Biological Journal of the Linnean Society, 2011, 103, 305–315. With 4 figures



Palaeogeography and palaeoenvironments of northern Patagonia from the Late Cretaceous to the Miocene: the Palaeogene Andean gap and the rise of the North Patagonian High Plateau

EUGENIO ARAGÓN^{1,2,3}*, FRANCISCO J. GOIN^{3,4}, YOLANDA E. AGUILERA², MICHAEL O. WOODBURNE^{5,6}, ALFREDO A. CARLINI^{3,4} and MARTHA F. ROGGIERO^{2,3,7}

¹Centro de Investigaciones Geológicas (UNLP-CONICET) La Plata, Calle 1 n°644, B1900FWA La Plata, Argentina

²Universidad de Nacional de La Plata, Facultad de Ciencias Naturales y Museo, Av. 60 y 122, B1900FWA La Plata, Argentina

³CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas)

⁴División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina

⁵Department of Geology, Museum of Northern Arizona, Flagstaff, AZ 86001, USA

⁶Research Associate, Department of Vertebrate Paleontology, American Museum of Natural History ⁷Centro Parasitológico y de Vectores (UNLP-CONICET CCT La Plata), Calle 2 No. 584, Universidad Nacional de La Plata, Av. 60 y 122, (1900) La Plata, Argentina.

Received 9 March 2011; accepted for publication 9 March 2011

We summarize the geotectonic history of the southern (mostly Patagonian) Andean Cordillera, and its possible influence on the regional expression of global climates, biogeography, and important aspects of mammalian evolution in South America. The northern Patagonian segment of the Andes contrasts with neighbouring sections in that, during Palaeogene times, there was a transform margin stage; this influenced the Andean climate in addition to global climate changes. This segment underwent alternating subduction and transform episodes that suggest the existence of a proto-Andes and an Oligocene Andean gap for the San Carlos de Bariloche area. Coeval with this gap (and at the backarc region of this segment), the 1200-1500 m uplift of the Northern Patagonian Massif took place, resulting in an altiplano (high plateau), or Northern Patagonian High Plateau (NPHP), of 100 000 km², which dominated northern Patagonia during the Oligocene. It is estimated that, by these times, climate in the NPHP was humid and seasonally cool, in contrast to the seasonally more uniform, humid climates of the lower lands peripheral to it. The NPHP may have acted as a biogeographical barrier between central and southern Patagonia, on one side (as part of the Austral Biogeographical Kingdom), and the rest of South America (Holotropical Kingdom) on the other. The most important Paleogene mammalian turnover transpired at the Early Oligocene, concomitantly with the full opening of the Drake Passage and associated global cooling. The latitudinal climate gradient that began at the Eocene-Oligocene transition affected sharply the entire Patagonian region, an effect that was enhanced by the uplift of the NPHP. © 2011 The Linnean Society of London, Biological Journal of the Linnean Society, 2011, 103, 305-315.

 $ADDITIONAL \ KEYWORDS: \ biogeography-geotectonics-Mammalian\ evolution-palaeoclimates-South \ America-Southern\ Andes$

^{*}Corresponding author. E-mail: earagon@cig.museo.unlp.edu.ar

Se resume la historia geotectónica del sector sur (principalmente Patagonia) de la Cordillera Andina y su posible influencia en la expresión regional de los climas globales, biogeografía e importantes aspectos de la evolución de los mamíferos en Sud América. El sector norte de los Andes Patagónicos contrasta con los sectores vecinos en que durante el Paleógeno existió un estadio de margen transformante; esto influenció el clima en los Andes en forma adicional a los cambios climáticos globales. Este segmento fue sometido a la alternancia de episodios de subducción y margen transformante, que sugieren la existencia de un proto-Andes y la existencia de un gap Oligoceno de los Andes para el área de San Carlos de Bariloche. Contemporáneo a este gap (y en la región del retroarco de este segmento) tiene lugar el levantamiento del Macizo Norpatagónico a una altura de 1200-1500 m, dando como resultado la formación de un altiplano (plateau elevado), o Plateau Elevado del Macizo Norpatagónico (NPHP), con una superficie de 100.000 km² la cual dominaba el norte de Patagonia durante el Oligoceno. Se estima que para esos tiempos, el clima en el NPHP fue húmedo con estaciones frías, en contraste con el clima estacionalmente más uniforme y húmedo de las tierras bajas de la periferia. El NPHP pudo haber actuado como una barrera biogeográfica entre Patagonia sur y central por un lado (como parte del Reino biogeográfico Austral) y por otro, con el resto de Sud América (Reino Holotropical). El 'turnover' más significativo para los mamíferos ocurrió en el Oligoceno Temprano, concomitante con la apertura del Pasaje de Drake y el enfriamiento global asociado. El gradiente latitudinal del clima que se inicio en la transición Eoceno-Oligoceno afectó profundamente la región Patagónica, un efecto que fue realzado por el levantamiento del NPHP.

PALABRAS CLAVE: América del Sur – Andes del Sur – biogeografía – evolución mamíferos – geotectónica – palaeoclimas.

INTRODUCTION

As a result of its large regional extent, the Andes comprise an east—west barrier that, in many ways, affects the distribution of South American climates. From a geological perspective, the Andean mountain system is a supra-subduction feature at the active South American plate margin. This plate margin has been active since the Late Jurassic.

The modern configuration of the Andes and its large north—south variations are the result of Miocene tectonic processes and the particular characteristics of each segment as regards the subduction angle, the angle of convergence, the thickness of the oceanic plate, the relations between the segments, the composition of the continental crust, etc. To understand the events that drove the Palaeogene geography and climates of Patagonia, its pre-Miocene orogenic developments have to be addressed.

