TOWARDS THE ORIGIN OF SOUTH AMERICAN NATIVE UNGULATES AND THEIR PALEOCENE AND EOCENE DIVERSITY

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1. INTRODUCTION

The biological history of South America is characterized by the strong endemicity of its taxa. This was a direct consequence of geographic isolation, since South America was an island during most of the Cenozoic (Simpson, 1980; Marshall et al., 1983). The origin, evolution, and later extinction of the so-called South American native ungulates (SANU) were tightly related to this geographic context. It has been argued that Notoungulata, Litopterna (including Notopoterna, see below), Astrapotheria (including Trigonostylopoidea, see below), Pyrotheria and Xenungulata evolved *in situ* from a Laurasian ancestor, widely supposed to have arrived during the Late Cretaceous or earliest Paleocene (Simpson, 1948; Cifelli, 1983b, 1993; Muizon and Cifelli, 2000). This immigration may have been facilitated by dry-land connections that existed between Laurasia and Gondwana in the present day Caribbean region (Iturralde-Vinent and Macphee, 1999; Case *et al.*, 2004). However, Notoungulata and Astrapotheria have been closely related to Afrotheria, a clade that includes the African taxa Proboscidea, Hyracoidea, Sirenia, Tubulidentata, Tenrecoidea and Macroscelidea (Agnolin and Chimento, 2011).

The SANU first appear in the fossil record during the early Paleocene in Bolivia (Muizon and Cifelli, 2000; Gelfo, 2006), while the geologically youngest representatives occur in association with humans, 8,500 years ago (*i.e.*, *Toxodon* sp. Tonni *et al.*, 1992). The wide evolutionary radiation of the SANU during the Paleocene and earliest Eocene, led to a high pick in their taxonomic and morphological diversity in the Eocene-Oligocene span.

Outcrops hosting Paleocene and Eocene mammals are concentrated in several localities of southern South America, particularly in Argentina. The main sites producing native ungulates in Argentina are in Patagonia, followed by other localities in the northwest, and isolated sites in the central Argentinean basin of great biogeographic significance this record also extends to the Antarctic Peninsula, as well as to isolated sites in Chile, Bolivia, Brazil, Peru, and Colombia.

The biotic history of South America Cenozoic mammals is described via a succession of biochronological units: the South American Land Mammal Ages (SALMAs) based mostly on the “Etages” of Ameghino (Ameghino, 1906), but which follow the North American Land Mammal Ages (NALMAs) concept (Pascual et al., 1965).

Here we review the relationships between several South American and Antarctic Paleocene-Eocene localities with SANU fossils and, also, we integrate their record for this span. The significance of these mammals in the establishment of a biostratigraphical and biochronological framework is enhanced by the cluster analysis performed here. The relationships of SANU to each other, and their inclusion in a new phylogenetic framework for the living placental mammals are also discussed.

2. GEOLOGICAL AND BIOCHRONOLOGICAL CONTEXT

Many localities where Paleocene and Eocene native ungulates occur lack isotopic data, meaning that only a relative ages can be inferred for them, through faunistic comparison. Native ungulates are important in this regard since they are high in diversity, widely distributed, and abundantly presserved in Paleogene outcrops. The biochronologic scheme followed below shows the provisional consensus about the age relationship of these localities following, with few modifications, Gelfo et al. (2009a, 2009b).

In this section we review and update the main native ungulate bearing Paleocene-Eocene localities of South America clarifying their stratigraphic context. For practical purposes we have divided this overview in a Patagonian and Antarctic component and the remainder of South American component.

2.1. Patagonian setting

The Paleogene stratigraphic succession of Patagonia is characterized by alternating marine and continental sequences with a very rich fossil record. In the austral sector, south of 48º S marine sedimentation prevailed from the end of the Cretaceous to the Oligocene. In contrast, in the northern Patagonia, Danian marine outcrops were gradually replaced by epiclastics sedimentation, particularly from the Paleocene onward, and then by pyroclastics deposits, particularly during the Eocene – Miocene span.

