretation of the age of the Divisaderan assemblage (López 2010). These are fully discussed in Appendix I.

Floral Background

Late Cretaceous Floras and Climate in South America

The global floral record indicates that angiosperms progressively overtook gymnosperms as the dominant plant group during the Late Cretaceous. In Patagonia, angiosperms diversifed from the middle Albian, ca 105 Ma (Archangelsky et al. 2009; Quattrocchio et al. 2011). In the Austral Basin (6, Fig. 2a), Iglesias et al. (2007c) discussed the Mata Amarilla flora derived from a littoral coastal plain of Cenomanian age (ca 96 Ma; Varela et al. 2012). Abundant megafossils demonstrated an important diversification of angiosperm shrubs and small trees, along with a canopy of podocarp and araucarian forests with a rich understory of ferns. Cupressaceae *s.l.* reflect very wet conditions, and widespread fungi, including epiphyllous forms, may indicate tropical conditions of high temperatures and humidity. Similar inferences were made based on analyses in the Mata Amarilla Formation where Varela (2011) recognized paleosols that reflected a MAT of about 20 °C (subtropical) and MAP above 100 cm, but with markedly seasonal rainfall. This is the oldest record of an angiosperm-dominated flora in southwest Gondwana. Other angiosperm-dominated floras of Cenomanian-Coniacian age include Portezuelo flora in the Neuquén Basin and the Bajo Barreal Formation in the San Jorge Basin (Archangelsky et al. 2009). Angiosperm pollen are an important part of the record from the Campanian onward (Prámparo et al. 2007).

During the Early Cretaceous (to the Albian), several fossil records of xerophilic plants (Ephedraceae, Gnetaceae, Cheirolepidiaceae, some conifers, and a few small-leafed angiosperms) infer a large area with dry conditions in equatorial and tropical South American regions, which extended from northern Brazil Crato Formation to central Argentina La Cantera Formation (Mohr et al. 2006; Sucerquia and Jaramillo 2007; Kunzmann et al. 2009; Prámparo 2005; Puebla 2010), and isolated northern wetter areas from those in the far south. Later Cretaceous and Paleocene elements of this tropical dry area could have continued the isolation of wet floras in the north from those of southern South America (Iglesias et al. 2011).

Maastrichtian and early Paleocene (Danian) marine transgressions flooded most Patagonian areas, including the Salado, Colorado, Neuquén, and Golfo San Jorge basins, as well as the Austral and Malvinas basins in the south (Malumián and Náñez 2011: Fig. 1). This figure (Fig. 2a) also shows the extent of marine transgressions elsewhere in South America, with a narrow zone on the eastern margin of the proto-Andes on the western side of the continent. A number of minor marginal re-entrants along the eastern Brazilian coastline are not shown.

Both in Patagonia and elsewhere in South America, it appears that the positive areas still were of relatively low relief and elevation, except for elements of the proto-Andes, which generally experienced a strong episode of tectonic activity in the preceding Campanian (Viramonte et al. 1999; Jaillard et al. 2008; Vallejo et al. 2009), although the ranges were not high enough to interfere with circulation patterns, or to produce a rain shadow, as characterizes the modern Andes (Folguera et al. 2011).

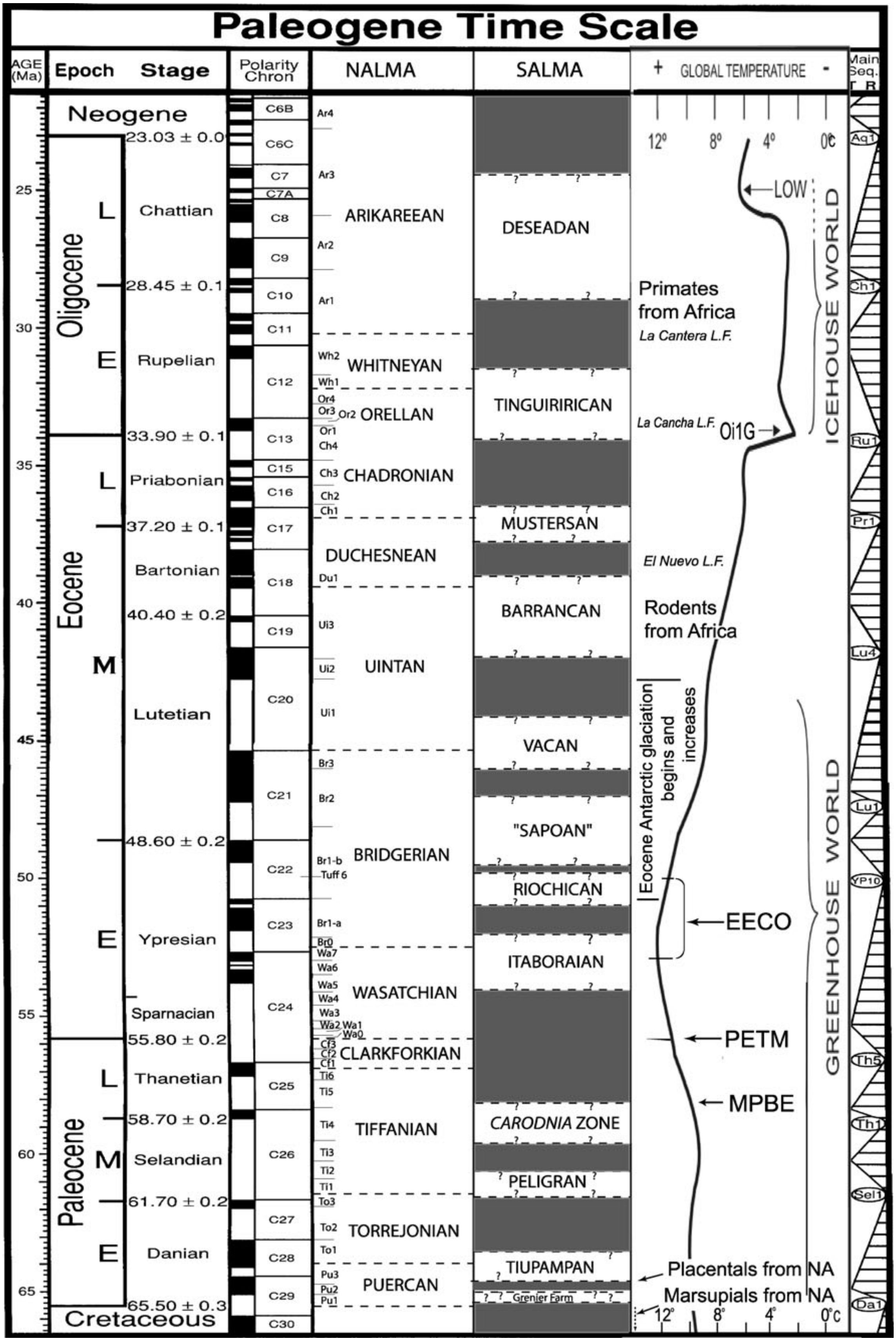
Representative Maastrichtian and Danian units in the Neuquén Basin, southern Mendoza and La Pampa provinces, include the Loncoche, Jagüel, and Roca formations (columns 1–3, Fig. 3), and the Pedro Luro Formation in the Colorado Basin to the east (Fig. 2a). In addition, the Allen and Los Alamitos formations of Río Negro Province (Colorado Basin) are important nonmarine units (columns 3, 4, Fig. 3), as are the Chubut Province Chubut Group, the La Colonia Formation, and the estuarine and littoral Lefipán and Salamanca formations in the northwestern and central parts of the Golfo San Jorge Basin to the south (Malumián and Náñez 2011; Fig. 2a; columns 5 and 7, Fig. 3).

Fig. 1 Paleogene Time Scale, showing the North American and South American Land Mammal ages. Age, Epoch, Stage and Polarity Chrons follow Luterbacher et al. (2004). Arikareean biochrons after Albright et al. (2008). Chronology of NALMAs and SALMAs is discussed in the text. The Global Temperature curve is after Zachos et al. (2001) ▶

Angiosperms exhibit a progressive diversification through the Late Cretaceous and become abundant in the Paleogene (Prámparo et al. 2007; Archangelsky et al. 2009). Cretaceous floras are strongly represented by the Proteaceae (rain forest Gondwanan elements), Nothofagaceae (southern beech), Myrtaceae (*Eucalyptus* family), Ulmaceae (elms), and Bombacacoideae (baobab tropical family) (Prámparo et al. 2007). *Nothofagus* is represented by pollen grains in the Jagüel Formation (3, Fig. 2a) in Río Negro Province (medial Maastrichtian according to Prámparo et al. (2007), but the first well-identified macrofossils of Nothofagaceae in Patagonia are from the early Danian Palacio de los Loros flora (3* [* indicates star symbol], Fig. 2b), with leaves as large as those found in present-day tropical New Guinea (Iglesias et al. 2007a). Well established pollen records and leaves having more temperate-like sizes in this family are recorded subsequently in the late Eocene of southernmost Patagonia.

Cúneo et al. (2007) discussed new Late Cretaceous megafossil floras from the Lefipán Formation, Chubut Province, Argentina (4, Fig. 2a; Figs. 3, 4, 5, 6, 7, and 8), and noted that a suite from the lower part of the formation is a diverse assemblage composed of angiosperms (including aquatic *Nelumbo* leaves and fruits) and conifers. A suite from the upper part of the formation is represented by extremely diverse angiosperms (about 70 species), as well as monocots, conifers, and ferns. The leafy flora suggests a warm climate. Previously, Baldoni and Askin (1993) indicated that the 35 angiosperm and minor gymnosperm pollen species from this unit probably represent a shrubby angiosperm-fernland vegetation with patchy wooded areas in a warm temperate, possibly subtropical, climate. The somewhat cooler, more temperate, setting as compared with other Late Cretaceous floras may reflect the presence of the adjacent highlands noted by Scasso et al. (2012).

To the east, Gandolfo and Cúneo (2005) discussed then-new *Nelumbo* (lotus) fossils from the Campanian-Maastrichtian La Colonia Formation (5, Fig. 2a; Figs. 3, 4 and 8), and indicated that today this group is typically found in subtropical to tropical aquatic settings. These La Colonia lotuses were associated with aquatic ferns as well as other angiosperms and gymnosperms, and may represent a wet lowland area (wetland) where a diverse mammal fauna also was present (Pascual et al. 2000; Albino 2000; Gasparini and De La Fuente 2000). As suggested in Figs. 3 and 4, the


Paleogene Time Scale
AGE (Ma)
Epoch
Stage
Polarity Chron
NALMA
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Main Seq.
T R
Neogene
23.03 ± 0.0
28.45 ± 0.1
33.90 ± 0.1
37.20 ± 0.1
40.40 ± 0.2
48.60 ± 0.2
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58.70 ± 0.2
61.70 ± 0.2
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Cretaceous
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C6B
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ORELLAN
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CHADRONIAN
DUCHESNEAN
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Ui3
Ui2
Ui1
UINTAN
Br3
Br2
Br1-b
Tuff 6
BRIDGERIAN
Br1-a
Br0
Wa7
Wa6
Wa5
Wa4
Wa3
Wa2
Wa1
Wa0
WASATCHIAN
Cf3
Cf2
Cf1
CLARKFORKIAN
Ti6
Ti5
Ti4
Ti3
Ti2
Ti1
TIFFANIAN
To3
To2
To1
TORREJONIAN
Pu3
Pu2
Pu1
PUERCAN
DESEADAN
TINGUIRIRICAN
MUSTERSAN
BARRANCAN
VACAN
"SAPOAN"
RIOCHICAN
ITABORAIAN
CARODNIA ZONE
PELIGRAN
TIUPAMPAN
Grenier Farm
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8°
4°
0°C
LOW
Primates from Africa
La Cantera L.F.
La Cancha L.F.
Oi1G
El Nuevo L.F.
Rodents from Africa
Eocene Antarctic glaciation begins and increases
EECO
PETM
MPBE
Placentals from NA
Marsupials from NA
ICEHOUSE WORLD
GREENHOUSE WORLD
Aq1
Ch1
Ru1
Pr1
Lu4
Lu1
YP10
Th5
Th1
Sel1
Da1

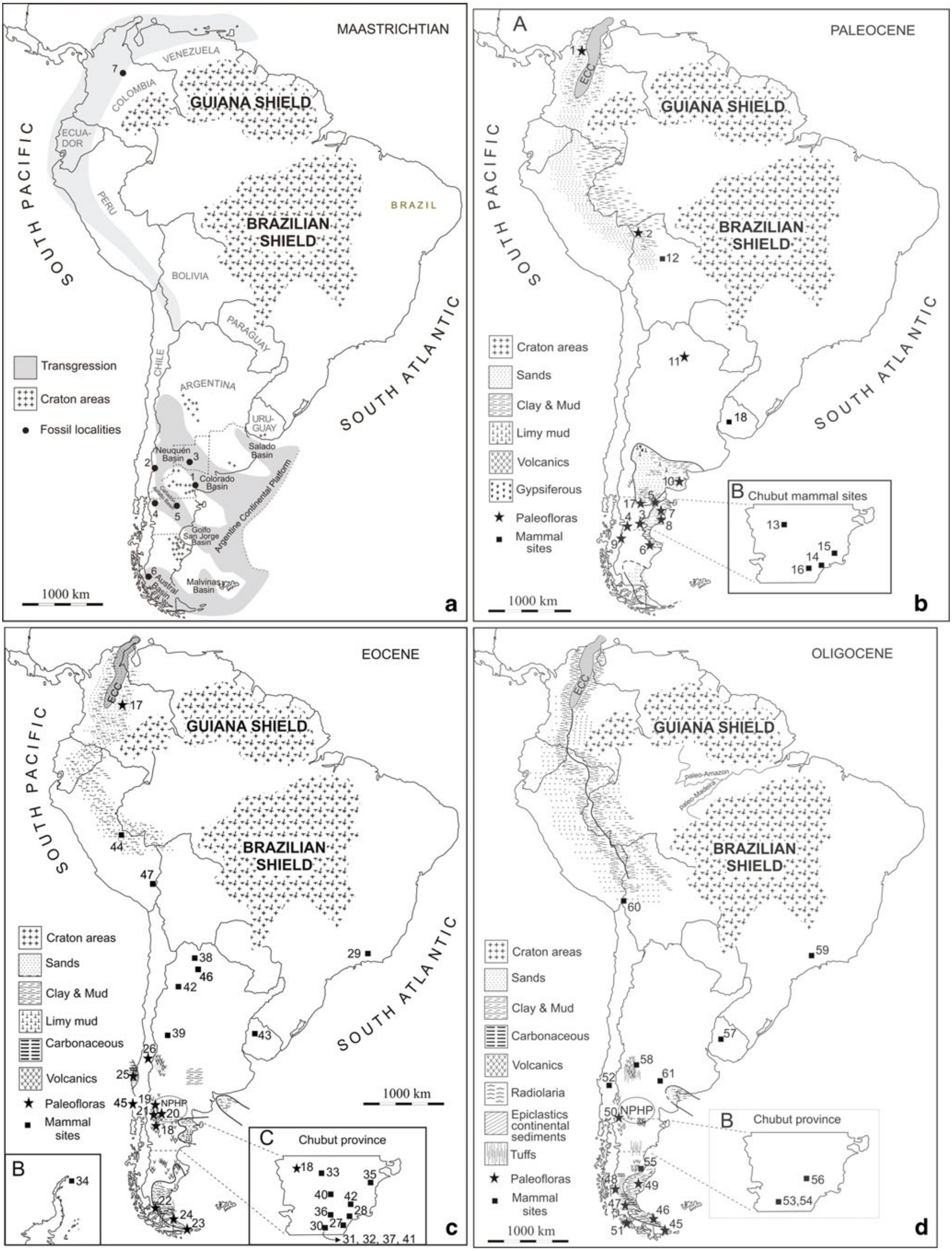
Fig. 2 Paleogeographic maps of South America showing the plant and mammal localities discussed in the text. **a** Maastrichtian transgressions for the South American continent, with emphasis on Patagonia, with named basins, Argentine provinces, and details of formation units. After Malumián and Náñez (2011: fig. 3). The dark pattern shows the major transgressions; most of the continental platform also was inundated. Crosses show positive areas. Localities discussed in the text are: 1, Los Alamitos and Allen Formation sites, Rio Negro Province; 2, Colipilli Group sites, Neuquen Province; 3, Jäguel Formation sites, La Pampa Province; 4, Lefipán Formation sites, Chubut Province; 5, La Colonia Formation sites, Chubut Province; 6, Mata Amarilla Formation (middle Cenomanian) and Calafate Formation (Maastrichtian), Santa Cruz Province. **b** Danian transgressions and Paleocene localities. After Malumián (1999: fig. 1) and Malumián and Náñez (2011). The major transgression is located in Venezuela. The other incursions in Patagonia are partly shallow marine. **Plants***: (1*) Cerrejón flora; early Paleocene; Guajira, northern Colombia; (2*) Flora Formation flora, late Paleocene; Bolivia; (3*) Palacio de los Loros flora, early Paleocene, Chubut Province. The Ormaechea Petrified Forest is about 30 km. NE of this point; (4*) Szlápelis Petrified Forest, early Paleocene, Salamanca Formation, Chubut Province; (5*) Ameghino Petrified Forest, early Paleocene, Salamanca Formation, Chubut Province; (6*) Estancia Laguna Manantiales, Salamanca Formation, Santa Cruz Province; (7*) Las Violetas Flora, Salamanca Formation; (8*) Puerto Viser and Bajo Palangana petrified forests, middle Paleocene, Peñas Coloradas Formation; (9*) Ligorio Márquez Flora, latest Paleocene, Chile; (10*) Pedro Luro Formation, core drill, Buenos Aires Province; (11*) Maíz Gordo Formation, Paleocene, Salta Province; (17*) Cerro Bororó Flora, early Danian, correlated to Salamanca Formation; (18) paleosols with calcretes, Queguay Formation, Paleocene, Uruguay. **Mammals**: (12) Tiupampa, Santa Lucía Formation, Cochabamba Department, Bolivia; Tiupampan SALMA, early Paleocene; (13) Grenier Farm, Lefipán Fm, Chubut Province; earliest Paleocene); (14) Punta Peligro, Hansen Member, Salamanca Formation, Chubut Province; Peligran SALMA, middle Paleocene; (15) Cerro Redondo (lowermost levels, Hansen Member, Salamanca Formation, Peligran SALMA, middle Paleocene; lower levels, Peñas Coloradas Fm, *Carodnia* Faunal Zone, late Paleocene; upper levels, *Ernestokokenia* Faunal Zone, Riochican SALMA, early Eocene; (16) Bajo Palangana, Chubut Province; lower fossiliferous level, Peñas Coloradas Formation, *Carodnia* Faunal Zone, middle Paleocene. **c**. Middle Eocene transgressions and Eocene localities. After Malumián (1999: fig. 2). **Plants***: (17*) Piñalerita flora; early Eocene; Colombia; (18*) Laguna del Hunco flora, early Eocene, Chubut Province; (19*) Pampa de Jones flora; early Eocene, Neuquen Province; (20*) Confluencia flora, middle Eocene, Neuquen Province; (21*) Río Pichileufú flora; middle Eocene, Río Negro Province; (22*) Río Turbio Flora, late Eocene, Santa Cruz Province; (23*) Sloggett Formation, latest Eocene, Tierra del Fuego Province; (24*) Estancia La Sara well, late Eocene, Tierra del Fuego Province; (25*) Lota Coronel and Caleta Cocholgüe floras, early Eocene, Chile; (26*) Quinamávida Flora, early Eocene, Chile. **Mammals**: (27) Bajo Palangana, Chubut Province, upper fossiliferous level, Koluel Kaike Formation, *Ernestokokenia* Faunal Zone, Riochican SALMA, early Eocene; (28) Las Flores fauna, and Peñas Coloradas flora, Las Flores Fm, Chubut Province; Itaboraian SALMA, early Eocene; (29) Itaboraí Quarry, Itaboraí Formation, Niteroi State, Brazil; Itaboraian SALMA, early Eocene; (30) Las Flores locality, Las Flores Fm, Chubut Province; Itaboraian SALMA, early Eocene; (31) Cañadón Hondo, Las Flores Fm, Chubut Province; Itaboraian SALMA, early Eocene; (32) Gran Barranca, Koluel Kaike Formation, *Ernestokokenia* Faunal Zone, Riochican SALMA, early Eocene; (33) Laguna Fría and La Barda mammal localities and Laguna del Hunco flora, near Paso del Sapo Volcanic-Pyroclastic Complex of Middle Chubut River, Chubut, Province, middle Eocene; (34) La Meseta Fauna, Seymour (Marambio) Island, Antarctic Peninsula; (35) Cerro Pan de Azúcar (basal sandstones, ?Río Chico Group; but see Tejedor et al. 2009); (36) Cañadón Vaca, Sarmiento Formation, Chubut Province; Vacan Subage, middle Eocene; (37) Gran Barranca, type "Barrancan" levels, Gran Barranca Member, Sarmiento Formation, Chubut Province; Barrancan Subage, middle Eocene; (38) Several localities in Salta and Jujuy provinces, Lumbrera Fm, ?Barrancan Subage, middle Eocene; (39) Divisadero Largo, Divisadero Largo Formation, Mendoza Province; middle Eocene); (40) Gran Hondonada, Sarmiento Formation, Chubut Province, Mustersan SALMA, middle Eocene; (41) Gran Barranca, El Rosado levels, Sarmiento Formation, Chubut Province, Mustersan SALMA, middle Eocene; (42) Antofagasta de la Sierra, Geste Formation, Catamarca Province, Mustersan SALMA, middle Eocene; (43) Paso del Cuello, Fray Bentos Fm, Santa Lucía Basin, Canelones Department, Uruguay, Deseadan SALMA, late Oligocene; (44) Santa Rosa, ?Yahuarango Formation, Ucayali Department, Perú, ?Eocene-?early Oligocene, likely Mustersan); (45*) San Pedro Formation, Valdivia Basin, Chile; middle Eocene flora; (46) Santa Bárbara subgroup-equivalent beds of Río Loro Formation, Tucuman Province, Argentina, ?early-middle Paleocene; (47) Laguna Umayo faunal sites, Puno Department, Peru, ?Itaboraian. **d**. Early Oligocene transgressions and Oligocene mammal sites. After Malumián (1999: fig. 4). **Plants***: (45*) Sloggett Formation, Tierra del Fuego Province, latest Eocene - early Oligocene; (46*) Estancia La Sara well, Tierra del Fuego Province, Oligocene; (47*) Río Guillermo, Santa Cruz Province, early Oligocene; (48*) Río Leona, Santa Cruz Province, early Oligocene; (49*) Monte León Formation, Santa Cruz Province, latest Oligocene - early Miocene; (50*) Río Foyel, Río Negro Province, latest Oligocene - early Miocene; (51*) Loreto Formation, southern Chile, latest Eocene. **Mammals**: (52) Termas del Flaco, Abanico Formation, Upper Tinguiririca Valley, central Chile; Tinguirirican SALMA, early Oligocene; (53) Gran Barranca, La Cancha locality, Vera Member, Sarmiento Fm, Chubut Province, Tinguirirican SALMA, early Oligocene; (54) Gran Barranca, La Cantera locality, Unit 3, Upper Puesto Almendra Member, Sarmiento Formation, Chubut Province, early Oligocene; (55) La Flecha, Sarmiento Formation, Santa Cruz Province, Deseadan SALMA, late Oligocene; (56) Cabeza Blanca, Sarmiento Formation, Chubut Province, Deseadan SALMA, late Oligocene; (57) Rancho Verde area, Fray Bentos Formation, Canelones Department, Uruguay, Deseadan SALMA, late Oligocene); (58) Quebrada Fiera, Agua de la Piedra Formation, Mendoza Province, Deseadan SALMA, late Oligocene; (59) Taubaté, Tremembé Formation, Sao Paulo Basin, Brazil, Deseadan SALMA, late Oligocene; (60) Salla-Luribay and Lacayani localities, Salla Beds, La Paz Department, Bolivia, Deseadan SALMA, late Oligocene); (61) Gran Salitral Formation and flora, La Pampa Province, early Eocene. Base maps used here were based on ones obtained from http://d-maps.com/index.php?lang=es

▶

La Colonia flora likely was about the same age as that from the Lefipán Formation. As indicated in Fig. 8, plant species diversity is still not known from the La Colonia site.

The Late Cretaceous floras of South America reviewed here reflect a variety of subtropical to tropical aquatic to woodland conditions and a diversity of gymnosperm and angiosperm plants as well as ferns, cycads, and conifers. Ottone (2007) examined Late Cretaceous palm pollen and trunks from the Colipilli Group, Neuquén Province (2, Fig. 2a), and noted that these and the associated trunks of diverse cycads there and in Río Negro Province (Artabe et al. 2004) indicated a frost-free, warm, and humid climate for this region at that time (75–65 Ma). This is comparable to the conditions inferred from the other floras reviewed above, although the growth rings in the Colipilli tree trunks suggest a seasonal climate.

Farther north in South America, Correa et al. (2010) reported on the late Maastrichtian (ca 68 Ma) Rhamnaceae (buckthorns) from the Guaduas Formation of Colombia (7, Fig. 2a), that lived under a MAT of 22.1±3.4 °C and a MAP of


MAASTRICHTIAN
VENEZUELA
COLOMBIA
GUIANA SHIELD
ECUA-DOR
PERU
SOUTH PACIFIC
BRAZILIAN SHIELD
BRAZIL
BOLIVIA
PARAGUAY
CHILE
ARGENTINA
URU-GUAY
SOUTH ATLANTIC
Transgression
Craton areas
Fossil localities
Neuquén Basin
Salado Basin
Colorado Basin
Argentine Continental Platform
Golfo San Jorge Basin
Austral Basin
Malvinas Basin
1000 km
1
2
3
4
5
6
7
a
A
PALEOCENE
ECC
Craton areas
Sands
Clay & Mud
Limy mud
Volcanics
Gypsiferous
Paleofloras
Mammal sites
B Chubut mammal sites
1000 km
b
EOCENE
Craton areas
Sands
Clay & Mud
Limy mud
Carbonaceous
Volcanics
Paleofloras
Mammal sites
NPHP
B
C Chubut province
31, 32, 37, 41
1000 km
c
OLIGOCENE
paleo-Amazon
paleo-Madeira
Craton areas
Sands
Clay & Mud
Carbonaceous
Volcanics
Radiolaria
Epiclastics continental sediments
Tuffs
Paleofloras
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53,54
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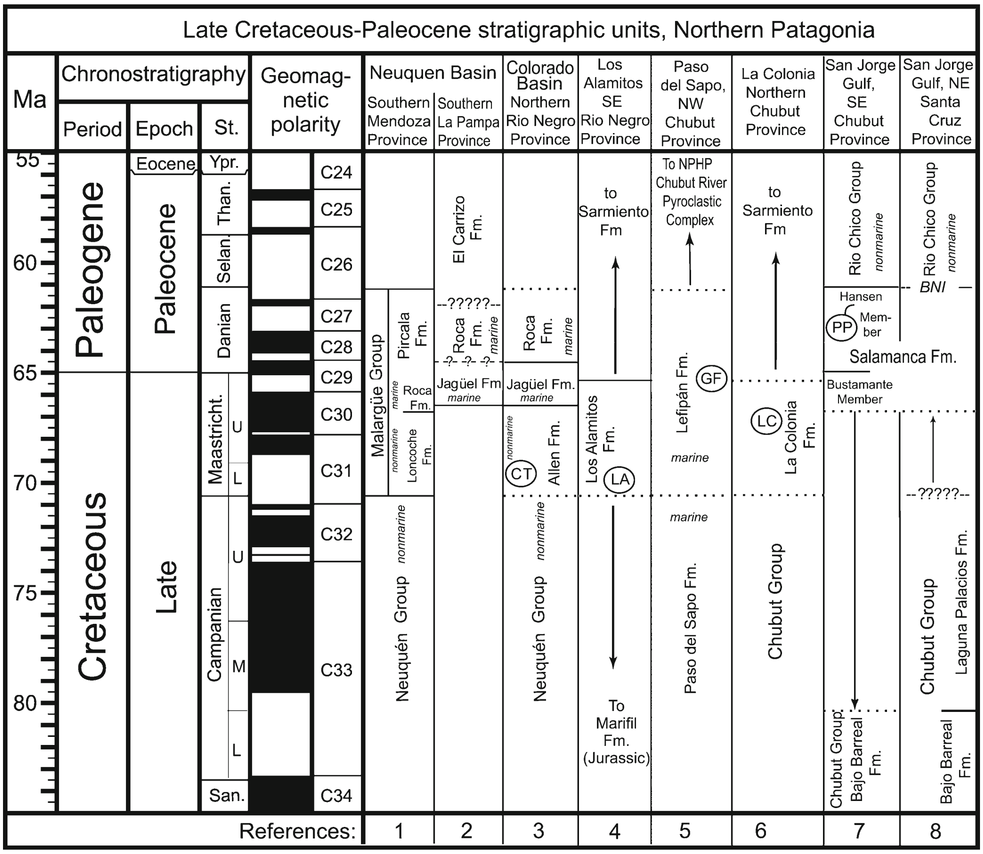


Fig. 3 Late Cretaceous to Paleocene stratigraphic units with palynofloras and fossil land mammals. References: 1. southern Mendoza Province after Parras et al. (1998), Casadio et al. (2005). 2. southern La Pampa Province, after Massabie (1995). 3. northern Río Negro Province, after Rougier et al. (2009a). CT = Cerro Tortuga mammal site. 4. Los Alamitos, southeastern Río Negro Province, after Bonaparte (1987), Spalletti et al. (1999). LA = Los Alamitos mammal site. 5. Paso del Sapo, NW Chubut Province, after Ruiz (2006). GF = Grenier Farm mammal site. 6. La Colonia, northern Chubut Province, after Pascual et al. (2000). LC = La Colonia mammal site. 7. Golfo San Jorge Basin, SE Chubut Province, after Andreis et al. (1975); Iglesias et al. (2007a); Riccardi (1988) for the age of the Bajo Barreal Formation 8. Golfo San Jorge Basin, NE Santa Cruz Province, after Hechem and Strelkov (2002, Mesozoic), Malumián (1999, Cenozoic); Riccardi (1988) for the age of the Chubut Group and formations

240 cm, but otherwise did not discuss the floral diversity there. Consistent with the MAT and MAP, the group is typically found in hot to warm tropical to subtropical lowlands.

Paleogene Floras and Climate in South America

Figure 2b shows the distribution of Paleocene sedimentary basins in South America. As for the Cretaceous, the most extensive such record is found in Patagonia, with the Maracaibo Basin of Venezuela having a landward southwesterly extension to the Eastern Cordillera region (ECC) of Colombia. Other districts in western Amazonia reflect erosion from elevated parts of the proto-Andes, as discussed by Mann et al. (2006) and Escalona and Mann (2011) regarding the geohistorical development of northern South America, with emphasis on the Maracaibo Basin in western Venezuela and adjacent districts both east and west. Parra et al. (2010) provided a tectonic context for adjacent Colombia; Hungerbühler et al. (2002) and Vallejo et al. (2009) for Ecuador; Contreras et al. (1996) and Jaillard et al. (2005, 2008) for Perú; McQuarrie et al. (2005), Horton (2005), and Garzione et al. (2006) for Bolivia; Mpodozis et al. (2005) and Arriagada et al. (2006a, b) for Chile; Carrapa et al. (2005) and Deeken et al. (2006) for northwestern Argentina; and Nullo and Combina (2011) for Patagonia in southern Argentina.

Cúneo et al. (2007) proposed that the pattern of plant extinction and recovery in South America during and subsequent to the K-Pg interval was comparable to that seen in North America, with a major early Paleocene renovation. But, as shown on Figs. 4 and 8, and discussed further below, Patagonian Paleocene floras apparently achieved renewed diversity well in advance of their North American counterparts, as recorded by the 62 Ma age, diversity and renovated composition reported by Iglesias et al. (2007a, b) for the Palacio de los Loros flora in the Salamanca Formation of Patagonia (3*, Fig. 2B; Figs. 4, 5 and 8). Figure 8 indicates that the Palacio de los Loros flora is represented by at least 40 species per fossil outcrop (as a minimum number),

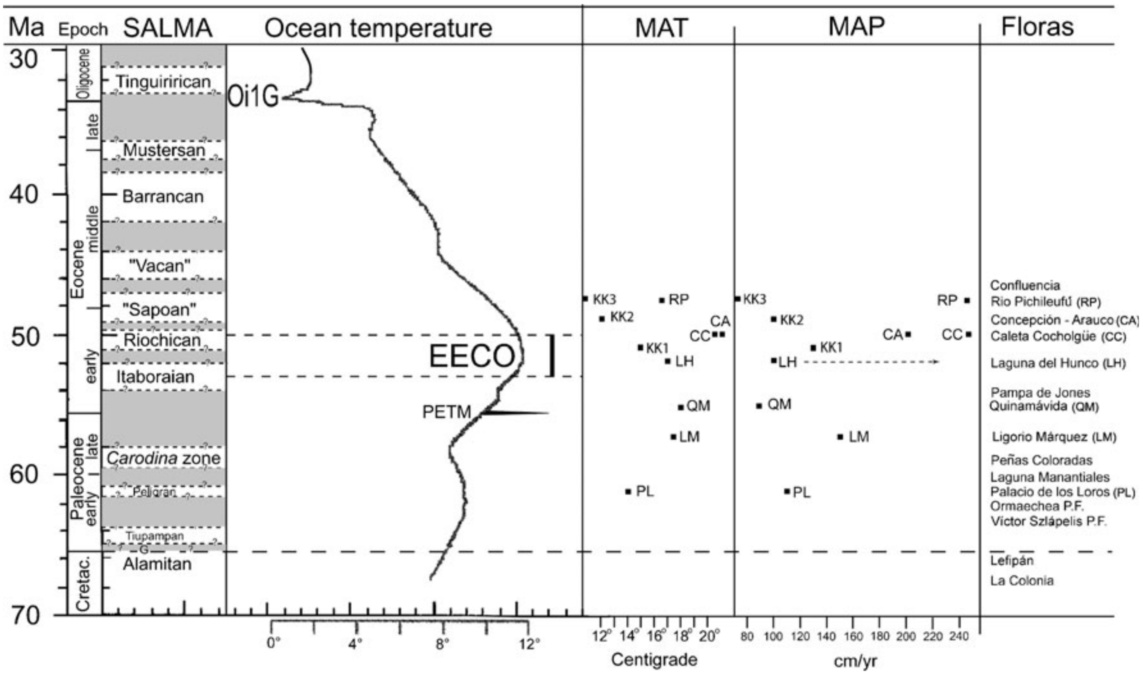


Fig. 4 Chart of SALMAs, deep ocean temperatures, MAT, MAP and South American floras discussed in the text. Ocean temperatures after Zachos et al. (2001). G in SALMA column refers to Grenier Farm site. KK1-KK3 are Koluel-Kaike Fm. paleosols after Krause et al. (2010). Rio Pichileufú and Laguna del Hunco floras after Wilf et al. (2005); Palacio de los Loros flora after Iglesias et al. (2007a)

whereas temporally comparable floras in North America have only about 30. Subsequently, the floral diversity in South America increased dramatically to 186 species in the early Eocene Laguna del Hunco flora, as compared to about 50 in North American suites, in which case the Paleocene recovery of Patagonian floras would have been outstandingly greater than recorded in North America (Iglesias et al. 2007a).

The following discussion is directed at an appraisal of the paleoclimatic setting for Paleocene and Eocene land mammals derived from a consideration of contemporaneous paleofloras in South America, with especial focus on those of Patagonia where the record of both groups is best developed, although the Neotropical paleofloras are also assessed as representing the basic floral background for the continent.

In addition to floral diversity, it has proven useful to compare floras regarding the MAT and MAP inferred from their foliar morphology. Recently, Little et al. (2010) have raised questions regarding the methodology commonly used in deriving such estimates, although Spicer and Yang (2010) have offered reasons in support of MAT and MAP calculations. Whereas the record for such analyses in North America is represented by a relatively large number of fossil floras in a well-developed chronologic framework (Woodburne et al. 2009a, b), and therefore might be internally consistent (Little et al. 2010), this is not yet the case in South America. As shown in Fig. 8, the three Patagonian floras that have been assessed regarding MAT and MAP occur within a span of about 20 m.y. (Palacio de los Loros, ca 62 Ma; Laguna del Hunco, ca 52 Ma; Río Pichileufú, ca 47 Ma), and provide only a general framework of climate change during this time. Fortunately others, from Chile (Quinamávida, Concepción-Arauco, and Caleta Cocholgüe) and more northern Argentina (Gran Salitral), help fill in the pattern. Whereas these estimates are helpful, further consideration of the important South American floras can be realized by invoking a more general characterization, such as tropical, humid, and the like, without reliance on MAT and MAP values. In fact, MAP derived from fossil leaves should be treated as a minimum value for a paleoflora (Wilf et al. 1998), and precise taxonomic identifications at the generic and specific levels should be taken as yielding better precipitation estimates, as based on modern relatives (Wilf et al. 2009).