The Northern Patagonian Massif (also referred as the Somún Curá Massif; Figs. 1, 2) is a geological province on its own (Ramos, 1999). It is one of the two major positive regions in extra-Andean Patagonia: the other one being the Deaseado Massif. Located between 41°30′–44°S and 65°30′–70°30′W, its basement has metamorphic rocks of Precambrian age (Dalla Salda, Varela & Cingolani, 1999). Several units of Palaeozoic and Mesozoic age were deposited above this basement (Rabassa, 1974; Kokogian *et al.*, 1999; Page *et al.*, 1999). During Palaeogene times, the Northern Patagonian Massif was the subject of successive uplift and erosion processes, which led to the development of a high plateau during the Late Eocene–Oligocene; this geomorphological unit is here

named the Northern Patagonian High Plateau (NPHP); see below and Figs 1B, 3). Subsequently, a series of basalt lava flows (the Somún Curá Fm.) covered its south-eastern flank, forming the Somún Curá plateau (Fig. 3C) (Ardolino *et al.*, 1999; Malumian, 1999). As suggested below, the NPHP may have been an important, north–south biogeographical divide during the first half of the Cenozoic.

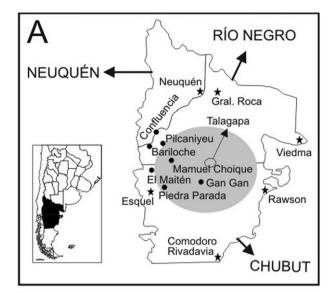
We summarize the historical development of the southern Andean range during the first two-thirds of the Cenozoic, including the Middle Eocene-Oligocene uplift of the NPHP, and its effect on the regional sedimentary and magmatic cycles, as well as climatic events. We also suggest how these events impacted southern South America climates, biogeography, and major trends in mammalian evolution.

ABBREVIATIONS AND DEFINITIONS

NPHP, Northern Patagonian High Plateau, which is a morphological unit; Northern Patagonian batholith includes Jurassic to Miocene plutons at the southern Andes axis (Rapela, 1999); Northern Patagonian Massif: this is a geological province in northern Patagonia (Ramos, 1999); Somún Curá Massif: Late Oligocene—Early Miocene plateau basalts (Ardolino et al., 1999). EECO, Early Eocene Climatic Optimum; LOW, Late Oligocene Warming.

PALAEOGEOGRAPY AND THE MAIN MAGMATIC AND SEDIMENTARY CYCLES

Southern South America is a slim continental plate that has a western active margin at which elements of



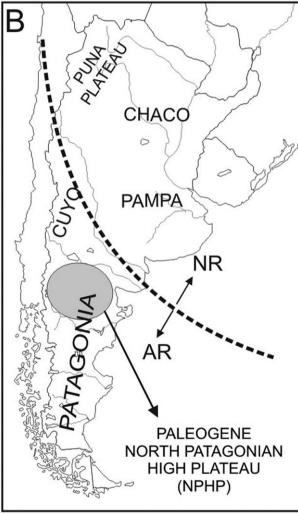


Figure 1. A, map of central and northern Patagonia (provinces of Neuquén, Río Negro, and Chubut) showing localities the described in the text (black circles). Stars indicate major towns. B, map of Argentina indicating natural regions, and the present divide between the Neotropical Region (NR) of the Holotropical Biogeographic Kingdom, and the Andean Region (AR) of the Austral Kingdom. The shaded areas in (A) and (B) indicate the location of the Palaeogene Northern Patagonian High Plateau.

the Pacific Plate were subducted (Fig. 3). In this context, a majority of the regional mountain building processes can be related to the tectono-magmatic changes that occurred in this supra-subduction system since the Late Jurassic (Jordan *et al.*, 1983, 2001; Munizaga *et al.*, 1988; Rapela & Kay, 1988). These subduction processes were not homogeneous throughout but, instead, varied greatly along strike and from segment to segment. This variability included intervals of normal to flat subduction (Barazangi & Isacks, 1979; Cahill & Isacks, 1992), and the evolution of the transform margin (Aragón *et al.*, 2008) that resulted in episodes of deactivation and erosion of the mountain belts, with drastic along-strike changes in topography.

The Cenozoic tectono-magmatic evolution of Northern Patagonia includes four magmatic cycles (Ardolino *et al.*, 1999) and five sedimentary cycles (Malumian, 1999) that can be arranged in four main stages of its palaeogeographical development (Figs 3, 4):

- 1. The Late Cretaceous to Danian interval (Fig. 3A) saw the subduction of the Aluk plate with the development of an arc represented by the emplacement of the Northern Patagonian batholith. This supra-subduction system may have developed a proto-Andes range (Suarez & de la Cruz, 2000). At its back arc counterpart, the most extensive Atlantic Ocean transgression drowned most of northern Patagonia, expressed by the Salamanca, Pedro Luro, and Jaguel Formations at the Colorado and Neuquén basins (Figs 2, 4), deposited in a shallow sea on a continental platform.
- 2. During the Late Palaeocene, the Farallón–Aluk ridge collided with the South American plate at the latitude of northern Patagonia with a very small convergence angle (Cande & Leslie, 1986; Somoza & Ghidella, 2005). This resulted in the development of a transform margin (Aragón et al., 2008) and regional uplift, the development of a broad extensional setting, and the migration of the volcanic locus to the former back arc (Fig. 3B). The regional uplift included the Northern Patagonian Massif, the elevation of which began by the Middle

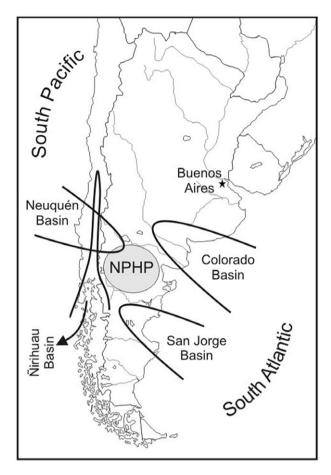


Figure 2. Map of Argentina indicating the sedimentary basins described in the text. Note that the Northern Patagonian High Plateau (NPHP), and, previously, the Northern Natagonian Massif, influenced the drainage of all of these basins.