The oldest fossil therian mammal in South America is an isolated tooth of the marsupial *Cocatherium lefipanum* and came from the earliest Paleocene (5 meters above the Cretaceous – Paleocene limit) in the Lefipán Formation, which crops out in the middle course of the Chubut River, in Patagonia (Figure 1). No native ungulate has been found in this level yet. In contrast, basal levels of the 'Banco Negro Inferior' (BNI), in the Hansen Member of the Salamanca Formation (Andreis et al. 1975), the latter of which is widely distributed in southeastern Chubut and northeastern Santa Cruz Provinces of Argentina, bear several basal native ungulates. The richest fossil locality for the BNI sediments is Punta Peligro, where a diverse fauna composed of leptodactylid frogs, chelid turtles, alligatorid crocodiles (Bonaparte et al. 1993), and a mixture of non-tribosphenic Gondwanan mammals, as well as native marsupials and ungulates was found (Bonaparte et al. 1993; Bond et al. 1995). This fauna was initially considered as the southern equivalent of the Tiupampan SALMA (Pascual and Ortiz-Jaureguizar, 1990) but later, the Peligran SALMA was defined (Bonaparte et al. 1993) and recognized as a distinctive and younger unit. Since no radioisotopic dates are available for Punta Peligro or Tiupampa, calibrating these faunas through their mammal content and magnetostratigraphy have been attempted. Results have been inconsistent, however, with both of the two possible age relationships of the Peligran and Tiupampan SALMAs being advocated by different workers. A complete and critical review of all the various alternatives, and a biochronological analysis of the SALMAs, allowed the Peligran SALMA to be referred to the Selandian Age (Gelfo et al. 2009a).

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An important set of epiclastic sediments overlies the Salamanca Formation, in several localities of eastern and central Chubut; these were termed the Rio Chico Formation by Simpson (1935b) consisting (from the base to top) of the "*Carodnia* Zone", "*Kibenikhoria* Zone" and "*Ernestokokenia* Zone". The Rio Chico Formation was later divided into the Las Violetas and Visser members (Andreis et al., 1975). Legarreta and Uliana (1994) made a new lithostratigraphic interpretation elevating Simpson's original unit to group status (Rio Chico Group), and correlating Simpson's zones with the Peñas Coloradas, Las Flores and Koluel Kaike formations, respectively.

Raigemborn (2008) added Las Violetas Formation to the base of the Rio Chico Group, where no fossil mammals have been found yet. The mammalian assemblages of the "*Kibenikhoria*" and "*Ernestokokenia*" zones were later referred to the Itaboraian and Riochican SALMAs respectively (Bond et al. 1995), leaving the oldest "*Carodnia* Zone" as intermediate between Peligran and Itaboraian SALMAs (Gelfo et al., 2009a). The age of these biochronological units was long debated. The Itaboraian and Riochican SALMAs were usually referred to the earliest late Paleocene and late Paleocene respectively (e.g., Flynn and Swisher, 1995; Pascual and Ortiz Jaureguizar, 2007) but the lack of numerical dates or magnetostratigraphic data forces their relative temporal placement to be based on indirect inferences. Las Flores and Koluel Kaike formations were considered Eocene in age based on stratigraphic analysis (Bellosi and Madden, 2005). Even though the Itaboraian and Riochican faunas recognized within these units, likely represent the late Paleocene and earliest Eocene span (Gelfo et al., 2009a).

The Rio Chico Group is overlain by an important, broadly distrubuted tuff unit (the Sarmiento Formation), covering the San Jorge Basin and the east-central Patagonia. In several localities this transition is difficult to determine but in others, such as Cañadón Hondo, in Chubut Province, the pyroclastic sediments of the Sarmiento Formation clearly unconformably overlie the Rio Chico Group (Andreis, 1977).

The whitish pyroclastic outcrops known as "*Tobas de Sarmiento*" (Feruglio, 1938) or, more recently, as the Sarmiento Formation (Bellosi, 2010), form a 319 m thick succession of sediments composed of tuffaceous mudstones, bentonites, paleosols, intraformational conglomerates and sandstones (Bellosi, 2010). Sedimentation was caused by the Plinian eruptions, along the western margin of Patagonia. The most widespread and characteristic unit of Eocene sedimentary rocks in central Patagonia, the Sarmiento Formation recorded a wide range of fossil mammals, and particularly SANU (Ré et al., 2010). Important faunal synthesis of these localities in the Sarmiento Formation may be found in Simpson (1948, 1967a and b); Marshall *et al.* (1983).