Neotropics

The discussion begins with the Neotropical record in that floras there were already well developed in the early Paleocene, and form a background to which more southern floras may be compared. The concept of the Neotropical Region used here follows Morrone (2002, 2006), which included most of Central and South

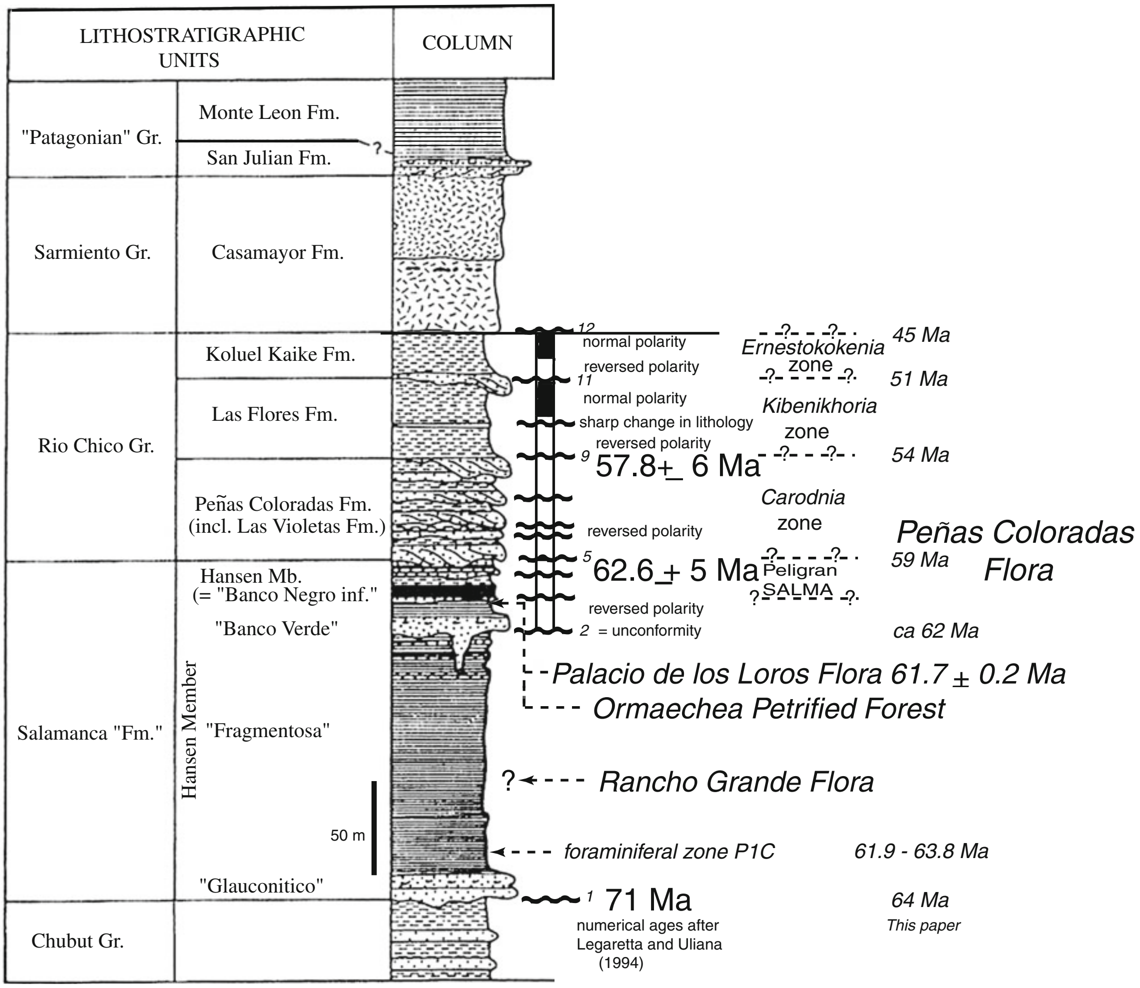


Fig. 5 Paleogene stratigraphic units of the Golfo San Jorge Basin, Patagonia, after Bond et al. (1995). The magnetostratigraphic profile given in Marshall et al. (1981: fig. 2) is shown in relation to unconformities shown or inferred from the indicated lithologic relationships. Legarreta and Uliana (1994: fig. 3) inferred numerical ages for these units based on an interpretation of the sea level fluctuation history for these strata. In that example, the base of the Salamanca Formation was interpreted as 71 Ma, rather than 64 Ma as shown here (right hand numbers). The unconformity 2 at the base of the Banco Verde (sediment-filled fissures) was interpreted as 63 Ma; the top of the Hansen Mbr. (vitreous tuff) dated at 62.6 Ma (between unconformities 2 and 5, after Andreis, 1977). This is now considered as 62 Ma after Iglesias et al. (2007a). The Palacio de los Loros Flora date is after Iglesias et al. (2007a) as is the 57.8 ± 6 Ma age near unconformity 9. The foraminiferal zone P1C age (61.9–63.8 Ma) is after Luterbacher et al. (2004). The base of the Peñas Coloradas Formation was interpreted as 60 Ma (unconformity 5; about 59 Ma here); the basal conglomeratic sandstone of the Koluel Kaike Formation was interpreted as 57 Ma (unconformity 11; about 51 Ma here; see text); the base of the Casamayor Formation is interpreted as 55 Ma (unconformity 12; about 45 Ma here)

America, with the exception of its southernmost part (the Andean Region, including Patagonia and the southern Andes), as well as a narrow strip of the Andean Range up to the low latitudes of Colombia. This strip is regarded by Morrone (2006) as a transitional zone of mixed biotas between both regions.

Jaramillo et al. (2006) noted that the South American Neotropics have the highest plant diversity in the world. Their study is based on a high-resolution pollen and core record from Paleogene to early Neogene of Colombia and western Venezuela that shows tropical plant diversity generally following long-term global climatic changes. The data are derived from well cores in which the sediments range from Campanian (80 Ma) to medial Miocene (16 Ma) and encompass fluvial to coastal plain environments.

As indicated in Fig. 8, the pattern of standing diversity is considered to have been relatively low in the early Paleocene (about 200 morphospecies). This is followed by an increase to about 300 morphospecies in the late Paleocene, and a drop at the end of that time (to about 250 morphospecies). Diversity then steadily increased during the Eocene toward a mid-Eocene peak (nearly 350 morphospecies). Diversity then declined during the middle and late Eocene, with a sharp drop at the Eocene - Oligocene boundary.

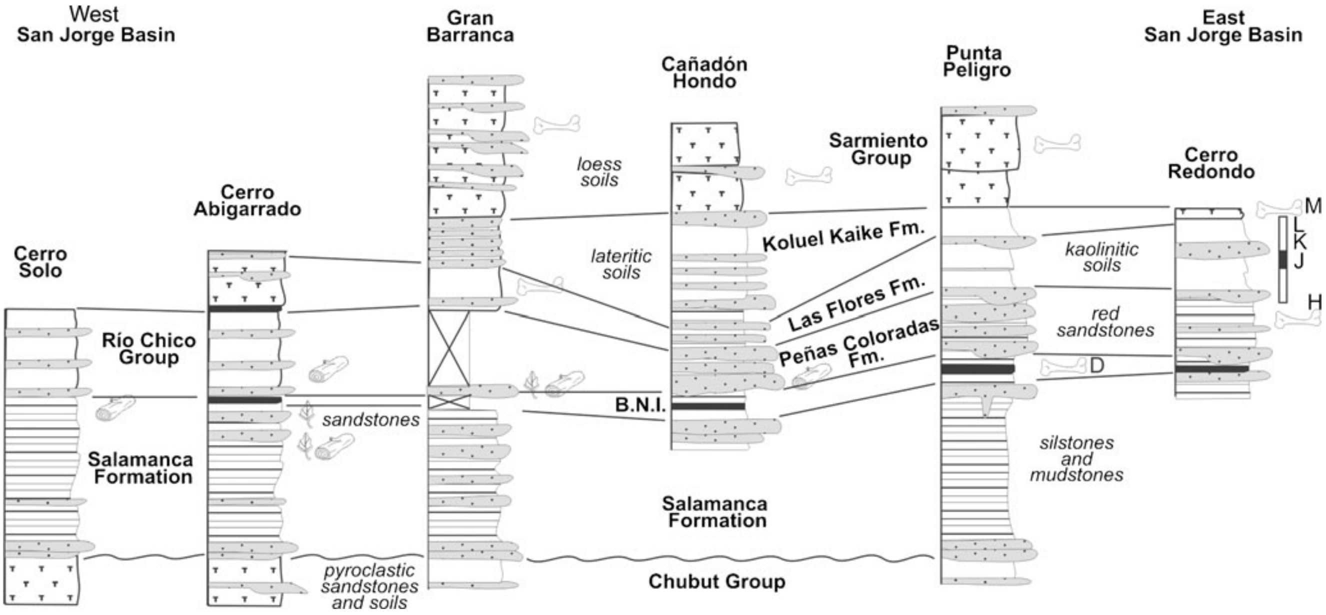


Fig. 6 Stratigraphic relationships of Upper Cretaceous and Paleogene strata in the Golfo San Jorge Basin of Patagonia (Fig. 2A). Geological sections at Cerro Solo, Cerro Abigarrado, Gran Barranca, Cañadon Hondo, and Punta Peligro after Feruglio (1949) and Raigemborn et al. (2010). The sequence at Cerro Redondo is from Simpson (1935) with the approximate locations for normal magnetic intervals after Marshall et al. (1981). The strata of the Peñas Coloradas Formation and that part of the Las Flores Formation below the normal magnetozone in unit J are of reversed polarity. Strata of unit K and the lower part of unit L in the Koluel Kaike Formation also are of reversed polarity. The D mammal horizon reflects the location of the Peligran SALMA. The H mammal horizon represents the location of the *Carodnia* Zone. The Upper Mammals horizon M is the location of the *Ernestokokenia* Faunal Zone

Jaramillo et al. (2006: fig. 2a) also showed a stable diversity during the Oligocene, with a slight fall toward the early Miocene. Overall, the Paleocene flora was of generally low diversity; the early to mid-Eocene flora was more diverse; that of the later Eocene and Oligocene was less diverse but more so than in the Paleocene.

During the same Paleogene interval, Jaramillo et al. (2006) indicated that extinction rates were relatively uniform, with a moderate increase in the late Paleocene and during the Eocene-Oligocene transition. Origination rates generally decreased slightly over the entire interval, but showed a somewhat higher rate that mirrored extinctions in the late Paleocene and early Eocene. Originations continued to decline in the later Eocene and Oligocene, comparable to extinctions. This is consistent with the overall diversity decrease seen in this part of the time scale (Fig. 8).

Jaramillo et al. (2006) also showed a relatively strong floral turnover at the end of the Paleocene, as well as at the beginning of the Oligocene Oi-1 glaciation. Overall, the pattern of palynological diversity followed the general increase in global temperature from the early Paleocene to the EECO, although the floral pattern is slightly offset from (later than) the temperature trend (Fig. 8). The long drop in temperature from the EECO to the early Oligocene also is generally paralleled by a somewhat later and more gradual pattern of diminished floral diversity in the Neotropics, including the sharp drop in both temperature and floral diversity at the Eocene-Oligocene boundary.

Whereas change in global temperature appears to have been the major factor reflected in the floral diversity pattern, it also is possible that there was an areal component (Jaramillo et al. 2006). In that context, global warming likely also expanded the area that experienced increased temperatures, as well as precipitation (Jaramillo and Dilcher 2000; Jaramillo 2002), with a positive effect on speciation. As indicated by Wilf et al. (2005), the northern Patagonian Laguna del Hunco (18*, Fig. 2c) and Río Pichileufú floras (21*, Figs. 2c and 8) were very diverse and located in a wet and warm tropical region. It is possible that the greater areal extent of wet tropical conditions provided an enlarged platform for speciation, and contributed to diversity increases into the middle Eocene. Subsequent cooling would not only have promoted a decline in plant diversity in and of itself, but the areal restriction of tropical conditions likely was an important factor, as well.

A late Paleocene megafossil flora (ca 58 Ma) is known from the Cerrejón Formation (1*, Figs. 2b and 8) of Guajira, northern Colombia (Jaramillo et al. 2007; Doria et al. 2008; Herrera et al. 2008, 2011; Gómez-Navarro et al. 2009; Wing et al. 2010). It contains a

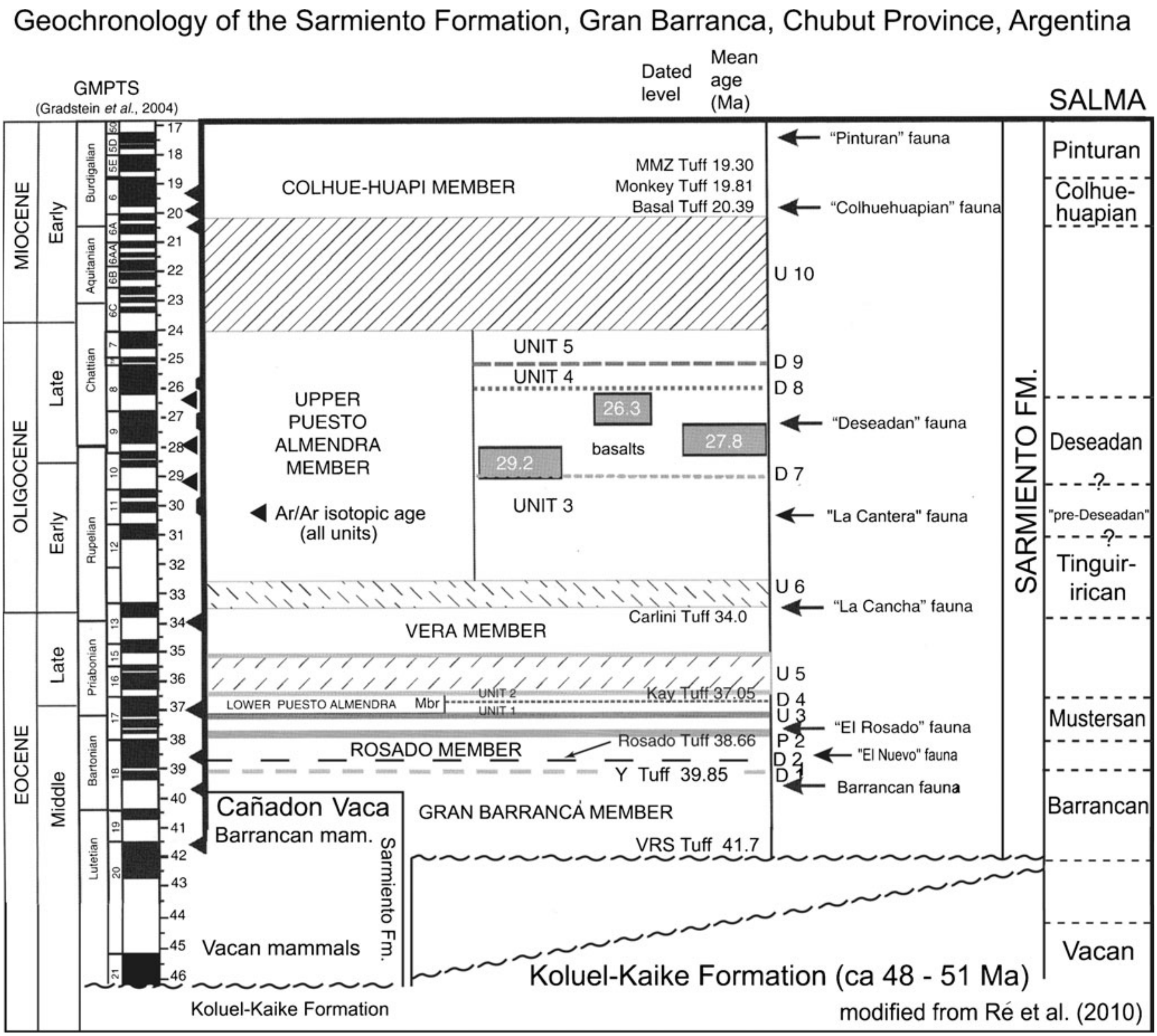


Fig. 7 Stratigraphic and geochronologic distribution of elements of the Sarmiento Formation in the Gran Barranca, with ranges of indicated SALMAs, after Ré et al. (2010a: fig. 4.1). Changes relative to Ré et al. (2010a: fig. 4.1) include adding SALMA intervals, locating the Ar/Ar arrowheads to the age indicated by the basalts they represent in upper unit 3 of the Upper Puesto Almendra Member; lowering the age of the "La Cantera" fauna to agree with the text; insert the "El Nuevo" fauna and D2 disconformity as indicated; adding an arrow relative to the "El Rosado" Tuff to indicate its chronologic location; adding the VRS Tuff at its chronological location; revising the basal contact of the Sarmiento Formation to agree with the discussion in the text. The numerical ages for the Koluel Kaike Formation are as in the text, modified from Krause et al. (2010). The Cañadón Vaca sequence is indicated to illustrate the age and faunal content of the Sarmiento Formation at that location in contrast to the Gran Barranca (after Cifelli 1985), and to demonstrate the extent of the unconformable contact between the Sarmiento and Koluel Kaike formations at Gran Barranca

diverse suite of tropical palms and legumes reflective of coastal river and mangrove swamp-lake environments. Doria et al. (2008) indicated that Neotropical rain forests have a unique combination of high plant species diversity, a distinct floristic composition, and a multistory forest structure. Wing et al. (2010) noted that the diversity and relative abundance of Cerrejón plant families are similar to those of modern Neotropical rain forests. At about 58 Ma, the Cerrejón Formation plants are the oldest Neotropical megafossil flora yet recovered, both in terms of its geography as well as its floral characteristics. The Late Cretaceous Guaduas Formation flora of Colombia may obtain this position when more fully described.

Cerrejón plants include leaves of 46 non-monocot angiosperms, 13 monocots, five ferns, and one conifer,

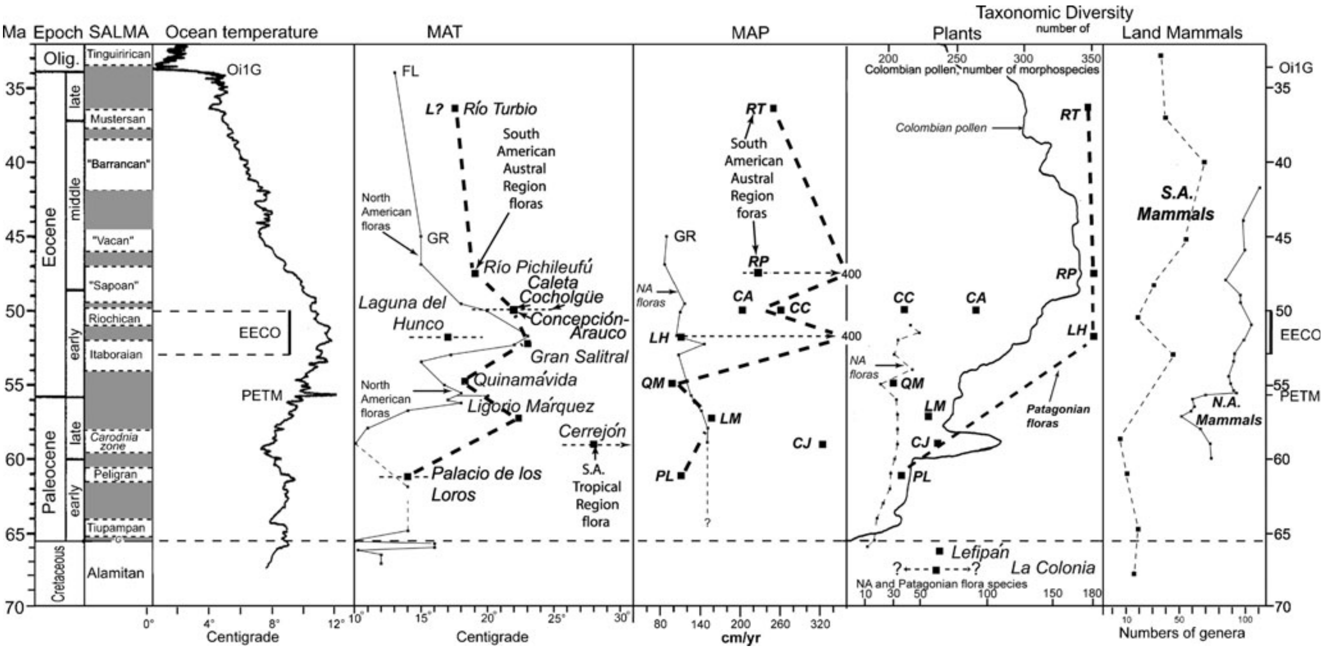


Fig. 8 Chart of Paleogene oceanic temperatures, MAT and MAP of North American and selected South American megafloras, taxonomic diversity of North American megafossil plants and Neotropical pollen, as well as North American and South American mammals. Global time scale after Luterbacher et al. (2004); deep sea ocean temperatures after Zachos et al. (2001), North American MAT and MAP record after Woodburne et al. (2009a). MAT and MAP record for South American megafossil floras after Wilf et al. (2005), Iglesias et al. (2007a), and Hinojosa et al. (2006). Taxonomic diversity: Colombian pollen from Jaramillo et al. (2007). North American floras after Wing (1998) and Wing et al. (1995); South American floras from Wilf et al. 2005; Iglesias et al. (2007a). Mammal diversity for North America after Woodburne et al. (2009b). South America, this paper. Note that although the diversity pattern for Colombian pollen physically crosses that for North American floras, the numerical scale higher in the figure indicates that at the beginning of the Paleocene, Colombian pollen represented about 175 taxa as compared to about 20 for North American megafloras. Megafloral diversity for the Correjón flora likely exceeded that indicated by the dashed line for Patagonian floras. Heavy dashed line indicates MAT and MAP for South American Austral Region floras as distinct from the Tropical Region Cerrejón flora

along with 33 kinds of compressed fruits and seeds. This suggests a diversity of at least 65 taxa, but that figure likely is conservative. The Cerrejón flora plots along the line that represents a conservative estimate of Paleocene Patagonian taxonomic diversity on Fig. 8 but, with likely greater ultimate diversity, it seems to potentially reflect the coeval pollen diversity pulse for floras from the same area in Colombia.

The most abundant and diverse plant orders are: Araceae (6–7 leaf types), Arecaceae (2 leaf, 3 fruit); Fabaceae (5–7 leaves; 7 fruit); Lauraceae (2 leaf); Malvaceae (2–4 leaf); Menispermaceae (4 leaves, 11 fruits); and Zingiberales (2 leaf). Sub-familial level taxa include *Montrichardia* (Neotropical aquatic aroid monocot), *Stephania* (Australian menispermaceaean liana), *Palaeoluna* (fossil Menispermaceae), and two palms: Euterpeinae and the hydrophylous *Nypa*. Four rare ferns are the pantropical, floating-aquatic *Salvinia*; an Old World tropical swamp climber *Stenochlaena*; the cosmopolitan *Lygodium*; and the pantropical freshwater mangrove swamp fern, *Acrostichum*. The Menispermaceae is a pantropical angiosperm family, with its predominantly climbing habit indicating that the multistory structure of tropical rain forests had been established by the time of the Cerrejón flora (Doria et al. 2008; Herrera et al. 2011). Early members of this family (*Palaeoluna*) reflected trans-Caribbean Paleocene connections between Colombia and Wyoming, in North America. The Cerrejón genus, *Stephania*, is a possible precursor of modern Australian members (Herrera et al. 2011), but this dispersal scenario is hindered by the lack of information regarding fossil occurrences of the group in India and southeastern Asia, as well as Australia.

Modern Araceae (aroids, including the arum lily; Heywood 1993) are one of the most diverse monocotyledenous plant families, and are most diverse in the modern tropics. The group ranges from the Late Cretaceous (Campanian) of Holarctica as well as the Maastrichtian of India and South America, the early Paleogene of Holarctica and northern South America, to the Recent.

Wing et al. (2010) calculated that MAT was about 28 °C (tropical), comparable to that estimated from large-bodied fossil snakes from the same unit (32°–33 °C; Head et al. 2009: fig. 8). Subsequently, MATs about 30 °C likely were experienced by the Neotropics in the early Eocene when global climates increased substantially. The Cerrejón MAP likely was at least 324 cm (Fig. 8; considered an underestimate), and plant morphology is compatible with that value and those above.

With respect to other Paleocene South American floras, the Cerrejón floral diversity appears to be significantly greater than that of the Patagonian Palacio de los Loros flora from the Paleocene (ca 62 Ma), but only 80 % of that seen in modern tropical litter samples and 60 % of the highly diverse Paleocene Castle Rock Flora of Colorado, in North America. Wing et al. (2010) also indicated that PIE values (a measure of taxon evenness) are not different from those of modern tropical forest litter, the Palacio de los Loros flora, or Castle Rock, but are strongly higher than those of most Paleocene-Eocene North American sites. This continues to reflect the greater floral diversity of South American Paleogene floras as compared to those from North America.

Cerrejón pollen samples (Jaramillo et al. 2007) show mean rarified richness about 66 % of that seen in Quaternary Amazonian samples; mean evenness is 85 % of that of Quaternary tropical forest samples. Insect predation was 50 % of specimens seen; greater than mid latitude Paleocene floras, but is comparable to that of modern Neotropical forests.

Overall, the Cerrejón flora shows that the basic plant components characteristic of modern Neotropical floras were present in the late Paleocene, with somewhat reduced levels of insect herbivory and lesser plant leaf and pollen diversity than at present. In that context both the megafossil and pollen data reinforce the interpretation that Neotropical floras were well established as such by the Paleocene in South America. As discussed below, coeval floras from Patagonia were more like their Neotropical counterparts than obtains as the present time, but still of a subtropical character.

The Bolivian Flora Formation (Vajda-Santiváñez 1999) is considered to be Danian age (Vajda-Santiváñez and McLoughlin 2005). The flora (2*, Fig. 2b) consists almost entirely of angiosperm pollen grains, in which those of *Aquillapollenites* are conspicuously absent. Vajda-Santiváñez and McLoughlin (2005) reported on an extensive record of the fern, *Azolla*, from this and the underlying Eslabón Formation (Maastrichtian). The Flora Formation is largely lacustrine in origin. The microspore assemblages, and particularly the abundant pollen of palms, as well as ferns, are suggestive of a tropical, warm and humid, climate.

The above data suggest that the basic character, structure, and framework of diversity of Neotropical floras was strongly under way by the Paleocene in northern South America and, although the episodically rising Andes certainly influenced the floras in those regions, the overall character and climatic setting of Neotropical floras was maintained to the present day.

Andean Region

As indicated in Biogeographical terminology (above), this refers to the austral part of South America: Patagonia and Chile south of about 38°S. As shown in Fig. 2a–d, most Patagonian fossil localities were found in lowland coastal areas with fluvial, lacustrine, and swamp environments. The Paleocene and Eocene floral climatic conditions in the Andean region are presently best represented by paleofloras found in the Golfo San Jorge Basin in eastern Patagonia and adjacent areas. The floras and associated mineralogical data suggest that early Paleocene climate reflected warm temperate conditions dominated by podocarpacean and auraucariacean trees, with many angiosperms of warm-temperate affinity. These included many types of palms (including the mangrove, *Nypa*), along with Myrtaceae (*Eucalyptus* family), Pandanaceae (mangrove trees), and Olacaceae (*Anacolosa*). Groups of Gondwanan affinity include the Proteaceae (trees), Cuoniaceae (subantarctic shrubs and trees), and Elaeocarpaceae (tropical trees), along with a few northern elements such as Ulmaceae (elms) (Petriella 1972; Archangelsky 1973; Palazzesi and Barreda 2007). Based on clay mineralogy of paleosols, an episode of increased seasonality is recorded in the late Paleocene. Thus, the Paleocene-Eocene transition changed from a warm-temperate and humid climate with seasonal precipitation to a wetter subtropical climate with year-around rainfall (Raigemborn et al. 2009). Subsequently, this relatively uniform early and middle Eocene climate led to cooler and drier conditions in the late Eocene and early Oligocene (Barreda and Palazzesi 2007). From then until the middle Miocene, it appears that semi-arid to arid conditions generally dominated northern Chile (Pinto et al. 2004; Le Roux 2012). In addition, studies on lacustrine sediments in the Potosi Basin of Bolivia (Rouchy et al. 1993) indicate that the area was situated in the intertropical convergence zone during the Paleocene, where arid conditions prevailed after a more humid interval in the Maastrichtian (Le Roux 2012). These conditions appear to coincide with the generally arid region postulated to intervene between the more tropical conditions found in the Neotropical and Austral regions during the Late Cretaceous and Paleogene (Iglesias et al. 2011). The more tropical and wetter conditions would have been found north of the Guiana Shield and south of Paraguay on Fig. 2a and b. Intervening areas would have been more arid, but data are scarce.

A number of floral samples have been obtained from the mostly marine to estuarine Salamanca Formation of late Danian age (Fig. 3); many of the Salamanca floras cannot be distinguished chronologically, but they show paleobiogeographic differences within the basin. The Ameghino Petrified Forest, located in the northwestern part of the Golfo San Jorge Basin (5*, Fig. 2b), was dominated by evergreen coniferous forests, with angiosperms and diverse palms also present. Conifers (*Podocarpoxylon mazonii*) are estimated to have been 17–29 m tall, and show regular growth rings indicative of a yearly regular (not seasonal) climate (Brea et al. 2011). This would be consistent with the warm off-shore sea water temperatures recorded in the uppermost Cretaceous-lowermost Danian Bustamante Member of the lower part of the Salamanca Formation (Andreis et al. 1975).

The Cerro Bororó flora (17*, Fig. 2b) is also preserved in a similarly northwestern part of the basin, in the Bororó Formation, considered (Scafati et al. 2009) as contemporaneous with the Salamanca Formation. The flora consists of spores and pollen of bryophytes, ferns, and angiosperms, including *Nypa* (mangrove palm; as well as other palms), Araceae (aroids), Sparganiaceae/Typhaceae (bulrush, cattails) that, together with fossil wood of the Rhyzophoraceae (mangrove trees), Elaeocarpaceae (clinodendrons), Cunoniaceae (lightwood), as well as Cycadales (cycads), indicate a lowland mangrove-swamp environment in the vicinity of a marine embayment (Petriella 1972; Scafati et al. 2009). The Sparganiaceae, *Nypa* palms, the extreme diversity in palm pollen, and the presence of other thermophilous taxa also indicate a warm, humid, subtropical-tropical climate for this region.

Salamanca Formation floras also are recorded in the Victor Szlápelis Petrified Forest, and the Ormaechea Petrified Forest (3* and 4*, Fig. 2b). In the former (Brea et al. 2005), podocarp tree trunks are >1 m in diameter, which, along with associated angiosperms, show growth rings that indicate a warm-temperate, humid, seasonal climate. The setting evokes a flora likely similar to that of present-day southeastern Brazil, with savannas in a subtropical, humid climate with markedly seasonal rains. The presence of palms also suggests winter temperatures above 10 °C. This is consistent with the presence of crocodilians in these Salamanca beds at the same latitude, but farther east along the present coast.

Pollen from the Estancia Laguna Manantiales are found somewhat farther south (6*, Fig. 2b), in Santa Cruz Province, but still within southern part of the Golfo San Jorge Gulf. The floras are from the southernmost outcrops of the Banco Negro Inferior (Zamaloa and Andreis 1995), and on that basis they are here considered to be stratigraphically comparable to the Palacio de los Loros Flora (PL, Fig. 4). In addition to a minor component of ferns, podocarp gymnosperms are next most abundant group. Angiosperm pollen predominates over all others in both abundance and diversity. Nevertheless, the flora is sparsely documented. As elsewhere, the material was deposited in fresh water to swampy environments.

The Palacio de los Loros flora, southern Chubut Province (3*, Fig. 2b; Figs. 4 and 5) was recovered (Iglesias et al. 2007a) from the Salamanca Formation of about middle Paleocene age (ca 62 Ma, about equivalent to the Danian/Selandian boundary; Fig. 1). The Salamanca Formation unconformably overlies (column 7, Fig. 3) the Bajo Barreal Formation (Chubut Group; Riccardi 1988; Data Repository in Iglesias et al. 2007a), and is unconformably overlain by the continental Río Chico Formation (Fig. 3). Based on Iglesias et al. (2007a), the Palacio de los Loros flora correlates as shown in Figs. 4, 5, and 8, and is about coeval with the Peligran SALMA, as also noted by Iglesias et al. (2007a, Data Repository) and Raigemborn et al. (2010).

The Palacio de los Loros assemblage is diverse and richly populated taxonomically. The 36 angiosperm leaf species correspond to a large-leafed *Nothofagus* (southern beech), Menispermaceae (moonseed), Akaniaceae (also known in the Australian rain forest as well as in the early Eocene of Patagonia (Romero and Hickey 1976), Lauraceae (laurels), Urticaceae (nettles), Fabaceae (being one of the oldest records of this legume family), Sapindaceae (litchee), palmate-lobed Malvaceae, and Rosaceaae. The presence of the oldest record of Fabaceae (legume family) is notorious for this site (Brea et al. 2008a), and a new rich food source for animals. Conifers also are associated with the angiosperms, which are represented by flowers, fruits, and seeds as well as leaves. The conifers include Auracariaceae (cone scales) and Podocarpaceae (leaves and cones), along with at least two species of fern, including *Lygodium*. Taxa such as *Nothofagus*, *Akania*, and the conifers indicate a Gondwanan affinity. Furthermore, the leaf diversity of angiosperms recovered at the single Palacio de los Loros floral site exceeds the diversity known in most other comparable floras in the world, with the exception of those from wet tropical climates. Yet, the diversity may be still higher due to the extremely conservative leaf taxonomy employed (Wilf et al. 2005).

Leaf analysis suggests that the flora lived under a MAT of about 14 °C (subtropical), with a MAP of at least 115 cm/year in the absence of an Andean rain shadow. Brea et al. (2008a) considered the Palacio de los Loros to have been a mesothermal flora that reflected a warm temperate climate and strongly seasonal precipitation. The associated remains of thermophilic palms found throughout the exposures are compatible with this climatic setting, as is the presence of alligatorid reptiles (Bona 2005). The large-sized *Nothofagus* leaves are indicative of warm, humid conditions (Iglesias et al. 2011), and a frost-free climate also is supported by modern podocarps inhabiting only high-rainfall environments and *Akania* living today only in eastern Australian tropical rain forests.

Analysis of alpha diversity of angiosperm leaves shows that the Palacio de los Loros flora (Fig. 8; see *PL* under Taxonomic Diversity); greatly exceeds the diversity of contemporaneous floras in North America on the one hand, but is less diverse than Patagonian floras of Eocene age (heavy dashed line, Fig. 8). Still, Wilf et al. (2005) considered the Palacio de los Loros diversity to be conservative and that the actual figure approached the diversity seen at Laguna del Hunco. The relative, but not yet fully established, diversity pattern (increasing with younger geologic age) is comparable to the situation seen in North America (Fig. 8). At the same time, there is a sharp break in taxonomic continuity from the Paleocene to the Eocene floras in Patagonia suggesting that a number of turnover events took place in the interim. Notably, the Paleocene Patagonian floras show a much greater continuity with those of Late Cretaceous age than is the case for North America. The cause of this earlier diversity is not known, but its effect continued subsequently in South American floras up to the present time.

The late Paleocene floras from the Peñas Coloradas and Las Flores formations of the Golfo San Jorge Gulf Basin (8*, Fig. 2b) are represented by phytoliths in addition to fossil wood and other plant remains (Raigemborn et al. 2009). The Peñas Coloradas flora (Figs. 4, 5, and 8) is composed of podocarp conifers and angiosperms. The latter are represented by the Cunoniaceae (trees and shrubs), along with the Styracaceae (modern tropical trees, silverbell, snowbell), Chrysobalanceae (tropical and subtropical trees), and Araliaceae (tropical - temperate ivy and other shrubs). The herbaceous component appears to be represented mainly by the Zingiberales (ginger family) and the Poaceae (grasses). Such plants populated mixed temperate to subtropical forests that lived under warm and humid conditions. Associated clay mineralogy indicates a strongly seasonal climate for this late Paleocene flora.

A late Paleocene flora of a more western and potentially higher elevation location is represented by the Ligorio Márquez flora of eastern central Chile (9*, Fig. 2b), about 300 km southwest of the Peñas Coloradas Formation, and almost immediately west of the Chile - Argentina border at 46°45’S. As discussed by Suárez et al. (2000), the Ligorio Márquez Formation unconformably overlies the Flamencos Tuffs of Lower Cretaceous age [128±3 Ma; 125±3 Ma; 123 ±3 Ma], and is overlain unconformably by ?early or mid-late Eocene basalts or the coeval San José Formation. The unconformably overlying basalts have been dated via K-Ar at 47.6±0.78 Ma (Yabe et al. 2006) based on feldspar crystals in the basalt. Whole-rock ages from sites to the north yielded an age of 57±1–44±5 Ma (Suárez et al. 2000); these authors also obtained a whole rock age of 41.6±1.4 Ma from a site immediately above the the Ligorio Márquez Formation Whether or not there are two basalt units above the the Ligorio Márquez remains to be determined (Yabe et al. 2006). In any case, the basalts provide an upper limit for the Ligorio Márquez flora, which is likely to be of late Paleocene or possibly earliest Eocene age. The pulse in MAT and MAP (Fig. 8) could be compatible with correlation to the PETM.