Eocene, and probably continued to the Middle Oligocene. These movements configured a new, outstanding feature in the Patagonian landscape: the Northern Patagonian High Plateau, or NPHP.

The marine regression from the Golfo San Jorge, Colorado, and Neuquén basins was replaced by successive continental sedimentation, as reflected by the Río Chico, El Carrizo and Ombucta formations, respectively (Fig. 4). The volcanic activity was concentrated at the Pilcaniyeu volcanic belt (Fig. 3B), the 'Faja Oriental o externa' of Ardolino $et\ al.\ (1999)$, with isotopic dates that range from 60 ± 5 to 42 ± 5 Mya (Rapela $et\ al.\ (1984,\ 1987)$. This volcanism was essentially explosive, with the development of a large caldera field (more than $400\ \mathrm{km}$ wide) that produced widespread deposits of ignimbrites. At a later stage of this volcanism, shield volcanoes were also developed. The most important volcanic districts of this large volcanic

- field are: Confluencia, Pilcaniyeu, and Mamuel Choique in Río Negro Province, and Piedra Parada in Chubut Province. The volumes of erupted ash were calculated in more than 1200 km³, during a time span of less than 10 Myr. Most of the Eocene ash deposits concentrate towards the southeast and east of the Pilcaniyeu belt.
- 3. By the Late Oligocene–Early Miocene, the proto-Andes underwent a major period of erosion to the extent that some of the region (the San Carlos de Bariloche area) was bridged and flooded by the Pacific Ocean (Nirihuau Basin; Figs 2, 3C). This new palaeogeographical interval is characterized by Atlantic and Pacific transgressions reflective of global eustatic changes (Malumian, 1999; Malumian et al., 2008). Volcanism changed from a single belt to widespread activity, extending from the Atlantic Ocean to the Pacific coast (Fig. 3C).

The NPHP became the new topographic barrier between the Atlantic and Pacific oceans, and probably between Patagonia and the rest of South America (Fig. 1). Its relative elevation and steep transition with respect to the surrounding countryside was preserved by the Late Oligocene basalt flows of the Somún Curá Fm. as well as by sediments of the Sarmiento Fm. At the locality of Gan Gan (Fig. 1), the Somún Curá lava flows descended more than 400 m from the edge of the NPHP to the surrounding countryside. The altitude that the NPHP was estimated as having at least 1200 m a.s.l. by the Late Oligocene, as determined from the position of the Danian marine sediments that lie undeformed at the top of the NPHP and beneath the Late Oligocene basalt flows. The western, sharp edge of the NPHP was bounded on the south-west by the Nirihuau Basin (Fig. 3C). The NPHP provided the sediments for the Nirihuau Basin, which show facies transitions related to a Pacific transgression, with more continental sediments found toward the NPHP and marine facies toward the southwest (Spalletti, 1983). By contrast, sediments on top of the NPHP are composed of loess. The Atlantic transgression counterpart is known as 'Patagoniense' or 'Patagoniano' and is characterized by a shallow sea with cold water associations (Malumian, 1999; Fig. 3C).

Volcanism during this palaeogeographical stage was broadly distributed from the Pacific to the Atlantic coasts. It was profuse but mainly dominated by lava flows. Moderate explosive activity was restricted to the El Maitén belt, and minor activity in the Somún Curá district (Fig. 3C). There was a moderate increase of volcanism from west to east: the coastal belt is made of sparse andesitic outcrops, whereas the El Maitén belt is composed of stratovolcanos that stand at the

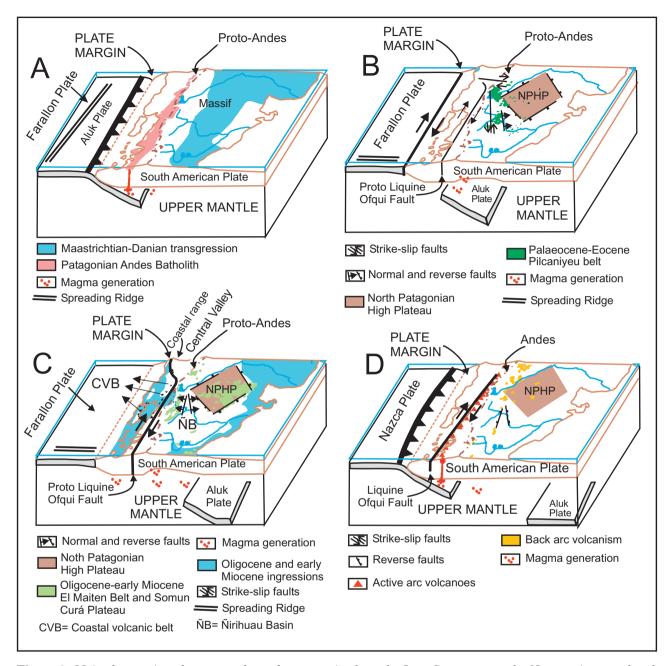


Figure 3. Main changes in palaeogeography and geotectonics from the Late Cretaceous to the Neogene in central and northern Patagonia. A, Late Cretaceous; the subduction of the Aluk plate develops the proto-Andes, and most of the back arc is below sea level. B, Eocene; the collision of the Farallon/Aluk spreading ridge with the South American plate at the northern Patagonia latitude, and the very low convergence angle between the oceanic/continental plates, develop a transform margin because the former back arc is subject to uplift and extension. C, Late Oligocene, the Northern Patagonian High Plateau reaches it maximum elevation (probably more than 1200 m a.s.l) and approximately 500 m with respect to the surrounding countryside. The transform plate margin jumps inland to the proto-Liquiñe—Ofqui fault system with the development of the coastal magmatic belt. The peninsular region of Chile is attached to the ocean plate and moves northward 400 km (Beck et al., 2008). The Ñirihuau basin develops through the former fore-arc, arc and back arc and along the Central Valley. Widespread volcanism at the former back arc is included in the El Maitén Belt and in the Somón Curá plateau basalts. D, Neogene; the break up of the Farallón plate to give birth to the Nazca and Cocos plates and the dramatic change of convergence angle between Nazca/South American plates develop the re-establishment of subduction beneath South America at this latitude, and the rise of the Patagonian Andes. The Northern Patagonian High Plateau remains as an elevated plateau (1200 m a.s.l.) up to present times.