Exposures of the Sarmiento Formation outcrop at Cañadón Vaca, located west of the Río Chico River approximately 60 kilometers northeast of Colhué-Huapi Lake. The Vaccan subage of the Casamayoran SALMA was recognized based on the lowest fossil horizon of Cañadón Vaca (Cifelli, 1985b), presently considered middle Eocene in age based on a date of 45 Ma. (Carlini com pers.) The age of this fauna indicates a gap between the Riochican and the Casamayoran SALMAs in central and eastern Patagonia.

This hiatus is partially filled by the Paso del Sapo fauna in northwest Patagonia (see below).

The locality of Gran Barranca at the southern cliff of the Colhué-Huapi Lake in central Chubut Province (Figure 1: 5) provides the best exposure of the Sarmiento Formation, revealing a nearly complete sequence from the Eocene (Lutetian) up to the Miocene (Burdigalian), recording the only continuous middle Eocene to early Miocene continental fossil record for the southern hemisphere (Ré et al., 2010). To make the Sarmiento Formation in its type area at Gran Barranca the standard reference section for the middle Cenozoic, Ameghino originally divided this sequence, from base to top, based on the most characteristic mammal taxon found in each "couche": "*Notostylopéen*", "*Astraponotéen*", "*Pyrotheréen*" and "*Colpodonéen*"; more recently these divisions have been equated with the Casamayoran, Mustersan Deseadan, and Colhuehuapian stages of Simpson (1948) or SALMAs (Pascual et al., 1965), respectively. The current stratigraphic framework shows the Sarmiento Formation as divided into the following members, from base to top: Gran Barranca, Rosado, Puesto Almendra Inferior, Vera, Puesto Almendra Superior and Colhue Huapi (Bellosi and Madden, 2005; Bellosi, 2010). The first three members represent Eocene sedimentation and the Eocene-Oligocene transition occurs within the Vera Member. The Gran Barranca Member, the most widespread, was dated by ^{40}Ar-^{39}Ar, between 41.6 and 38.7 Ma and was referred to middle Eocene (Ré et al., 2010). Fossil mammals from Gran Barranca Member pertain to the Barrancan subage of the Casamayoran SALMA (Simpson, 1948, 1967a; Cifelli, 1985b). Cañadon Tournouër in Santa Cruz Province and Valle Hermoso, Cerro del Humo, Cañadon Hondo, Laguna de la Bombilla in Chubut (Figure 1) are some of the Patagonian localities where classic Barrancan faunas have been recovered.

The more restricted Rosado Member is bounded by upper and lower unconformities (Bellosi and Madden, 2005). Fossil mammals from this unit have been assigned to the Mustersan SALMA (López et al., 2005), and referred to the middle late Eocene based on an isotopic age of 37.8 Ma (Bellosi and Madden, 2005). The overlying Puesto Almendra Member represents the transition between the middle and earliest late Eocene (Ré et al., 2010). A prominent unconformity in the middle of this unit divides it into upper and lower Puesto Almendra submembers (Bellosi and Madden, 2005). Mustersan mammals are also known from the lower submember (Simpson, 1948; 1967b). Other Patagonian localities with Mustersan taxa are La Gran Hondonada, Cerro

Blanco, Cerro del Humo and Laguna del Mate (Figure 1). At the top of the Eocene sequence the Vera Member has yielded a mammal fauna assigned to the Tinguiririan SALMA (López et al., 2005).

Laguna Fría and La Barda are the westernmost Paleogene mammal-bearing sites in Patagonia; collectively they are informally known as the "Paso del Sapo" locality, in northwestern Chubut Province, Argentina (Figure 1). The fossil levels of Laguna Fría occurs within the Tufolitas Laguna del Hunco Formation which unconformably overlies the Ignimbrita Barda Colorada Formation and unconformably underlies lava flows of the Andesitas Huancache Formation. La Barda occurs within the Andesitas Huancache interbedded tuff. Numerical dates of the surrounding sediments constrain the age of Laguna Fría between 52.05 ± 0.23 Ma and 47.89 ± 1.21 Ma and the mammal-bearing tuff of the La Barda between 45–47 Ma (Tejedor et al., 2009). The faunal similarity between Paso del Sapo and the Antarctic La Meseta Formation fauna (see below) could represent a new biochronological unit for the early Eocene between the Riochican and the Vacan subage of the Casamayoran SALMAs (Tejedor et al., 2009).