Plant remains obtained from near the middle of the unit in its measured section (44 m, but stratigraphically incomplete), include Podocarpaceae (*Podocarpus inopinatus*), eight species of Lauraceae, and one of the Melastomataceae (Troncoso et al. 2002). The diversity of the Lauraceae is best compared with the late Paleocene Concepción-Arauco paleoflora, which indicates a wet subtropical setting (also Gayó et al. 2005).

The flora is consistent with a late Paleocene age for the Ligorio Márquez Formation. A small pollen sample of *Nothofagidites* was taken from near the top the unit, which would imply a cooler climate than suggested by the macroflora, although this could be accounted for by relating it to a short cool interval that apparently is recorded in the early late Paleocene, about 61 Ma (Dingle et al. 1998; Dingle and Lavelle 1998), as suggested by Suárez et al. (2000). In addition, Zachos et al. (2001) showed short-lived cool episodes just before and after the PETM, one somewhat younger than 56 Ma, and the other at about 54 Ma, which also could fit the temporal intervals discussed here. Alternatively, Iglesias et al. (2007a) indicated that Paleocene leaf records of Nothofagaceae can be associated with warm-temperate forests. Hinojosa et al. (2006) interpreted the Ligorio Márquez flora as indicating subtropical, frost-free, and humid conditions, with a MAP of 155 cm and MAT of 23 °C. Peppe et al. (2011), however, considered these analyses to be overestimated.

From the preceding discussion, it appears that the Paleocene floras of Patagonia were largely preserved in lowland, coastal, settings. They were generally dominated by podocarp and araucarian conifer forests that lived under warm, humid, and at least subtropical climates; in lowlands typically of mangrove swamps and woodlands. Some of the floras record a seasonal climate, but others do not.

As indicated in Fig. 4, the Eocene floral record in Patagonia begins with the Pampa de Jones flora, discussed further below. In the Golfo San Jorge Basin, the Las Flores Formation, located about 40 km NE of 3* (Fig. 2b), contains a range of phytoliths, wood, and other materials comparable to that of the Peñas Coloradas. Associated fossil mammals indicate an Itaboraian age for the Las Flores (Raigemborn et al. 2009; Oliveira and Goin 2011, and literature cited therein; Fig. 4). In the lower part of the unit, palm (Arecaceae) phytoliths are abundant, along with those of Mimosoideae (*Acacia*-like), Chrysobalanaceae (Coco plum), and Lauraceae, characteristic of tropical to subtropical lowland forests, along with a grass understory (see also Brea et al. 2008b). This is one of the earliest occurrences of grasses (but not grasslands) in South America (Brea et al. 2008b; Prasad et al. 2005, indicated a Late Cretaceous record, as well). Cione et al. (2011) reported on a ceratodontid lungfish tooth plate from the lower Las Flores Formation, compatible with the indicated climatic setting.

In the upper part of the Las Flores Formation, palms and herbaceous forms decrease, to be replaced by more arboreal elements: Magnoliaceae, Annonaceae (tropical trees, shrubs), Burseraceae (tropical trees and shrubs; frankinsence), and Boraginaceae (herbs, shrubs, trees). The herbaceous component is represented by the tropical Zingeberales (wetland monocots) and Poaceae (grasses). As indicated by their geologic setting (Raigemborn et al. 2009), these Golfo San Jorge Basin sites are fundamentally coastal lowland records, and reflect humid subtropical to tropical conditions.

The coastal lowland record continues with the late early Eocene lateritized Koluel Kaike Formation (Krause et al. 2010) of Riochican age (Fig. 5). The sequence is about 50 m thick and displays a succession of five major pedotypes. The lower, strongly lateritized, units reflect humid megathermal conditions (subtropical) with MAP of 120–130 cm and MAT of 15^{0}C. Stratigraphically higher parts of the formation are less strongly lateritized, and indicate sub-humid and mesic-megathermal conditions with a MAP of about 100 cm and MAT of ca 12 °C. The highest few meters of the unit show cooler and more arid conditions with MAP and MAT of about 60–70 cm and 10 °C, respectively. The sequence is interpreted to range in age from about 54 Ma at the base to about 42 Ma at the top, with the cooler conditions beginning at about 40 m and 45 Ma, and the drier period beginning at about 50 m and 42 Ma (Krause et al. 2010: fig. 10). Under this chronologic scenario, the overall pattern is considered to closely resemble that of global ocean temperature (Zachos et al. 2001; see Figs. 4 and 8). In Fig. 4 the base of the Koluel-Kaike section (KK1) is correlated as about 51 Ma, instead of 54 Ma because the underlying Las Flores Formation is considered to be of Itaboraian age. Similarly, the upper parts of the section (KK2, KK3) are considered as about 48 Ma because the overlying Sarmiento Formation contains fossil mammals of "Vacan" and "Barrancan" age. [Note that these and other mammal biochrons that are not formally designated as SALMAs are bracketed by ".."] These potential revisions in age of KK1-KK3 still comply with warmer and cooler parts, respectively, of the ocean temperature profile in Figs. 4 and 8. In any case, the interpretations of Krause et al. (2010) result in the 50-m thick Koluel Kaike Formation having a duration of nearly 10 m.y., a distinctly greater interval than the other, but comparably thick, Las Flores and Peña Coloradas formations of the Río Chico Group. The geochemical analyses point to a climatic change from effectively subtropical at the base of the Koluel-Kaike Formation to a cooler and more arid setting at its top.

The early Eocene Pampa de Jones (19*, Fig. 2c) and the middle Eocene Río Pichileufú sites (21*, Fig. 2c) represent more western examples of Patagonian Eocene floras, that likely also reflect somewhat higher elevations. The Pampa de Jones flora has been recovered from the lower part of the Huitrera Formation (Wilf et al. 2010), dated at 54.25± 0.45 Ma. Melendi et al. (2003) described the taxa as having constituted a podocarp cool-temperate rain forest, with gymnosperms having dominated (32 %–46 %) over angiosperms (23 %–33 %) and pteridophytes/bryophytes (3 %–4.5 %), in association (Wilf et al. (2010) with a pipid frog, *Llankibatrachus truebae*, as well as insects. As shown on Fig. 2c, the Pampa de Jones is slightly farther north than other early Eocene Patagonian floras. The activity generated by the Pilcaniyeu volcanic belt and initial uplift of the North Patagonian High Plateau (NPHP, Fig. 2c) (Aragón et al. 2011) also likely contributed to the elevation of these cool-temperate rain forest sites.

The Laguna del Hunco flora (18*, Fig. 2c) was originally recorded by Berry (1925). It is now known to occur in Tufolitas Laguna del Hunco tuffaceous mudstones and sandstones related to the activity of the Pilcaniyeu volcanic belt, and to contain megafossil plants in addition to fish, insects, caddis-fly cases, and pipid frogs (Wilf et al. 2005). The flora is very diverse. Radioisotopic dates obtained from the sequence center on 52.13±0.32 (Wilf et al. 2003), and magnetic polarity data indicate that most samples fall within chron C23n.2n, and coeval with the Early Eocene Climatic Optimum (Figs. 4 and 8).

Wilf et al. (2005) showed that the Laguna del Hunco flora is composed of conifers, a cycad, a *Ginkgo*, three monocots (including palms) and seven ferns. In addition, angiosperms are very diverse and include Proteaceae, Myrtaceae (eucalypts), Cunoniaceae, Lauraceae (laurels), Akaniaceae, Sapindaceae (litchee), Sterculiaceae, and Fabaceae (legumes), as well as many other families (Zamaloa et al. 2006). Zamaloa et al. (2006) added three species of *Gymnostoma* (Casuarinaceae), the genus also being known from the Recent of Malesia, Fiji, New Caledonia, and northeastern Australia. Gandolfo et al. (2011) recorded the presence of *Eucalyptus* at this site, indicating a setting marginal to the main rain forest in this volcanically disturbed caldera lake context. The sample represents the only and oldest non-Australian occurrence of the genus. Of the 30 most abundant species, thermophilic families are strongly represented, including Myrtaceae (eucalypts), Sapindaceae, Fabaceae, Lauraceae, and Araucariaceae (conifers), and it is apparent that diversity would increase with further collecting. At present, the diversity of the Laguna del Hunco flora (186 species; Fig. 8) is comparable to, or greater than, the most diverse Eocene floras of North America.

As summarized by Zamaloa et al. (2006), megafossil Casuarinaceae are known from the Paleogene and Neogene of Australia and Miocene of New Zealand as well as the Eocene of Patagonia. Fossil pollen pertaining to this group extends the Patagonian record from early Paleocene to Eocene, and such pollen also has been recorded from Paleogene deposits of Australia and the Antarctic Peninsula (as well as from younger rocks in other Gondwanan locations). The Casuarinaceae thus provide a Gondwanan scope for Patagonian floras, as does the genus, *Eucalyptus*. Both are notable for their absence in the Río Pichileufú flora (ca 47 Ma; see below), so it is likely that both groups were extinct by then in South America, in contrast to Australasia.

Paleoclimatic reconstruction for the Laguna del Hunco flora suggests that it was neither warm nor humid enough to qualify as a tropical rain forest, although Wilf et al. (2005) noted that it showed Neotropical affinities. The effect of a maritime setting to the west (Fig. 2c) narrowed the potential range of temperature and precluded frost. MAT is estimated to have been about 17 °C (subtropical), and a minimum MAP about 110 cm/year, with the latter incompatible with an elevated Andes at this time. Wilf et al. (2005) interpreted the climate as having been moist and equable. As indicated above, the present values may have been conservative, and likely approached those of more tropical character (arrows on Fig. 8), although the potential ecological and elevational influence of the Pilcaniyeu volcanism and the rising North Patagonian High Plateau (NPHP) should be considered. Wilf et al. (2009) noted that the presence of the rain forest podocarp *Papuacedrus* in the flora indicates a minimum MAP of 400 cm/year. These new estimates invigorate a completely new idea regarding the availability of water and thus forest type in the Eocene of Patagonia, such that MAP and MAT values would have reached those found today in the warm temperate rain forests of New Guinea.

In central Chile, early Eocene floras are known from the Lota Coronel-Arauco and Caleta Cocholgüe (*25, Fig. 2c), and Quinamávida floras (26*, Fig. 2c; Fig. 8). These floras demonstrate warm, humid, subtropical conditions (Troncoso 1992; Gayó et al. 2005). Based on multiple regression analyses of the macroflora, Hinojosa et al. (2006) obtained MAT and MAP estimates of 203 cm/year and 22 °C for Lota Coronel-Arauco, and 260 cm/year and 19–26 °C for Caleta Cocholgüe. Comparable estimates for Quinamávida (Fig. 8) are 91 cm/year and ~18 °C (Hinojosa 2005). Peppe et al. (2011) considered these figures to be over estimated, however, consistent with more subtropical conditions.

From the preceding discussion, it appears that the Paleocene and early Eocene floras of Patagonia were largely preserved in lowland coastal settings, although Patagonian early Eocene floras attest to variations in climatic setting, with more cool-temperate elements at perhaps somewhat higher elevations contemporaneous with those of wetter and more subtropical character in lowland area, and seasonally more arid settings found locally (Gran Salitral; below).

The floras were generally dominated by podocarp and araucarian conifer forests that lived under warm, humid, and at least subtropical climates, typically in mangrove swamp woodlands, likely at elevations below 1200 m (Quattrocchio et al. 2011). Angiosperms also were diverse and recorded the oldest legumes and bamboo-like grasses (Brea et al. 2008b). Early Eocene *Papuacedrus*, *Gymnostoma*, *Akania*, *Eucalyptus*, and several conifers (González et al. 2007; Zamaloa et al. 2006; Wilf et al. 2009; Gandolfo et al. 2011) reflected an old Gondwanan influence that was already present between Australia and South America via Antarctica in the Late Cretaceous. The Ligorio Márquez flora of Chile likely recorded a short-lived cool pulse at about 56 Ma (possibly coeval with the PETM), and the Peñas Coloradas flora may be another example of that or, at least, of a locally more seasonal climate. The Chilean sample, as well as that from Pampa de Jones (cool-temperate), also may reflect its somewhat higher elevation as compared to most of the other floral sites. Overall, the diversity of these floras was notable from the outset, in strong contrast to North American analogs.

In the Chaco-Paraná Basin, Uruguay (18, Fig. 2b), evaporate beds in the Mariano Boedo and Laguna Paiva formations suggest at least temporarily arid conditions during the early Paleocene (Padula and Minggram 1968). A change in climate from temperate to humid at the base of the sequence to hot and dry in the upper part is suggested by del Papa (2006). In the same basin, the development of a paleosol in the Maíz Gordo Formation also indicates an overall aridification and decrease in seasonality leading up to the Thanetian-Ypresian warm interval. However, the basal interval of the middle Eocene Lumbrera Formation of the Salta Basin, Argentina (38, Fig. 2c) to the north, reflects the deposition of permanent sandy fluviatile systems and the presence of a perennial fresh-water lake indicative of more humid conditions (Le Roux 2012).

The middle Eocene Río Pichileufú flora (21*, Fig. 2c; Figs. 4 and 8) was recovered (Berry 1938) from sites near Bariloche, Río Negro Province, Argentina. As summarized in Wilf et al. (2005), the flora was obtained from volcanic lacustrine deposits of the Ventana Formation. Preliminary analysis of collections indicates that megafossils of flowers, fruits, seeds, and leaves are preserved, as well as remains of ants and frogs. The Río Pichileufú flora is the most diverse assemblage known from Cenozoic deposits in Austral South America. Tuff beds directly associated with the fossil sites yielded a mean age of 47.46±0.05 Ma for the flora.

The Río Pichileufú flora indicates that the diversity of the early assemblages continued into the medial Eocene. Wilf et al. (2005) showed that this later flora is as diverse (180+ species) as the extremely differentiated Laguna del Hunco Flora of Patagonia (Fig. 8). Whereas some aspects of diversity at Laguna del Hunco appear to be related to distance from shoreline for a given fossil site, this does not seem to apply to the Río Pichileufú flora. Collectively, these floras are the most diverse assemblages known from Cenozoic deposits in South America as well as the entire Southern Hemisphere. The Río Pichileufú contains the oldest record of the Asteraceae (sunflowers) based on a complete inflorescence (Barreda et al. 2010), although dominance of this group begins in the Oligocene.

Río Pichileufú MAT is suggested as having been about 19 °C, somewhat higher than at Laguna del Hunco, and somewhat out of line with the proposed global increase in temperature based on oceanic data (Zachos et al. 2001; Fig. 8). Minimum MAP was suggested as having been between 200–250 cm (Wilf et al. 2005; Barreda et al. 2010). The presence of *Papuacedrus* (rain forest podocarp) in both floras points to an underestimation of MAP, and suggests the presence of a large area in western Patagonia that supported floras similar to the modern subtropical or montane tropical rain forests (Wilf et al. 2009).

Other than Rio Pichileufú, Barreda and Palazzesi (2007) summarized the Patagonian floras of middle to late Eocene age. The sites, which are mostly in southern Patagonia, include Confluencia (20*, Fig. 2c), and Río Turbio (22*, Fig. 2c), but also include Loreto in Chile (51*, Fig. 2d; Terada et al. 2006; Otero et al. 2012). The continued presence of *Nothofagus* forests in these floras is compatible with the concurrent occurrence of other groups of micro- to mesothermal aspect, such as podocarp and araucarian conifers of Gondwanan heritage, as well as Cunoniaceae and Proteaceae, gunneracean herbs, and caryophyllacean carnations. Associated megathermal elements include laurels, Tiliaceae-Bombacaceae (tropical balsa, jute), Malpighiaceae (tropical climbers), Sapindaceae (tropical trees, lianas), Rubiaceae (gardenia shrubs), and Aquifoliaceae (holly). These floral elements suggest that in general a mesothermal setting was beginning a transition to cooler and drier climates, with an increase in seasonality indicated by the presence of marked growth rings in nothofagacean wood at Río Turbio to the south. This climatic change would be compatible with locally similar indications in some of the early Eocene floras. Megathermal conditions likely persisted in coastal regions.

Tófalo and Morrás (2009) studied paleosols in continental deposits of the Chaco-Paraná Basin, Uruguay (18, Fig. 2b). These indicate important climatic changes during the Late Cretaceous and Cenozoic. Paleocene palustrine carbonates of the Queguay Formation are associated with phreatic calcretes that indicate a seasonally-contrasted, semi-arid climate that might coincide with the Santonian-Danian cooling interval (Le Roux 2012). In the early Eocene Asencio Formation of the Chaco-Paraná Basin, fluvial deposits contain ultisols that developed under a warm and humid climate, and were indurated after periods of intense aridity marked by the development of ferricretes.

Middle Eocene units of the San Pedro Formation in the Valdivia Basin (45*, Fig. 2c; Elgueta et al. 2000) contain fossil floras with *Sabal ochseniusi*, *Tetracera ellipitica*, and *Bennettia grosseserrata*, together with abundant conifers, which suggest a subtropical climate, possibly coinciding with the Lutetian warming (Le Roux 2012).

Megathermal elements appear to have been absent in the later parts of the Eocene and early Oligocene in Patagonia (Barreda and Palazzesi 2007). Late Eocene – earliest Oligocene sites include the Sloggett Formation, Tierra del Fuego Province, Argentina (Panti et al. 2007; 45*, Fig. 2d), Estancia La Sara Well (Menéndez and Caccavari 1975; 46*, Fig. 2d), and Loreto, Chile (Otero et al. 2012; 51*, Fig. 2d). Early Oligocene floras are found in the Río Guillermo (47*, Fig. 2d) and Río Leona (48*, Fig. 2d) formations of Patagonia. In the latest Eocene to early Oligocene, the relatively homogeneous forests were composed of *Nothofagus*, podocarps and araucarian conifers, as well as cunoniaceaean angiosperms that are now well represented in tropical to subtropical and drier climates in the Americas, Australasia, and southern Africa (Heywood 1993). Understorys would have been composed of ferns and herbs. All wood described from the Río Leona flora resembles extant species that today inhabit the Patagonian Andean forest (Pujana 2009). Overall the flora of this time interval reflects high rainfall in a cool-temperate climate.

Oligocene coal seams higher in the San Pedro Formation also contain an association of *Microthyriaceae* and *Cyathidites patagonicus* spores, together with pollen of *Araucariacites australis*, *Nothofagus cinta*, and *Podocarpities* species, implying a forest environment of high to very high humidity and a cold to temperate climate similar to present-day conditions in southern Chile (Palma-Heldt and Alfaro 1982; Le Roux and Elgueta 2000).

Late Oligocene floral sites are rare (Barreda and Palazzesi 2007, 2010; 49*, 50*, Fig. 2d), but have been dominated by forests of *Nothofagus*, podocarp and araucarian conifers, southern beech, an understory of abundant ferns, along with persistently megathermal lowland elements in the north that include palms (Arecaceae), tropical climbers (Malpighiaceae), gardenia shrubs (Rubiaceae), and largely tropical trees and lianas (Combretacea, Sapindaceae). Shoreline elements include the first Asteraceae (sunflowers), and Convolvulaceae (morning glory), associated with Poaceae (grasses), Chenopodiaceae (sugar beet), and Ephedraceae (Mormon tea), a seasonally drier climate indicator. Climates overall were cool-temperate and humid. Apparently the climate rebounded somewhat from the initial Oligocene cooling in the late Oligocene warm interval (LOW) with a new southward dispersal of megathermal elements in Patagonia. Although as noted by some eastern floras, such as the Río Foyel (50*, Fig. 2d) Patagonian Subantarctic Floras were well established, and reach sea level in southern Chile (Terada et al. 2006) in the Loreto Formation (*51, Fig. 2d).

Arid conditions during the Oligocene are indicated by gypsiferous units in the Salar de Antofalla region of the

Salta Basin (Adelmann 2001; Carrapa et al. 2005), which might coincide with Chattian warming (Le Roux 2012).

The Oligocene – lower Miocene Fray Bentos Formation of the Chaco-Paraná Basin is composed of loess that was deposited under semi-arid conditions, with paleosols and pedogenic tubular calcretes also indicating a seasonal, semi-arid, climate (Tófalo and Morrás 2009).

Discussion

Based on the above summary, it appears that both North and South American Paleogene floras responded generally similarly to the global temperature pattern, but that the southern floras were considerably more diverse than their northern counterparts, with the possible exception of the Castle Rock flora of Colorado. The available data indicate that the Neotropical region had achieved its basic floral and ecological structure from the Paleocene, if not earlier, and that coeval floras from Patagonia were nearly as diverse and lived in nearly tropical conditions, as well, until about the middle Eocene.

Under the conventions of Morley (2000), the Patagonian fossil sites could occur within the Southern Megathermal rain forest, but Wilf et al. (2005) noted that these Patagonian forests lived under conditions cooler and drier (but still quite moist) than expected for rain forests. To the north, in La Pampa Province, the early Eocene Gran Salitral Formation (61, Fig. 2d) is a lacustrine sequence that records seasonally semiarid conditions with MAT above 20 °C (about 24 °C; Melchor et al. 2002), in contrast to about 17 °C–19 °C for those in Patagonia (but note above comments on the likely conservative calculations for the Patagonian floras). As indicated in Fig. 8, the Gran Salitral Formation is estimated at about 52 Ma old (early Eocene; Melchor et al. 2002). In this regard, Wilf et al. (2005) suggested that the Patagonian forest setting remained exceptionally diverse during the 4.5 m.y. between the Laguna del Hunco and Río Pichileufú floras, demonstrating a floral/climatic coherence in Patagonia through at least 52–47 Ma, with a cooler setting to the south and one of more seasonal aridity to the north. During this time, a corridor along the eastern margin of South America likely connected the Patagonian with Neotropical regions to the north (Wilf et al. 2005: 637) comparable to the modern situation (Morley 2000), with implications for the climatic setting of the nearly contemporaneous Itaboraian fauna of Brazil (29, Fig. 2c) and the Australasian region via Antarctica to the south (Iglesias et al. 2011). The Patagonian floras contain significant numbers of genera with disjunct distributions in the Neotropics and Australasia that may be Eocene relicts (Davis et al. 1997; Villagrán and Hinojosa 1997).

Barreda and Palazzesi (2007) proposed a rain forest-dominated setting in the Paleocene and early Eocene, but pointed out the presence of certain taxa indicative of a local presence of more arid-adapted shrubs and low trees. Cool-temperate *Nothofagus* is first recorded from the early Eocene and, with other more mesothermal elements, shows the beginning of at least locally cooler environments in Patagonia. Pulses of cooler or more seasonal conditions also are suggested by the Ligorio Márquez flora (late Paleocene) of Chile, and even by the early Paleocene Victor Szlápelis flora and the later Paleocene Peñas Coloradas flora of the San Jorge Golfo area. Grasses (Poaceae) are also recorded in the early Eocene (Brea et al. 2008b; Raigemborn et al. 2009), although grasslands are not represented until the late Oligocene (Barreda and Palazzesi 2007), and local seasonal aridity is recorded in central Argentina by the early Eocene Gran Salitral biota and paleosols.

The record in the later middle Eocene into the Oligocene is consistent with the global drop in temperatures after the EECO, including the development of more open areas with grasses, which continue into the late Oligocene. *Nothofagus* forests expand, with persisting cooler conditions. More mesothermal groups such as Juglandaceae (hickory) and Aquifoliaceae (holly), Tiliaceae (jute), Bombacaceae (balsa), and Sapindaceae (lianas) became extinct at the end of the Paleogene in Patagonia (Barreda and Palazzesi 2007).

In the late Oligocene, the southward dispersal of Neotropical elements (such as palms, Rubiaceae, and Combretaceae) reflects a return of warmer climates, and the addition of xerophytic and halophytic shrubs and herbs (Convolvulaceae, Asteraceae, Poaceae, Chenopodiaceae, Ephedraceae) reflects the beginning of modern-aspect floras (Barreda and Palazzesi 2007).

The Land Mammal Record

Alamitan As background, the Late Cretaceous Alamitan SALMA is based on the mammals of the Los Alamitos Formation, Río Negro Province, Argentina (1, Fig. 2a; 4, Fig. 3; see also Pascual and Ortiz-Jaureguizar 2007). The Alamitan is considered to be of Campanian-Maastrichtian (Bonaparte 1986) or Maastrichtian age (Pascual et al. 2000; Rougier et al. 2009a, b). The Alamitan SALMA contains 17 genera (Table 1), all pertaining to non-tribosphenic groups that include an austroconodontid 'triconodont,' a 'symmetrodont,' 12 dryolestoids, and a sudamericid as well as a ferugliotheriid gondwanathere (Pascual and Ortiz-Jaureguizar 2007; Rougier et al. 2009a). Based on a specimen from the La Colonia Formation, Pascual et al. (2000) referred *Reigitherium bunodontum* to the Docodonta, but later Rougier et al. (2009a) argued in favor of its dryolestoid affinities. Finally, a single multituberculate was recorded (Kielan-Jaworowska et al. 2007).

Table 1 South American Paleogene Mammal Faunas

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
Superfamilial taxon	Family	Genus													
Multituberculata			1	0	0	0	0	0	0	0	0	0	0	0	La Colonia; Kielan-Jaworowska et al. (2007)
Triconidonta	Austroconodontidae	*Austrotriconodon*	1	0	0	0	0	0	0	0	0	0	0	0	
"Symmetrodonta"	Bondesiidae	*Bondesius*	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1990)
Dryolestoidea		*Paraungulatum*	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1990)
	Dryolestidae	*Groeberitherium*	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1986)
		Leonardus	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1990)
	Mesungulatidae	*Mesungulatum*	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte and Soria (1985)
		Coloniatherium	1	0	0	0	0	0	0	0	0	0	0	0	Rougier et al. (2009b)
	Peligrotheriidae	*Peligrotherium*	0	0	1	0	0	0	0	0	0	0	0	0	Rougier et al. (2009b)
	Regitheriidae	*Reigitherium*	1	0	0	0	0	0	0	0	0	0	0	0	Rougier et al. (2009b)
	Brandoniidae	*Brandonia*	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1990)
	Casamiguelidae	*Casamiguelia*	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1990)
		Alamatherium	1	0	0	0	0	0	0	0	0	0	0	0	
		Rougeritherium	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1990)
	Barbereniidae	*Barberenia*	1	0	0	0	0	0	0	0	0	0	0	0	Rougier et al. (2009a)
		Quirogatherium	1	0	0	0	0	0	0	0	0	0	0	0	Rougier et al. (2009a)
Gondwanatheria	Sudamericidae	*Sudamerica*	0	0	1	0	0	0	0	0	0	0	0	0	Scillato-Yane and Pascual (1964)
		Gondwanatherium	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1986)
	Ferugliotheriidae	*Ferugliotherium*	1	0	0	0	0	0	0	0	0	0	0	0	Bonaparte (1986)
Gondwanatheria, Indet.		New genus	0	0	0	0	0	0	1	0	0	0	0	0	Goin et al. (2012b)
Monotremata	Ornithorhynchidae	*Monotrematum*	0	0	1	0	0	0	0	0	0	0	0	0	Pascual et al. (1992)
Metatheria															
"Ameridelphia"	Pediomyidae	*Khasia*	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
	Pucadelphyidae	*Pucadelphys*	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
		Andinodelphys	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
		Mizquedelphys	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
	Jaskhadelphyidae	*Jaskhadelphys*	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
	Mayulestidae	*Mayulestes*	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1998)
	Protodidelphidae	*Carolocoutoia*	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011), Goin et al. (1998b)
		Guggenheimia	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
		Protodidelphis	0	0	0	0	1	0	1	0	0	0	0	0	Oliveira and Goin (2011)
		Periprotodidelphis	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
		Zeusdelphys	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
	Derorhynchidae	*Derorhynchus*	0	0	1	0	1	0	1	0	0	0	0	0	Oliveira and Goin (2011)
		Pauladelphys	0	0	0	0	0	0	1	0	0	0	0	0	Tejedor et al. (2009)
		Coona	0	0	0	0	0	0	0	1	1	0	0	0	Goin and Abello (2013)
	Sternbergiidae	*Carolopaulacoutoia*	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
		Itaboraidelphys	0	0	0	0	1	0	1	0	0	0	0	0	Oliveira and Goin (2011)
		Didelphopsis	0	0	1	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
	Family indeterminate	*Incadelphys*	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
		Tiulordia	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
		Szalinia	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
		Reigia	0	0	0	0	0	0	0	0	1	0	0	0	Pascual (1983)
		Eobrasilia	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
		Marmosopsis	0	0	0	0	1	0	1	0	0	0	0	0	Oliveira and Goin (2011)
		Gaylordia	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
		Minusculodelphis	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
		Monodelphopsis	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
		Sternbergia	0	0	0	0	1	0	0	0	0	0	0	0	
Sparassodonta	Basal Sparassodonts	*Argyrolestes*	0	0	0	0	0	0	0	0	1	0	0	0	Forasiepi (2009)
		Allqokirus	0	1	0	0	0	0	0	0	0	0	0	0	Forasiepi (2009), Muizon (1991)
		Procladosictis	0	0	0	0	0	0	0	0	1	1	0	0	Forasiepi (2009)
		Pseudocladosictis	0	0	0	0	0	0	0	0	1	0	0	0	Forasiepi (2009)
		Nemolestes	0	0	0	0	1	0	1	0	1	0	0	0	Forasiepi (2009)
		Patene	0	0	0	0	1	1	0	0	1	0	0	0	Forasiepi (2009)
	Hathliacynidae	*Notogale*	0	0	0	0	0	0	0	0	0	0	0	1	Forasiepi (2009)
		Sallacyon	0	0	0	0	0	0	0	0	0	0	0	1	Forasiepi (2009)
		Andinogale	0	0	0	0	0	0	0	0	0	0	0	1	Forasiepi (2009)
	Proborhyaenidae	*Arminheringia*	0	0	0	0	0	0	0	0	1	1	0	0	Forasiepi (2009)
		Paraborhyaena	0	0	0	0	0	0	0	0	0	0	0	1	Forasiepi (2009)
		Proborhyaena	0	0	0	0	0	0	0	0	0	0	0	1	Forasiepi (2009)
		Callistoe	0	0	0	0	0	0	0	0	1	0	0	0	Forasiepi (2009)
	Borhyaenidae	*Angelocabrerus*	0	0	0	0	0	0	0	0	1	0	0	0	Forasiepi (2009)
		Plesiofelis	0	0	0	0	0	0	0	0	0	1	0	0	Forasiepi (2009)
		Pharsophorus	0	0	0	0	0	0	0	0	0	0	0	1	Forasiepi (2009)
		Fredszalaya	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
Marsupialia															
Didelphimorphia	Peradectidae	New genus	0	0	0	0	0	0	1	0	0	0	0	0	Tejedor et al. (2009)
		Peradectes	0	1	0	0	0	0	0	0	0	0	0	0	Muizon (1991)
	Caroloameghiniidae	*Caroloameghinia*	0	0	0	0	0	0	0	0	1	0	0	0	Goin (2006)
		Procaroloameghinia	0	0	0	0	1	0	1	0	0	0	0	0	Oliveira and Goin (2011)
		Canchadelphys	0	0	0	0	0	0	0	0	0	0	1	0	Goin et al. (2010)
		New genus	0	0	0	0	0	0	1	0	0	0	0	0	Tejedor et al. (2009)
Paucituberculata	Family indeterminate	*Riolestes*	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
		Bardalestes	0	0	0	0	0	0	1	0	0	0	0	0	Goin et al. (2009)
	Caenolestidae	*Evolestes*	0	0	0	0	0	0	0	0	0	0	0	1	Goin et al. (2010)
	Pichipilidae	*Pseudhalmaripus*	0	0	0	0	0	0	0	0	0	0	0	1	Abello (2007)
	Palaeothentidae	*Pilchenia*	0	0	0	0	0	0	0	0	0	0	1	1	Abello (2007), Goin et al. (2009)
		Acdestodon	0	0	0	0	0	0	0	0	0	0	0	1	Abello (2007)
		Palaeothentes	0	0	0	0	0	0	0	0	0	0	0	1	Abello (2007)
	Abderitidae	*Parabderites*	0	0	0	0	0	0	0	0	0	0	0	1	Abello (2007)
Australidelphia															
Microbiotheria	Microbiotheriidae	*Eomicrobiotherium*	0	0	0	0	0	0	1	0	1	0	1	0	Goin et al. (2010)
		Clenia	0	0	0	0	0	0	0	0	0	0	1	0	Goin et al. (2010)
		Microbiotherium	0	0	0	0	0	0	0	0	0	0	1	0	Goin et al. (2010)
		Mirandatherium	0	0	0	0	1	0	0	0	0	0	0	0	Goin et al. (2010)
Polydolopimorphia	Family indeterminate	New genus and species	0	0	1	0	0	0	0	0	0	0	0	0	Goin et al. (2009)
		Bobbschaefferia	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
	Glasbiidae	*Periakros*	0	0	0	0	0	0	0	0	0	0	1	0	Goin et al. (2010)
		Palangania	0	0	0	0	0	1	1	0	0	0	0	0	Goin et al. (1998a)
	Prepidolopidae	*Prepidolops*	0	0	0	0	0	0	0	0	1	0	0	0	Pascual (1980a, b)
		Punadolops	0	0	0	0	0	0	0	0	0	1	0	0	Goin et al. (1998a)
	Bonapartheriidae	*Bonapartherium*	0	0	0	0	0	0	0	0	1	1	0	0	Goin et al. (1998a)
		New genus	0	0	1	0	0	0	0	0	0	0	0	0	Goin et al. (2009)
		Epidolops	0	0	0	0	1	0	0	0	0	0	0	0	Oliveira and Goin (2011)
	Gashterniidae	*Gashternia*	0	0	0	0	1	1	1	0	0	0	0	0	Goin et al. (2009), Tejedor et al. (2009)
	Rosendolopidae	*Rosendolops*	0	0	0	0	0	0	0	0	1	0	1	0	Goin et al. (2010)
		Hondonadia	0	0	0	0	0	0	0	0	0	1	1	1	Goin et al. (2010)
	Basal Argyrolagoidea	*Klohnia*	0	0	0	0	0	0	0	0	0	0	1	0	Flynn et al. (2003), Goin et al. (2010)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
		Epiklohnia	0	0	0	0	0	0	0	0	0	0	0	1	Goin et al. (2009), (2010)
		Praedens	0	0	0	0	0	0	0	0	0	0	1	0	Goin et al. (2010)
	Groeberiidae	*Groeberia*	0	0	0	0	0	0	0	1	1	0	0	0	Pascual et al. (1994)
	Argyrolagidae	*Proargyrolagus*	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
	Family indeterminate	*Roberthoffstetteria*	0	1	0	0	0	0	0	0	0	0	0	0	Muizon and Cespedes, in press
	Polydolopidae	*Amphidolops*	0	0	0	1	0	0	1	1	1	0	0	0	Chornogubsky (2010)
		Eudolops	0	0	0	0	0	0	0	1	1	0	0	0	Chornogubsky (2010)
		Polydolops	0	0	0	0	0	0	0	1	1	1	0	0	Chornogubsky (2010)
		Kramadolops	0	0	0	0	0	0	0	1	1	1	1	1	Chornogubsky (2010), Goin et al. (2010)
		Archaeodolops	0	0	0	0	0	1	0	1	1	0	0	0	Chornogubsky (2010)
		Pseudolops	0	0	0	0	0	0	0	0	1	0	0	0	Chornogubsky (2010)
		Pliodolops	0	0	0	0	1	1	1	1	1	0	0	0	Chornogubsky (2010)
		New genus	0	0	0	0	1	0	1	0	0	0	0	0	Chornogubsky (2010)
Eutheria															
Cingulata	Dasypodidae	*Prostegotherium*	0	0	0	0	0	1	1	1	1	0	0	0	Carlini et al. (2010)
		Riostegotherium	0	0	0	0	1	0	1	0	0	0	0	0	Carlini et al. (2010)
		Astegotherium	0	0	0	0	0	0	1	1	0	0	0	0	Carlini et al. (2010)
		Pseudostegotherium	0	0	0	0	0	0	0	0	1	0	0	0	Carlini et al. (2010)
		Stegosimpsonia	0	0	0	0	0	0	1	1	1	0	0	0	Carlini et al. (2010)
		Barrancatatus	0	0	0	0	0	0	0	0	0	0	1	0	Carlini et al. (2010)
		Sadypus	0	0	0	0	0	0	0	0	0	1	1	1	Carlini et al. (2010)
		Parutaetus	0	0	0	0	0	0	0	0	0	1	1	0	Carlini et al. (2010)
		Orthutaetus	0	0	0	0	0	0	0	0	0	1	0	0	Carlini et al. (2010)
		Anteutatus	0	0	0	0	0	0	0	0	0	1	0	0	Carlini et al. (2010)
		Archaeutatus	0	0	0	0	0	0	0	0	0	0	0	1	Carlini et al. (2010)
		Mazzoniphractus	0	0	0	0	0	0	0	0	0	1	0	0	Carlini et al. (2010)
		Meteutatus	0	0	0	0	0	0	0	1	1	1	1	1	Carlini et al. (2010)
		Pseudoeutatus	0	0	0	0	0	0	0	0	0	1	0	1	Carlini et al. (2010)
		Utaetus	0	0	0	0	0	0	0	1	1	0	0	0	Carlini et al. (2010)
		Kuntinaru	0	0	0	0	0	0	0	0	0	0	0	1	Billet et al. (2011)
	Incertae sedis	*Machlydotherium*	0	0	0	0	0	0	0	0	1	1	1	0	Carlini et al. (2005)
	Peltephilidae	New genus	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		New genus	0	0	0	0	0	1	0	0	0	0	0	0	Carlini et al. (2005)
		New genus	0	0	0	0	0	0	0	0	1	0	0	0	Carlini et al. (2005)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
		New genus	0	0	0	0	0	0	0	0	0	0	1	0	Carlini et al. (2005)
	Glyptodontidae	*Glyptatelus*	0	0	0	0	0	0	0	0	0	1	0	1	
		Clypeotherium	0	0	0	0	0	0	0	0	0	0	0	1	Scillato-Yané (1977)
		Glyptatelinae, indet.	0	0	0	0	0	0	0	0	0	0	1	0	Carlini et al. (2005)
		Propalaeohoplophorinae, indet.	0	0	0	0	0	0	0	0	0	0	0	1	Scillato-Yané (1977)
	Palaeopeltidae	*Palaeopeltis*	0	0	0	0	0	0	0	0	0	0	0	1	
	Indeterminate	*Eocoleophorus*	0	0	0	0	0	0	0	0	0	0	0	1	Carlini and Scillato-Yané (1999)
Pilosa	Mylodontidae	*Paroctodontotherium*	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2011)
	Orophodontidae	*Octodontotherium*	0	0	0	0	0	0	0	0	0	0	0	1	Carlini and Scillato-Yané (2004), Vizcaíno et al. (2012)
		Orophodon	0	0	0	0	0	0	0	0	0	0	0	1	Carlini and Scillato-Yané (2004), Pujos and de Iuliis (2007)
		Chubutherium	0	0	0	0	0	0	0	0	0	0	0	1	Carlini and Scillato-Yané (2004), Pujos and de Iuliis (2007)
	Megalonychidae	unnamed genus	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Pseudoglyptodon	0	0	0	0	0	0	0	0	0	0	1	1	Shockey and Anaya (2008), Pujos and de Iuliis (2007)
		Deseadognathus	0	0	0	0	0	0	0	0	0	0	0	1	Carlini and Scillato-Yané (2004), Pujos and de Iuliis (2007)
Astrapotheria	Astrapotheriidae	*Albertogaudrya*	0	0	0	0	0	0	0	1	1	0	0	0	Carlini et al. (1990)
		Astraponotus	0	0	0	0	0	0	0	0	0	1	0	0	Kramarz et al. (2011)
		Scaglia	0	0	0	0	0	0	0	1	0	0	0	0	
		Parastrapotherium	0	0	0	0	0	0	0	0	0	0	0	1	Kramarz and Bond (2008)
		Maddenia	0	0	0	0	0	0	0	0	0	0	0	1	Kramarz and Bond (2009)
		Liarthrus	0	0	0	0	0	0	0	0	0	0	0	1	Kramarz and Bond (2008)
		Eoastrapostylops	0	0	0	0	1	0	0	0	0	0	0	0	
		Shecenia	0	0	0	0	1	0	0	0	0	0	0	0	
		Tetragonostylops	0	0	0	0	1	0	0	1	0	0	0	0	
	Trigonostylopidae	*Trigonostylops*	0	0	0	0	0	1	1	1	1	1	0	0	Bond et al. (2011)
'"Condylarthra"	Mioclaenidae														
	Kollpaniinae	*Molinodus*	0	1	0	0	0	0	0	0	0	0	0	0	
		Tiuclaenus	0	1	0	0	0	0	0	0	0	0	0	0	
		Pucanodus	0	1	0	0	0	0	0	0	0	0	0	0	
		Silmoclaenus	0	1	0	0	0	0	0	0	0	0	0	0	