Figure 4. Stratigraphic chart of central Patagonia from the Late Cretaceous to the Miocene (Malumian, 1999). The column at the right indicates each of the four stages of its palaeogeographic evolution (for an explanation, see text).

western edge of the Ñirihuau Basin with a potential ash production of 500 km³. The Somún Curá district shows extensive plateau basalts and volcanic centres such as Talagapa (Fig. 1) that reflect a small number of explosive events with a potential ash production of 100 km³. Most of this ash production was confined to the Ñirihuau Basin, or to the Oligocene–Miocene deposits of southeastern Chubut province (San Jorge Basin area) (Fig. 2).

4. The next major palaeogeographic phase (Figs 3D, 4) occurred during the Miocene. The break-up of the Farallón Plate gave rise to the Nazca and Cocos plates at approximately 23 Mya (Lonsdale, 2005). The newly formed Nazca plate also changed its relative movement to a large convergence angle with respect to the South American plate (almost 90°; Cande & Leslie, 1986), promoting the events:

(1) reinstallation of subduction beneath the South American plate at the latitude of northern Patagonia; (2) the rise of the Andes and the tectonic inversion that put an end to the Ñirihuau Basin (Giacosa & Márquez, 1999); (3) the reinstallation of arc volcanism locus to the Andes axis; and (4) the development of the Andes as a geographical barrier for the easterly and westerly winds.

Volcanic activity shows a major explosive event at 15 Mya with the wide-spread distribution of the Collón Curá Formation and its pyroclastic deposits (Fig. 4). Since the Pliocene, typical stratovolcanos spread along the present volcanic arc axis, and sparse basaltic colada flows are erupted at the back arc.

REGIONAL CLIMATES AND THE ANDEAN CORDILLERA

Continental-scale mountain belts interfere with atmospheric and oceanic circulation patterns, and produce climate changes and gradients in precipitation that affect surface processes (Isacks, 1992). Thus, in addition to the complexity of global climate changes, the mountain building changes at each Andean segment must be considered as an additional factor to be taken into account when considering palaeoclimate changes of a particular area.

Even though the Andes comprises a continuous belt that splits South America, the distribution of humid and arid conditions alternate in a chess-board pattern along it. This is a result of the fact that the Andes stand perpendicular to moisture-bearing winds that vary along strike. The northern and central Andes are exposed to the moist easterlies that come from the Atlantic Ocean across the Amazon basin, leaving all moisture on the eastern flanks of the northern and central Andes, and leading to aridity on the western flanks. By contrast, the southern Andes receive the moist Southern Hemisphere westerlies that leave all the moisture on their western flanks, with resultant aridity on their eastern side (Patagonia). It is important to point out that the southern Andes with an elevation of 2000 m a.s.l. are as effective a moisture barrier as the central and northern Andes are, with elevations of 5000 m and the Puna at 3700 m a.s.l.

Global climate changes through Palaeogene times record two thermal optimums (EECO and LOW) that extended sub-tropical climates to extreme high latitudes. Palaeocene–Eocene climates in this region were humid and subtropical on both sides of the proto-Andes (Aragón & Romero, 1984; Suarez, de la Cruz & Troncoso, 2000; Wilf et al., 2005). The existence of the proto-Andes suggests that the humidity in eastern Patagonia may have been provided by the easterly Atlantic monsoon.

Contrary to northern-central South America, which had an arid western flank and a humid eastern flank throughout the Cenozoic (Strecker et al., 2007), Patagonia Eocene palaeofloras suggest that a subtropical climate was present as far as 48°S (Wilf et al., 2005) on the eastern flank of the southern Andes. This was abruptly interrupted by the global cooling that took place during the Early Oligocene, which established the beginning of the cool-arid conditions that characterize modern Patagonia. During the Early Eocene climatic optimum, the climate throughout Patagonia was humid and subtropical; it is suggested that the humid easterlies (Atlantic monsoon) extended as far south as to dominate continental Patagonia (see Compagnucci, this volume).

During the Oligocene, as global cooling was in progress and the Patagonian climate became gradually more arid, the proto-Andes were diminished as an effective barrier because they were eroded sufficiently as to let Pacific marine transgressions reach the former backarc region (at least in the San Carlos de Bariloche area). From the Late Oligocene to the Early Miocene, the NPHP, with its 100 000 km² area and 1200 m altitude, may have been the most important topographic feature remaining to interact with the monsoon (if present), as suggested by floral data.

After the Miocene, major plate rearrangement and the building of the present Andes began, along with its role as a barrier to humid westerly circulation. The NPHP must have also remained as an important topographical barrier during this time.

An additional factor to be considered is that the Eocene–Oligocene rise of a plateau at the former back arc, split South America into a southernmost part (most of Patagonia south of the NPHP), and a northern part (the remaining, much larger portion of the continent). This may have had considerable climatic and biogeographical influence in southern South America (see below). Palaeofloras also show a sharp change between the Oligocene-Early Miocene deposits of the northern Patagonian lowlands (the Ñirihuau Formation) and those of the NPHP (the La Pava Formation). In the lowlands, abundant Nothophagus and coal deposits of economic interest are present, whereas, in the NPHP, only diatom-bearing deposits (shallow lakes) in loess sediments and strata made of wasp nests are found (Franchi et al., 1984). This shows coeval climate stratification from the high plateau to the surrounding lowlands. The Nirihuau Formation shows that subtropical floras of the middle section suffered the effect of progressive desertification toward the top of the sequence. Instead, the NPHP appears to show sufficient humidity to sustain diatomaceous lake deposits (Oligocene and Miocene). Nevertheless, the abundant wasp nests suggest a more seasonal climate, perhaps including cool winter conditions.