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2.2. Antarctic setting

The James Ross Basin is located in the Weddell Sea, on the south side of the northeastern boundary of the Antarctic Peninsula. The Paleogene beds of the James Ross Basin are exclusively marine and crop out on Seymour and nearby Cockburn islands. Terrestrial fossil mammals have been disovered in NW Seymour (=Marambio) Island, Antarctic Peninsula. The mammal-bearing La Meseta Formation is divided into six erosionally bounded members. The unit reaches a maximum thickness of 720 m and fills a 7 km wide valley incised into the Paleocene Marambio Group. The taxonomic diversity of the La Meseta Fauna (LMF, Allomember *Cucullaea* I, natricid horizon) give reference for this subdivision is modest, including three avian and seven mammalian ordinal groups. The terrestrial mammalian assemblage was likely even more diverse than presently recorded given that fewer than 60 specimens have been recovered from a small number of sites. Strontium isotopic ages where the mammals were collected indicate an age between 49 and 51 Ma (Ivany, 2007).

2.3. Other South American settings

The oldest South American fauna, containing a diverse array of the therian mammals (see Muizon and Céspedes in this volume), derives from the middle section of the Santa Lucía Formation (Marshall et al., 1997), in the Tiupampa locality, southeast of Cochabamba, Bolivia (Figure 1). The fossil bearing levels of the Santa Lucia Formation are characterized by medium-grained to conglomeratic sandstones, intercalated with commonly rooted red-brown mudstones and some paleosols. This sequence was deposited in a meandering fluvial environment (Marshall et al., 1997). The Tiupampan mammal-bearing levels were initially interpreted as Late Cretaceous in age (Marshall et al. 1983), subsequently as early Paleocene (Ortiz-Jaureguizar and Pascual, 1989; Bonaparte et al. 1993), earliest late Paleocene (Marshall et al. 1997) and, finally, as Puercan NALMAequivalent, i.e., early Paleocene (Muizon and Cifelli, 2000). The fauna became the basis of the Tiupampan SALMA, originally interpreted as Danian in age (Pascual and Ortiz Jaureguizar, 1990). Mammals from Tiupampa represent the oldest and most primitive South American eutherians know, closely related to those of the Puercan of North America (Gelfo et al. 2009a).

An important Paleogene sequence in northwest Argentina is, the Santa Bárbara Subgroup of the Salta Group, the former of is subdivided into the Mealla, Maíz Gordo and Lumbrera formations (from bottom to top). The pelitic sediments of the Mealla Formation crop out in eastern ranges of Salta and Jujuy and north of Tucumán Provinces. southwest of Tres Cruces, in the area between Sierra del Mal Paso and Sierra de Aguilar in Jujuy this unit was correlated at the with the base of the Santa Lucía Formation in Tiupampa, Bolivia and also with the base of the Banco Negro Inferior of the Salamanca Formation in Patagonia Argentina (Marshall et al., 1997). Due to their stratigraphic position, the Mealla mammals were considered equivalent to those of the Peligran SALMA (Selandian) represented at the base of the BNI, in Punta Peligro (Marshall et al., 1997). In view of the lack of data about deposition rates, the long distances between these localities, and their differing mammal content Gelfo et al (2009a) rejected this correlation, providing a revised age for the Mealla Formation. The presence of a henricosborniid suggests that the Mealla fauna is probably related to the Riochican SALMA an interval over which this family is diverse (Pascual et al. 1981).

The overlying Maíz Gordo Formation shows a similar regional distribution as Mealla Formation. This unit formed by rocks deposited in a lacustrine basin of mixed carbonate-clastic sedimentation, is dominate by mudstone, with abundant fossils of turtles, crocodiles, fishes and insects. Maíz Gordo Formation has been correlated with the upper part of the Santa Lucía Formation, in Bolivia, and also has been considered a distal equivalent of the Impora Formation. It was considered late Paleocene (Marshall et al., 1997) or probably late Paleocene to early Eocene in age (Del Papa, 1999).