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
		Andinodus	0	1	0	0	0	0	0	0	0	0	0	0	
		Pascualodus	0	0	0	0	0	0	0	0	1	0	0	0	Gelfo (2004)
	Didolodontidae	New genus	0	0	0	0	0	0	1	0	0	0	0	0	New genus recorded only
		New genus	0	0	0	0	0	0	1	0	0	0	0	0	New genus recorded only
		Didolodus	0	0	0	0	0	0	0	1	1	0	0	0	
		Escribania	0	0	1	0	0	0	0	0	0	0	0	0	
		Raulvaccia	0	0	1	0	0	0	0	0	0	0	0	0	
		Xesmodon	0	0	0	0	0	0	0	0	0	1	0	0	
		Paulogervasia	0	0	0	0	0	0	0	0	1	1	0	0	Gelfo (2010)
		Ernestokokenia	0	0	0	0	1	1	0	1	1	1	0	0	Gelfo (2010)
		Lamegoia	0	0	0	0	1	0	0	0	0	0	0	0	
		Paulacoutoia	0	0	0	0	1	0	0	0	0	0	0	0	
		Umayodus	0	0	0	0	1	0	0	0	0	0	0	0	Gelfo and Sigé (2011)
Pantodonta	Alcidedorbignyidae	*Alcidorbignia*	0	1	0	0	0	0	0	0	0	0	0	0	
Litopterna	Adianthidae	*Thadanius*	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Tricoelodus	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Proectocion	0	0	0	0	0	0	0	0	1	0	0	0	
	Protolipternidae	*Miguelsoria*	0	0	0	0	1	0	0	0	0	0	0	0	
		Protolipterna	0	0	0	0	1	0	0	0	0	0	0	0	
		?*Asmithwoodwardia*	0	0	0	0	1	0	1	1	0	0	0	0	
	Anisolambdidae	*Wainka*	0	0	0	1	0	0	0	0	0	0	0	0	Pascual and Ortiz-Jaureguizar (2007)
		Decanonus	0	0	0	0	0	0	0	0	0	1	0	0	
		Anisolambda	0	0	0	0	1	1	0	1	1	0	0	0	
	Notonychopidae	*Notonychops*	0	0	0	0	1	0	0	0	0	0	0	0	
		Requisia	0	0	1	0	0	0	0	0	0	0	0	0	
	Sparnotheriodontidae	*Sparnotheriodon*	0	0	0	0	0	0	0	1	0	0	0	0	
		Victorlemoinea	0	0	0	0	1	1	1	1	0	0	0	0	
		Phoradiadius	0	0	0	0	0	0	0	1	1	0	0	0	
	Macraucheniidae	*Polymorphis*	0	0	0	0	0	0	0	0	0	1	0	0	
		Coniopternium	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
	Proterotheriidae	*Heteroglyphis*	0	0	0	0	0	0	0	0	0	1	0	?	
		Polyacrodon	0	0	0	0	0	0	0	0	0	1	0	?	
		Salladolodus	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
Notopterna	Indaleciidae	*Adiantoides*	0	0	0	0	0	0	0	1	1	0	0	0	
		New genus	0	0	0	0	0	0	0	0	0	0	1	0	Croft et al. (2008b)
		Indalecia	0	0	0	0	0	0	0	1	1	0	0	0	
Notoungulata		*Satshatemnus*	0	0	0	0	1	0	0	0	0	0	0	0	
	Perutheriidae	*Perutherium*	0	0	0	0	1	0	0	0	0	0	0	0	Gelfo and Sigé (2011)
	Archaeohyracidae	*Acoelohyrax*	0	0	0	0	0	0	0	0	1	0	0	0	
		Eohyrax	0	0	0	0	0	0	0	1	1	1	0	0	Reguero and Prevosti (2010)
		Pseudhyrax	0	0	0	0	0	0	0	0	0	1	1	0	Reguero and Prevosti (2010)
		Protoarchaeohyrax	0	0	0	0	0	0	0	0	0	0	1	1	Reguero and Prevosti (2010)
		Archaeohyrax	0	0	0	0	0	0	0	0	0	0	0	1	Reguero and Prevosti (2010)
		Archaeotypotherium	0	0	0	0	0	0	0	0	0	0	1	1	Reguero and Prevosti (2010)
		Punahyrax	0	0	0	0	0	0	0	0	0	1	0	0	Reguero and Prevosti (2010)
	Hegetotheriidae	*Prohegetotherium*	0	0	0	0	0	0	0	0	0	0	1	1	Reguero and Prevosti (2010)
		Propachyrucos	0	0	0	0	0	0	0	0	0	0	0	1	Reguero and Prevosti (2010)
		Prosotherium	0	0	0	0	0	0	0	0	0	0	0	1	Reguero and Prevosti (2010)
	Mesotheriidae	*Trachytherus*	0	0	0	0	0	0	0	0	0	0	1	1	Reguero and Prevosti (2010), Croft et al. (2008a)
		Anatrachytherus	0	0	0	0	0	0	0	0	0	0	0	1	Reguero and Prevosti (2010)
	Archaeopithecidae	*Archaeopithecus*	0	0	0	0	0	1	1	1	1	?	0	0	
		Acropithecus	0	0	0	0	0	1	1	1	0	0	0	0	
	Henricosborniidae	Genus indet.	0	1	0	0	0	0	0	0	0	0	0	0	
		Henricosbornia	0	0	0	0	1	1	1	1	1	0	0	0	
		Othnielmarshia	0	0	0	0	0	1	1	1	0	0	0	0	
		Peripantostylops	0	0	0	0	1	0	0	1	0	0	0	0	
		Simpsonotus	0	0	0	0	1	0	0	0	0	0	0	0	see text
		Acamana	0	0	0	0	0	0	0	1	1	0	0	0	Bond and Vucetich (1983)
	Interatheriidae	*Johnbell*	0	0	0	0	0	0	0	0	0	0	1	0	Hitz et al. (2006)
		unnamed genera	0	0	0	0	0	0	0	0	0	0	0	2	Shockey and Anaya (2008)
		Antepithecus	0	0	0	0	0	0	0	0	1	1	1	0	Reguero and Prevosti (2010), Hitz et al. (2006), Scarano et al. (2011)
		Guilielmoscottia	0	0	0	0	0	0	0	0	0	1	0	0	Reguero and Prevosti (2010)
		Notopithecus	0	0	0	0	0	1	0	1	1	?	0	0	Reguero and Prevosti (2010)
		Punapithecus	0	0	0	0	0	0	0	0	0	1	0	0	López and Bond (1995)
		Eopachycros	0	0	0	0	0	0	0	0	0	0	1	0	Reguero and Prevosti (2010)
		Plagiarthrus	0	0	0	0	0	0	0	0	0	0	0	1	Reguero and Prevosti (2010), Scarano et al. (2011)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
		Santiagorothia	0	0	0	0	0	0	0	0	0	0	1	0	Reguero and Prevosti (2010), Scarano et al. (2011)
		Proargyrohyrax	0	0	0	0	0	0	0	0	0	0	1	0	Reguero and Prevosti (2010), Scarano et al. (2011)
		Archaeophylus	0	0	0	0	0	0	0	0	0	0	0	1	McKenna and Bell (2002), *Progaleopithecus*; Scarano et al. (2011)
		Transpithecus	0	0	0	0	0	0	0	0	1	0	0	0	
		Sallatherium	0	0	0	0	0	0	0	0	0	0	0	1	Reguero and Prevosti (2010)
	Campanorcidae	*Campanorco*	0	0	0	0	0	0	0	0	1	0	0	0	Reguero and Prevosti (2010)
	Isotemnidae	*Isotemnus*	0	0	0	0	1	1	1	1	?	0	0	0	
		Anisotemnus	0	0	0	0	0	0	0	1	1	0	0	0	Tejedor et al. (2009)
		Pampatemnus	0	0	0	0	0	0	0	1	1	0	0	0	
		Pleurostylodon	0	0	0	0	0	0	0	1	1	0	0	0	
		Rhyphodon	0	0	0	0	0	0	0	0	0	1	0	0	
		Thomashuxleya	0	0	0	0	0	0	0	1	1	0	0	0	
		Distylophorus	0	0	0	0	0	0	0	0	0	1	0	0	
		Periphragnis	0	0	0	0	0	0	0	0	0	1	1	0	
	Leontiniidae	*Leontinia*	0	0	0	0	0	0	0	0	0	0	0	1	Ribeiro et al. (2010)
		Ancylocoelus	0	0	0	0	0	0	0	0	0	0	0	1	Ribeiro et al. (2010)
		Scarittia	0	0	0	0	0	0	0	0	0	0	0	1	Ribeiro et al. (2010)
		Henricofilholia	0	0	0	0	0	0	0	0	0	0	0	1	Ribeiro et al. (2010)
		Taubatherium	0	0	0	0	0	0	0	0	0	0	0	1	Ribeiro et al. (2010)
		Anayatherium	0	0	0	0	0	0	0	0	0	0	0	1	Ribeiro et al. (2010)
		Coquenia	0	0	0	0	0	0	0	1	1	0	0	0	Deraco et al. (2008)
		Martinmiguelia	0	0	0	0	0	0	0	0	0	1	0	0	Bond and López (1995)
	Homalodtheriidae	*Trigonolophodon*	0	0	0	0	0	0	0	0	0	0	1	0	
		Asmodeus	0	0	0	0	0	0	0	0	0	0	0	1	Vizcaíno et al. (2012)
	Notohippidae		0	0	0	0	0	0	0	0	0	0	2	0	Croft et al. (2008b)
		Coelostylodon	0	0	0	0	0	0	0	0	1	0	0	0	Bond and López (1993)
		Eomorphippus	0	0	0	0	0	0	0	0	0	0	1	0	López et al. (2010)
		Plexotemnus	0	0	0	0	0	0	0	0	1	0	0	0	López et al. (2010)
		Puelia	0	0	0	0	0	0	0	0	0	1	1	0	López et al. (2010)
		Trimerostephanus	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)
		Patagonhippus	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)
		Moqueguahippus	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)
		Rhynchippus	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
		Morphippus	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)
		Argyrohippus	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)
		Eurygenium	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)
		Pascualihippus	0	0	0	0	0	0	0	0	0	0	0	1	López et al. (2010)
		Pampahippus	0	0	0	0	0	0	0	1	1	0	0	0	Bond and López (1993)
		Coresodon	0	0	0	0	0	0	0	0	0	0	0	1	López (2010)
	Notostylopidae	gen. nov.	0	0	0	0	0	0	0	0	0	0	1	0	Croft et al. (2008b)
		Boreastylops	0	0	0	0	0	0	0	1	1	0	0	0	
		Brandmayria	0	0	0	0	0	1	0	0	0	0	0	0	
		Edvardotrouessartia	0	0	0	0	0	0	1	1	0	0	0	0	
		Homalostylops	0	0	0	0	0	0	1	1	1	0	0	0	
		Notostylops	0	0	0	0	0	1	1	1	1	0	0	0	
		Otronia	0	0	0	0	0	0	0	0	0	1	?	0	
		notostylopid indet.	0	0	0	0	1	0	0	0	0	0	0	0	Las Flores Fm., this paper
	Toxodontidae	*Proadinotherium*	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008b)
	Oldfieldthomasiidae	*Acoelodus*	0	0	0	0	0	0	0	1	1	0	0	0	
		Colbertia	0	0	0	0	1	0	0	1	1	1	0	0	
		Itaboraitherium	0	0	0	0	1	0	0	0	0	0	0	0	
		Kibenikhoria	0	0	0	0	1	0	0	0	0	0	0	0	
		Maxschlosseria	0	0	0	0	0	1	0	1	0	0	0	0	
		Oldfieldthomasia	0	0	0	0	0	1	0	1	1	0	0	0	Reguero and Prevosti (2010)
		Paginula	0	0	0	0	0	0	0	1	0	0	0	0	
		Tsanmichoria	0	0	0	0	0	0	0	0	0	1	0	?	
		Ultrapithecus	0	0	0	0	0	0	0	0	1	0	0	0	
		Dolichostylodon	0	0	0	0	0	0	0	1	1	0	0	0	García-López and Powell (2009)
		Suniodon	0	0	0	0	0	0	0	0	0	1	0	0	López (1995)
	New Family	*Brachystephanus*	0	0	0	0	0	0	0	1	1	0	0	0	López and Bond (2003)
		Xenostephanus	0	0	0	0	0	0	0	1	1	0	0	0	
		Allalmeia	0	0	0	0	0	0	0	1	1	0	0	0	
Pyrotheria	Pyrotheriidae	*Carolozittelia*	0	0	0	0	0	0	0	1	?	0	0	0	
		Propyrotherium	0	0	0	0	0	0	0	0	0	1	0	0	
		Baguatherium	0	0	0	0	0	0	0	0	0	0	1	0	Salas et al. (2006)
		Pyrotherium	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
Xenungulata	Carodniidae	*Carodnia*	0	0	0	1	1	0	0	0	0	0	0	0	Paula-Couto (1952)

Table 1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
		Notoetayoa	0	0	0	1	0	0	0	0	0	0	0	0	Gelfo et al. (2008)
		Etayoa	0	0	0	0	1	0	0	0	0	0	0	0	Villarroel (1987)
Rodentia															
Caviomorpha, Indeterminate		*Cachiyacuy*	0	0	0	0	0	0	0	0	1	0	0	0	Antoine et al. (2011)
		Canaanimys	0	0	0	0	0	0	0	0	1	0	0	0	Antoine et al. (2011)
Cavioidea	Dasyproctidae		0	0	0	0	0	0	0	0	0	0	0	1	Croft et al. (2008b)
		Andemys	0	0	0	0	0	0	0	0	0	0	1	0	Bertrand et al. (2012)
		Litodontomys	0	0	0	0	0	0	0	0	0	0	0	1	
		Incamys	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Cephalomys	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Branisamys	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Eobranisamys	0	0	0	0	0	0	0	0	1	0	0	?	Antoine et al. (2011), Vucetich et al. (2010)
	Eocardiidae	*Astemorys*	0	0	0	0	0	0	0	0	0	0	0	1	Wood and Patterson (1959)
		Chubutomys	0	0	0	0	0	0	0	0	0	0	0	1	Wood and Patterson (1959)
Octodontoidea		cf. *Eoespina*	0	0	0	0	0	0	0	0	1	0	0	0	Antoine et al. (2011)
	Octodontidae	*Migraveramus*	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Sallamys	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
		Platypittamys	0	0	0	0	0	0	0	0	0	0	0	1	Wood and Patterson (1959)
	Echimyidae	*Deseadomys*	0	0	0	0	0	0	0	0	0	0	0	1	Wood and Patterson (1959)
	indet.	*Draconomys*	0	0	0	0	0	0	0	0	0	0	0	1	Vucetich et al. (2010)
	indet.	*Vallehermosomys*?	0	0	0	0	0	0	0	0	0	0	0	1	Vucetich et al. (2010)
Chinchilloidea	Chinchillidae	*Eoviscaccia*	0	0	0	0	0	0	0	0	0	0	1	0	Bertrand et al. (2012)
		Scotamys	0	0	0	0	0	0	0	0	0	0	0	1	Wood and Patterson (1959)
		?*Prolagostomus*	0	0	0	0	0	0	0	0	0	0	0	1	Croft et al. (2008b)
Erethizondoidea	Erethizontidae	*Protosteiromys*	0	0	0	0	0	0	0	0	0	0	0	1	Wood and Patterson (1959)
Primates	Incertae sedis	*Branisella*	0	0	0	0	0	0	0	0	0	0	0	1	Shockey and Anaya (2008)
Total number of genera			17	19	10	4	51	21	34	55	73	42	40	90	
Number of FADs			17	19	10	4	48	13	12	34	29	28	27		
Number of LADs			17	19	8	3	31	2	16	15	58	29	33		
Through going			0	0	0	0	1	8	13	15	8	4	3		
Number of taxa		Total	17	19	10	4	51	21	34	55	73	42	40		
		FADs	17	19	10	4	48	13	12	30	29	29	28		
		LADs	17	19	8	3	31	2	16	14	58	30	30		

Table 1 (continued)

Biochron		Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.	Vac.	Bar.	Mus.	Ting.	Des.	Remarks
	Through going	0	0	0	0	1	8	13	15	8	4	4		
Percent of taxa	FADs	100	100	100	100	94	62	35	54	40	67	70		
	LADs	100	100	80	75	61	10	47	25	79	71	75		
	Through going	0	0	0	0	2	38	38	27	11	10	10		

All except Carodnian, Sapoan, Mustersan, and Tingiririican after Gelfo et al. (2009). Carodnian after Pascual and Ortiz-Jaureguizar (2007). Sapoan after Tejedor et al. (2009). Mustersan after Cladera et al. (2004). Tinguirircan afer Flynn et al. (2003), Pascual and Ortiz-Jaureguizar (2007), and Croft et al. (2008a, b). La Cancha taxa included in Tinguirirican after Goin et al. (2009). La Colonia multituberculate after Kielan-Jaworowska et al. (2007). Deseadan taxa are only those relevant to prior SALMAs and may not be a complete list. See citations for individual taxa. If not listed, metatherians and non-therians after Gelfo et al. (2009), placentals after Gelfo et al. (2009) and Mckenna and Bell (2002).

The 17 taxa are scored (Figs. 9 and 10) as an equal number of FADs and LADs (Table 1) in that there are no antecedent or subsequent forms known. The fauna is clearly dominated by the 12 dryolestoids (Fig. 11), distributed among seven families (Table 1). Of these, casamiquelid dryolestoids comprise the most diverse family (three genera), with mesungulatids, dryolestids, and barbereniids each represented by two genera. The Sudamericidae is of Gondwanan distribution in the Late Cretaceous through the mid-Paleocene (Table 1) and, along with the Late Cretaceous South American endemic Ferugliotheriidae, reflects the gondwanathere influence here (Goin et al. 2012b). The Alamitan multituberculate recovered from levels of the La Colonia Formation reflects, along with those of the Early Cretaceous of Australia (Rich et al. 2009), the rare Gondwanan occurrence of the group that is much better known in faunas of Jurassic and Cretaceous age in North America (and Holarctica; McKenna and Bell 2002) as well as the Early Cretaceous of Africa (Morocco; Sigogneau-Russell 1991; Hahn and Hahn 2003).

With the possible exception of multituberculates, this diverse group of pre-tribosphenic taxa had its origin in Late Jurassic faunas of Gondwana, and underwent a successful radiation in the Cretaceous (Rougier et al. 2009a), during an interval termed the Gondwana Episode by Pascual and Ortiz-Jaureguizar (2007). Goin et al. (2012b) suggested that the radiation of these endemic mammals was a Late Cretaceous (Cenomanian-Maastrichtian) event (their “Late Gondwanan Phase”), and that it was triggered by the global warming that developed since the Cenomanian. Bertini et al. (1993) and Candeiro et al. (2006) noted the presence of a potentially therian mammal from the Turonian-Santonian (ca 85 Ma) Adamantina Formation of Brazil, but this awaits further discoveries.

Pascual and Ortiz-Jaureguizar (2007: fig. 18) suggested that the Alamitan taxa can be ecologically categorized as insectivorous, insectivorous-carnivorous, omnivore-browsers, and browsers. The preponderance of dryolestoids in Alamitan faunas indicates a strong exploitation of the insectivorous niche (Kielan-Jaworowska et al. 2004: 377), with members possibly also having been somewhat arboreal. Apparently the ‘triconodont’ and ‘symmetrodont’ also likely were insectivorous, with the multituberculate perhaps having been omnivorous, and the gondwanathere a likely herbivore (Prasad et al. 2005, but potentially also beaver-like, Koenigswald et al. 1999).

Tiupampan The Tiupampan SALMA is based on the Tiupampa fauna of Bolivia (12, Fig. 2b), considered to be of early Paleocene age (ca 63 Ma), and holds the oldest record of placental mammals in South America along with the first diversity of metatherians. Based on Tables 1 and 2, and Figs. 3 and 9, the Tiupampa fauna contains 19 genera of

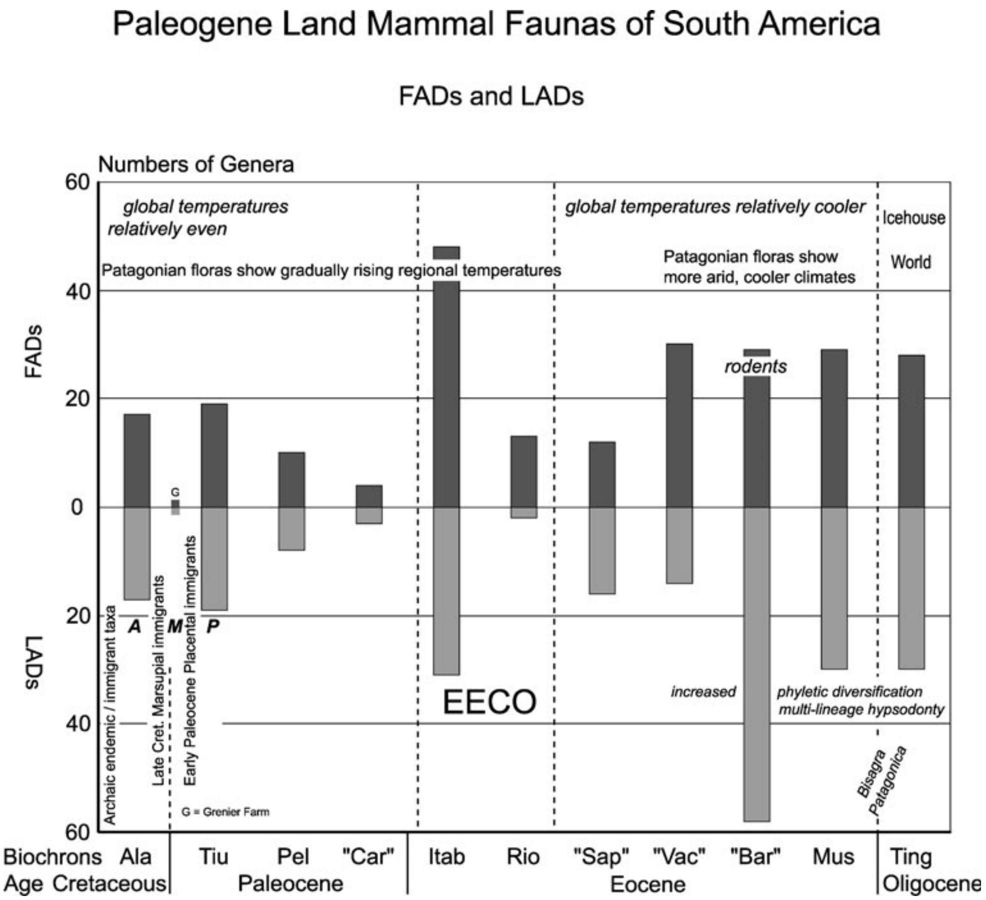


Fig. 9 Paleogene land mammal faunas of South America showing the numbers of genera of FADs and LADs for Alamitan to Tinguirirican biochronologic units. Biochron abbreviations are: Ala = Alamitan; Tiu = Tiupampan; Pel = Peligran; "Car" = "Carodnian"; Itab = Itaboraian; Rio = Riochican; "Sap" = "Sapoan"; "Vac" = "Vacan"; "Bar" = "Barrancan"; Mus = Mustersan; Ting = Tinguiririican. The Grenier Farm site is the earliest Paleocene unit in South America, with a single taxon (Goin et al. 2006a). *Bisagra Patagonica* refers to the sharp change (hinge) in climatic change at the beginning of the Oligocene (from Goin et al. 2012a). EECO = Early Eocene Climatic Optimum. To reflect likely times of immigration, the ***M*** is located below the G (Grenier Farm site) to represent the likely Late Cretaceous dispersal of metatherians to South America from the north. The ***P*** is located below the bar for the Tiupampan to point out the likely early Paleocene entry of placental mammals in South America. ***A*** represents the Late Cretaceous and earlier immigration and diversification of non-therian mammals

mammals, of which over two-thirds (12 genera) are metatherians, followed by a diversity of placentals (eutherians) that includes five genera of mioclaenid 'condylarths,' a pantodont, and a henricosborniid notoungulate (Table 1; Figs. 11 and 12). In that there are no antecedent or succeeding records of these Tiupampan genera in South America (see Goin et al. 2006a; Gelfo et al. 2009), all 19 are scored as FADs and LADs (Table 2).

Regarding metatherians, *Cocatherium* from the pre-Tiupamian, earliest Paleocene, Grenier Farm fauna (13, Fig. 2b) is considered (Goin et al. 2006a) to be a polydolopimorphian. A recent phylogenetic analysis led Goin et al. (2009) to suggest that polydolopimorphians are members of the Australidelphia clade, as are the microbiotheres (Nilsson et al. 2010). Along with the Tiupampan polydolopimorphian, *Roberthoffstetteria*, the clear early Paleocene presence of this relatively derived group contributes to the evidence in favor of there having been a Late Cretaceous entry and evolution of metatherians in South America. Paleogene South American polydolopimorphians and microbiotheres are not suggested as having an affinity with known Australian taxa, but the likely Late Cretaceous presence of these australidelphians in South America would provide a potential early biotic link between the two continents (Muizon 1991; Muizon and Brito 1993; Woodburne and Case 1996; Nilsson et al. 2010; Beck 2012). This link also may be reflected by the later Paleocene presence of monotremes in Peligran faunas of Patagonia (Table 1; Pascual et al. 1992).

The great metatherian diversity in the Tiupampan supports the inference of there having been a strong prior endemic radiation of the group. In Table 1, a majority of the 'ameridelphians' are considered to reflect this South American radiation (three pucadelphyids, a jaskhadelphyid, and a mayulestid). *Mayulestes* was once regarded as the

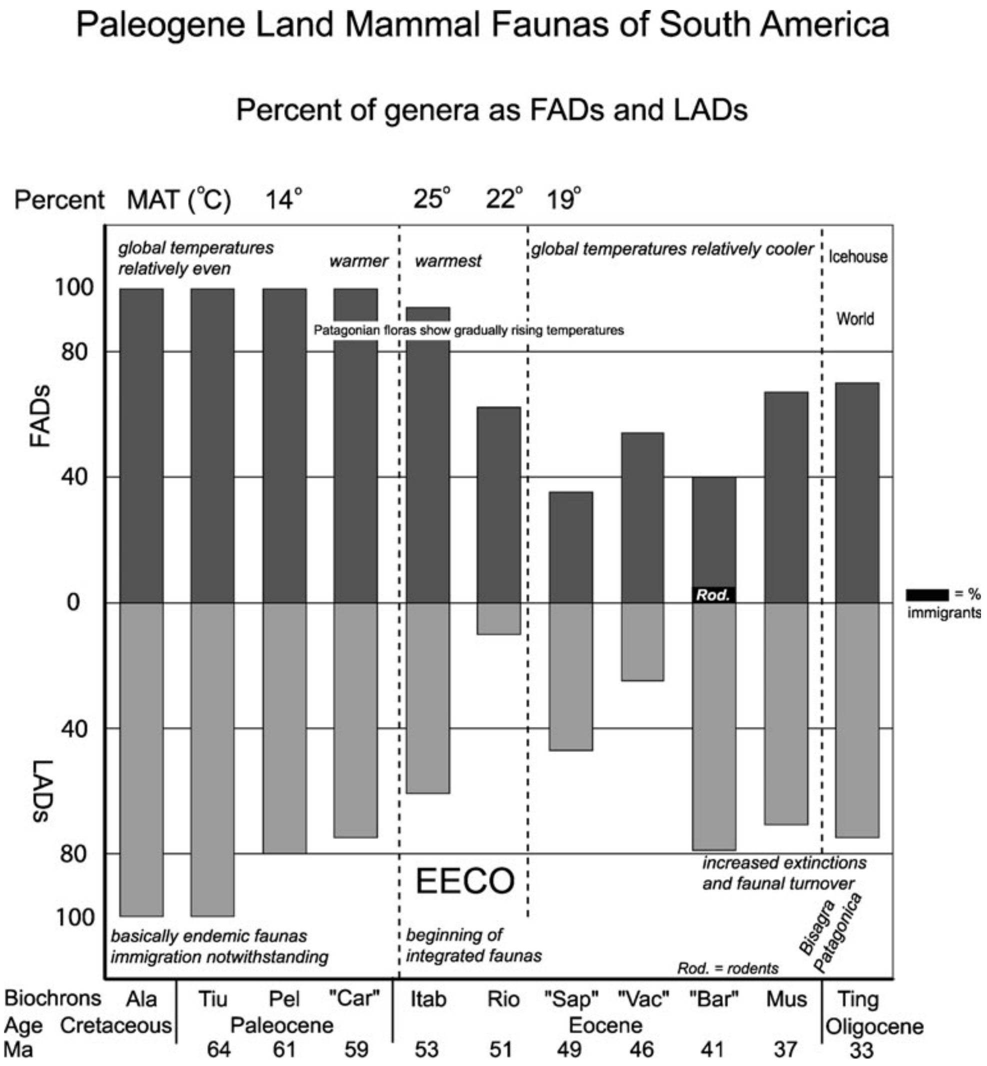


Fig. 10 Paleogene land mammal faunas of South America showing the percent of genera that represent FADs or LADs in the faunal units. Biochronological and other abbreviations as in Fig. 9. Ma refers to megannum

earliest, and basalmost, sparassodontan (Muizon 1991, 1998), whereas it now is considered as a basal taxon to other South American metatherians (e.g., Forasiepi 2009). The other, indeterminate 'ameridelphians,' *Incadelphys*, *Tiulordia*, and *Szalinia*, further broaden the endemic Tiupampan diversity, as does the ?sparassodontan *Allqokirus* (Table 1), all of which points to a pre-Tiupampan radiation of the group.

The 'ameridelphian' *Khasia* is an enigmatic taxon whose precise affiliations are still to be proven. Originally regarded as a microbiothere (Muizon 1991), more recently it has been argued to have pediomyid affinities (Goin et al. 2013). If the latter is the case, it would also argue in favor of close affinities between South American and North American early metatherians (Case et al. 2005). The didelphimorphian *Peradectes* (Horovitz et al. 2009) is the last element of that archaic marsupial clade from North America (but see Goin and Abello 2013). Pediomyids are not known from younger deposits in South America. In summary, the basic ancestry of South American metatherians was in North America. The early Paleocene South American diversity of the group suggests its Late Cretaceous entry.

Regarding placental mammals, *Molinodus* and four other taxa (Table 1; Fig. 12) provide a major, but also nearly final, diversity of kollpaniine 'condylarths,' which have a lingering presence in the "Barrancan" (*Pascualodus*, Table 1). The archaic placental group Pantodonta is last represented in South America by the Tiupampan *Alcidedorbignia*. Muizon and Cifelli (2000) noted the basic similarity between Puercan-aged North American 'condylarths' and those of South America, and suggested a close temporal link between them (Fig. 1). The first henricosborniid signals the beginning of the notoungulates, a conspicuous group in Itaboraian and later Paleogene faunas (Fig. 12), as well as continuing into the Pleistocene (McKenna and Bell 2002).