BIOGEOGRAPHICAL PATTERNS IN SOUTHERN SOUTH AMERICA

A series of successive papers published in the last decade (Morrone, 2002; Donato et al., 2003; Morrone, 2004a, b, 2006) summarized previous evidence and argued that, in biogeographical terms, South America was not a unit (the region traditionally referred to as the Neotropics) but, instead, that the continent is a composite. As previously proposed by several specialists belonging to different disciplines, especially by palaeobotanists, it was argued that the southernmost tip of South America belongs not to the Neotropical region but, instead, to a distinct biogeographical unit, the Andean Region of the Austral Kingdom. This intercontinental biogeographical realm includes the Southern Andes (central Chile, Puna Plateau (Fig. 1B), and the Subantarctic Andean region) and Patagonia, as well as Antarctica, southernmost Africa, eastern and southern Australia, New Zealand, and New Guinea. In later works, Morrone (2006) regarded the remaining portion of the Andean Range, its central and northern sections, as a transitional zone between the Neotropical and Andean regions. In turn, the remaining areas of South America, as well as southernmost North America and the Caribbean, were included in the Neotropical Region of the Holotropical Kingdom (Morrone, 2002).

The biogeographical distinction of Patagonia in comparison with the remaining (central and northern) South America has been supported by several lines of palaeo- and neontological evidence. For example, a recent review of the biogeographical history of South American arid lands, taking in account selected, recent arthropod taxa, led Roig-Junent et al. (2006: 416) to state that the areas of endemism of Patagonia form a natural (biogeographical) group, '... showing that this biota evolved as a unit'. Interestingly, the natural area immediately north of central and southern Patagonia, as defined by these authors (the Austral Monte area; Roig-Juñent et al., 2006: fig. 2 and table 1 in that paper) matches quite strictly with the geographical placement of the Northern Patagonian Massif.

Several aspects of the geological history of South America had been suggested as primary drivers of its biotic evolution (Pascual, 2006; Pascual & Ortiz Jaureguizar, 2007; Donato et al., 2003). From our perspective, and putting aside the Andean Cordillera, the most prominent feature responsible of the isolation of Patagonia during post Middle Eocene times was the Northern Patagonian High Plateau. It should be noted that the Austral Biogeographical Kingdom largely predates the Mid-Eocene uplift of the NPHP; Goin et al. (in press b) suggest that its origin could be traced back to the Late Triassic.

Evidence of an Austral realm previous to the uplift of the NPHP is abundant. For example, Quattrocchio & Volkheimer (2000) found that, during the Late Cretaceous and Palaeogene, a southern, high latitude, cool temperate, biogeographical province extended from Patagonia in South America, across Antarctica (mainly Western Antarctica) to New Zealand and southeastern Australia. They named it the 'Weddellian Province' (Zinsmeister, 1979, 1982) and included within it both shallow marine faunas, as well as the terrestrial biotas. Similarly, Quattrocchio (2006) and Quattrocchio et al. (2005) recognized two major Danian microfloral provinces in Argentina: an Ulmaceae pollen province north of Santa Cruz Province, and a Nothofagidites province south of the Chubut-Santa Cruz boundary in central Patagonia. Goin et al. (in press a) suggested that these palynological 'provinces' actually correspond to the Neotropical and Andean biogeographical regions, respectively. Briefly, it can be concluded that the boundary between these northern and southern regions may have shifted with time since the Late Cretaceous to the Early Eocene, until the uplift of the Northern Patagonian High Plateau set a more permanent boundary for both regions from the Mid-Eocene onwards.

A cautionary note should be made on the nature of the palaeontolological evidence regarding Tertiary South American mammals: most of it comes from central Patagonia (i.e. from sites south of the NPHP). However, when faunas from low latitude localities are known, radical differences with approximately contemporary Patagonian associations can be observed. This is the case, for example, of the Late Eocene (?)-Early Oligocene Santa Rosa mammalian assemblage in Peruvian Amazonia. Goin & Candela (2004) noted the uniqueness of this (Neotropical) metatherian association as compared to the (Austral) Patagonian ones of similar age.

Also regarding metatherian mammals, Goin et al. (in press a) postulated that the radiation of basal 'opossum-like' taxa ('Ameridelphia') may have been a largely Neotropical event, including both southern North America and northern South America. Second, they postulated that the origin and radiation of Australidelphia marsupials (microbiotherians, polydolopimorphians, and Australasian taxa) was predominantly an Austral Kingdom event (Andean Region + Antarctica + Australasia). An example of this is the Late Palaeocene (?)-Early Eocene faunal assemblages of Las Flores (central Patagonia) and Itaboraí (southeastern Brazil; Itaboraian age). Both share many taxa in common, except for the Polydolopidae (an australidelphian clade of marsupials), which are exclusively present in Patagonia. In specimen numbers, polydolopids comprise approximately

50% of all the Las Flores metatherian association (Goin *et al.*, in press a).

A more general hypothesis, this time regarding nontherian mammals, could also be made: that monotremes (and gondwanatherians?) are Austral Kingdom elements that would not be found in Cenozoic levels of South America north of the NPHP. Finally, we wonder whether the whole Australosphenidan clade may have had an Austral Kingdom centre of origin, rather than a Gondwanian or a Southern Hemisphere one (on contrasting views regarding the concept and entity of the Australosphenida, compare Luo, Kielan-Jaworowska & Cifelli, 2002 with Woodburne, Rich & Springer, 2003).