The lacustrine deposits of the Lumbrera Formation, at the top of the Santa Bárbara Subgroup, are a 600 m thick sequence dominated by reddish claystones and mudstones. In the locality Pampa Grande (Alemania area, Salta Province, figure 1) two lacustrine deposits occur, Faja Verde I and Faja Verde II. Most of the native ungulates discovered in this unit were found below the Faja Verde I (*e.g*. Pascual et al., 1981). The astrapotherian *Albertogaudrya? carahuensis* Carbajal et al., 1977 was recovered from Faja Verde I and, over it, the notoungulates *Coquenia bondi* Deraco et al., 2008 (Leontiniidae), *Campanorco inauguralis* Bond *et al.* (Campanorcidae) and *Dolichostylodon saltensis* García López and Powell, 2009 (Oldfieldthomasiidae), suggesting that the upper levels of Lumbrera Formation are younger than hitherto supposed. Faunistic comparisons to Patagonian localities tentatively suggest the mammals below Faja verde I to be Casamayoran SALMA (Pascual et al., 1981), and thus middle Eocene in age. Based on magnetostratigraphy, Marshall et al (1997) suggested an early late Paleocene age for the lower section of Lumbrera Formation. Also correlated this level and the Faja Verde I, with the lowermost part of the Potoco Formation, including La Cabaña Member, which overlies the Santa Lucía Formation in Tiupampa, Bolivia. Despite this interpretation, based on sedimentary facies and palynofacies, Del Papa et al., (2002) considered, the Lumbrera Formation as probably early Eocene in age, and the lower part of the Santa Bárbara Subgroup, as probably late Paleocene-early Eocene (Del Papa, 1999; Gelfo et al., 2009a).

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The Río Loro Formation in Tucumán Province, in the northwest Argentina consists of pink, friable and ocassionaly calcareous sandstones. This unit, correlated with the Mealla Formation (Powell and Palma, 1981), crop out around 30 km from the city of San Miguel de Tucumán, where several well preserved native ungulates have been exhumed (Soria and Powell, 1981; Soria, 1987, 1989b and c). The Río Loro Formation was originally considered Late Cretaceous in age but once the first described native ungulate from the region was assigned to the Trigonostylopidae (Powell and Palma, 1981), a Paleogene age became favored. Several attempts to refine this age estimation have been made. Mammal-bearing levels were considered middle to late Paleocene (Powell and Palma, 1981) and, as middle Paleocene (Selandian) given their assumed correlation with the Mealla Formation (Marshall et al., 1997). The fauna from the Río Loro Formation is strongly similar with the fauna of Itaboraí in Río de Janeiro Brazil, the latter of which is referred to the Itaboraian, or Riochican SALMAs when the validity of the first was questioned (Soria 1987). Itaboraian SALMA was traditionally regarded as late Paleocene but most probably could be referred to the late Paleocene - early Eocene span (Gelfo et al., 2009a).

Comentario [AW1]: Unl ear—did Soria first propose Itaboraian and this Riochican in response to criticism. If so, from whom?

The Geste Formation in Salta and Catamarca Provinces (northwest Argentina) is composed of conglomerates and purple medium to coarse grained sand. Two localities within the Geste Formation have yielded Eocene mammals and including native ungulates. Antofagasta de la Sierra, in northern Catamarca Province, at an elevation of ~3440 m, occurs on the southernmost Puna plateau. Also, on the Puna but in Salta Province, occurs the Pozuelos locality, at an elevation of about 3900 m, between Salar de Pozuelos and Salar de Pastos Grandes, near the Argentina–Chile border (Figure 1). Considering the mammal content, the faunistic assemblages of the Geste Formation were related tentatively to the Mustersan SALMA (López, 1997). Detrital zircons from the Geste Formation of the central Puna yielded U-Pb ages between 37-35 Ma confirming the assignment to the late Eocene (DeCelles et al., 2007).