The fauna appears to have been dominated by metatherian insectivorous-omnivorous taxa of minute to small size (Fig. 11). All insectivores are below 50 g in body mass, and a very small taxon of 5 g (*Jaskhadelphys*) occurs in this trophic category (Zimicz 2012). The carnivore niche is also

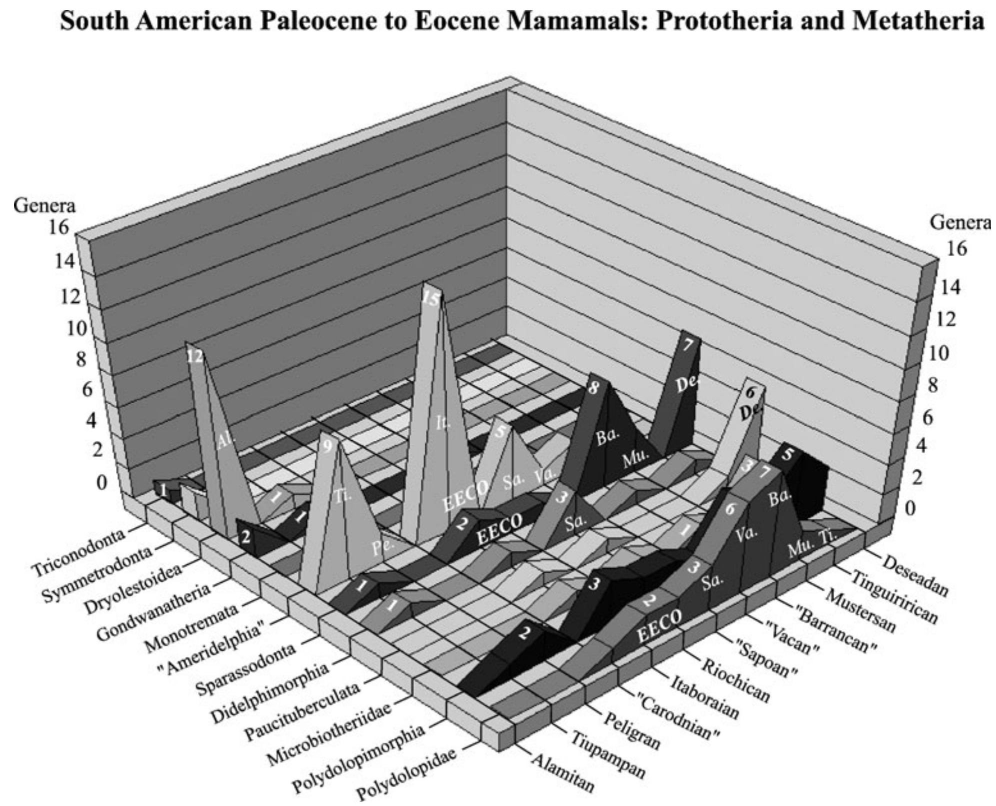


Fig. 11 South American Prototherian and Metatherian Paleocene to Eocene mammals, from Alamitan to Deseadan, showing numbers of genera for each group, as listed. Numbers refer to the genera as indicated. *EECO* is the interval from the Itaboraian through the "Vacan" that corresponds to the Early Eocene Climatic Optimum. Abbreviations such as *Ba*., *It*. refer to the equivalent SALMA. Due to visual layout, the "Sapoan" presence of a gondwanathere and the Peligran presence of a monotreme are not displayed. The Alamitan dryolestoid record includes the seven families indicated in Table 1; only a single peligrotheriid is found later (Peligran) in Paleogene mammal faunas. The nine 'ameridelphians' are unique to the Tiupampan. Beginning in the Peligran a derorhynchid and a sternbergiid continue later, showing the beginning of faunal continuity. The Itaboraian surge reflects five protodidelphids, three sternbergiids, six indeterminate genera, and a derorhynchid. The last episode of major diversity is recorded in the "Sapoan," with a protodidelphid, two derorhynchids, a sternbergiid and *Marmosopsis*. The three "Sapoan" didelphimorphs continue the diversity of that biochron (a peradectid and two caroloameghiniids). The Sparassodonta show a beginning diversity (one genus) in the Tiupampan, but their major pulse is recorded with eight genera in the "Barrancan" (three borhyaenoids and five basal forms), with hathliacynids (three) and borhyaenoids (four) being emphasized in the Deseadan. Paucituberculatans begin in the Itaboraian, but are rare until the Deseadan, with a caenolestid, a pichipilid, three palaeothentids, and an abderitid. Microbiotheriids begin in the Itaboraian, but only diversify in the Tinguiririca (three). Polydolopids begin in the "Carodnian" and increase in diversity from the Itaboraian. Major development is seen in the "Vacan" (six) and "Barrancan" (seven), but the family terminates by the Deseadan. Other polydolopimorphians begin in the Tiupampan, with small peaks in the Peligran and Itaboraian, but increase to four in the "Barrancan" and five in the Tinguiririca

Table 2 South American paleocene and eocene mammal faunal evolution

SALMA	Genera	FADs	% FADS	LADS	%LADS	Through	%Through
Alamitan	17	17	100	17	100	0	0
Tiupampan	19	19	100	19	100	0	0
Peligran	10	10	100	8	80	0	0
Carodnian	4	4	100	3	75	0	0
Itaboraian	51	48	94	31	61	1	2
Riochican	21	13	62	2	10	8	38
Sapoan	34	12	35	16	47	13	38
Vacan	55	30	54	14	25	15	27
Barrancan	73	29	40	58	79	8	11
Mustersan	42	28	67	30	71	4	10
Tinguiririca	40	28	70	30	75	4	10

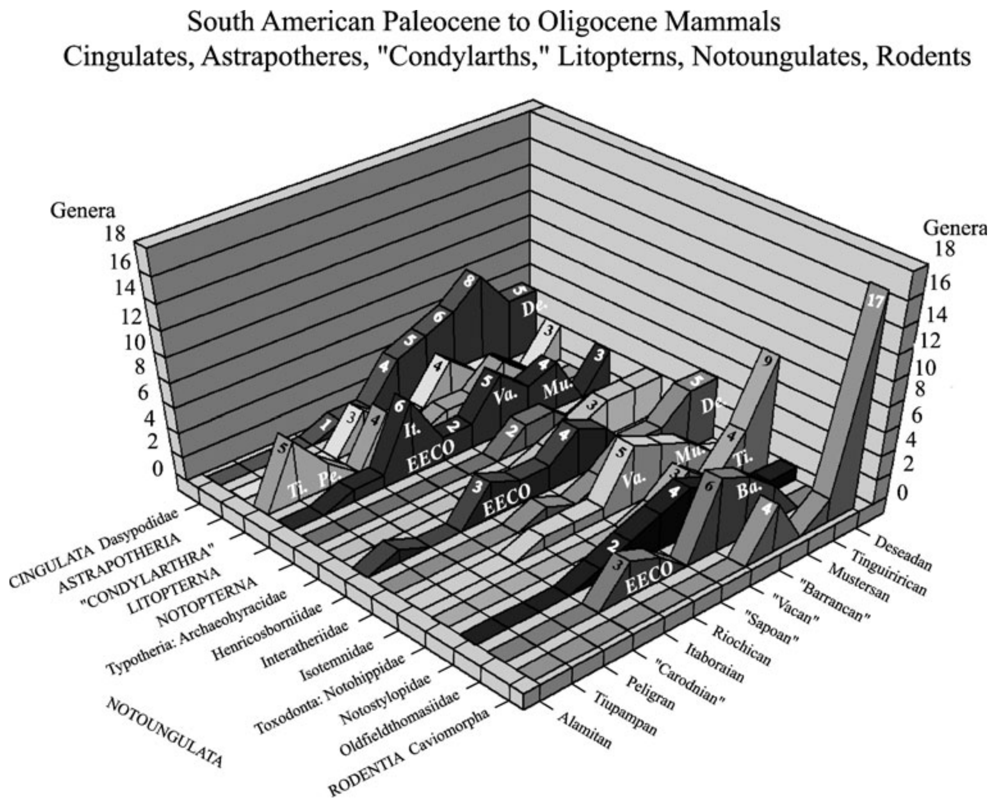


Fig. 12 South American Paleocene to Eocene placental mammals represented by genera of cingulates, astrapotheres, 'condylarths,' litopterns, notoungulates, and rodents. Numbers, *EECO*, and abbreviations are as in Fig. 11. The dasypodid cingulates are the only family shown. Other families are of later origin: Mustersan for the Glyptodontidae, and Deseadan for the Palaeopeltidae and Mylodontidae. Megalonychidae begin in the Tinguirirican. Of the astrapotheres, the trigonostylopids (not shown) are relatively unimportant, but the astrapotheriids begin in the Itaboraian and carry through to the Deseadan. Kollpaniid 'condylarths' have a strong presence (five genera) in the Tiupampan, but are otherwise not present. The didolodontids begin in the Peligran, and from the Itaboraian to Mustersan maintain a relatively continuous record of about three genera. Litopterns are represented by eight families, beginning in the Peligran (Notonychopidae) and "Carodnian" (Anisolambdid), but the group begins its diversification in the Itaboraian with three protolipternids, another anisolambdid, and another notonychopid and a sparnotheriodontid. This diversity is continued in the "Vacan," but diminishes subsequently, and doesn't survive the "Barrancan." Subsequently, new macraucheniids (one genus) and two proterotheriids begin in the Mustersan, and these families carry on into the Deseadan. Notopterna pulse briefly in the "Vacan" and "Barrancan" and persist (one genus) in the Tinguirirican. Notoungulates comprise the Typotheria and Toxodonta. Typothere groups begin with a Tiupampan henricosborniid, but the family typically diversifies in the Itaboraian with three genera, two of which carry through to the "Vacan," where two more are added. The family doesn't survive the "Barrancan." The Archaeohyracidae begins in the "Vacan" and begins to diversify in the "Barrancan" (three) and maintains three genera into the Deseadan. The Hegetotheriidae and Mesotheriidae are fundamentally Deseadan groups and not shown here, and the Archaeopithecidae is represented by two genera from Riochican to "Vacan," with a single taxon in the "Barrancan." The Interatheriidae about mirrors the Archaeohyracidae after its beginning in the Riochican, a single taxon in the "Vacan," and a count of three each from the "Barrancan" to the Deseadan. The Isotemnidae originated in the Itaboraian and like many others, has a pulse in the "Vacan," but is extinct after the Tinguirirican. Toxodont notoungulates typically originate in the Itaboraian and show a reasonable diversity through the "Barrancan," with many still being present in the Deseadan. The Leontiniidae (ten genera), Homalodotheriidae (two), and Toxodontidae (one), not shown, have a post-"Vacan" record (the last two being only from the Tinguirirican and Deseadan, respectively). The Notohippidae has a similar record, but is more diverse (16 genera), begins in the "Vacan," and by the Deseadan has expanded to nine genera. The Notostylopidae begin somewhat earlier (Itaboraian), increase to a maximum of four genera in the "Vacan," but then decline to a single genus in the Deseadan. The Oldfieldthomasiidae begins with a reasonable diversity (three) in the Itaboraian, increases to a peak of six in the "Vacan," and diminishes to extinction by the Tinguirirican (no taxa). The Pyrotheria (single taxa in the "Vacan," Mustersan, Tinguirirican, and Deseadan) and the Xenungulata (two genera in the "Carodnian" and Itaboraian) are not illustrated. The Rodentia are first known in the "Barrancan" (three basal caviomorphs and an octodontoid), re-occur in the Tinguirirican (a cavioid and a chinchilloid) and the Deseadan (seven cavioids, six octodontoids, two chinchilloids, and an erethizontoid). The single Deseadan primate is not shown

filled by metatherians, the small sparassodontan (*Allqokirus*), and the medium-sized 'ameridelphians' *Mayulestes* and *Andinodelphys*. Other small-sized metatherians occupy the mixed insectivory-frugivory niche (e.g., *Roberthoffstetteria*). The remainder of the fauna appears to have been adapted to largely browsing herbivory. The Bolivian Tiupampa fauna occurs far to the north of Argentina (12, Fig. 2b), but the preceding discussion on distribution and paleoecology suggests that its climate would have been tropical to subtropical and similar to that of the Palacio de los Loros flora of Argentina (3*, Fig. 2b), or the Cerrejón flora of Colombia (1*, Fig. 2b).

None of the 19 Tiupampan genera is related to any genus or higher taxonomic category of Alamitan age (Gelfo et al. 2009; Table 1). The totally new fauna can only have been derived from immigration from North America in the latest Cretaceous or earliest Paleocene (as discussed above). A similar statement applies to the ?basal polydolopimorphian, *Cocatherium*, from the earlier Paleocene Grenier Farm Local Fauna, Lefipán Formation of Chubut Province, Argentina (G, Figs. 9 and 10; Case et al. 2005; Goin et al. 2006a). Although the exact affinities of *Cocatherium* are not known, it certainly belongs to the Polydolopimorphia, and probably represents a basal Polydolopiformes close to *Roberthoffstetteria*. It thus is a derived, rather than stem, metatherian and its early Paleocene age supports the interpretation that 'ameridelphian' and other stem-group metatherians, as well as their more derived lineages now found in the Tiupampa fauna, reflect a Late Cretaceous dispersal from North to South America. The 'condylarths' support an early Paleocene dispersal from North America as well. Except for the possible therian from the Adamantina Formation of Brazil (see above) such mammals have not been found in South American Late Cretaceous faunas as currently known, so the matter remains unresolved. The above discussion of the menispermacean podocarp *Palaeoluna* from the Cerrejón flora of Colombia also supports these dispersals, and the early Paleocene presence of australidelphians raises the possibility of a link between South America and Australia at that time or possibly in the Late Cretaceous.

Peligran The fauna from Punta Peligro, Chubut Province, Argentina (14, Fig. 2b) forms the basis of the next-younger Peligran SALMA (Fig. 1) and is considered to be middle Paleocene in age (Gelfo et al. 2009). This fauna likewise contains a diversity of non-therian mammals, such as a peligrotheriid dryolestoid, a sudamericid gondwanathere, and the only South American monotreme (Pascual et al. 1992). The metatherians (Table 1) are represented by two genera of 'ameridelphians' and two others of polydolopimorphian affinities. Goin et al. (2009) indicated that trends toward insectivory, carnivory, frugivory, and omnivory were already established in these taxa. The insectivorous and frugivorous forms are small-sized, with body mass below 100 g and 400 g, respectively. Derorhynchid 'ameridelphians' were strict insectivores while polydolopimorphians were mainly frugivores (Zimicz 2012). Other 'ameridelphians' such as *Didelphopsis* were omnivorous (Zimicz 2012) or carrion-eaters (Clemens 1966). The gondwanatheres are represented by the hypsodont *Sudamerica ameghinoi*, an herbivorous taxon with presumably fossorial and possibly semi-aquatic habits (Koenigswald et al. 1999). The monotreme *Monotrematum sudamericanum* likely fed on invertebrates, as do living monotremes that also have semi-aquatic and fossorial habits (Koenigswald et al. 1999). Dryolestoids are generally considered to have fed on insects or invertebrates (Kielan-Jaworowska et al. 2004). Placental mammals from Punta Peligro include two genera of didolodontid 'condylarths,' a notonychopid litoptern, and a single henricosborniid notoungulate (Table 1).

Gelfo et al. (2009) discussed the paleobiology of the Peligran fauna. Vegetation was forested; climate subtropical, humid, also reflected by the presence of crocodiles and chelyid turtles (freshwater swamps; Pascual and Ortiz-Jaureguizar 1991; Pascual et al. 1996). Pollen indicates the presence of swamp and mangrove communities (Petriella and Archangelsky 1975; Romero 1986, 1993; Troncoso and Romero 1998), as does sedimentological evidence (Andreis et al. 1975; Andreis 1977).

As indicated in Tables 1 and 2, and Figs. 9 and 10, the 11 Peligran genera are grouped as ten FADs (100 %) and eight LADs (80 %), with two taxa continuing onward (the 'ameridelphian' *Derorhynchus* - to "Sapoan," and *Didelphopsis* - to Itaboraian). In that context, the Peligran is the first biochron to have a link to subsequent (but still not previous) units. Although total numbers are small, this represents 20 % of the Peligran fauna. The Peligran also contains some of the last Gondwanan elements in South America: the dryolestsoid (*Peligrotherium*), the hypsodont sudamericid gondwanathere (*Sudamerica*), and the monotreme (*Monotrematum*). Hypsodont gondwanatheres are also known from the mid Eocene of Antarctica (Goin et al. 2006b), Perú (Goin et al. 2004; Antoine et al. 2011), and Patagonia (Goin et al. 2012b). Monotremes still live in Australia, of course, and *Necrolestes* (early Miocene, Argentina) has been considered as related to *Peligrotherium* (Rougier et al. 2012; Chimento et al. 2012).

As for the Tiupampan, the placental mammals apparently were omnivorous or browsing herbivores and, considered together, it appears that this niche was also reasonably well represented in the overall small-sized sample of taxa. The 'condylarths,' 'ameridelphians,' and polydolopimorphians are about equally diverse, with two species each, so that the insectivorous and omnivorous-herbivorous niches are about equally represented. The nearby Palacio de los Loros flora (3*, Fig. 2b) indicates the presence of tropical to subtropical, warm, and moist climates.

To the extent that this fauna is representative of its community, the low number of carnivorous species in relation to the potential prey population, as well as the apparently small number of actual carnivore specimens, is in line with the demonstration by Croft (2006) that metatherian carnivores in South American faunas were never developed either numerically or as in diversity and adaptive range to the extent seen in the faunas of the Northern Hemisphere or Africa where carnivores are basically placental mammals.

As mentioned by various authors (e.g., Patterson and Pascual 1972; Marshall 1978; Prevosti et al. 2011), both predatory birds and crocodiles may have had a more definite structural role and feeding strategy in the South American faunas, in contrast to their more marginal roles in restricted biotopes as seen in other continents.

Whereas the therian mammals likely were indigenous descendants of a Late Cretaceous or earliest Paleocene immigration event (or events) from North America, the monotreme (Pascual et al. 1992) documents a distinct southern Gondwanan distribution, with their earliest record being the Early Cretaceous of Australia (Rich et al. 2001; Musser 2006; Rowe et al. 2008). The sudamericid gondwanathere represents a similar Gondwana context.

Herrera et al. (2011) noted the presence of the menispermacean podocarp *Stephania* in the medial Paleocene of Colombia (Cerrejón flora) and the Recent of India and Australasia, and suggested a possible South Amerian origin for the Australian distribution of this genus. It is clear from discussions in Renner et al. (2010) and Michalak et al. (2010) that land-based dispersals are preferred for land plants, and that whereas trans-oceanic dispersals may be aided by wind or bats, vegetations mats are the preferred method in such cases. At the moment dispersal scenarios for *Stephania* are hindered by the lack of fossil data from India and Australasia.

Carodnian This informal biochron (see Appendix I) corresponds to the *Carodnia* faunal zone of Simpson (1935). It is considered to be of late Paleocene age, and about 58 Ma old (Fig. 1), originally developed from what is now known as the Peñas Coloradas Formation of the Río Chico Group (Fig. 5) in Chubut Province, Argentina (15, Fig. 2b). The "Carodnian" lacks non-therian mammals (Fig. 11), in contrast to older SALMAs - and resembles younger Paleogene mammal intervals in that respect - but the sparse faunal content may not be definitive in that regard. At present, the "Carodnian" (Tables 1 and 2) is composed (Table 1) of only four taxa (Pascual and Ortiz-Jaureguizar 2007; Gelfo et al. 2009). These include the oldest polydolopid metatherian, *Amphidolops*, the anisolambdid litoptern, *Wainka*, and the oldest xenungulates, *Carodnia* and *Notoetayoa* (Gelfo et al. 2008). The fauna shows a nearly equal number of FADs and LADs (Table 2; Figs. 9 and 10).

The "Carodnian" unit is linked with later faunas by the FAD of *Amphidolops* (to "Barrancan"). *Notoetayoa* and *Carodnia* are unknown elsewhere and scored as FADs and LADs as sole South American "Carodnian" xenungulates. On this weak basis, the "Carodnian" would be most similar to the Brazilian Itaboraian interval, elements of which are also found in the Las Flores fauna of Patagonia (28, Fig. 2c). If the similarity between the "Carodnian" and Itaboraian intervals is borne out by further evidence, then the development of the increasingly integrated Paleogene faunas in South America may have its base in the "Carodnian," possibly coeval with the MPBE (Fig. 1).

Presumably these placental groups represent browsing herbivores. Based on groups found before and after the Carodnia Zone, the presence there of a variety of metatherians, including didelphimorphians, sparassodontans, and polydolopimorphians, would be expected, along with didolodontid 'condylarths.' The climatic setting for this fauna presumably was similar to that of the Peligran. The presence of vertical Hunter-Schreger bands in *Carodnia* suggests at least local presence of abrasive foodstuff (Line and Bergqvist 2005).

Itaboraian The Itaboraí fauna of Brazil (Fig. 1; 29, Fig. 2c) is one of the most diverse Paleogene faunas of South America (Table 1), and is the basis for the Itaboraian SALMA. We regard the mammalian fauna from the *Kibenikhoria* Faunal Zone (e.g., the Patagonian Las Flores fauna) as contemporary with the Itaboraian. Although not directly dated isotopically, it is here (Appendix I) considered to be about 53 m.y. old and to correspond with the early part of the EECO (Figs. 1, 9, 10, 11, and 12). See Oliveira and Goin (2011) for a slightly older age. Bellosi and Madden (2005) and Gelfo et al. (2009) provide additional context.

In northwestern Argentina, the Río Loro Formation of Tucumán Province (46, Fig. 2c; Soria and Powell 1982) has yielded a group of very primitive ungulates, as well as fish, crocodiles, and turtles. The mammals include a small notoungulate, *Satshatemnus*, possibly related to the Henricosborniidae; a notonychopid litoptern, *Notonychops*, related to *Reqisia* from the Patagonian Peligran SALMA; and a generalized astrapotherian, *Eoastrapostylops*, that is clearly more primitive than either *Trigonostylops* (Riochican to Mustersan) or *Tetragonostylops* (Itaboraian to "Vacan"). The beds with this fauna overlie ones of Cretaceous age and are not clearly correlated with the nearby Santa Bárbara Subgroup of late Paleocene to early Eocene age (Quattrocchio et al. 1997; Marquillas et al. 2005), but such a correlation would be compatible with a potential Peligran or "Carodnian" evolutionary status of the fossil mammals. If this is confirmed by future work, it would result in earlier FADs of *Satshatemnus*, *Notonychops*, and *Eoastrapostylops*, all of which now are first known in the Itaboraian (Table 1).

In Perú, mammals of the Laguna Umayo local fauna and the 140 m superjacent Chulpas level (47, Fig. 2c) are considered very probably to be of late Paleocene-early Eocene age (Sigé et al. 2004). An approximate correlation with the Brazilian Itaboraian (Gelfo et al. 2009) is based on a shared notoungulate and a didolodontid. Faunal differences between the Peruvian and Brazilian faunas likely reflect paleobiogeographic factors (Gelfo and Sigé 2011).

The metatherian diversity is continued from the Tiupampan (Fig. 11), with 15 genera of 'ameridelphians,' two sparassodontans, a caroloameghiniid, a paucituberculatan, a microbiothere, and several polydolopimorphians. Among the last are *Bobbschaefferia* (family indet.), a bonapartheriid, a gashterniid, and two polydolopids (Table 1). Especially with respect to sparassodontans (eight) and polydolopids (seven), this overall degree of metatherian diversity will continue into the "Barrancan" SALMA (Fig. 11). Notable metatherian novelties include the first protodidelphids and a number of indeterminate 'ameridelphian' genera, the first basal paucituberculatans, microbiotheres, gashternids, and a beginning diversity of polydolopids (Fig. 11).

Itaboraian placental mammals are represented by South America's oldest cingulate dasypodid (*Riostegotherium*) and basal astrapotheres (*Eoastrapostylops*, *Shecenia*, *Tetragonostylops*; Table 1; Fig. 12). The first members of several other groups (Table 1) include protolipternid litopterns (*Miguelsoria*, *Protolipterna*, and *Asmithwoodwardia*), sparnotheriodontid (*Victorlemoinea*, to "Vacan") litopterns, the isotemnid notoungulate (*Isotemnus*), and the oldfieldthomasiids (*Colbertia*, to Mustersan, *Itaboraitherium*, and *Kibenikhoria*).

New diversity (Table 1) is also indicated by four didolodontid 'condylarths,' the above diversity of litopterns (including an anisolambdid), and five more notoungulates (*Satshatemnus*, *Perutherium*, *Henricosbornia*, *Peripantostylops*, and *Simpsonotus*). Figure 12 shows the three henricosborniids, the first isotemnid, as well as the first notostylopid and oldfieldthomasiids (three).

Numerous FADs demonstrate the basic coherence in community structure from the Itaboraian to later biochrons. 'Ameridelphian' metatherians include *Protodidelphis*, *Itaboraidelphys*, and *Marmosopsis* (to "Sapoan"), and *Derorhynchus* is a through-going genus (to the "Sapoan"). The sparassodontans, *Nemolestes* and *Patene*, continue to the "Barrancan," *Procaroloameghinia* is the oldest (and sole) member of the caroloameghiniid didelphimorphians (to "Sapoan"), but the family continues on to at least the Tinguirirican (*Canchadelphys*; Table 1). Polydolopimorphian continuity is shown by the FADs of *Gashternia* (to "Sapoan"), *Pliodolops* (to "Barrancan"), and an unnamed genus (to "Sapoan"; Chornogubsky 2010). The 'ameridelphian' *Didelphopsis* is the sole LAD from a prior biochron (Peligran).

Placental FADs that contribute to community coherence are represented by the xenarthran *Riostegotherium* (to "Sapoan"), a first astrapotheriid astrapothere, *Tetragonostylops* (to "Vacan"), the didolodontid 'condylarth,' *Ernestokokenia* (to Mustersan), the protolipternid litoptern *Asmithwoodwardia* (to "Vacan"), the anisolambdid *Anisolambda* (to "Barrancan"), the sparnotheriodontid *Victorlemoinea* (to "Vacan"), the henricosborniid notoungulates *Henricosbornia* (to "Barrancan") and *Peripantostylops* (to "Vacan"), the first isotemnid, *Isotemnus* (to "Vacan"), and a first oldfieldthomasiid, *Colbertia* (to Mustersan).

Taxa that are both FADs and LADs, and thus serve to illustrate endemic diversity (Table 1), are the 'ameridelphian' taxa *Carolocoutoia*, *Guggenheimia*, *Periprotodidelphis*, *Zeusdelphys*, *Carolopaulacoutoia*, *Eobrasilia*, *Gaylordia*, *Minisculodelphis*, *Monodelphopsis*, *Sternbergia*, the paucituberculatan *Riolestes*, the microbiotheriid *Mirandatherium*, and the polydolopimorphians *Bobbschaefferia* and *Epidolops*. Among the placentals, comparable new taxa are the other two first astrapotheriid astrapotheres, *Eoastrapostylops* and *Schecenia*, the didolodontids *Umayodus*, *Lamegoia*, and *Paulacoutoia*, the protolipternid litopterns *Miguelsoria* and *Protolipterna*, the first notostylopid, *Notonychops*, the notoungulates *Perutherium* and *Satshatemnus*, the henricosborniid *Simpsonotus*, the other first oldfieldthomasiids, *Itaboraitherium* and *Kibenikhoria*, and the xenungulate *Etayoa*.

The Itaboraí fauna is not only the largest, but also the most diverse yet discussed, shown in part by the high percentage of LADs (61 %) indicated in Tables 1 and 2 and Fig. 10. This figure is the greatest for any well-integrated SALMA until the "Barrancan," Mustersan, and Tinguirirican (the "Carodnian" and Divisaderan are based on samples that are too small to be instructive here and virtually all Alamitan and Tiupampan taxa are endemic and unique). The Itaboraian also is the first biochronological unit in the sequence in which taxa are extensively shared with both previous and subsequent units. In that sense, the South American land mammal faunas began to demonstrate interrelationships with others at this time, rather than being essentially isolated entities. Under current appraisals, the Itaboraian is the earliest Eocene fauna of South America. At ca 53 Ma (above) it post-dates the beginning of the Eocene by about 2 m.y. and is within the early part of the EECO (Fig. 1).

In being located essentially within the present as well as former Neotropical region, the Itaboraí fauna likely enjoyed warm and humid tropical environments, likely more so than those recorded by the Laguna del Hunco flora of Patagonia (Fig. 8; also 18*, Fig. 2c). The metatherians inhabited the insectivore, frugivore, herbivore (folivore), and carnivore niches. Their sizes ranged from small to medium (Zimicz 2012). The apparently smallest metatherian known (*Minusculodelphys*) is recorded in the Itaboraian (Table 1), with a body mass similar to a pigmy shrew (Goin et al. 2013). The insectivore niche was mainly occupied by the Derorhychidae and Peradectidae, whereas frugivorous taxa are represented by the Protodidelphidae, Bonapartheriidae, and Caroloameghiniidae. The folivorous niche was occupied by members of the Gashternidae; sparassodontans were carnivores. The latter were represented by a mesocarnivore, *Patene*, and a hypercarnivore *Nemolestes* (Zimicz 2012).

The placental mammals apparently reflect a diversity of browsing herbivorous niches. The trigonostylopid astrapotheres were omnivorous browsers comparable to suids (Soria and Bond 1984). The didolodontid 'condylarths' probably were omnivores. The notonychoipid litopterns likely were browsers, as was the notoungluate *Satshatemnus*, along with the henricosborniids, isotemnids, oldfieldthomasiid, and notostylopid. The sparnotheriodontids, protolipternids, and anisolambdids may have been browsing forms, as well. Sparnotheriodontids and astrapotheres possess teeth with vertical Hunter-Schreger bands, interpreted as an adaptation to resist cracking when consuming tough materials as in modern rhinoceroses (Boyde and Fortelius 1986).

Riochican The Riochican SALMA was based on the *Ernestokokenia* faunal zone of the Río Chico Formation, Chubut Province, Argentina (Simpson 1933, 1935; Fig. 5). Note that the Koluel Kaike Formation now represents the *Ernestokokenia* faunal zone as the uppermost part of the Rio Chico Group (Fig. 5). The Riochican is considered to be late early Eocene in age (Fig. 1), rather than late Paleocene as in Flynn and Swisher (1995: Fig. 3; see Appendix I). Potential sample bias likely underestimates the metatherian and ungulate components but, at present, the Riochican is composed of fewer taxa than the Itaboraian (Tables 1 and 2). Still, the overall diversity increased, as shown by the prevalence of FADs (13; 62 %) versus LADs (two; 10 %; Tables 1 and 2; Figs. 9 and 10).

Of the total of 21 land mammal genera (Table 1), metatherians include a sparassodontan, a glasbiid, a gashterniid, and two polydolopid polydolopimorphians. Among this group FADs are represented by the glasbiid, *Palangania* (to the "Sapoan"), and the polydolopid, *Archaeodolops* (to the "Barrancan"). No taxa are LADs. The other taxa show continuity with preceding and succeeding biochrons. Polydolopids are somewhat more diverse (two) than other metatherians (Fig. 11).

Eleven placental mammals are FADs (Table 1), such as the dasypodid xenarthran *Prostegotherium* (to "Barrancan"), the trigonostylopid *Trigonostylops* (to Mustersan), the archaeopithecids *Archaeopithecus* (to "Barrancan") and *Acropithecus* (to "Vacan"), the henricosborniid *Othnielmarshia* (to "Vacan"), the interatheriid typothere *Notopithecus* (to "Barrancan"), the notostylopid notoungulate *Notostylops* (to "Barrancan"), and the oldfieldthomasiid notoungulates *Maxschlosseria* (to "Vacan") and *Oldfieldthomasia* (to "Barrancan"). Additionally, the notostylopid notoungulate, *Brandmayria*, is a single occurrence, and thus both FAD and LAD. *Acropithecus*, an archaeopithecid notoungulate, is the first hypsodont mammal recorded in South America. It continues to the "Vacan" (Table 1).

Eight taxa are known before and after the Riochican, contributing to the 38 % index of through-going genera (Table 2). Thus, Riochican taxa can be grouped as representing 13 FADS, two LADs, with eight known before and after that time. Originations somewhat exceed the combined last and continuing occurrences. Litopterns and notoungulates clearly dominate the placental group, although no particular family prevailed (Table 1), and all placentals attest to a diversity of herbivorous habitats. The increased diversity and integration of its taxa with preceding and succeeding faunas (38 % are through-going) continues the trend established in the Itaboraian with its high number of FADs (19 of 48, or 40 %) that persist in younger biochrons.

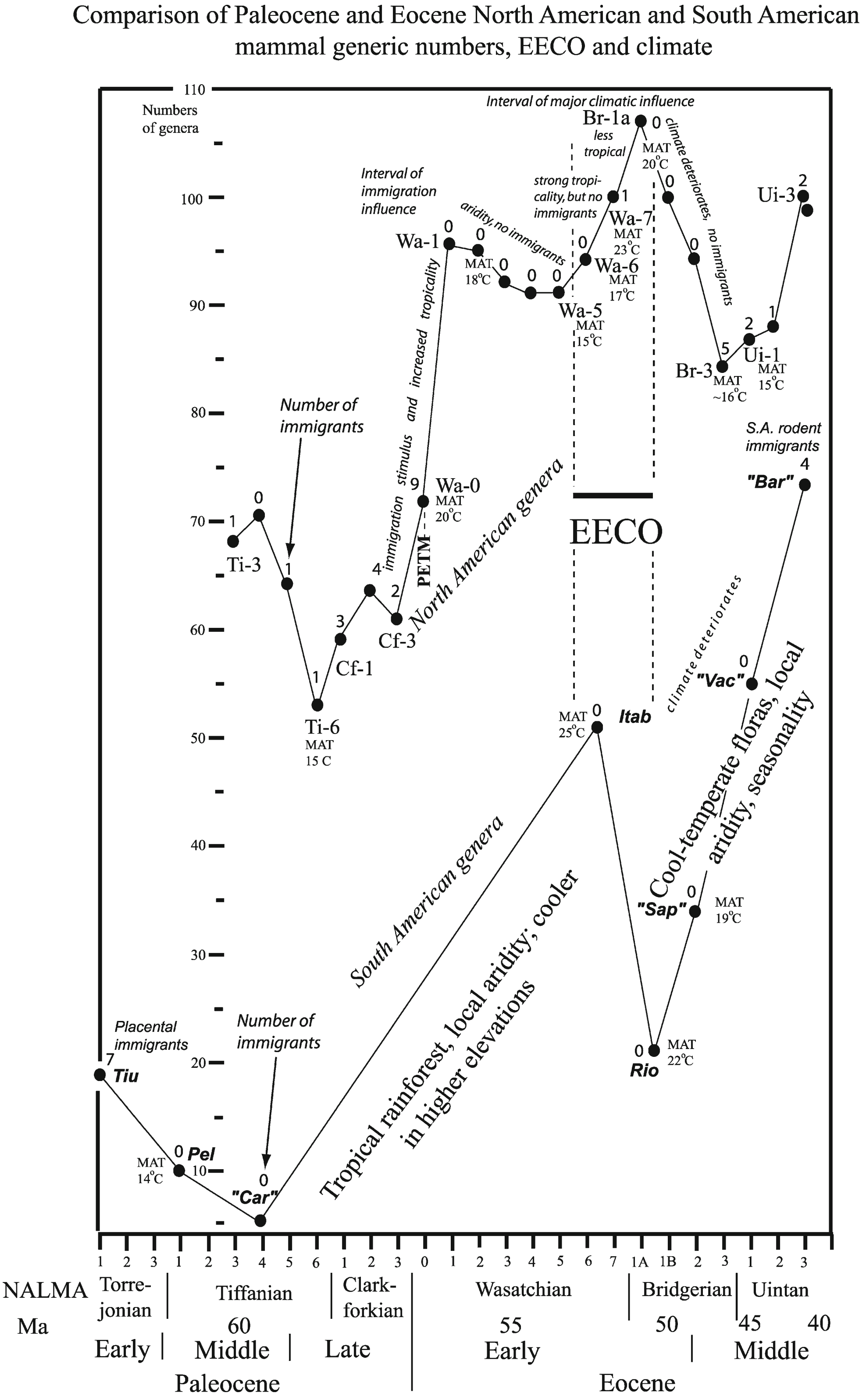
With ten notoungulates, two litopterns, a 'condylarth,' and an astrapothere (Fig. 12), it appears that the majority of fauna is composed of moderate-sized herbivores, with the five metatherians and the single xenarthran likely occupying a variety of insectivore-omnivore niches. It should be noted, however, that screen-washing efforts in Riochican-aged beds have been significantly less than those made in older (e.g., Itaboraian) or younger (e.g., "Sapoan") levels. This may account for the bias clearly shown by the less represented small-sized taxa.

If the Laguna del Hunco flora is representative of the Patagonian region, it would appear that the climatic setting was essentially subtropical. The Riochican is within the later part of the EECO (Figs. 1, 9, 10 and 13). In that context, Riochichan metatherians are well adapted to a tropical or subtropical forest. Although the record is sparse, the trophic types for the Riochican SALMA are frugivorous-insectivorous taxa of small size, and medium-sized folivorous and carnivorous forms. It is apparent that the strong diversity of ungulate groups also reflects a comparable diversity in floral ecololigies, as a continuation of those from the Itaboraian.

Sapoan The Paso del Sapo fauna, and the "Sapoan" informal biochron, is derived from deposits that flank Laguna del Hunco in Chubut Province, Argentina (33, Fig. 2c). As discussed in the Appendix, as well as in Tejedor et al. (2009), the mammal-bearing sediments are associated with volcanic rocks that provide an isotopic age range of 47–49 Ma for the fauna, thus considered to be of about early middle Eocene age (Fig. 1); it also is considered to be essentially coeval with the La Meseta fauna (34, Fig. 2c) of the Antarctic Peninsula (Goin et al. 2012b). Elevating this biochronological unit to full "Sapoan" SALMA status awaits the complete description of the taxa contained within it. As indicated on Figs. 1, 9, 10, and 13 the "Sapoan" appears to shortly post-date the end of the EECO, in which global cooling had commenced.

Tables 1 and 2 show that there now are 34 land mammals in the Paso del Sapo Fauna, about equally balanced between

Fig. 13 North American Paleocene and Eocene Mammals, percent FADs and LADs. After Woodburne (2009b: fig. 6). Allowing for fewer data points in South America and the less precise allocation of SALMAs to numerical ages, the pattern of generic numerical diversity is overall comparable between North and South America. The very small number of genera (four) in the "Carodnian" (***Car***) likely is not representative, but the strong increase in generic numbers in the Itaboraian (***Itab***) as compared to earlier South American units is comparable to the approximately coeval in North America (Br-1a), as is the strong increase in MAT (ca 20–25 °C; ***Itab***, Wa-7, Br-1a). The first response to strong climatic deterioration similarly results in a diminution of taxa and temperature (Br-3, ***Rio***), with subsequent change to more cool-temperate conditions and decreased temperatures reflected by a renewed development of generic diversity (***Bar***, Ui-3). SALMAs are: ***Tiu*** (Tiupampan), ***Pel*** (Peligran), ***Car*** ("Carodnian"), ***Itab*** (Itaboraian), ***Rio*** (Riochican), ***Sap*** ("Sapoan"), ***Vac*** ("Vacan"), ***Bar*** ("Barrancan"). After the initial number of placental immigrants in the Tiupampan (seven), there is no further such input until the four Barrancan rodents



FADs (12) and LADs (16; Fig. 9). The Gondwanatheria persisted from Peligran and Alamitan faunas (Fig. 11, Table 1) and is similar in that respect to the La Meseta fauna of Antarctica (Goin et al. 2012b). Metatherians are distributed among five 'ameridelphians,' a sparassodontan, a paucituberculatan, three didelphimorphians, a microbiothere, and five polydolopimorphians (a glasbiid, a gashterniid, and three polydolopids; Fig. 11).