The NPHP probably acted not only as a general barrier between the Andean and Neotropical regions of South America, but also as a selective filter for biotic migrations between these two regions. This may be the case for two major groups of mammals that arrived in South America by Middle Cenozoic times: caviomorph rodents and platyrrhini primates. None have vet been recorded from pre-Tinguirirican (latest Eocene-earliest Oligocene) levels in South America; however, molecular evidence strongly suggests that at least caviomorphs may have been present in this continent since the Middle or Late Eocene (Poux et al., 2006). Most favoured hypotheses dealing with the arrival of these mammals suggest a trans-Atlantic dispersal from Africa, first to intertropical South America and then to Patagonia (Vucetich et al., 2010). If a pre-Tinguirirican age for the Santa Rosa mammalian assemblage proves to be correct (as partially hypothesized by Goin & Candela, 2004; see also Madden et al., 2010), this fauna, which includes a wide variety of caviomorphs, would be an empirical proof of a north-south dispersal of rodents in South America. In that case, the NPHP may well have been the filter for a (later) southern dispersal of these mammals, as well as primates, into Patagonia after their arrival to lower latitudes in this continent.

THE BEGINNING OF ARID-ADAPTED MAMMALS IN SOUTH AMERICA

An interesting corollary of these inferences is whether the isolation of Patagonia, by means of the Northern Patagonian High Plateau, triggered the evolution of arid-adapted mammalian taxa after the 'big chill' that transpired by the Eocene–Oligocene boundary (EOB). At this time (33.9 Mya), climatic conditions changed toward an Icehouse phase, probably as a consequence of the opening of the Southern Ocean with the Drake Passage, an event that led to the formation of the Antarctic Circumpolar Current (Livermore *et al.*, 2004). The result was the first major expansion of

Antarctic ice in the Cenozoic, together with a sharp decrease in global temperatures. In turn, these changes promoted generalized turnovers in the Palaeogene marine and terrestrial biota. In southern South America, subtropical biomes and savannas became the dominant biomes just after the EOB (Ortiz-Jaureguizar & Cladera, 2006). During this time, there was an expansion of micro- and mesothermal floristic elements (Barreda & Palazzesi, 2007), and a sharp increase in seasonality (Hinojosa, 2005). All these elements may have promoted the evolution of lineages that exploited the new environmental conditions, initially not distributed throughout South America but found at its souternmost tip: approximately comprising the areas encompassed by the Austral Kingdom.

Most of the South American mammalian fossil associations known from the EOB are known from high latitudes, such as those of Patagonia and other regions of the Austral Kingdom. Marsupials, especially sensitive to low temperatures (Goin et al., in press a), underwent a major turnover by the earliest Oligocene that implied a modernization of several lineages and the extinction of some of the earlier, archaic taxa (Goin, Abello & Chornogubsky, 2010; Goin et al., in press b). Among the most notable of these changes is the origin and radiation of the Argyrolagoidea, a lineage of hypsodont marsupials most probably adapted to granivorous and (at least partial) herbivorous feeding habits. Among native ungulates, there is a noticeable increase in the diversity of hypsodont notoungulates (e.g. Archaeohyracidae, Interatheriinae, Hegetotheriidae, and Mesotheriidae) after the Early Oligocene. Judging from the Miocene South American record, the few persisting taxa of lowcrowned, bunodont ungulate types were restricted to lower latitudes (Cifelli & Villarroel, 1997; Carlini, Gelfo & Sánchez, 2006; Goin et al., in press b).

In summary, we suggest that: (1) the first major expansion in South America of xeric environments after the EOB took place in the southernmost latitudes: Patagonia and the southern Andes; (2) this change promoted the evolution of arid-adapted lineages among mammals; and (3) the subsequent expansion of open, xeric environments in other regions of South America may have promoted the expansion of these arid-adapted taxa throughout northern parts of the continent, probably via the xeric corridors provided by the Andean Range.

ACKNOWLEDGEMENTS

F. Goin thanks CONICET (Argentina) and the Alexander von Humboldt Foundation (Germany) for their support. E. Aragón thanks CONICET for the support for field work.PIP 00916. This paper is based on our

presentation at the Symposium on 'Palaeogeography and Palaeoclimatology of Patagonia: Effects on Biodiversity', held at the La Plata Museum in Argentina in May 2009 and organized by Jorge Rabassa, Eduardo Tonni, Alfredo Carlini, and Daniel Ruzzante.

REFERENCES

- Aragón E, Romero JE. 1984. Geología, Paleoambientes y Paleobotánica de yacimientos Terciarios del occidente de Río Negro, Neuquén y Chubut. 9° Congreso Geológico Argentino, Actas 4: 475–507.
- Aragón E, Aguilera Y, Cavarozzi C, Ubaldón MC, Ribot A. 2008. La Caldera de Piedra Parada. Un volcán gigante de 50 millones de años, testimonio de cambios. Buenos Aires: Sitios de Interés Geológico Ed. Servicio Geológico Minero Argentino.
- Ardolino A, Franchi M, Remesal M, Salani F. 1999. El volcanismo en la Patagonia extraandina. In: Caminos R, ed. 579–612. Geología Argentina. Buenos Aires: Instituto de Geología y Recursos Minerales, Anales 29 (15).
- Barazangi M, Isacks BL. 1979. Subduction of Nazca plate beneath Peru: evidence from spatial distribution of earthquakes. *Geophysical Journal of the Royal Astronomical* Society 57: 537–555.
- Barreda V, Palazzesi L. 2007. Patagonian vegetation turnovers during the Paleogene–Early Neogene: origin of aridadapted floras. *The Botanical Review* 73: 31–50.
- Beck RMD, Godthelp H, Weisbecker V, Archer M, Hand SJ. 2008. Australia's Oldest Marsupial Fossils and their Biogeographical Implications. *PLoS ONE* **3**(3): e1858. doi:10.1371/journal.pone.0001858.
- Cahill T, Isacks BL. 1992. Seismicity and shape of the subducted Nazca plate. *Journal of Geophysical Research* 97: 17503–17529.
- Cande SC, Leslie RB. 1986. Late Cenozoic tectonics o the Southern Chile trench. *Journal of Geophysical Research* 91: B1 471–496.
- Carlini AA, Gelfo JN, Sánchez R. 2006. First record of the strange Megadolodinae (Mammalia: Litopterna: Proterotheriidae) in the Urumaco Formation (Late Miocene), Venezuela. Journal of Systematic Palaeontology 4: 279–284.
- Cifelli RL, Villarroel C. 1997. Paleobiology and affinities of Megadolodus. In: Kay RF, Cifelli RL, Madden RH, eds. 265–288. A history of the Neotropical fauna: vertebrate paleobiology of the Miocene of Tropical South America. New York, NY: Springer-Verlag.
- Compagnucci R. this volume. Atmospheric circulation over Patagonia since the Jurassic to present: a review through proxy data and climatic modeling scenarios. *Biological Journal of the Linnean Society*.
- Dalla Salda L, Varela R, Cingolani C. 1999. El basamento pregondwánico del centro-oeste del Macizo Nordpatagónico. In: Caminos R, ed. *Geología Argentina*. Buenos Aires: Instituto de Geología y Recursos Minerales, Anales 29 (15), 107–112.
- Donato M, Posadas P, Miranda-Esquivel DR, Ortiz Jaureguizar EO, Cladera G. 2003. Historical biogeography of

- the Andean region: evidence from Listroderina (Coleoptera: Curculionidae: Rhytirrhinini) in the context of the South American geobiotic scenario. *Biological Journal of the Linnean Society* **80:** 339–352.
- Franchi MB, Nullo FE, Sepúlveda EG, Uliana MA. 1984.
 Las sedimentitas Terciarias. 9° Congreso Geológico Argentino, Relatorio I-(9): 215–266.
- Giacosa RE, Márquez MJ. 1999. El volcanismo en la Patagonia Extraandina. In: Caminos R, ed. Geología Argentina. Buenos Aires: Servicio Geológico Minero Argentino, Anales 29, 444–459.
- Goin FJ, Abello MA, Chornogubsky L. 2010. Middle Tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America's Grande Coupure. In: Madden RH, Carlini AA, Vucetich MG, Kay RF, eds. The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. New York, NY: Cambridge University Press, 71–107.
- Goin FJ, Candela A. 2004. New Paleogene marsupials from the Amazon Basin of Eastern Perú. In: Campbell KE Jr, ed. In: *The Paleogene mammalian fauna of Santa Rosa, Ama*zonian Perú. Sciences Series 40. Los Angeles: Natural History Museum of Los Angeles County, 15–60.
- Goin FJ, Zimicz AN, Forasiepi AM, Chornogubsky LC, Abello MA. in press a. The rise and fall of south American metatherians: contexts, adaptations, radiations, and extinctions. In: Rosenberger AL, Tejedor MF, eds. Origins and evolution of Cenozoic south American mammals. New York: Springer.
- Goin FJ, Gelfo JN, Chornogubsky L, Woodburne MO, Martin T. in press b. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. In: Patterson BD, Costa L, eds. Bones, clones, and biomes: an 80-million year history of recent Neotropical mammals. Chicago: University of Chicago Press.
- Hinojosa LF. 2005. Cambios climáticos y vegetacionales inferidos a partir de paleofloras cenozoicas del sur de Sudamérica. Revista Chilena Historia Natural 32: 95– 115
- Isacks BL. 1992. Long term land surface processes: erosion, tectonics and climate history in mountain belts. In: Mather PM, ed. Terra-1: understanding the terrestrial environment. London: Taylor and Francis, 21–36.
- Jordan TE, Isacks BL, Ramos V, Allmendinger RW. 1983. Mountain building in the central Andes. Episodes 3: 20-25.
- Jordan TE, Matthew Burns W, Veiga R, Pángaro F, Copeland P, Kelley S, Mpodozis C. 2001. Extension and basin formation in the southern Andes caused by increased convergence rate: a mid-Cenozoic trigger for the Andes. *Tectonics* 20: 308–324.
- Kokogian DA, Spalletti L, Morel E, Artabe A, Martínez RN, Alcober OA, Milana JP, Zavattieri AM, Papú OH. 1999. Los depósitos continentales triásicos. In: Caminos R, ed. *Geología Argentina*. Buenos Aires: Instituto de Geología y Recursos Minerales, Anales 29 (15), 377–398.
- Livermore R, Eagles G, Morris P, Maldonado A. 2004.

- Shackleton Fracture Zone: no barrier to early circumpolar ocean circulation. *Geology* **32:** 797–800.
- **Lonsdale P. 2005.** Creation of the Cocos and Nazca plates by fission of the Farallon plate. *Tectonophysics* **404:** 237–264.
- Luo Z, Kielan-Jaworowska Z., Cifelli RL. 2002. In quest for a phylogeny of Mesozoic Mammals. Acta Paleontologica Polonica 47: 1–78.
- Madden RH, Kay RF, Vucetich MG, Carlini AA. 2010. Gran Barranca: a 23-million-year record of middle Cenozoic faunal evolution in Patagonia. In: Madden RH, Carlini AA, Vucetich MG, Kay RF, eds. The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. New York, NY: Cambridge University Press, 419–435.
- Malumian N. 1999. La sedimentación en la Patagonia Extraandina. In: Caminos R, ed. Geología Argentina. Buenos Aires: Instituto de Geología y Recursos Minerales, Anales 29, 557–578.
- Malumian N, Asencio MA, Cornou ME, Martinez MA, Quattrocchio ME. 2008. Formación Rio Foyel, La transgresión Pacífica en la Cordillera Norpatagónica. 17° Congreso Geológico Argentino, Actas, 861–862.
- Morrone JJ. 2002. Biogeographical regions under track and cladistic scrutiny. *Journal of Biogeography* 29: 149–152.
- Morrone JJ. 2004a. Panbiogeografía, componentes bióticos y zonas de transición. Revista Brasileira de Entomologia 48: 149–162.
- Morrone JJ. 2004b. La Zona de Transición sudamericana: caracterización y relevancia evolutiva. Revista Entomológica Chilena 28: 41–50.
- Morrone JJ. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology* **51:** 467–494.
- Munizaga F, Hervé F, Drake R, Pankhurst R, Brook M,
 Snelling N. 1988. Geochronology of the granitoids of the
 Andean lake region 39a-42aLat. South central Chile, preliminary results. *Journal of South American Earth Sciences* 1: 309-316.
- Ortiz-Jaureguizar E, Cladera GA. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. Special issue: historical biogeography and origin and evolution of arid and semi-arid environments. *Journal of Arid Environments* 66: 498–532.
- Page R, Ardolino A, de Barrio RE, Franchi M, Lizuain A, Page S, Silva Nieto D. 1999. 3. Estratigrafía del Jurásico y Cretácico del Macizo de Somún Curá, Provincias de Río Negro y Chubut. In: Caminos R, ed. Geología Argentina. Buenos Aires: Instituto de Geología y Recursos Minerales, Anales 29 (15), 460–488.
- Pascual R. 2006. Evolution and geography: the biogeographic history of South American land mammals. Annals of the Missouri Botanical Gardens 93: 209–230.
- Pascual R, Ortiz Jaureguizar E. 2007. The Gondwanan and South American episodes: two major and unrelated moments in the history of the South American mammals. *Journal of Mammalian Evolution* 14: 75–137.