Of these, the five 'ameridelphians' (Fig. 11) include one FAD/LAD (*Pauladelphys*), and four LADs (the protodidelphid *Protodidelphis*, the derorhynchid *Derorhynchus*, the sternbergiid *Itaboraidelphys*, and the indeterminate *Marmosopsis*). The sparassodontan *Nemolestes* is a through-going taxon. The three didelphimorphians (Fig. 11) include a FAD/LAD peradectid (un-named), whereas the caroloameghiniid *Procaroloameghinia* is a LAD in association with another FAD/LAD (un-named). The paucituberculatan *Bardalestes* is yet another of the seven FADs-LADs in the fauna. The microbiothere *Eomicrobiotherium* is a FAD (to Tinguiririean), whereas through-going taxa include two of the three (Fig. 11) polydolopids, *Amphidolops* and *Pliodolops*. Another polydolopid (un-named) is a LAD, along with the gashternid *Gashternia* and the glasbiid *Palangania* (both LADs).

As regards placental mammals, the Paso del Sapo assemblage shows a strong diversity of cingulate xenarthrans (4; Fig. 12) as compared to previous biochrons, with two new genera (*Astegotherium*, *Stegosimpsonia*) as well as the through-going *Prostegotherium* (to "Barrancan"), and the *Riostegotherium* LAD. The trigonostylopid astrapothere, *Trigonostylops*, is a through-going taxon.

Two genera of didolodontid 'condylarths' (Fig. 12) are recognized (new un-named FADs/LADs). The through-going protolipternid litoptern (*Asmithwoodwardia*, to "Vacan") along with the sparnotheriodontid *Victorlemoinea*, survive an otherwise "Sapoan" low point for the group. Notongulate diversity continues (Table 1; Fig. 12), with the through-going archaeopithecids (*Archaeopithecus* and *Acropithecus*, to "Barrancan" and "Vacan," respectively) and the henricosborniids, *Henricosbornia* and *Othnielmarshia*, to "Barrancan" and "Vacan," respectively). Isotemnids show the through-going *Isotemnus* (to "Vacan"). Three notostylopids (Fig. 12) are represented by the FADs, *Edvardotrouessartia* (to "Vacan"), *Homalostylops* (to "Barrancan"), and the through-going, *Notostylops* (to "Barrancan"). Oldfieldthomasiids record a temporary lapse in the "Sapoan" (Fig. 12), which is a likely sampling bias.

The above results in a total of 34 genera distributed among 12 FADs and 16 LADs. Overall, the number of supra-generic clades in the "Sapoan" assemblage is comparable to that of the preceding Riochican and Itaboraian. Beginning with the Itaboraian, South American land mammal faunas exhibit a new presence and beginning diversity of cingulate xenarthrans (quadrupled in the "Sapoan"), and notoungulates, with henricosborniids and ("Sapoan") notostylopids being relatively numerous. It seems likely that the overall community structure and climatic setting was comparable to that of the Riochican and Itaboraian. The single gondwanathere reflects the indigenous persistence of this formerly more widespread clade, and presumably favored semi-aquatic to possibly fossorial habits. The 13 through-going genera represent 38 % of the fauna (Table 2), which, along with the 12 FADs, show a strong link to the "Vacan" SALMA. Overall the metatherians seem to favor a continuity from the Itaboraian, but less so with the "Vacan." In contrast, the placental mammals continue a "Vacan" affinity that began in the Itaboraian (Table 1).

The "Sapoan" metatherian assemblage is dominated by insectivorous-frugivorous, strictly frugivorous, and strictly insectivorous types. These categories account for 76 % of the metatherian species richness (Zimicz 2012). The other 24 % is distributed among the folivorous, folivorous-frugivorous, and hypercarnivorous niches. Body mass attained by the "Sapoan" metatherians extends from small to medium size, with the exception of the hypercarnivorous species of *Nemolestes* which probably exceeded 6 kg of body mass (Zimicz 2012).

Vacan Cifelli (1985) distinguished the Vacan and Barrancan biochrons as sub-ages of the Casamayoran SALMA. Both are preserved in the Sarmiento Formation, Chubut Province, Argentina (37, Fig. 2c). Carlini et al. (2005, 2010) proposed an age of 45 Ma for the Vacan sub-age (Fig. 1). The Vacan and Barrancan biochrons are here treated as informal SALMAs, and include taxa referred to the Divisaderan (see below). These taxa are indicated by *.

Fossils of "Vacan" age were recovered from Cañadón Vaca, located about 65 km northeast of the Gran Barranca (36, Fig. 2c), where the thickest and younger part of the Sarmiento Formation crops out. As discussed by Cifelli (1985), the lower 80 m of the Cañadón Vaca section of the Sarmiento Formation is older than at Gran Barranca, where fossils of "Barrancan" age occur close to the local base (Fig. 7). Most "Vacan" fossils occur about 5–19 m above the base of the Sarmiento Formation at Cañadón Vaca, whereas those with "Barrancan" affinities occur about 86 m above that base (Cifelli 1985; see Appendix I, here). Except for those at the top of the fossil section (86 m level), the taxa at Cañadón Vaca are distinctly different from those of Gran Barranca, and hence the basis for the "Vacan" SALMA. Cifelli (1985) considered that "Vacan" taxa are more similar to those then known from the Río Chico Formation (Koluel Kaike Formation of current literature; e.g., Ré et al. 2010a: fig. 5) than to those of the Gran Barranca (Fig. 7). Thus, the assemblages termed "Vacan" differ both faunally and stratigraphically from those assigned to the "Barrancan." If the 86 m level at Cañadón Vaca correlates with the basal part of the Sarmiento Formation at Gran Barranca, then nearly 86 m of section have been removed at the unconformity between the Sarmiento and Koluel-Kaike formations shown on Fig. 7.

The Santa Bárbara subgroup (Salta Group) in Salta and Jujuy provinces also bears a very interesting mammal fauna. The Lumbrera Formation has yielded a series of mammals that differ from those of Patagonia, apparently a reflection of biogeographic differences. The upper and lower intervals of the Lumbera Formation apparently extend from the "Vacan" to the "Barrancan," and the uppermost levels could be referred to the Mustersan (see below). The preceding units, the Mealla and Maíz Gordo formations, have yielded a few remains of the peculiar henricosborniid notoungulate, *Simpsonotus*, which, except for specialized incisors, has a primitive molar morphology. The Mealla and Maíz Gordo formations are likely of pre-Itaboraian early and middle Paleocene age (Selandian; Quattrocchio et al. 1997). Table 1 shows *Simpsonotus* as being of Itaboraian age.

The "Vacan" SALMA is composed of 55 genera, of which 30 are FADs and 14 are LADs (Fig. 9), and 15 are through-going (Tables 1 and 2). Because of the scarce screen-washing methods applied to strata of "Vacan" age, very few metatherians have been recovered to date. The 'Ameridelphia' are represented by the derorhynchid *Coona* (FAD to "Barrancan"). Based on prior and subsequent records, sparassodonts and microbiotheres would be expected, but have not yet been found. In spite of possible sample bias, polydolopids are very diverse, with six genera (Fig. 11). Of these, *Amphidolops*, *Archaeodolops*, and *Pliodolops* are through-going taxa (to "Barrancan"). FADs are *Eudolops* (to"Barrancan"), *Polydolops* (to Mustersan), and *Kramadolops* (to Tinguiririncan; Chornogubsky 2010). The polydolopimorphian FAD *Groeberia** also occurs in the "Barrancan."

Regarding placental mammals, the five cingulate xenarthrans (Fig. 12) increase the "Sapoan" diversity, with the through-going *Prostegotherium* and *Stegosimpsonia*. *Astegotherium* is a LAD, and FADs being *Meteutatus* (to Deseadan) and *Utaetus* (to "Barrancan").

The astrapotheriid astrapotheres, *Albertogaudrya* and *Scaglia*, are FADs ("Barrancan" and LAD, respectively), with *Tetragonostylops* being a LAD. The trigonostylopid *Trigonostylops* is a through-going form, to the Mustersan.

The two didolodontid 'condylarths' (Fig. 12) include the FAD *Didolodus* (to "Barrancan") and the through-going *Ernestokokenia*.

Litopterns are represented by five taxa (Fig. 12), the LAD *Asmithwoodwardia* (protolipternid); sparnotheriodontids show the FAD/LAD *Sparnotheriodon*, the LAD, *Victorlemoinea*, and the FAD, *Phoradiadius**. The anisolambdid *Anisolambda* is through-going. Notopterns (*Adiantoides*, *Indalecia*) are first recorded in the "Vacan" and continue to the "Barrancan."

Notoungulates are very diverse. These include the through-going forms such as the archaeopithecid, *Archaeopithecus*, the henricosborniid *Henricosbornia*, the interatheriid *Notopithecus*, the moderate-sized notostylopids *Notostylops* and *Homalostylops* (Elissamburu 2012), and the oldfieldthomasiids *Colbertia* and *Oldfieldthomasia*. Other notoungulates include the FADs/LADs represented by the single occurrences of the oldfieldthomasiid *Paginula*, and the pyrotherian *Carolozittelia*. LADs include the henricosborniids *Othnielmarshia* and *Peripantostylops*, the isotemnid *Isotemnus*, the notostylopid *Edvardotrouessartia*, and the oldfieldthomasiid *Maxschlosseria*. FADs are reflected in the hypsodont archaeohyracid *Eohyrax* (to Mustersan), the henricosborniid *Acamana**, the isotemnids *Anisotemnus*, *Pampatemnus*, *Pleurostylodon*, and *Thomashuxleya*, the leontiniid *Coquenia*, the notohippid *Pampahippus*, the notostylopid *Boreastylops*, the oldfieldthomasiids *Acoelodus* and *Dilochostylodon* (all to "Barrancan"), and *Brachystephanus**, *Xenostephanus**, and *Allalmeia**, that pertain to a new family (Table 1). It is noted that *Coquenia* and *Dolichostylodon* may prove to be of Mustersan age, but are portrayed as "Vacan" on Table 1.

The strong diversity of five cingulate xenarthrans, five litoperns, and 28 notoungulates, including four notostylopids, four henricosborniids, four isotemnids, and six oldfieldthomasiids (Fig. 12) speaks in favor of their having been an equally diverse set of cursorial herbivore niches, although directly coeval floral data are absent. *Acropithecus* is considered as the oldest hypsodont notoungulate (Reguero et al. 2010; Riochican, Table 1) and likely attests thereby to the presence of locally more open conditions (Pascual and Ortiz-Jaureguizar 1990).

"Vacan" metatherians are composed of insectivorous species of small size, frugivores of small to medium size, and medium-sized frugivorous-folivorous species. The conspicuous "Divisideran" genus *Groeberia* is a small-sized taxon with inferred granivorous-folivorous feeding habits (Zimicz, unpublished observations). Presumably, additional collecting will discover large carnivorous sparassodontans that responded to the indicated strong ungulate diversity.

The strong percentage (27 %; Table 2) of continuing taxa maintains continuity with subsequent SALMAs. It is noteworthy that the increase in ungulate diversity well postdated the EECO.

Divisaderan The SALMA status of the Divisaderan has been challenged (López 2008, 2010). The specimens derive from the type locality of the Divisadero Largo Formation, Mendoza Province, Argentina (39, Fig. 2c) and consist of only eight genera, of which six are FADs and seven are LADs (Tables 1 and 2).

These include a single metatherian, the argyrolagoidean *Groeberia* (FAD/LAD), and several placentals: the through-going trigonostylopid, possibly assigned to *Trigonostylops*; the single entry FADs/LADs of the sparnotheriodontid litoptern *Phoradiadius*, the henrocosborniid notoungulate *Acamana*, as well as the other notoungulates *Brachystephanus*, *Xenostephanus*, and *Allalmeia*. The indalecid notoptern *Adiantoides* is a LAD. Presumably, the ecological settings that obtained in the "Vacan" prevailed here as well, although as shown in Fig. 1, global temperatures had been declining since the Riochican. Sedimentological and biological inferences suggest warm and humid environmental conditions with abundant water availability, and plant cover with the development of trees (López 2008).

The Divisaderan fauna was referred originally to the late Eocene, because it would partially fill the gap between the Mustersan and Deseadan biochrons in the South American record (Pascual et al. 1965). This mammal assemblage was recognized as significantly older, and could be referred to the early Eocene (López 2010). One plausible explanation for the record of exclusive taxa in this fauna is that it may represent the hiatus between the "Barrancan" and "Vacan" SALMA (almost 2 Ma; Fig. 1) not recognized so far in any other locality. In Table 1, we place the Divisaderan and Lumbrera genera (the last also referred to early Eocene by Pascual et al. 1981) in both "Vacan" and "Barrancan" columns, because those taxa do not represent, at the moment, individual SALMAs. The presence of sebecid crocodiles in the Lumbrera Formation (Gasparini 1984; Reguero et al. 2008) suggests a wet, tropical climate, which may coincide with the Lutetian warming interval (Le Roux 2012). Del Papa et al. (2010) clarified the Lumbrera Formation stratigraphy, and show that in its upper part, near 40 Ma, the climate became more arid.

Barrancan The "Barrancan" SALMA is contained within the Gran Barranca Member of the Sarmiento Formation that crops out in the Gran Barranca of southern Chubut Province, Argentina (37, Fig. 2c). As indicated in Fig. 7, the Gran Barranca Member extends from the base of the formation, a few meters below the VRS Tuff, and up to Disconformity 2, which is directly overlain by the Rosado Tuff and ranges in age from about 42 to 39 Ma. Much of the type "Barrancan" fauna was recovered from the Y Tuff, but other specimens occur both above and below that fossiliferous tuff bed (Ré et al. 2010a). The "Barrancan" SALMA is calibrated as being between about 42 to 39 Ma (Fig. 1)

With the addition of the formerly Divisaderan taxa, the "Barrancan" SALMA is composed of 73 genera, with 29 FADs (40 %) and 58 LADs (79 %; Figs. 9 and 10), as well as eight taxa (11 %; Table 2) that continue on from a prior unit. The large proportion of LADs and the small number of continuing taxa indicate that the "Barrancan" seems to have recorded the beginning of a major turnover in mammalian faunas of South America. Whether this turnover coincided with the MECO (Fig. 1) remains to be determined.

Among metatherians, "Barrancan" taxa exhibit a minor component (two) of 'ameridelphians,' eight sparassodontans, a didelphimorphian, a microbiothere, and 11 polydolopimorphians, of which seven are polydolopids (Fig. 11). The derorhynchid *Coona* is a LAD, whereas the other 'ameridelphian,' *Reigia*, is a singular FAD/LAD, as are most of the sparassodontans (*Argyrolestes*, *Pseudocladosictis*, the proborhyaenid *Callistoe*, and borhyaenid *Angelocabrerus*). FADs include *Proacladosictis* and the proborhyaenid *Arminheringia* (both to Mustersan). LADs are *Nemolestes* and *Patene*. The caroloameghiniid didelphimorphian *Caroloameghinia* is a FAD/LAD, whereas the microbiotheriid *Eomicrobiotherium* is a through-going genus.

The 11 polydolopimorphians are assorted as two FADs/LADs (the prepidolopid *Prepidolops* and the polydolopid *Pseudolops*), two FADs (the bonapartheriid *Bonapartherium*, to Mustersan), the rosendolopid *Rosendolops*, to Tinguiririican), four LADs (polydolopids *Amphidolops*, *Eudolops*, *Archaeodolops*, and *Pliodolops*), and two through-going forms (*Polydolops*, *Kramadolops*). Later polydolopids and sparassodontans are much reduced (to two and three, respectively) so that the "Barrancan" represents a strong turnover episode for these metatherians (Fig. 11).

Among placental mammals, the cingulate dasypodid xenarthrans *Prostegotherium*, *Stegosimpsonia*, and *Utaetus* are LADs, which, with the FAD/LAD of *Pseudostegotherium* show a general downsizing of this group (Fig. 12). Only *Meteutatus* is a through-going taxon. *Machlydotherium* is a FAD. Other LADs include the astrapotheriid *Albertogaudrya*, the didolodontid 'condylarth' *Didolodus*, the anisolambdid *Anisolambda*, the sparnotheriodontid litoptern *Phoradiadius*, and indaleciid notopterns *Adiantoides* and *Indalecia*, the archaeopithecid *Archaeopithecus*, the henricosborniids *Acamana* and *Henricosbornia*, the interatheriid *Notopithecus*, the isotemnids *Anisotemnus*, *Pampatemnus*, *Pleurostylodon*, and *Thomashuxleya*, the leontiniid *Coquenia*, the notohippid *Pampahippus*, the notostylopids *Boreastylops*, *Homalostylops*, and *Notostylops*, and the oldfieldthomasiids *Acoelodus*, *Oldfieldthomasia*, and *Dolichostylodon*, as well as *Brachystephanus*, *Xenostephanus*, and *Allalmeia*. This group of taxa clearly reflects a post-"Barrancan"—pre-Mustersan major faunal change in South American mammal faunas.

Other singular entities (FADs/LADs) further reflect this turnover: the probable kollpaniine *Pascualodus*—which needs confirmation, the adianthid litoptern *Proectocion*, the archaeohyracid *Acoelohyrax*, the interatheriid *Transpithecus*, the campanorcid *Campanorco*, the notohippids *Coelostylodon* and *Plexotemnus*, and the oldfieldthomasiid *Ultrapithecus*. The didolodontid *Paulogervasia* (to Mustersan) and the interatheriid *Antepithecus* (to Tinguiririican) are the only placental FADs.

In addition to the xenarthran (above) other through-going groups include the trigonostylopid *Trigonostylops*, the didolodontid 'condylarth' *Ernestokokenia*, the hypsodont archaeohyracid *Eohyrax*, and the oldfieldthomasiid *Colbertia*.

In summary, the greatest diversity of endemic "Barrancan" faunas is shown by the eight sparassodontan and seven polydolopid metatherians, as well as the persistence of five dasypodid cingulates, three litopterns, two astrapotheres, four ‘condylarths,’ three litopterns, two notopterns, two archaeohyracids, an archaeopithecid, two henricosborniids, three interatheriids, a campanorcid, four isotemnids, a leontiniid, three notohippid, three notostylopids, five oldfieldthomasiids, and four rodents (Fig. 12). At the same time (except for the cingulates) these same groups tend to exhibit a strong decrease in the Mustersan (in some cases—interatheriids, notohippids, rodents—to be re-invigorated in the Tinguirirican and/or the Deseadan; Fig. 12). The astrapotheres as well as the isotemnid, notohippid, and one half of the notostylopid and oldfieldthomasiid notoungulates persist. Medium- to large-sized toxodonts include *Pleurostylodon* (54 kg) and *Thomashuxleya* (338 kg, Elissamburu 2012).

Only the dasypodid cingulates, astrapotheres, didolodontid ‘condylarths,’ litopterns, notopterns, henricosborniids, isotemnids, henricosborniids, isotemnids, notostylopids, and oldfieldthomasiids demonstrate a strong connection (two or more genera) to the “Vacan.” Overall, the endemic mammal community tends to emphasize discontinuity, rather than continuity with the Mustersan and later Paleogene biochrons, shown in part by the 79 % of the “Barrancan” fauna that are LADs (Fig. 10).

In this context, a major innovation for the “Barrancan” is the immigration of rodents as seen in the Contamana Fauna of Perú (Antoine et al. 2011). Five species (four genera, Fig. 12) of caviomorph rodents, pertaining to *Cachiyacuy*, *Canaanimys*, *Eobranisomys*, and *Eoespina*, are considered to represent plesiomorphic members of their groups and to have resulted from a sweepstakes dispersal from Africa. Associated floral elements reflect tropical rain forest conditions in this Neotropical region, in contrast to the more seasonal and drier settings of the Austral region. The “Barrancan” rodent record precedes that of the Tinguiririсan (Wyss et al. 1993; Vucetich et al. 2010) by about 15 m.y., with continued expansion in the Deseadan (Fig. 12). Figueirido et al. (2012) noted the role played by immigration at various times in the North American Cenozoic mammal record. Whereas the”Barrancan” immigrant taxonomic diversity does not approach that commonly seen in North American examples, it is tempting to suggest that rodent immigration played a role in the “Barrancan” taxonomic increase just prior to the major pre-Mustersan faunal change.

To review, “Barrancan” faunas are represented by strong metatherian components that include polydolopids, proborhyaenids-borhyaenids, and basal sparassodontans (Fig. 11). Among placentals, dasypodid xenarthrans, didolodontid ‘condylarths,’ isotemnid, interatheriid, notohippid, notostylopid, and oldfieldthomasiid notoungulates are well represented (Figs. 11 and 12). Of these, the ‘condylarths’ and interatheriids tend to be strongly reduced or become absent in the Mustersan SALMA This signals a clear change from subsequent ages, and may equate with a major faunal (?and climatic) turnover, although still in the waning stages of a Greenhouse world (Fig. 1). In the Neotropical region, extremely wet tropical conditions (?rain forests) are associated with the immigration of the first South American rodents which may have affected the “Barrancan” faunal change.

The “Barrancan” metatherians show clear ecological differences with respect to the previous ages. The dominant trophic types are the hypercarnivores of large size, along with small-sized frugivore-insectivores. However, the folivore-frugivore niche is well occupied by medium-sized polydolopimorphians *Kramadolops* and *Eudolops* (Zimicz 2012), and the granivorous and strictly frugivorous niches are also filled, although to a lesser degree, by rosendolopids and polydolopids. Sparassodontan carnivores of medium size are also present, but in low diversity relative to their hypercarnivorous counterparts (Zimicz 2012). The major feature of “Barrancan” metatherian ecology is the explosive radiation of the large-sized predatory types (Proborhyaenidae and several basal borhyaenoids), and the coeval decline of the strictly frugivorous types and an increase of medium-sized folivorous taxa (Zimicz 2012). This event represents an adaptive and taxonomic turnover most probably related to climatic changes, at least in Patagonia.

Mustersan Bond and Deschamps (2010) reviewed the Mustersan SALMA, originally described (Ameghino 1906) from the Gran Barranca area, with the “Faune Astraponoteén” originally considered to be notable for the hypsodonty of ungulates. Bond and Deschamps (2010) noted, however, that stratigraphic revisions have resulted in most of the so-called Mustersan hypsodont taxa being actually of Tinguiririсan age. Reguero et al. (2010) showed virtually no Mustersan hypsodont notoungulates. The archaeohyrachid *Pseudhyrax* is hypsodont, and apparently was adapted to an abrasive diet (Reguero and Prevosti 2010).

At Gran Barranca, the Mustersan SALMA is contained within the Rosado Member and unit 1 of the Lower Puesto Almendra Member of the Sarmiento Formation (41, Fig. 2c), bracketed by discontinuities 2 and 5 (Fig. 7), with an age range of about 39 to 36.5 Ma. The Mustersan is the last SALMA prior to the early Oligocene climatic deterioration. It is composed of 42 genera, with nearly equal numbers of FADs (29) and LADs (30), and four throughgoing taxa, a pattern that demonstrates a strong faunal turnover at this time.

As mentioned above, the uppermost levels of the Lumbrera Foramation in NW Argentina are probably coeval with the Casa Grande Formation of Jujuy Province, and bear a faunal assemblage of notoungulates comparable to that of Mustersan localties in Patagonia.

Metatherians differ from prior units in having no 'ameridelphians,' didelphimorphians, or microbiotheres, although the latter two groups would be expected (Table 1). The sparassodontans are diminished over those of the "Barrancan," to three genera. The singular borhyaenid (*Plesiofelis*) is a FADs/LAD, with the hathliacynid *Procladosictis* and proborhyaenid *Arminheringia* being LADs. Polydolopimorphians show a similar pattern relative to the "Barrancan," but with six fewer taxa. On the other hand, some of the metatherian absences likely reflect sampling biases in that many families present in the "Barrancan," but absent in the Mustersan, re-occur in the Tinguirirican, and the 10 % of continuing taxa recorded in Table 2 likely underrepresents the actual situation.

The rosendolopid polydolopimorphian *Hondonadia* is a FAD (to at least the La Cantera assemblage, here recorded as Deseadan; Table 1). In the following text a FAD (to Deseadan) carries the implication that the taxon may occur later than that, but is not recorded here. The prepidolopid *Punadolops* is a FAD/LAD, the bonapartheriid *Bonapartherium* a LAD. Polydolopids include the LAD of *Polydolops* and the through-going *Kramadolops*, but are overall diminished by six taxa relative to the "Barrancan" (Fig. 11).

Three of the eight dasypodid cingulates (Fig. 12) are FADs/LADs (*Ortheutaetus*, *Anteutatus*, and *Mazzoniphractus*). FADs are *Sadypus* and *Pseudoeutatus* (to Deseadan), and *Parutaetus* (to Tinguirirican). *Machlydotherium* and *Meteutatus* are through-going cingulates.

The new large and hypsodont astrapotheriid astrapothere *Astraponotus* (Kramarz et al. 2011) is a FAD/LAD, whereas the 200 kg trigonostylopid *Trigonostylops* is a LAD and the second large-sized ungulate recorded. Other LADs include the didolodontid 'condylarths' *Paulogervasia* and *Ernestokokenia*. The didolodontid 'condylarth,' *Xesmodon* and the ?anisolambdid *Decanonus* are FADs/LADs, as are the macraucheniid (*Polymorphis*) and the two proterotheriid (*Heteroglyphus*, *Polyacrodon*) litopterns, the archaeohyrachid notoungulate *Punahyrax*, the interatheriids *Guilielmosottia* and *Punapithecus*, the isotemnids *Rhyphodon* and *Distylophorus*, the leontiniid *Martinmiguelia*, the notostylopid *Otronia*, the oldfieldthomasiids *Tsanmichoria* and *Suniodon*, and the pyrothere *Propyrotherium*.

In addition to the above, notoungulates continue having a strong diversity, with the archaeohyracid typothere *Pseudhyrax*, the isotemnid *Periphragnis* being true FADs (to Tinguirirican). Other typotheres are LADs, such as the hypsodont archaeohyracid *Eohyrax*, and the oldfieldthomasiid *Colbertia*.

Notoungulates undergo a distinct radiation, indicated by the above FADs/LADs, along with the notohippid *Puelia* FAD (to Tinguirirican). The pyrothere group continues from the "Vacan" to at least Deseadan (Table 1).

In comparison with preceding biochrons, the Mustersan shows a diminished diversity of polydolopimorphian metatherians (Fig. 11), an increase in dasypodid cingulates (Fig. 12), the first macraucheniid and proterotheriid litopterns, an increase in archaeohyracids, and a decrease in notohippids, notostylopids, and oldfieldthomasiids.

Mustersan metatherian associations show an increase in the small granivorous types (rosendolopids) that dominate the Patagonian assemblage along with large hypercarnivores (*Procladosictis* and *Plesiofelis*). The frugivorous and insectivorous trophic types are present, but are scarce in Patagonia, as are folivorous-frugivorous forms (Zimicz 2012). In the northern latitudes, the dominant trophic types are the frugivorous and insectivorous forms of small size, although granivorous forms are also represented. In low latitudes, the carnivorous niche is occupied by hypercarnivores (*Arminiheringia*) and mesocarnivores of large and medium size, respectively (Zimicz 2012). In general, the Mustersan metatherians are suggestive of more open environments in Patagonia with respect to the more northern sites. The differential species richness of granivorous and frugivorous types between both associations (diminished in Patagonia) also attests to this interpretation. Evidence from paleosols of the El Rosado Member of the Sarmiento Formation at Gran Barranca is consistent with a period of increased aridity for the Mustersan (Bellosi and González 2010), which agrees with the open environments suggested by the metatherians.

In summary (Table 1), Mustersan faunas demonstrate a strongly diminished diversity in metatherians, which, for taxa still present, reflect lingering archaic elements such as bonapartherians and polydolopids. Among placental mammals, the Mustersan shows a comparable pattern wherein archaic elements are, or have been, phased out, and new groups are inaugurated that have ties to later biochrons. Most of the didolodontid 'condylarths,' which were prominent elements of earlier faunas, are here becoming extinct. In contrast, dasypodid cingulates undergo a new diversity, and the beginings of a radiation of new interatheriid and notohippid notoungulates is also seen. The astrapothere *Astraponotus* achieved large size among other distinct specializations (Kramarz and Bond 2008; Kramarz et al. 2011), as did the isotemnid *Periphragnis* (350 kg, Elissamburu 2012). This diversity is in contrast to eighteen notoungulates that had a pre-Mustersan record, but became extinct subsequent to the "Barrancan" including a majority of the previous large-sized ungulates. Faunal turnover also is shown by the advent of the first proterotheriid and macraucheniid litopterns relative to other members of that group. Overall, the Mustersan record indicates that the the modernization of the South American land mammal fauna was now under way.

As indicated above, floras of this age generally are increasingly cooler, but still relatively humid, with temperate to warm-temperate climates, open spaces being developed, and grasses importantly recorded. Seasonal climates are recognized from the presence of growth-rings in *Nothofagus* trunks.

*Tinguiririca*n The Tinguiririca*n* SALMA was originally described from the Termas de Flaco district of central Chile (Wyss et al. 1990; Flynn et al. 2002, 2003) (52, Fig. 2d). Radioisotopic dates (^{40}Ar/^{39}Ar) from the succession range from 35.6±0.85 Ma to 31.34±0.17 Ma, with the Tinguiririca Fauna being assigned an age of about 31.5 Ma, although suggested as likely ranging older (Fig. 1).

The Tinguiririca*n* has been recognized subsequently in the Gran Barranca sequence (Fig. 7), notably represented by the La Cancha fauna (53, Fig. 2d) as well (Goin et al. 2009, 2010, 2012a). Historically, Roth (1903) described some taxa from Cánadon Hondo (Chubut Province) that were later recognized of Tinguiririca*n* age (Croft et al. 2008b). Other localities in Patagonia referred to this biochron are Lomas Blancas and Rinconada de los López in Chubut, and Rocas Bayas in Rio Negro province. Based on its correlation to the Gran Barranca an age for the Tinguiririca*n* SALMA is here taken as likely 34.5 to 31.5 Ma. With the Eocene-Oligocene boundary dated at about 34.9 Ma (Fig. 1), the Tinguiririca*n* only briefly post-dates the beginning of the Oligocene.

The Tinguiririca*n* SALMA is composed of 40 genera, with 28 FADs and 30 LADs (Fig. 9), as well as four through-going forms (Table 1). The large number of LADs (75 %) and comparably high number of FADs (70 %; Fig. 10; Table 2) is consistent with the thesis of strong climatic change relative to that under which the preceding Mustersan SALMA flourished.

As indicated in Table 1, metatherians show seven FADs, including the palaeothentid paucituberculatan *Pilchenia* (to Deseadan), the caroloamethiniid didelphimorphian *Canchadelphys*, and the microbiotheriids *Clenia* and *Microbiotherium* (each also a LAD, as are the glasbiid polydolopimorphian *Periakros*, and the argyrolagoids *Klohnia* and *Praedens*; Fig. 11). These groups show a diversification relative to the “Barrancan” or Mustersan SALMAs.

The remaining metatherian groups are comparable to those of the next older units. The microbiothere *Eomicrobiotherium* and the polydolopid *Kramadolops* are LADs, as is the rosendolopid polydolopimorphian *Rosendolops*, with *Hondanadia* being a through-going form. Sparassodontans are absent here, but the group regains diversity in the Deseadan (Fig. 11; Table 1), so their Tinguiririca*n* record reflects a sampling bias.

In spite of the lack of sparassodontans and reduced number of polydolopids (Fig. 11), the main differences relative to “Barrancan” and earlier faunas are indicated by the numerous FADs noted above, which tend to show an increase in their respective groups and identify a new metatherian diversity in the Tinguiririca*n*.

Among placental mammals, the dasypodid cingulates are diminished relative to earlier biochrons (Fig. 12). A FAD (and LAD) is represented by *Barrancatatus*, but the other taxa are either LADS (*Parutaetus*) or through-going forms (*Sadypus*, *Meteutatus*).

A notable new xenarthran is represented by *Pseudoglyptodon*, the earliest member of the megalonychid group (Table 1), which is diverse in Deseadan and later biochrons (e.g., McKenna and Bell 2002; McKenna et al. 2006; Pujos and de Iuliis 2007; Shockey and Anaya 2011).

There are no astrapotheres, ‘condylarths,’ pantodonts, or litopterns in contrast to “Barrancan” and older or younger (astrapotheres, litopterns) units. A FAD/LAD for interatheriid notoungulates is represented by *Johnbell hatcheri*, along with a LAD of *Antepithecus* (Hitz et al. 2006). The small size of these taxa relative to other interatheriids may reflect their more northern occurrence. Whereas ‘condylarths’ and pantodonts are now extinct, astrapotheres reappear later, in the Deseadan (Table 1). Pyrotheres occur in Tinguiririca*n*-equivalent faunas of Peru (*Baguatherium*) (Salas et al. 2006).

Notoungulates continue to be well represented, with 15 FADs, and three LADs. FADs include a new notoptern, the archaeohyracids, *Protoarchaeohyrax* and *Archaeotypotherium*, which continue into the Deseadan along with the hegethoteriid, *Prohegetotherium*, and the mesotheriid, *Trachytherus*. *Johnbell*, *Eopachycros*, *Santiagorothia*, and *Proargyrohyrax* are interatheriid FADs/LADs, as is the homalodotheriid *Trigonolophodon*; two notohippids (Croft et al. 2008b), as well as *Eomorphippus* (López et al. 2010), and a new genus of notostylopid (Croft et al. 2008b). LADs include the archaeohyracid *Pseudhyrax*, the interatheriid *Antepithecus*, the isotemnid *Periphragnis*, and the notohippid *Puelia*. As indicated in Fig. 12, the main diversity is seen in dasypodids, archaeohyracids, interatheriids, and nothohippids.

Rodents are not yet known from the Mustersan, but Tinguiririca*n* rodents continue the diversity initiated in the “Barrancan” by means of the chinchillid *Eoviscaccia* (FAD/LAD), and a new genus of dasyproctid rodent, *Andemys* (Bertrand et al. 2012), belongs to a group that continues into the Deseadan (Table 1).

Croft et al. (2008b) indicated that the Chilean Tinguiririca*n* taxa are dominated by 17 notoungulates, comprising 71 % of the land mammal species. In addition, two-thirds of the taxa are hypsodont, a remarkable example of convergence in this feature across several notoungulate clades. Among these, archaeohyracids (six species) represent the highest diversity of this group yet known, followed by four species of notohippids and two interatheriids. In contrast, large and brachydont forms are rare. On a regional basis, hegetotheriids are absent in Chile, but found in coeval faunas in Patagonia (Gran Barranca; Fig. 7). López et al. (2010) inidcated that the notohippid, *Eomorphippus*, is one of the earliest notoungulates to develop hypsodont dentitions, potentially suitable to more abrasive diets such as grasses. The body morphology, including tridactyl feet, is consistent with cursorial adaptations, possibly suited to living in more open spaces.

The Tinguiririцan contains the oldest mammalian herbivore assemblage dominated by species with hypsodont cheek teeth (Flynn et al. 2003) with clear inferences as to the renovation in floral structure, the development of grasslands, and the 'modernization' of the mammal fauna (Shockey and Anaya 2011). Jardine et al. (2012) noted that North American rodents (mostly fossorial, but some semi-aquatic) became hypdosont in the late Eocene whereas ungulates (mainly artiodactyls—oreodonts, camels) only evolved hypsodonty at about 30 Ma.

Goin et al. (2009) noted that the 18 species of metatherians from the Tinguiririca-equivalent La Cancha fauna of Patagonia represent the most remarkable faunal turnover for this group in the Paleogene of South America. This turnover (the *Bisagra Patagónica* or "Patagonian Hinge") coincides with a sudden fall of global temperatures by the latest Eocene-early Oligocene times, and apparently led to the development of the first major open-area landscapes in South America. Metatherians show an expansion of polydolopimorphians, but also the last records of caroloameghiniids didelphimorphians and polydolopid polydolopimorphs, the last represented by *Kramadolops* with the largest body size yet recorded for a polydolopid polydolopimorphian.

Trophic types in the Tinguiririцan metatherian assemblage show a predominance of granivorous (rosendolopids) and insectivorous-frugivorous (caroloameghiniids, microbiotheriids, paucituberculatans, and glasbiids) forms. The folivorous/frugivorous and folivorous/granivorous niches are occupied by the large-sized polydolopids (*Kramadolops*) and the small basal argyrolagoids (*Klohnia*), respectively. The carnivorous niche contains a medium-sized hathlyacinid hypercarnivore. Overall, the metatherian reorganization in the Tinguiririцan and later times appears to be in response to the development of more open habitats and cooler climates, comparable to the pattern seen in placental mammals.