- Poux C, Chevret P, Huchon D, De Jong WW, Douzery EJP. 2006. Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. Systematic Biology 55: 228–244.
- **Quattrocchio ME. 2006.** Palynology and palaeocommunities of the Paleogene of Argentina. *Revista Brasileira de Paleontologia* **9:** 15–22.
- Quattrocchio ME, Volkheimer W. 2000. Danian microfloral provinces in Argentina. Revista Española de Paleontología 15: 3-11
- **Quattrocchio ME, Volkheimer W, Marquillas RA, Salfity JA. 2005.** Palynostratigraphic, palaeobiogeographic and evolutionary significance of the Late Senonian and Early Paleogene floras of northern Argentina. *Revista Española de Micropaleontología* **37:** 259–272.
- Rabassa J. 1974. Geología de la región Pilcaniyeu-Comallo, Prov. de Río Negro. San Carlos de Bariloche: Fundación Bariloche, Publicación 17.
- Ramos V. 1999. Las provincias geológicas del territorio argentino. In: Caminos R, ed. Geología Argentina. Buenos Aires: Instituto de Geología y Recursos Minerales, Anales 29 (15), 41–96.
- Rapela CW. 1999. El plutonismo Triásico-Jurásico de la Patagonia. In: Caminos R, ed. *Geología Argentina*. Buenos Aires: Instituto de Geología y Recursos Minerales, Anales 29 (15), 364–372.
- Rapela CW, Kay SM. 1988. Late Paleozoic to recent magmatic evolution of Northern Patagonia. *Episodes* 11: 176–182.
- Rapela CW, Spalletti LA, Merodio JC, Aragón E. 1984. El vulcanismo Paleoceno-Eoceno de la Provincia Volcánica Andino Patagónica (40 a 43 Latitud Sud). En: *IX Congreso Geológico Argentino (S.C. de Bariloche) 1984 RELATORIO I (8)*, 189–213.
- Rapela CW, Spalletti L, Merodio JC, Aragón E. 1987. Temporal evolution and spatial variation of the lower tertiary Andean volcanism (40–42 30'S). *Journal of South American Earth Sciences* 1: 1–14.
- Roig-Juñent S, Domínguez MC, Flores GE, Mattoni C. 2006. Biogeographic history of South American arid lands: a view from its arthropods using TASS analysis. *Journal of Arid Environments* 66: 404–420.
- Somoza R, Ghidella ME. 2005. Convergencia en el margen

- occidental de América del Sur durante el Cenozoico: subducción de las placas de Nazca, Farallón y Aluk. *Revista de la Asociación Geológica Argentina* **60:** 797–809.
- Spalletti LA. 1983. Paleogeografía de la Formación Ñirihuau y sus equivalentes en la región occidental de Neuquén, Río Negro y Chubut. Revista de la Asociación Geológica Argentina 38: 454–468.
- Strecker MR, Alonso RN, Bookhagen B, Carrapa B, Hilley GE, Sobel ER, Trauth MH. 2007. Tectonics and Climate of the Southern Central Andes. *Annual Review of Earth and Planetary Science Letters* 35: 747–787.
- Suarez M, de la Cruz R. 2000. Tectonics in the eastern central Patagonian Cordillera (45°30′-47°30′S). Journal of the Geological Society, London 157: 995-1001.
- Suarez M, de la Cruz R, Troncoso A. 2000. Tropical/ subtropical Upper Paleocene-Lower Miocene fluvial deposits in eastern central Patagonia, Chile (46°45'S). *Journal of* South American Earth Sciences 13: 527–536.
- Vucetich MG, Vieytes EC, Pérez ME, Carlini AA. 2010. The rodents from La Cantera and the early evolution of caviomorphs in South America. In: Madden RH, Carlini AA, Vucetich MG, Kay RF, eds. The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. New York, NY: Cambridge University Press, 189–201.
- Wilf P, Johnson KR, Cúneo RN, Smith EM, Singer SB, Gandolfo MA. 2005. Eocene Plant Diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. American Naturalist 165: 634–650.
- Woodburne MO, Rich TH, Springer MS. 2003. The evolution of tribospheny and the antiquity of mammalian clades. *Molecular Phylogeny and Evolution* 28: 360–385.
- Zinsmeister WJ. 1979. Biogeographic significance of the Late Mesozoic and early Paleogene molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. In: Gray J, Boucot AJ, eds. *Historical biogeography, plate tectonics and the changing environment*. Proc. 37th Annual Biology Colloquium and Selected papers, Eds. Gray, J. and A. Boucot. Corvallis, Oregon: Oregon State University Press, 349–355.
- **Zinsmeister WJ. 1982.** Late Cretaceous–Early Tertiary molluscan biogeography of the southern CircumPacific. *Journal of Paleontology* **56:** 84–102.