Deseadan The La Cantera local fauna of the Gran Barranca is considered (Fig. 1) as pre-Deseadan, but its taxa are included in that SALMA in Table 1. The La Cantera suite (54, Fig. 2d) is represented by several granivorous species (rosendolopids), some granivorous-folivorous forms (basal argyrolagids), some insectivorous (pauciteruberculatans), some folivorous (*Kramadolops*), and large hypercarnivorous (*Pharsophorus*) taxa. Both *Kramadolops* and *Pharsophorus* show a clinal increase in body mass relative to their predecessors, which is interpreted as an adjustment with respect to Bergman's Rule.

In the Deseadan (including the La Cantera l.f. in Table 1), the above decrease is accompanied by the beginning of the Argyrolagoidea (and of hypsodonty in metatherians), the radiation of paucituberculatans, and the development of gigantism among borhyaenid sparassodonts. The record of the probably largest South American hypercarnivore metatherian, *Proborhyaena gigantea*, with a body mass estimated at 93 kg, together with other large proborhhaenids (e.g., *Paraborhyaena* at 76 kg), is the main ecological feature of Deseadan metatherian associations (Zimicz 2012), likely in response to the increased size of ungulates, including the gigantic *Parastrapothrium* (Kramarz and Bond 2008). Other large Deseadan ungulates (100–1000 kg) include the homalodotheriid *Asmodeus* (ca 1780 kg), the leontiniids *Scarrittia* (1400 kg), *Leontinia* (560 kg), and *Ancylocoelus* (440 kg), the notohippids *Rhynchippus* (100 kg) and *Morphippus* (98 kg), the mesotheriid *Trachytherus* (400 kg), and the toxodontid *Proandinotherium* (104 kg; data from Elissamburu 2012). In that context it may not be surprising that the carnivorous niche accounts for 66.6 % of the total Deseadan metatherian species richness, and the remainder is distributed among granivorous-folivorous (argyrolagid) and insectivorousl-frugivorous (paucituberculantan) types. However, there is a strong geographic bias in the percentage of carnivorous taxa. When the predator guild is evaluated for Patagonia only, the percentage falls to 33 % of the total metatherian association. Body mass range in Deseadan metatherians extends from a very few grams (*Proargyrolagus*) to the enormous proborhyaenids (Zimicz 2012).

Overall, the metatherian reorganization in the Tinguiririцan and Deseadan and the Deseadan resurgence of large-sized ungulates appears to be in response to the development of more open habitats and cooler climates as compared with those of prior times. The Deseadan radiation and diversification of sloths (Pujos and de Iuliis 2007) may reflect this situation, as well.

General Discussion

Late Cretaceous mammal faunas in South America, here grouped under the Alamitan SALMA, are notable in lacking therian mammals. Studies by Bonaparte (1987) and Rougier et al. (2007, 2009a, b) have greatly improved our knowledge of the land mammal fauna of this interval, but the continued absence of therians has not modified the basic dispersal situation reviewed by Woodburne and Case (1996) and Case et al. (2005). In any case, the Alamitan fauna of numerous dryolestoids, and the less prominent, but still important, 'triconodonts,' 'symmetrodonts,' and hypsodont gondwanatheres, flourished in a variety of ecologies within subtropical to tropical aquatic to woodland settings reflected by a diverse framework of gymnosperms, angiosperms, ferns, monocots, conifers, and grasses. This essentially endemic group of mammals is represented by ***A*** on Fig. 9.

The earliest Paleocene faunas in South America (Grenier Farm, and the Tiupampan SALMA) display a diversity of stem metatherian groups as well as early members of extant metatherian radicles. The 12 species distributed among four orders (nine 'Ameridelphia,' Sparassodonta, Didelphimorphia, and Polydolopimorphia) virtually demand a Late Cretaceous introduction and subsequent diversification of metatherians to account for this record. Similarly, the five Tiupampan placental 'condylarths,' along with a pantodont and notoungulate (Gelfo et al. 2009) record a North American affinity as well, although more likely with early Paleocene, rather than Late Cretaceous sources. The pantodont and notoungulate demonstrate an at least incipient phyletic diversification of placentals in the Tiupampan. The above is reflected in the ***M*** for metatherian immigrants on Fig. 9 being located below the G (Grenier Farm), whereas the ***P*** for placental immigrants is located below the bar for the Tiupampan.

In the middle Paleocene, Peligran faunas start to show continuity with subsequent units on one hand (two 'ameridelphians') as well as recording a dispersal from Antarctica (monotreme). Goin et al. (2009) noted the surprising diversity of the metatherian component of the Punta Peligro Fauna (four species pertaining to the 'Ameridelphia' and Polydolopimorphia; Table 1), inherited at least at the suprageneric level from the Tiupampan, as were the placental groups (two genera of didolodontid 'condylarth' and a single notonychopoid litoptern). The Peligran contains the first record of the Litopterna, but the henricosborniids and 'condylarths' are known from the Tiupampan.

As noted above, the polydolopimorphians, and possibly the dryolestoids, likely were insectivorous-frugivorous taxa, with the 'ameridelphian' metatherians being more insectivorous-omnivorous. It appears that the precocious hypsodonty exhibited by the gondwanatheres (*Sudamerica*) reflects an abrasive diet in semi-aquatic and possibly fossorial habitat, but grasses were present (Raigemborn et al. 2009). The monotremes were insectivorous-aquatic, the 'condylarths' browsers or omnivores.

The Cerrejón and Palacio de los Loros floras indicate that the early Paleocene vegetation of South America ranged from tropical (northern) to subtropical (southern) and enjoyed a substantially higher diversity as compared to coeval floras in North America. The shared presence of the menispermacean podocarp *Palaeoluna* in approximately coeval floras of Wyoming and South America (Cerrejón), supports an early to mid-Paleocene dispersal across the Caribbean (Herrera et al. 2011), compatible with the FAD of 'condylarths' in Tiupampan and Peligran mammal faunas.

For Patagonia, Iglesias et al. (2007a) showed that the medial Paleocene Palacio de los Loros macroflora of Argentina has a distinctly Gondwanan affinity as shown by taxa such as the southern beech (*Nothofagus*), *Akania*, Cunoniaceae, podocarps, and Araucariaceae. MAT for the Argentine flora is estimated at 14.1±2.6 °C (about 57 °F), with a humid (tropical or subtropical), frost-free environment (MAP about 115 cm/year; Fig. 8).

Iglesias et al. (2007a) also showed that, although diverse, the Patagonian late Paleocene megafossil plant associations still are substantially less diverse than such associations of the EECO interval (Fig. 8, Laguna del Hunco flora; Wilf et al. 2005), and the faunal compositions differ as well, as discussed below. It was proposed that the relatively high diversity in the Paleocene anchored the evolution of the floral diversity seen 10 m.y. later at Laguna del Hunco (Iglesias et al. 2007a), a pattern that is comparable to that of Colombia and Venezuela, based on pollen records (Fig. 8).

The floral records in northern and southern South America seem to be completely independent, without interchange of lower level taxa. The tropical Cerrejón flora is located within a Caribbean sphere of influence, whereas the Patagonian floras likely are related to a floristic corridor shared with Australasia via the Antarctic Peninsula (Iglesias et al. 2011). This is compatible with the Peligran record of Australian monotremes (Pascual et al. 1992).

Both floras record the first occurrence of several families that are major components of Tertiary floras and which provide new sources of food, such as the Fabaceae (legumes) and Arecaceae (palms). Alligators, turtles, birds, and riparian mammals are associated with these floras.

In the later Paleocene, the "Carodnian" witnessed the apparent beginning of integrated faunas, and an early glimpse of the diversification of South American metatherians (polydolopids) and placentals (litopterns, and the oldest xenungulates). Permineralized trunks and phytoliths of the Peňas Coloradas Formation reflect warm and humid, in contrast to subtropical, conditions, and the common presence of grasses and other understorey plants such as the Zingiberales (ginger family) record mixed-temperate conditions in which the absence of palms is notable (Raigemborn et al. 2009). These conditions in Patagonia are very different from those of the early Paleocene. The late Paleocene—early Eocene Ligorio Márquez flora of Chile could represent a yet different history in western Patagonia, with wetter conditions and closed forests.

At the beginning of the EECO, the Itaboraian is important in being very diverse and showing a substantially greater number and percent of FADs than LADs (Figs. 9 and 10; Table 2). The 15 'ameridelphians' (Fig. 11) were dominant metatherians, with the five polydolopimorphians being the next in diversity (Table 1), along with two sparassodontans, a didelphimorphian, a paucituberculatan, and a microbiothere (Fig. 11). The 26 placental mammals were strongly represented by astrapotheres, didolodontid 'condylarths,' protolipternid litopterns, and notoungulates. The Itaboraian documented the first cingulate, the first astrapotheriid, astrapotheres (three), the first protolipternids (three), and sparnotheriodontid (one) litopterns, the first perutheriid (one), the first isotemnid (one) typothere, and the first notostylopid (one) and oldfieldthomasiid (three) notoungulates (Table 1; Fig. 12).

In addition to the numerous (48) FADs, the Itaboraian through-going or continuing metatherians (ten) and placentals (ten) show a strong continuity with later SALMAs extending in many cases to the "Barrancan." The basic Paleogene SALMA structure was well established by the Itaboraian.

Itaboraian faunas have been recorded both at Itaboraí, southeastern Brazil (29, Fig. 2c), essentially within the present as well as former Neotropical region, and at Las Flores, in central Patagonia (28, Fig. 2c) in the heart of the Andean Region. The many taxa shared between them also suggest that the two districts likely enjoyed warm and humid tropical environments. However, the fact that polydolopids represent as least one-half of the specimens of Las Flores metatherians, in contrast to their complete absence at Itaboraí, suggests that somewhat cooler conditions obtained in the southern region, and that biogeographic distinctions were fully active by this time. The grasses, also seen in the "Carodnian"-equivalent Peňas Coloradas flora, were further developed in Las Flores Formation floras.

Most metatherians likely inhabited insectivore-omnivore ecologies, with the carnivorous niche occupied by the sparassodontans *Patene* and *Nemolestes*, which were mesocarnivorous and hypercarnivorous, respectively (Zimicz 2012). The placental mammals apparently reflected a growing diversity of small- to medium-sized herbivorous taxa, possibly indicative of the spread of tropical or nearly topical conditions across South America as the EECO reached its early surge in global temperature (Fig. 8). Palynological data from the Paleocene-Eocene interval of Colombia strongly supports a hyperdiverse Eocene tropical environment (Jaramillo 2002).

The later phase of the EECO is represented by the Riochican. Its smaller-sized but comparably diverse, faunas likely reflected conditions and evolutionary trends comparable to those of the Itaboraian. The Riochican diversity is demonstrated by the greatest number of FADs versus LADs than in any other Paleogene SALMA (Fig. 9). The ten notoungulates, two litopterns, a 'condylarth,' a cingulate, and an astrapothere (Fig. 12) suggest that the majority of the fauna was composed of moderate-sized herbivores, with the five metatherians (a sparassodont and four polydolopimorphians—two being polydolopids; Fig. 11) and the single xenarthran likely occupying a group of insectivore-omnivore niches. Based on the overall small number of taxa as well as the eight metatherians and five placentals not represented by genera that otherwise continue to "Sapoan" or younger units from the Itaboraian, the Riochican sample likely is biased.

If the Laguna del Hunco flora is representative of the Patagonian region, it would appear that the climatic setting was essentially subtropical, whereas to the north, the Gran Salitral paleosols (61, Fig. 2d) reflected paleotemperatures that appear to be comparable, but developed under seasonal aridity, during the height of the EECO (Fig. 8).

Iglesias et al. (2007a) inferred that a number of compositional turnovers transpired between the late Paleocene and EECO floras, facilitated by increased temperatures and driven by floral immigration as well as evolutionary diversification. Based on the floras, themselves, it appears that wet subtropical conditions obtained over virtually all of of Patagonia and northern South America in the late Paleocene through early medial Eocene and, as pointed out by Iglesias et al. (2007a) the enhanced diversity in South American Paleocene floras preceded the development of comparable diversity in North American floras by about 10 m.y. The Patagonian floras were limited to the north by drier conditions, which are shown by the Gran Salitral paleosols and some palynofloras from the subtropical seasonally dry biome (Iglesias et al. 2011). This implies that whereas mammalian faunas of the EECO in North America may have been responding to the newly evolved floral diversity in their hemisphere, contemporaneous mammalian assemblages in South America had already been evolving in relatively greater floral diversity since the early Paleocene. This is discussed further below.

The post-EECO interval begins with the "Sapoan" biochron, wherein the South American land mammal faunas develop a long-term trend in which FADs and LADs tend to be more nearly equal, along with generally cooling global temperatures (Figs. 8 and 10). Even though parts of the fauna remain to be fully studied, the "Sapoan" mammals continue the basic structure seen in the Itaboraian. Among metatherians, through-going 'ameridelphian' taxa and polydolopimorphians continue to dominate, as do a variety of placental notoungulates. Didelphimorphian metatherians also are strongly represented (Fig. 11). Xenarthrans show an increase in diversity (to four). Protolipternids are strongly diminished from the Itaboraian (as also in the Riochican), with *Asmithwoodwardia* continuing into the "Vacan." Oldfieldthomasiid notoungulates also appear to be diminished (absent, but three genera are present in the Itaboraian, two in the Riochican and, among those, *Colbertia*, *Oldfieldthomasia*, and *Maxschlosseria* are present in both pre- and post-"Sapoan" times; Table 1). In contrast (Fig. 12), notostylopids are more diverse (three) than in the preceding biochrons. The gondwanathere (Tejedor et al. 2011; Goin et al. 2012b; not seen on Fig. 11) is a remnant of the earlier presence of the group in South America (Table 1).

Gelfo and Tejedor (2007) and Tejedor et al. (2009) noted that Paleogene mammals in South America exhibited diversity in scarce protolipternid litopterns and didolodontid 'condylarths.' "Sapoan" bunodont ungulates are of small size; they include didolodontids and an abundance of the protolipternid *Asmithwoodwardia subtrigona*.

Patagonian floras suggest a diminishing temperature in the interval from 52 to 47 Ma, as indicated by the record from the Gran Salitral to Río Pichileufú samples (Fig. 8), which is in accord with global marine data (Zachos et al. 2001; Wilf et al. 2005) and paleoclimatic reconstructions of Antarctica (Pross et al. 2012). Whereas the Gran Salitral paleosol data may not be strictly comparable to those developed from paleofloras, the Calcheta Cohologüe and Concepción Auauco samples are consistent with the trend (Fig. 8). At the same time, the high precipitation suggested by the presence of *Papuacedrus* in the Laguna del Hunco and Río Pichileufú floras (Wilf et al. 2009) is compatible with their strong taxonomic diversity, comparable to that shown by pollen morphospecies from Colombia.

Middle Eocene "Vacan" taxa continue the main trends seen in the "Sapoan." Because of the lack of small mammal prospecting at "Vacan" sites, metatherians are highly under represented. Still, the reduction in 'ameridelphians' appears to continue an earlier trend. Microbiotheres and sparassodontans are momentarily absent, but return in the "Barrancan" (Fig. 11). The six polydolopids document a strong increase from the "Sapoan." Among placentals, dasypodids increase to five genera. Astrapotheriid astrapotheres (Kramarz and Bond 2009) are revitalized from a Riochican and "Sapoan" absence, didolodontid 'condylarths,' litopterns, and notoungulates maintain or increase their diversity (leontiniids and notohippids are new; isotemnids and notostylopids increase to five and four, oldfieldthomasiids to six; Fig. 12). Comparable numbers are one, three, and zero for the "Sapoan" (but there are two Riochican oldfieldthomasiids as well as *Colbertia* in the Itaboraian, so some should be found in the "Sapoan"). In any case, an increased diversity for the "Vacan" is notable, as is the major input of 17 large-sized ungulates among the above-listed groups.

From Figs. 1 and 8 it seems that the climate was substantially cooler during the "Vacan" than for the height of the EECO. The hypsodont notoungulate *Acropithecus* and the numerous large ungulates attest to the changed climatic conditions.

Near the end of the middle Eocene, the "Barrancan" faunas continued the basic structure seen in, but underwent a significantly greater number of extinctions than recorded for, the "Vacan" (Figs. 9 and 10), including a 50 % reduction in the number of large-sized ungulates. The "Barrancan" (79 %) and Mustersan (71 %) show the greatest relative extinctions of the Eocene. In the early Oligocene, the Tinguiririican has a comparable percentage of LADS (75 %, Table 2). This pattern appears to be consistent with an increased deterioration in global climate as seen in Fig. 8, and the large proportion of LADs along with the relatively small number of continuing taxa (Table 2) indicates that the "Barrancan" recorded the beginning of a major turnover in mammalian faunas of South America.

Extinctions include the last of the derorhynchids, a strong turnover in sparassodontans, and almost the last of the polydolopids (Table 1; Fig. 11). At the same time, there were the first records of borhyaenids and proborhyaenids. According to Forasiepi (2009), all lineages of Sparassodonta were already established by the Casamayoran ("Vacan" and "Barrancan"). This implies the existence of ghost lineages, especially among Thylacosmilidae. Taking into account that the oldest known record for representatives of the Thylacosmilidae is the Colhuehuapian (ca 19 Ma), the assumed ghost lineages had durations of about 20 m.y.

For placentals, the "Barrancan" saw the last henricosborniid notoungulate (Fig. 12). The "Barrancan" also records the loss of sparnotheriodontid and anisolambdid litopterns, the notopternids, and a reduction in dasypodid xenarthrans, as well as didolodontid 'condylarths' (Fig. 12). None of the large-sized ungulate genera persists, replaced in the Deseadan by new genera and families.

In addition to showing the first adianthid litopterns, the "Barrancan" witnessed a slight increase in didolodontid 'condylarths,' and a continued strong diversity of isotemnid, notostylopid, and oldfieldthomasiid notoungulates (Fig. 12). The first rodents reflect the first immigration of mammals to South America since the early Paleocene.

Overall, "Barrancan" reductions or extinctions focused on archaic groups that had been effectively continuous from at least the beginning of the Eocene. Even with their two continuing taxa, polydolopids are greatly diminished after the "Barrancan." Placental extinctions or reductions involved the members of clades that had been prominent in earlier biochrons when the basic phyletic structure of these South American mammals was being established and when climate had been substantially warmer (Fig. 8). Still it is significant that the "Barrancan" dasypodid cingulates, and, among notoungulates, archaeohyracids, interatheriids, isotemnids, leontiniids, and notohippids pertain to groups that are well represented in subsequent Paleogene biochrons (Table 1). Following on the changes seen in the "Vacan," including the development of hypsodont as well as the persistence of large-sized notoungulates, it appears that "Barrancan" changes hearld the increased "modernization" of the mammal faunas seen in the Mustersan and Tinguirircan.

During this time, Patagonian turnover probably was driven by a cooler temperate climate in which tropical plant taxa from extremely diverse Eocene floras were mixed with immigrants from lower latitudes (Wilf et al. 2005). Cool-temperate *Nothofagus* forests expanded in southern Patagonia and some mesothermal groups became extinct there at the end of the Eocene.

In the late Eocene, these general trends continue into the Mustersan, which, as noted above, has one of the highest (71 %) relative extinction rates of any Paleocene or Eocene SALMA, with LADs (30, or 71 %) slightly outnumbering FADs (29, or 67 %; Figs. 9 and 10; Table 2). Most groups present in the "Barrancan" suffer reduction in the Mustersan in apparent response to continued diminished temperatures, development of more open spaces, and spread of grassy areas under seasonal climates. The Mustersan recorded a diminished diversity of polydolopimorphian metatherians as reflected in the ultimate extinction of the Bonapartheriidae and Prepidolopidae. Placental extinctions include the trigonostylopid astrapotheres, didolodontid 'condylarths,' and oldfieldthomasiid notoungulates. One of the large-size ungulates (*Trigonostylops*) survives from the "Barrancan." The first Glyptodontidae (xenarthrans) is recorded here.

Diversity increases are seen in adaptive invigoration as shown by the dasypodid cingulates (with six new genera), one new didolodontid 'condylarth,' the first macraucheniid and proterotheriid litopterns, two new archaeohyracid typotheres, two new interatheriids, three new isotemnids, a new leontiniid, a notohippid, a notostylopid, two new oldfieldthomasiids, and a new pyrothere.

The Tinguiririca n is the first SALMA to follow the early Oligocene climatic catastrophe (Figs. 1 and 8), when global climate became strongly colder than previously, during a span of a few 100,000 years (Pälike et al. 2006). In Figs. 9 and 10, this is reflected by a strong faunal turnover, recorded by the initiation of 28 new FADs in association with a comparable number of LADs (30; see also Table 2). Among other features, these faunas record the first of the rodent family Chinchillidae, as well as the first Argyrolagoidea (hypsodont Polydolopimorphia). The seven new metatherian FADs identify a renewed diversification of that group, as well, with two new microbiotheres (Fig. 11) being recognized. The development of more open and generally drier conditions resulted in the biotic responses indicated below including the development of regional facies.

Tinguiririca n extinctions include most Paleocene-Eocene metatherian lineages (notably, the Caroloameghiniidae and Glasbiidae, as well as the placental mammal groups, the Notopterna, the isotemnids, and notostylopids. In contrast, the diverse representation of notoungulates (13 new genera) is noteworthy (Table 1). Carlini et al. (2010) reported a reduction in stegotheriini and euphractini dasypodids at this time, along with the appearance of five new eutatine species, and the attainment of larger size in dasypodid xenarthrans overall.

In bypassing extinctions, the numerous and diverse Tinguiririca n innovations record the continued renovation of South American mammal faunas. Goin et al. (2009) noted that the 18 species of metatherians from the Tinguiririca-equivalent La Cancha fauna of Patagonia represented the most remarkable faunal turnover for this group in the entire South American Cenozoic. This turnover (the *Bisagra Patagónica* or "Patagonian Hinge") coincides with a sudden fall of global temperatures by the latest Eocene-early Oligocene times, and apparently led to the development of the first major open-area landscapes in South America.

As discussed by Croft et al. (2008b), the Tinguiririca n notoungulates represent 71 % of the land mammal species. In addition, two-thirds of these taxa are hypsodont. This remarkable example of convergence is recorded by several notoungulate clades, chief of which are six species of archaeohyracids, four species of notohippids, and two interatheriids. In contrast, large and brachyodont forms are rare. On a regional basis, hegetotheriids are absent in Chile, but found in coeval faunas in Patagonia (Gran Barranca; Fig. 6).

Reguero and Prevosti (2010) reviewed the rodent-like notoungulates ("Archaeohyracidae," Hegetotheriidae, Mesotheriidae), recorded a beginning of this general morphology in the Mustersan (*Pseudhyrax*), and indicated that all three families diversified in the Tinguiririca n (five genera) and Deseadan (eight genera), as a reflection of the more open ecologic settings of those times. Reguero et al. (2010) pointed out that the fossorial mesotheriids are not found in low latitude faunas (north of 10° S) where Neotropical conditions persist. Similarly, the small, somewhat glirifiorm and cat-sized interatheriids are rare in apparently more closed ecologic settings of Neotropical latitudes. These constitute examples of developing regional biofacies.

In addition to the above, López et al. (2010) described the development of more hypsodont notohippids in the Tinguiririca n, their peak in the Deseadan, and the loss of lateral digits and body size increase in Deseadan taxa, as well. They suggested these trends were related to the development of more open environments and grasslands.

Croft et al. (2008b) assigned the Tinguiririca n rodents to the Dasyproctidae (*Andemus*; Bertrand et al. 2012). Under the scenario that portrays South American rodents having been introduced by rafting across the Atlantic Ocean from Africa (Wyss et al. 1993; Coster et al. 2010), there is the question of whether the South American record (which includes the ancestors of the sister-taxon Erethizontidae) was produced from a single taxon, or more than one.

Vucetich et al. (2010) described the rodent fauna from the La Cantera site at Gran Barranca, Chubut Province, Argentina (Figs. 1 and 2d). They noted that the three species of Octodontoidea and one each of Cavioidea and Chinchilloidea? are post-Tinguiririca n and pre-Deseadan, and reflected a post-Tinguiririean dispersal to the southern part of South America. They also suggested that it is most likely that the Santa Rosa fauna of Perú is younger than Mustersan in age, and might be as young as Deseadan, which would fit with the "Barrancan"-aged dispersal event to South America. However, the early late Eocene ("Barrancan" or earlier) fauna of Contamana, also from Perú, includes no fewer than half a dozen mammal genera in common with that of Santa Rosa (Antoine et al. 2011; Suppl. electronic material), thus implying that the latter also could be late Eocene in age.

In the Deseadan, mesothermal-megathermal forests dominated, and were highly diverse, with the first occurrences of modern shrubby and herbaceous groups, including the first record of abundant Asteraceae (sunflowers). Grasslands were well developed. Climates were warm-temperate and humid, an apparent reflection of the late Oligocene warm period (LOW, Fig. 1).

Summary

In summary, the initial stages of therian mammal development in South America reflected immigrations from North America in the Late Cretaceous and early Paleocene, with early diversification of metatherians (Tiupampan) and archaic placental groups such as 'condylarths,' and the first notoungulate (Tiupampan). Paleocene climates were wet and warm tropical in the northern part of South America, and somewhat less so in the south, but the floras still were relatively diverse. Subsequently, as climates became warmer in the early Eocene, the indigenous fauna flourished with distinct increased diversity in the Itaboraian and Riochican during the EECO. The didolodontid 'condylarths' continued to expand (Gelfo 2010), as did the 'ameridelphian' and sparassodontan lineages, as well as the polydolopids and bonapartheriids. As indicated in Fig. 12, many new placental mammals are recorded during the EECO, which shows the beginning of cingulates as well as increases in astrapotheres, didolodontid 'condylarths,' litopterns, and the growing importance of notoungulates. Floral diversity increased as well in the north as well as in the south.

Only the Tiupampan, Itaboraian, and "Sapoan" faunas are relatively well represented in smaller mammals (all being metatherians; the rodent-sized archaeohyracid notoungulates appear in the Mustersan, and rodents, themselves, in the "Barrancan"). 'Ameridelphian' metatherians are virtually unknown after the "Sapoan." The essentially omnivorous-insectivorous pucadelphyids, derorhynchids, sternbergiids, and protodidelphids as well as didelphimorphians are best represented in the Tiupampan and Itaboraian, but several taxa persist into the "Sapoan," and then to the "Vacan" and "Barrancan" with much reduced diversity. Overall this group appears to reflect diversity during the EECO.

More carnivorous sparassodontans (Fig. 11) show Itaboraian diversity but persist in low numbers until a strong pulse in the "Barrancan" that is repeated in the Deseadan. Carnivorous metatherians are only sparsely represented throughout the Paleogene, as noted by Croft (2006) and Forasiepi (2009).

Polydolopimorphian metatherians, which represent a major radiation of more omnivorous to herbivorous lineages, are largely unknown prior to the Peligran (recall the Grenier Farm *Cocatherium*), but are well represented from then into the "Barrancan" during an interval of initial EECO climatic warming, followed by cooling. Only the Argyrolagoidea persist into the Neogene. Polydolopids are present in the EECO but most of their diversity is subsequent to that time (Fig. 11). The decisive moment in the turnover for the whole order is the early Oligocene (Tinguiririean fauna), in which the polydolopids decrease sharply in diversity and gain large body sizes, whereas the argyrolagoid radiation gains momentum. It is noteworthy that the former had developed a variety of dental adaptations for frugivorous or omnivorous diets, while the Argyrolagoidea (with several hypsodont taxa) include more grazer/seed-eating types.

The presumptively ancient xenarthrans are virtually unknown prior to the Itaboraian, and begin to demonstrate a growing diversity from the "Sapoan" into the "Vacan" and "Barrancan," show a peak in the Mustersan, subside in the Tinguiririean and into the Deseadan (Fig. 12). The group peaks subsequent to the EECO, and continues in diversity until the Tinguiririean, with its strongly cooler climate.

The endemic South American didolodontid 'condylarths' are first seen in the Peligran SALMA and show a limited diversity in younger units (through the Mustersan, but are absent in the Tinguiririean and Deseadan). Gelfo (2010) noted their attainment of larger size in the "Barrancan" (when seven species had developed) and in the Mustersan, possibly as a response to the climatic cooling. Their diversity is definitely a post-EECO phenomenon.

Litopterns showed a comparable pattern to didolodontids, and a growing diversity of small to medium-sized herbivorous placental mammals is revealed in Itaboraian and younger units, also possibly reflective of the diversely tropical forests living in Patagonia under the influence of the EECO. A post-EECO growth in diversity recorded in the "Vacan" included the presence of very large-sized genera. The "Vacan" diversity diminished subsequently (Table 1).

Among notoungulates, the henricosborniids show a Tiupampan beginning but the "Vacan" diversity is post-EECO (Fig. 12), and whereas the isotemnids first appear in the Itaboraian, their main diversity is also "Vacan." The first notostylopids and (diverse) oldfieldthomasiids are recorded in the Itaboraian, but also show post-EECO diversity in the "Vacan." Some of the "Vacan" elements included large-sized taxa.

Grasses were noted from at least the Mustersan and reflected by the advent of medium and small-sized notoungulates with hypsodont dentitions, and as further developed in the early Oligocene (Tinguiririca), when floras indicated a decline to temperate—cool-temperate but still humid conditions with abundant rainfall. The understory of ferns demonstrates a persistence of soft-substrate conditions even though certain areas were developing more open habitats. Cool-temperate *Nothofagus* forests expanded northward in Patagonia and reached the Atlanntic coast, with persistent cooler conditions. Most mesothermal groups became extinct in Patagonia.

In the Deseadan, the climate apparently rebounded somewhat from the initial Oligocene cooling, in the late Oligocene warm interval (LOW) with a new southward dispersal of megathermal elements. These include the first occurrences of modern shrubby and herbaceous groups, living in a more humid climate. Soft substrates apparently were advantageous to the newly developed leontiniid notoungulates (Ribeiro et al. 2010). Other changes in the notoungulate faunas in the Tinguiririca and Deseadan have been noted above.

Conclusions

The Early Eocene Climatic Optimum recorded the strongest warming episode of the Tertiary Epoch (Wolfe 1978; Wolfe and Poore 1982; Miller et al. 1987; Prentice and Matthews 1988) recognized in northern and southern high latitudes (Askin and Spicer 1995), including Australia (Christophel 1995). The question asked here is to what extent is that manifested in the land mammal fauna of South America, and was that response similar to that of North America (e.g., Woodburne et al. 2009a, b)? Inasmuch as land mammal ecology is dependent to a large degree on the niches provided by contemporaneous floras, it also is important to compare the paleobotanical aspects of the two regions.

As summarized in Woodburne et al. (2009a, b), the North American record indicates the presence of high mean annual temperatures with nominally tropical or subtropical climates in the North American Western Interior during the EECO. The record there suggests that floras of Lostcabinian age (Wa-7, ca 52.5 Ma, Fig. 1) experienced a MAT of about 22 °C and a MAP of about 140 cm. in this early part of the EECO. The floral evidence (Fig. 8) also indicates that more tropical conditions were developed during the EECO, but began to wane after about 52 Ma (Br-1a, Fig. 13) as cooler and more arid conditions developed in the Western Interior, although precipitation did not decline as sharply as temperature. In any case, the numbers of mammalian genera began to decline after about 50 Ma in the 'Bridgerian Crash' (Woodburne et al. 2009a, b; Figs. 8 and 13).

The Patagonian record is less detailed chronologically than that of North America, but the overall pre- and syn-EECO patterns are comparable. The early Paleocene Palacio de los Loros flora (ca 62 Ma) likely developed under a MAT of 14 °C, and a MAP of 115 cm/year (Fig. 8; ***Pel***, Fig. 13), comparable to that at To-3 (Fig. 1) in North America. At about the time of the PETM, the Ligorio Márquez and Quinamávida floras of Chile indicate a warmer climate (MAT about 18–25 °C; MAP 140–155) during that global pulse. This is comparable to the PETM—post PETM MAT and MAP to the north (Figs. 1, 8, and 13). The data do not indicate whether or not there was an immediate post-PETM reduction in temperature in South America, but by about 55 Ma the Quinamávida flora estimates are ~18 °C and 91 cm/year (Hinojosa 2005). At the 52 Ma EECO peak, the Laguna del Hunco flora in Patagonia suggests a MAT of up to 20 °C, and a MAP near 400 cm. in a subtropical climate (see arrows on Fig. 8). The MAT is still well below the 23 °C recorded at the peak of the EECO in North America, perhaps reflecting its more montanne setting. On the other hand, the Gran Salitral Formation records seasonally more arid conditions in more northern regions of Argentina (61, Fig. 2d) at about this time, and a MAT of about 24 °C. Up to this point the MAT interpretations for South American floras seem generally compatible with the pre- and syn-EECO pattern in North America.

As regards precipitation, the pre-EECO record in South America is generally similar to that in North America (Fig. 8), but rainfall was much greater in the south during the EECO. The EECO-equivalent Laguna del Hunco flora of Patagonia suggests that MAP rose to 400 cm/year (Wilf et al. 2009) and a similarly high precipitation apparently continued to the Río Pichileufú flora at 47.5 Ma (Fig. 8), perhaps consistent with the relatively high MAT. Somewhat older floras toward the west in Chile (Caleta Cocholgüe and Concepción-Arauco, ca 49 Ma) demonstrate a lower precipitation, to about 220–240 cm/year. The subtropical character of these floras near the North Patagonian High Plateau (NPHP, Fig. 2c) is compatible with the MAT and MAP inferences derived therefrom. Toward the north and east it appears that drier subtropical conditions obtained. Apparently, the EECO rainfall in Patagonia was generally much greater than in North America, although the pattern of an EECO pulse, and possibly one after the EECO, is similar, if of smaller magnitude.

It thus appears that the MAT, and possibly the MAP, record of early Eocene floras of Patagonia and Chile (Fig. 8) may resolve into a pattern that generally corresponds to that preceeding and embracing the EECO shown in the North American Western Interior. It is clear that precipitation was significantly higher at and after the EECO in South America, likely indicative of greater tropicality of its floras. Subsequent to the EECO (see below), the

South American record appears to have retained a temperature that was up to 5 °C higher than seen to the north.

EECO mammal faunas in South America begin with the Itaboraian biochron. In this unit, mammalian generic numbers increased strongly from previous levels at the beginning of the EECO (Figs. 8 and 13), with the historical development of South American mammal faunas indicating that the basic taxonomic and ecologic structure of those faunas also was achieved by this time. The diversity increase is shown by a much higher percentage of FADs (94) versus LADs (61; Table 2) than any SALMA up to that point, and also with respect to the early EECO biochrons in North America (Wa-6, Wa-7; Fig. 14). The early EECO of North America differs in that LADs somewhat outnumber FADs. In contrast to maintaining a relatively even faunal structure in the early part of the EECO, as in in North America (Fig. 14), the Itaboraí fauna diversified strongly, apparently in response to the climatic change.

In the later part of the EECO (Riochican), South American mammal numbers decline in contrast to their pattern in North America (Figs. 8 and 13), but this may be in part an artefact of Riochican sample deficiency, discussed above and could mirror to some extent the "Bridgerian Crash" of the north. Nevertheless, the Riochican has the highest relative increase in FADs versus LADs of any South American or North American biochron. MAT is higher for the Riochican (22 °C) than for late or just post-EECO units in North America (Figs. 8 and 13; Br-1a, Br-1B; 20 °C and 17 °C). Thus, in spite of a general temperature similarity in both hemipsheres, the EECO for South America reflects a major increase in faunal diversity not shown in the north, which might be a reflection of the greater tropicality and rainfall of that interval in the south. The late EECO interval shows warmer climates than in North America, as demonstrated by the post-EECO South American floras.

Figure 8 indicates a strong decline in MAT and MAP after the EECO peak in North America. By about 50 Ma, MAT had declined to 20 °C, and was at 17 °C by 49 Ma, 15 °C by 47 Ma, with MAP at about 100 cm/year. In South America, Hinojosa et al. (2006) obtained MAT and MAP estimates of 22 °C and 203 cm/year for the Lota Coronel-Arauco flora at about 49 Ma, and 19–26 °C and 260 cm/year for Caleta Cocholgüe flora of similar age. Peppe et al. (2011) considered these figures to be over estimated but, overall, MAT and MAP ratings suggest higher temperatures and rainfall than for of the comparable interval in North America (ca 50–49 Ma; 17 °C, Br-1b, and 100 cm/year; Figs. 8 and 13).

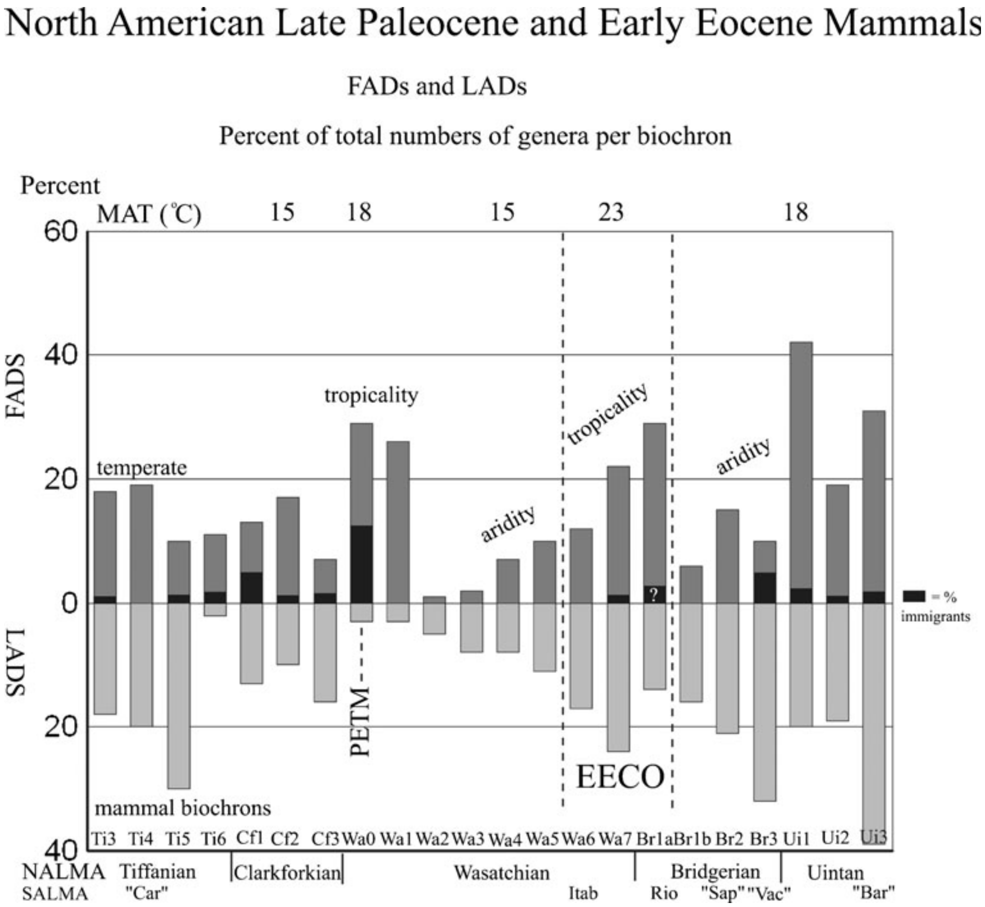


Fig. 14 Percentage of FADs and LADs for North American late Paleocene and early Eocene mammals. Positions of PETM, EECO, and mammalian biochrons are indicated. After Woodburne et al. (2009b)

The additionally post-EECO Río Pichileufú flora suggests a MAT of 19 °C and a MAP of 200–250 cm/year, substantially higher than for North America at 47 Ma (Fig. 8). Late Eocene floras in southern Patagonia (Río Turbio flora; 22*, Fig. 2c), and southernmost Chile (Loreto Formation, 51*, Fig. 2d; 36.5 Ma) reflect climatic deterioration with cool-temperate floras dominated by both pollen and leaves of *Nothofagus*. Panti (2010) recorded a MAT of 17.5±1.3 °C for the Río Turbio flora, but that for the Loreto is only approximated (***L***?) on Fig. 8. Whether MAT for the Loreto had declined to the level seen in the North American Florissant flora (13 °C; FL, Fig. 8) remains to be seen, but that would be consistent with a cool-temperate climate.

The 37 Ma Río Turbio flora (***RT***, Fig. 8; Taxonomic Diversity, Plants) shows a diversity of 178 species, comparable to that of the Rio Pichileufú (***RP***). Subsequently, Colombian pollen morphospecies drop about 18 %. If southern megafloras dropped a comparable amount in the early Oligocene, it would coincide with the time of major expansion of hypsodont mammals in Tinguiririican and Deseadan faunas.

Thus, in the post-EECO interval to about 40–36 Ma, temperatures in South America appear to have been warmer than in the north. If the Riochican (***Rio***, Fig. 13) represents the South American indication of part of the "Bridgerian Crash" in the north (Br-1a–Br-3, Fig. 13), the South American 'rebound' may have begun prior to that time in the north. Overall, from the "Sapoan" to "Barrancan," South American generic numbers follow a pattern comparable to that seen in North America (Figs. 8 and 13).

But the pattern is only part of the record. Whereas the number of taxa is less in the south at each step from the Riochican to the "Barrancan," the overall percent increase (ca 350 %; 21 to 73 genera) is significantly greater than in the north (ca 18 %; 85 to 100 genera). During a time of climatic deterioration in both hemispheres, the South American fauna apparently responded much more vigorously than the northern counterpart. Later, generic numbers fall to about 40 in the Mustersan and Tinguiririican (Fig. 8), a drop of about 40 %, but the development of hypsodonty still is on the rise.

In both continents, the biotic change is considered to have been coeval with a decrease in temperatures and an increase in aridity. The greater MAT during the ***Sap-Bar*** interval (ca 48–40 Ma) in South America versus the record to the north may have contributed to an earlier advent of grasslands and hypsodonty among southern mammals. Pascual and Ortiz-Jaureguizar (1990: Table 2) record an increase, each, of about 13 % hypsodont (protohypsodont) and 13 % hypselodont (euhypsodont) taxa during this interval [taking into account the Pancasamayoran and Divisaderan intervals of that paper are herein combined]. Grasses growing in local abundance are seen in the Itaboraian-equivalent Las Flores flora, and become more common and widespread as conditions deteriorated in the Mustersan through the Tinguirircan and Deseadan, by which time they were fully established in South America. The strong percentage (71 %) of hypsodont notoungulates is characteristic of the Tinguiririican, and precursors of that diversity are found in the Mustersan and "Barrancan," with earlier representatives in the Riochican through "Vacan." Thus, hypsodonty was definitely achieved by a diversity of South American notoungulates by about 32 Ma, and originated as early as at least the Riochican (*Acropithecus*) and "Vacan" (*Eohyrax*) and the other taxa noted by Pascual and Ortiz-Jaureguizar (1990), or at about 50–45 Ma. This precedes the record of North American hypsodont ungulates (camels and oreodonts) by about 15 m.y. (known from the Ar-1 early Arikareean NALMA at about 30 Ma; Jardine et al. 2012). Whereas the uplift of the modern Andes and the development of modern ecologic settings began about 23 Ma as the Nazca Plate began its descent beneath South America (Pardo-Casas and Molnar 1987; Spikings et al. 2010), local manifestations of aridity are known from the late Eocene of Argentina (Carrapa et al. 2005) and Chile (Dunai et al. 2005; Hartley and Evenstar 2010) at about 36–40 Ma. Additionally, the widespread distribution of pyroclastic deposits (grit) throughout the "Vacan,"—Mustersan interval (Pre-Patagonian, ca 45–35 Ma, Fig. 1) is well known (Pascual and Ortiz-Jaureguizar 1990). All of the above is compatible with a strong development of mammalian hypsodonty well in advance of its record in North America (Damuth and Janis 2011; Jardine et al. 2012).

An unexpected result of the present study was the realization that in total numbers of taxa, South American mammal faunas are less diverse than northern counterparts. In fact, the floral differences would suggest in favor of the reverse. Although not yet recorded in comparable stratigraphic density, Patagonian Paleogene forests appear to have been substantially more diverse than those represented in North America (Plants column, Fig. 8). In addition, the high plant diversity seen in the Late Cretaceous of Patagonia suffered a drop at the K/Pg, but that was almost completely recovered by the early Paleocene floras. Whereas floral diversity increased in North America at the time of the EECO, that diversity was already greater in South America than for North America in the Paleocene and early Eocene, and this increased in the later early and middle Eocene as seen in Fig. 8.

It appears that the ca 52 Ma early Bridgerian (Br1a, Fig. 13) peak in mammal numbers and diversity in North America was in response to increased niche diversity, abetted by relatively high temperature and rainfall, but the mammalian evolution in South America already had been responding, at least in theory, to an enhanced niche diversity.

The greater niche diversity reflected in Neotropical as well as Austral floras in South America would be compatible with the suggestions that MAT and MAP estimates for some of those floras are conservatively low and should be considerably higher, consistent with the apparently near-tropical ecologies reflected. Regardless of potential changes in these estimates, it remains difficult to reconcile the disparity of greater generic numbers and diversity of North American versus South American mammals, given the strong opposite discrepancy in their associated floras, and different collecting intensity notwithstanding.

Jaramillo and Dilcher (2000) and Jaramillo (2002) also noted that the pattern in South America differed from that interpreted for North America (Wing 1998; Wilf 2000) where early Eocene (PETM) warming is considered to have abetted intra- and intercontinental dispersal of plants (and land mammals; Gingerich 2003; Woodburne et al. 2009a; Wa-0, Fig. 13). Jaramillo et al. (2006) apparently favor temperature increase as the main driving factor in the northern South American examples, as well. Wing and Harrington (2001) noted, however, only minor palynological floral rearrangement across the Paleocene-Eocene boundary in North America, and suggested that the interaction between immigrant and endemic mammals was a major spur to mammalian faunal reorganization at that time; that climatic increase may have played a general background role, rather than having a direct influence, on mammalian evolution. Note, however, that Woodburne et al. (2009a, b) inferred a strong climatic deterioration subsequent to 52 Ma (Fig. 8; beginning in Br1a, Fig. 13) in the North American Western Interior as having had a pronounced affect on the mammal faunas then and subsequently. In addition, the general comparability in mammalian generic patterns in the two continents would be compatible with a climatic source rather than immigration. Whereas the above comments suggest that immigration had a major effect on Paleocene-Eocene transition in North America, it cannot have been a factor in South America. There, the Late Cretaceous to early Paleocene immigrations of therian mammals established the South American fauna (***Tiu***, Fig. 13) but, until the "Barrancan" (***Bar***, Fig. 13), no additional foreign input took place, and faunal evolution was endemic only.

Among some major differences in mammalian composition, it is noted that the Late Cretaceous and early Paleocene immigration to South America resulted in a variety of metatherians, 'condylarths,' and a pantodont. Carnivorous, insectivorous, and rodent- and primate-like taxa were not included. Subsequently, the metatherian diversity greatly surpassed that in North America, yet large carnivores were basically absent. Certain small notoungulates have been regarded as rodent-like (Reguero and Prevosti 2010), but these did not appear until the Musersan, after true rodents had immigrated in the "Barrancan." In a major innovation, hypsodonty and its implication of at least abrasive diets (Stirton 1947; Jardine et al. 2012) is first recorded in the Riochican (ca 50 Ma) in South America, or about 20 m.y. before its evolution in North America. The emphasis here is on cursorial mammals. Whereas Jardine et al. (2012) noted the presence of hypsodont fossorial rodents from about 36 Ma in North America, oreodont and camelid artiodactyls are recorded at about 30 Ma. The Riochican record may be cited as a local artifact, but in any case, the development of a diverse record of hypsodonty was underway at least from the "Barrancan," at ca 40 Ma, and was fully developed by the Tinguiririca n, apparently along with well-developed grasslands.

Thus, it appears that the pattern of floral and faunal change preceding and coeval with the EECO was generally comparable in both North and South America. As conditions deteriorated subsequent to the EECO peak, however, the South American climate retained higher temperatures and rainfall than to the north, at least to about 40 Ma. During this time, land mammal hypsodonty was achieved well before it evolved in North America. The apparent initial greater diversity and subsequent stability of South American floras during the Paleogene is not yet reflected in the numbers of mammalian taxa in that continent.

Acknowledgments It is with great pleasure and gratitude that we acknowledge the assistance of Dr. Peter Wilf and Dr. Viviana Barreda in helping with paleobotanical matters; Dr. Silvio Casadio aided in guiding Woodburne to relevant geological literature; and Drs. Darin Croft, Christine Janis, and Jussi Eronen provided valuable insights regarding mammalian ecofacies. These individuals do not necessarily agree with the interpretations presented here. Many thanks are offered to Marcela Tomeo for the design of several of the figures that illustrate this work. Two anonymous reviewers made valuable comments that improved the manuscript. Wilf and Iglesias gratefully acknowledge support from NSF grant DEB 0919071. F. Goin, M. Bond, A. Carlini, J. Gelfo, A. Iglesias, and N. Zimicz (PIP 0361) thank the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina) for its support.

Appendix I

Paleogene South American stratigraphy, mammalian faunas, and biochronology

Paleogene

As indicated in Fig. 1, the Paleogene begins at about 65.6 Ma, and lasts until about 23 Ma. The age and magnetic polarity signatures for the Epochs and Stages follows Luterbacher et al. (2004: fig. 20.4). The Sparnacian has been added, following the recommendations of Thiry et al.

(2006). The paleotemperature curve is after Zachos et al. (2001).

Oldest Mammal Fauna The Grenier Farm site is the currently oldest occurrence of a South American therian mammal for which the age is well documented (Goin et al. 2006a). This site has produced only a single (metatherian) taxon: *Cocatherium lefipanum*, from the Lefipán Formation, Chubut Province, Patagonia. Based on the associated marine invertebrate fauna the Grenier Farm Fauna is considered to be of Danian age. The position shown on Fig. 1 reflects the 5 m separation of the Grenier Farm site above the likely position of the K/Pg boundary (Goin et al. 2006a: fig. 2).

Tiupampan SALMA The Tiupampan SALMA is recognized in the Santa Lucia Formation of Bolivia (Gayet et al. 1991). Whereas this unit is not found in Patagonia, it is here taken as older than the Peligran SALMA of that region, following Gelfo et al. (2009).

The Tiupampa Fauna is found in the middle part of the Santa Lucía Formation of Bolivia (Fig. 1; 12, Fig. 2b). Marshall et al. (1997) and Sempere et al. (1997) reviewed the stratigraphy of the Santa Lucía Formation and associated strata. The Santa Lucía Formation is underlain by the El Molino Formation (?late Campanian; Maastrichtian—Danian) and unconformably overlain by the Cayara Formation (Thanetian equivalent). All of the Upper El Molino, the Santa Lucía and part of the Cayara formations are of reversed polarity, correlated to Chron C26r, or from 61.7–58.7 Ma in Luterbacher et al. 2004). The El Molino-Santa Lucía contact is correlated with a regression coeval with the Danian-Selandian boundary at 61.7 Ma, and with the base of chron C26r. Regarding the Tiupampan, this fauna is associated with the base of the Middle Santa Lucía Formation, for which an increase in grain size of the sediments is interpreted (Sempere et al. 1997) as a regression. The first major regression within chron C26r is near the top of the Selandian, or ca 59 Ma. This suggests that the Tiupampa SALMA is about 59 Ma old = very late Selandian; see also Marshall et al. (1997).

Mammal biochronology suggests an earlier age for the Tiupampan. The relative ages of the Peligran (Bonaparte et al. 1993) and Tiupampan (Pascual and Ortiz-Jaureguizar 1990) SALMAs have been revised by Gelfo et al. (2009). Qualitative analyses suggested that the Tiupampan is older than the Peligran, and may be phyletically closer to those of early Puercan age in North America. *Molinodus* is a member of the Panameriungulatan subfamily Kollpaniinae in the Tiupampa Fauna, and may represent an early dispersal event from North to South America (Muizon and Cifelli 2000: 145), perhaps of Puercan age. As summarized by Gayet et al. (1991) most metatherian and eutherian groups are permissive of an early Paleocene (essentially Puercan) age of many Tiupampan taxa, but *Alcedidorbignya* (Pantodonta) is first known in the Torrejonian of North America. A late Puercan to Torrejonian correlation for the Tiupampan is shown in Fig. 1, at about 64 Ma.

This scenario implies that the reversed magnetic polarity with which the Tiupampa Fauna is associated pertains to Chron 28r, rather than 26r (also Gelfo et al. 2009), and that the regression interpreted from the presence of coarse-grained material in the Tiupampa sediments is open to interpretations other than reflecting a global event.

On one hand, Sempere et al. (1997:719 L) indicated that the nonmarine sediments of the basal part of the Santa Lucía Formation reflect an eustatically-controlled regression, without tectonic influence. On the other hand, Sempere et al. (1997:715 L) portrayed the distribution of the red-brown lacustrine mudstones of the lower Santa Lucía Formation as having been controlled by remaining subsidence of the basin and by the structural framework in which they occur. This suggests a local, rather than regional, cause for these deposits and diminishes the interpretation for an eustatic origin. Thus, notwithstanding the proposed correlation of the Santa Lucía sediments with Chron C26r, there appears to be no compelling reason to equate the base of the Santa Lucía Formation with the Danian-Selandian boundary.

Sempere et al. (1997:715 L) indicated that the middle Santa Lucía Formation begins with a "somewhat coarser facies," but discussed this in the context of "highly subsident" areas, and also indicated that the paleostructural corridor in which they were deposited was reactivated at the time the top of the Middle Santa Lucía sandstone beds were deposited. The sandstone interval, which contains the Tiupampa Fauna, is about 50 m thick, according to Sempere et al. (1997: fig. 5). Again, the evidence of tectonic activity associated with the Middle Santa Lucía Formation (also Sempere et al. 1997:719 L) diminishes the interpretation of its regional correlation at ca 59 Ma. In summary, the 64 Ma age for the Tiupampan SALMA (Fig. 3) based on its fossil mammals appears plausible, comparable to that proposed by Flynn and Swisher (1995).

Peligran Through Riochican The Salamanca Formation and Río Chico Group in the San Jorge Basin of Patagonia (Figs. 3 and 5) contain a stratigraphic succession of Paleogene mammal faunas that is unequaled in South America. As reviewed by Bond et al. (1995), the succession begins with the largely marine Salamanca Formation (Fig. 5) of Danian age, with a basal glauconitic sandstone that rests unconformably on sediments of the Chubut Group. The basal sandstone is followed stratigraphically upward by about 150 m of siltstone and mudstone apparently deposited under transgressive conditions (Legarreta and Uliana 1994). K-Ar dates on basalts at the base of the Salamanca Formation are 64.0±0.8 Ma and 62.8±0.8 Ma (Marshall et al. 1981).

The Salamanca mudstones are overlain unconformably by Banco Verde green sandstones that cut down (locally deeply) into the underlying strata (Fig. 5), and are followed upward by about 8 m of mudstone that is unconformably overlain by the basal sandstone of the Banco Negro Inferior. Marshall et al. (1981) indicated that a tuff in the upper part of the Hansen Member yielded a K-Ar date of 61±5 m.y. Marshall et al. (1981) also showed that strata of the Banco Negro Inferior and adjacent strata of the Hansen Member carry a reversed magnetic signature, and that this pattern continues 80 m into the overlying Río Chico Group. This interval of reversed polarity is followed by a pair of normally magnetized intervals about 19 and 13 m thick, respectively, separated by a reversed interval also about 13 m thick (Marshall et al. 1981: fig. 2). This suggests that the Peñas Coloradas Formation in Fig. 5 is of reversed polarity (unless one or more of the numerous unconformities in the sequence have cut out normally magnetized strata), and that the upper part of the Las Flores and Koluel Kaike formations each are of normal polarity. Under the interpretation of Marshall et al. (1981), the faunas from the Río Chico Formation of their terminology (and the Riochican SALMA) correlates to magnetic chrons 25 and 26, or from about 56.5–61.7 Ma. As shown in Fig. 1, the Riochican SALMA is here correlated to about chron C22r, or at about 50–51 Ma. This is discussed further below. Iglesias et al. (2007a) dated a tuff horizon 35 m above the Banco Negro Inferior in the western part of the basin. It yielded an Ar-Ar date of 57.8±6 Ma, but the sanidines retrieved were clearly altered, and the resulting age has little interpretive value.

Peligran SALMA The monotreme *Monotrematum patagonicum* and the sudamericid *Sudamerica ameghinoi* were recovered from the Banco Negro Inferior (Pascual and Ortiz-Jaureguizar 1991; Pascual et al. 1992; Bonaparte et al. 1993) and, along with other non-tribosphenic Gondwanan as well as therian mammals of Laurasian affinity (Table 1), constitute the basis for the Peligran SALMA (Gelfo et al. 2009). In that context, the Peligran occurs in the unconformity-bounded package that includes the Banco Verde and Banco Negro units (Fig. 5). Foraminiferal evidence yields a Danian age for the Salamanca Formation (Bertels 1975a, b), compatible with the 61 Ma age (± 5 m.y.) for the Hansen Member and its reversed magnetic polarity (Marshall et al. 1981). Soria (1989), Pascual and Ortiz-Jaureguizar (1990, 2007), and Pascual et al. (1996), tentatively correlated the land-mammal fauna of the Río Loro Formation to the Itaboraian SALMA. More recently Gelfo et al. (2009) summarized the evidence that favors a post-Tiupampan age for the Peligran SALMA comparable to its position shown in Fig. 1.

Carodnian There is no SALMA for this zone. The next unconformity bounded unit, the Peñas Coloradas Formation, contains the "*Carodnia*" faunal zone (Fig. 5). Pascual and Ortiz-Jaureguizar (2007) indicated that the "*Carodnia*" biochron contains the first occurrence of the polydolopid polydolopimorphian, *Amphidolops* (also known from many younger units), the "didelphid" *Derorhynchus* (now considered as not being present; Table 1), the anisolambdid litoptern *Wainka* and the xenungulate *Carodnia feruglioi*. *Wainka* would be a FAD relative to its presence in the Riochican SALMA, and *Carodnia* would be a FAD relative to its occurrence in Riochican and younger biochrons. Bond et al. (1995) indicated that this unit correlates with that from the lower levels at Bajo de la Palangana and at Cerro Redondo, near Punto Peligro. Gelfo et al. (2009) summarized the presence of possibly correlative faunal sites in Colombia and northwestern Argentina (also Villarroel et al. 1987 - Bogotá Formation, Colombia; Soria 1989; Pascual and Ortiz-Jaureguizar 1990, 2007; Pascual et al. 1996; Bergqvist et al. 2004 - Río Loro Formation, Argentina).

Even though sparse, the taxa in the "*Carodnian*" fauna fit well as shown on Fig. 1, and this position is compatible with the general superposition of the Peñas Coloradas Formation indicated in Fig. 5 and the apparently reversed magnetic polarity of its sediments (Marshall et al. 1981). Figure 4 indicates that there are many unconformities of unknown duration in the Río Chico Group and the Hansen Member of the Salamanca Formation. Figure 5 also shows the stratigraphic location of the two normal magnetozones described by Marshall et al. (1981) as though no unconformities were present (none were recorded in Marshall et al. 1981). Based on additional field studies (Raigemborn et al. 2010), but also indicated by Simpson (1935: fig. 3), it is clear that numerous unconformities are present in Río Chico Group deposits at Cerro Redondo and elsewhere in the Golfo San Jorge Gulf Basin. In that context the integrity of the magnetic zonation proposed by Marshall et al. (1981) and utilized further in Marshall et al. (1997) appears to be doubtful. For the purposes of this report, location of the paleomagnetic signatures of Marshall et al. (1981) is accepted, but their use as a coherent profile for the purposes of correlation to patterns in the GPTS is strongly questioned.

Itaboraian SALMA Patagonia. The Peñas Coloradas Formation is followed stratigraphically by the Las Flores Formation and its faunal unit, in part known as the "*Kibenikhoria*" faunal zone (Fig. 5), which is a correlative of the Itaboraian SALMA. Bond et al. (1995) indicated that this faunal zone is from Cañadón Hondo (Figs. 2 and 5). Correlative faunas in the Las Flores Formation near Gran Barranca (Fig. 6; Raigemborn et al. 2010) occur above an ash dated at 57 Ma. This appears compatible with a revised age of the Itaboraian SALMA as utilized here (Fig. 1). We note that the Las Flores fauna occurs above unconformity *10* in Fig. 5, in rocks apparently correlative with those having a normal magnetic polarity signature (Marshall et al. 1981). If this magnetozone is chron C24n, that would be compatible with evidence in favor of an age of about 53 Ma for the Itaboraian SALMA.

Itaboraí The fresh water travertine deposits at São José de Itaboraí yield fossil mammals of the Itaboraian SALMA, conventionally considered to be about medial Paleocene in age (e.g., Marshall et al. 1997), who interpreted the succession as having been developed in a sequence stratigraphic context regardless of the nonmarine origin of the sediments. This correlation is maintained in Flynn and Swisher (1995: fig. 3). Medeiros and Bergqvist (1999) and Gomes Sant'Anna and Riccomini (2001) reiterated that the Itaboraí travertines formed in a tectonically active basin, which carries the implication that their genesis likely is locally controlled rather than in response to global eustatism. Medeiros and Bergqvist (1999) also demonstrated that the upper travertine unit is of Pleistocene age and inappropriate for Paleogene sequence stratigraphic analysis, and further indicate that an ankaramitic basalt flow rests unconformably on the travertines that elsewhere contain the post-depositional fissure fillings with Itaboraí mammals. Gomes Sant'Anna and Riccomini (2001) indicated that the basalt is dated at 52.6±2.4 Ma. On faunal grounds (e.g., Marshall et al. 1997), the Itaboraí mammals are not of Cretaceous aspect. If the basalt flow also postdates the genesis of the fillings, then the Itaboraí mammals should be post-Cretaceous and pre-53 Ma in age, but the above tectonic and stratigraphic considerations dictate against invoking a sequence stratigraphic analysis for these deposits. If the scenario proposed by Gomes Sant'Anna and Riccomini (2001) is reasonable, and that the cementation of the Itaboraí fissure fillings (and the contained fossils) took place at about this time, then a 53 Ma age for the Itaboraí fossils is plausible and is used here (Fig. 1).

Riochican SALMA Legarreta and Uliana (1994) indicated that the youngest unit in the faunal succession of the former Río Chico Formation or Group, the "*Ernestokokenia*" faunal zone of Simpson (1933), is contained in the Koluel Kaike Formation that unconformably overlies the Las Flores Formation and is unconformably overlain by the Casamayor Formation of the Sarmiento Group (Figs. 5 and 6), now designated as the Sarmiento Formation (Ré et al. 2010b). It also occurs at the upper levels at Bajo de la Palangania and at Cerro Redondo. This is the basis for the Riochican SALMA. See also Flynn and Swisher (1995: fig. 3, where the Riochican SALMA is considered as late Paleocene, rather than late early Eocene, as advocated here in Fig. 1).

In summary to this point, strata that contain type or correlated successions pertaining to the Peligran through Riochican SALMAs can be documented in superpositional relationships in the Golfo San Jorge Gulf Basin of Patagonia. The Tiupampan is reliably interpreted as preceding the Peligran. Whereas it cannot be directly shown as pre-Tiupampan, the documented early Paleocene age of the Grenier Farm site indicates that derived polydolopimorphian metatherians were present by that time in South America. This is compatible with the Late Cretaceous presence of that group in North America on the one hand and also with its plausibly Late Cretaceous dispersal to South America.

Sapoan Now that the "Barrancan" episode of the Casamayoran SALMA is known to be at least 36 Ma old (Kay et al. 1999), that aspect of the Sarmiento Formation is separated by a substantial hiatus (unconformity *12* in Fig. 5) from the underlying Koluel Kaike Formation. As indicated on Fig. 1, the post Riochican - pre "Barrancan" interval has a duration of about 8 m.y., and that from the Riochican to the "Vacan" SALMA is about 5 m.y. long.

Tejedor et al. (2009) described fossil mammals derived from a sequence of tuffs and sediments that crop out in the Chubut River drainage west of Paso del Sapo in north central Chubut Province (33, Fig. 2c). These deposits appear to be extra-caldera counterparts of the Tufolitas Laguna del Hunco Formation, an important plant-bearing succession that formed within the Piedra Parada Caldera at about 52 Ma and persisted later. An ignimbrite that underlies the "Sapoan" mammal-bearing sediments at the type locality of Laguna Fría has been dated (^{40}Ar/^{39}Ar) at 49.51±0.32 Ma. Correlative deposits with fossil mammals at a site known as La Barda occurs above the upper member of the Huancache Andesite, dated at 47.89±1.21 Ma and is overlain by basalts dated at 43 Ma. Tejedor et al. (2009) interpreted the Paso del Sapo mammals to occur within an interval of from 47 to 49 Ma and correlate these with the mammal fauna from the La Meseta Formation of the Antarctic Peninsula (Marenssi 2006; Ivany et al. 2008).

Vacan Cifelli (1985) distinguished the Vacan and Barrancan as sub-ages of the Casamayoran SALMA. "Vacan" fossils are preserved in the lower part of the Sarmiento Formation at Cañadon Vaca, located about 65 km northeast of the Gran Barranca (Fig. 1). The thickest and youngest part of the Sarmiento Formation crops out at Gran Barranca, with "Barrancan" fossils found near its local base (Fig. 7). Cifelli (1985) noted that the contact between the Sarmiento Formation and underlying Río Chico Formation is 'sharp but planar contact' (p. 16), and that fossils occur from about 5 m, 12 m, 18 m, and 86 m above the base of the contact in Section II. Most specimens are found from 5–19 m above the contact (p. 16), and all of those are of "Vacan" age (p. 23).

Cifelli (1985) considered that "Vacan" taxa are more similar to those then known from Río Chico Formation

(Koluel Kaike Formation of current literature; e.g., Ré et al. 2010a) than to those of the Gran Barranca. Andreis (1977) noted an angular unconformity between his Cañadon Honda Formation (basal Sarmiento) and the Río Chico Formation in the Cañadon Hondo site, located about 25 km E. of Cañadon Vaca on the E. side of Río Chico (see Fig. 1 in Cifelli). Carlini et al. (2005, 2010) have proposed an age of 45 Ma for the "Vacan" SALMA. Based on the pre-"Barrancan" age of the "Vacan" SALMA in the Sarmiento Formation, and its earlier age relative to early "Barrancan" elements, the 'conformable' relationship portrayed in Ré et al. (2010b) at Gran Barranca must contain a hiatus (Fig. 7). Both faunally and stratigraphically the assemblages termed "Vacan" differ from those assigned to the "Barrancan." If the 86 m level at Cañadon Vaca correlates with the basal part of the Sarmiento Formation at Gran Barranca, then nearly 86 m of section have been removed at the level of the unconformity between the Sarmiento and Koluel-Kaike formations shown on Fig. 7.

The Gran Barranca and the "Barrancan" through Pinturan SALMAs The Gran Barranca of the Colhue Huapi Lake (Lago de Colhue Huapi) in southern Chubut Province, Argentina (37, Fig. 2c) exposes primary outcrops of the Sarmiento Formation. The Sarmiento Formation contains the type sections of the "Barrancan," Mustersan, Deseadan, Colhuehuapian and Pinturan SALMAs, and fossils correlated with the Tinguiririican SALMA also occur in this unit (Ré et al. 2010a) as indicated in Fig. 7. The physical stratigraphy of the Sarmiento Formation at Gran Barranca is summarized by Bellosi and Madden (2005), Ré et al. (2005, 2010a, b), and Madden et al. (2005), and the following discussion is derived from these publications. They incorporated new litho-, bio-, magnetostratigraphic and geochronologic studies that build upon numerous prior investigations, including Ameghino (1906), Feruglio (1949), Simpson (1941), Spalletti and Mazzoni (1977, 1979), Cifelli (1985), Mazzoni (1985) and Kay et al. (1999).

The Sarmiento Formation (formerly Sarmiento Group) is a regionally extensive pyroclastic unit about 319 m thick that unconformably overlies the subjacent Koluel Kaike Formation (Río Chico Group), and is overlain unconformably by the marine Chenque Formation, followed by the nonmarine Santa Cruz Formation. The areally extensive subhorizontal Sarmiento succession contains numerous facies and hiatuses based upon lithologic changes and the development of paleosols (Ré et al. 2010a, b).

As indicated in Fig. 7 the Sarmiento Formation is considered in the context of six members wherein the SALMAs based on fossil mammals can be correlated to the global chronology via the interbedded paleomagnetic and radioisotopic data. Considered in this context, the "Barrancan" SALMA is contained within the Gran Barranca Member of the Sarmiento Formation. This unit extends from the base of the formation, a few meters below the VRS Tuff, and up to Disconformity 2, which is directly overlain by the Rosado Tuff and ranges in age from about 42 to 39 Ma (Fig. 7). Much of the type "Barrancan" fauna was recovered from the Y Tuff, but others occur both above and below that fossiliferous tuff bed (Ré et al. 2010a).

Mustersan SALMA The Mustersan SALMA is contained within the Rosado Member and unit 1 of the Lower Puesto Almendra Member of the Sarmiento Formation, bracketed by discontinuities 2 and 5 (Fig. 7), with an age range of about 39 to 36.5 Ma. As discussed by Ré et al. (2010a), the Rosado Member of the Sarmiento Formation is about 7 m thick, and is bounded above by Disconformity 3 (U3, Fig. 7). The Lower Puesto Member occurs between Disconformity 3 and Disconformity 5 (U5, Fig. 7), and is about 30 m thick. The Rosado Tuff occurs a few meters above the base of the Rosado Member and yielded a mean ^{40}Ar/^{39}Ar age of 38.66 Ma. The Kay Tuff occurs in Unit 2 of the lower Puesto Alamendra Member of the Sarmiento Formation, about 2 m above Disconformity 4. The mean age for the Kay Tuff is 37.05 Ma. Ré et al. (2010a) assigned a tentative age of about 38.0 to 36.5 Ma for the Mustersan SALMA at Gran Barranca, with the tentative aspect being the uncertainty of when, within Chron 18n.1n the Mustersan actually occurs. The Rosado Member strata correlated with the lower (but not lowest) part of that chron contain a transitional "Barrancan"-Mustersan fauna (El Nuevo L.F., Figs. 1 and 7) here suggested as being about 38.5 Ma.

Tinguiririican SALMA The Tinguiririican SALMA was nominated by Flynn et al. (2003) for fossil mammals recovered from the Abanico Formation in southeastern central Chile (Tinguiririca, 52, Fig. 2d), in a strongly volcaniclastic succession about 100 m thick. Radioisotopic dates (^{40}Ar/^{39}Ar) from the succession range from 35.6±0.85 Ma to 31.34±0.17 Ma, with the Tinguiririca Fauna being assigned an age of about 31.5 Ma, although suggested as likely ranging older. Based on its correlation to the Gran Barranca an age for the Tinguiririican SALMA is here taken as likely 34.5 to 31.5 Ma.

Fossil mammals correlated with the Tinguiririican SALMA occur in the Vera Member of the Sarmiento Formation which correlates to an age range of about 34.8 to 33.3 Ma. The La Cancha site that yields Tinguiririican mammals (Goin et al. 2010) corresponds to magnetic polarity Chron C13n, or from 33.7–33.3 Ma (Fig. 7). In Fig. 1 the age of the Tinguiririican SALMA is taken as from about 34–31 Ma.

Deseadan SALMA The Upper Puesto Almendra Member is dated radioisotopically as 30.4 to 25.9 Ma, The member is composed of three units, 3, 4, and 5, with the base of Unit 3 bounded by Disconformity 6 (U6, Fig. 7). Disconformity 7, within Unit 3, is the base upon which a basalt rests dated at 29.18±0.38 Ma. Two other basalts in this upper part of Unit 3 are dated at 27.78±0.08 Ma and 26.34±0.32 Ma, respectively. Although these basalts also rest locally on or near Disconformity 7, they represent different flow events. Disconformity 8 is cut into Unit 3 and forms the base of Unit 4. Disconformity 9 likewise forms the base of Unit 5. Neither units 4 or 5 are dated isotopically. Disconformity 10 separates the entire member from the overlying Colhue-Huapi Member (U9, Fig. 7).

Two fossil-bearing units occur in the Upper Puesto Almendra Member. The La Cantera L.F. occurs near the base of unit 3 below Disconformity 7, and just above Disconformity 6. The fauna is considered as pre-Deseadan in that it contains some Tinguiririican elements as well as Deseadan taxa. The La Cantera L.F. is considered to correlate with Chron C11n.1n to C11n.2n, and thus range in age from 31.1 to 29.5 Ma.

The Deseadan fossils are found in units 3 and 4 of the Upper Puesto Almendra Member of the Sarmiento Formation. The stratigraphic information supports a potential age range of 29.3 to about 26 Ma.

Neogene

Colhuehuapian SALMA The Colhue-Huapi Member of the Sarmiento Formation crops out only in the west end of the Gran Barranca. Four tuff beds occur in the unit. The Basal tuff is about 10 M above the basal contact, Disconformity 10 (U10, Fig. 7), and has a mean age of 20.39 Ma. The Big Mammal Tuff is about 6 m above the Disconformity 10, with a mean age of 19.75 Ma (not shown on Fig. 7). The Monkey Tuff lies about 22 m above the basal contact and has a mean age of 19.81 Ma. The highest tuff, MHZ 24.5 lies about 48.5 m above the base of the unit and has a mean age of 19.30 Ma. In that this tuff lies between beds with Colhuehuapian mammals on the on hand and Pinturan mammals on the other, it provides a boundary age between these SALMAs.

The beds of the lower fossil zone are the type section for the Colhuehuapian SALMA. The fossil-bearing beds in the Gran Barranca are correlated as being 20.2–20.0 Ma.

Pinturan SALMA Kramarz et al. (2010) strengthened a proposal for a new Pinturan SALMA, based on fossiliferous strata of the Pintura Formation, in the Pinturas River valley of Santa Cruz Province (Kramarz et al. 2010: fig. 18.1). This unit is considered to be post-Colhuehuapian and pre-Santacrucian in age, based on mammalian paleontology. The strata in the upper fossil zone of the Colhue-Huapi Member of the Sarmiento Formation contains taxa correlated with the Pinturan NALMA (Kramarz et al. 2010), who state that this unit thus ranges regionally in age from about 18.75 to 16.5 Ma.

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