The type locality of the Divisadero Largo Formation is located 8 km west of the city of Mendoza (west-central Argentina). This unit is characterized by maroon and gray, medium-grained sandstones alternating with thin beds of red and violet clay. The fauna exhumed from the Divisadero Largo Formation, formed the basis for recognizing the Divisaderan SALMA by Pascual et al. (1965), including a unusual ensemble of taxa, some with generalized features (comparable to Casamayoran and Mustersan taxa) along with others with much more modern aspect (comparable to Deseadan and post-Deseadan taxa). Based on this peculiar co-occurrence of archaic and advanced types, Pascual et al. (1965) suggested that the fauna partially filled the gap between the Mustersan and Deseadan SALMAs in the South American land mammal sequence. Accordingly, Pascual et al. (1965) referred the Divisaderan to the upper Eocene, although Bond (1991) suggested that it might be significantly younger. The discovery of mammal fossils in the overlying Mariño Formation (Cerdeño et al., 2008) and sedimentary-petrographic analyses (López and Manassero, 2008) established that the taxa with derived characters supposedly exhumed from the Divisadero Largo Formation came from a different stratigraphic level than the rest of the fauna (*i.e.*, from the overlying Mariño Formation). Thus the fossil assemblage from the Divisadero Largo region could no longer be viewing as comprising a single cohesive fauna, consisting instead of a stratigraphically unrelated mix of primitive taxa, more closely related to Casamayoran than to Mustersan associations, and advanced taxa from younger deposits. Cerdeño et al. (2008) and López (2010) referred the older component of this "composite fauna" tentatively to the early Eocene, and questioned its status as a biochronologic unit. López (2010) suggested the possibility that the fauna which in fact came from Divisadero Largo Formation, might be referred to the temporal hiatus between the Vacan and the Barrancan subages.

Southwest of La Pampa Province, in the Cerro El Fresco, occur greenish pelitic sediments with a significant input of pyroclastics were described as the Vaca Mahuida Formation. Icnofossils, gastropods, bivalves, fishes, anurans (Báez and Púgener, 1998), birds (Tambussi and Noriega, 1998) and remains of oldfieldthomasiid notoungulates (Montalvo and Bond, 1998) were recovered from this unit. According to the faunistic comparison, the fossil level was tentatively considered Eocene in age.

In the Valle de Punilla in Córdoba Province occurs a continental sequence of red to reddish limestones and claystones with minor carbonate intercalations, informally known as "Estratos Cosquín" (Linares et al., 1961). The only mammal from the area, recovered from the western side of the Sierra Chica Hills, is *Eohyrax rusticus* (Notoungulata, Hegetotheriidae), a species recorded in Casamayoran levels of Patagonia (Linares *et al*., 1961).

Several South American localities outside Argentina have produced other Paleocene and Eocene mammals, particularly native ungulates. The Itaboraí Formation, of the São José de Itaboraí basin in Rio de Janeiro state, is a limestone with fissure infillings wherein fossil vertebrates, mostly mammals, occur. This fauna was first related to fossil mammals in Patagonia, as the "*Notostylopéen*" of Ameghino (1901) or Casamayoran of Simpson (1948), later it was considered equivalent to the Riochican SALMA (Paula Couto, 1978). Lately the Itaboraian was formally recognized as a new SALMA, (Marshall, 1985; Bonaparte et al., 1993), older than the Riochican and younger than the *Carodnia* zone of Simpson (1935b). The Itaboraian fauna was correlated to the Las Flores Formation in Patagonia, (Pascual and Ortiz-Jaureguizar, 1991; Bond et al., 1995). The age of the Itaborian SALMA has long been debated, not only because of the absence of isotopic data but also because of the probable asynchrony between the fossils in different fissure fills (Soria, 1987; 2001). At present a late Paleocene – early Eocene span is considered most likely for the Itaboraian SALMA (Gelfo et al., 2009a and literature therein).

An Etayoidae xenungulate, *Etayoa bacatensis*, from the Bogotá Formation compares closely was compared to *Carodnia vierai* from Itaboraí in Brazil, and *C. feruglioi* from Patagonia, Argentina, suggesting a middle Paleocene age for the Colombian site (Villarroel, 1987). The presence of this family in Patagonia (Gelfo et al., 2008) highlights the biogeographic relevance of this taxa.

A fossiliferous red mudstone sequence belonging to the lower Muñani Formation of the Puno Group outcrops on the northwestern shore of the Laguna Umayo, in southeastern Peru (Sigé et al. 2004). Fossils include the Laguna Umayo local fauna (LU-3) and the 140 m stratigraphically higher Chulpas level . These widely diverse assemblages comprise charophytes, several osteichthyan orders and representatives of Anura, Chelonia, Squamata, Crocodylia and several mammals, represented by marsupials and native ungulates (updated list in Sigé et al., 2004). This stratigraphic sequence is entirely reversely magnetized, suggesting a correlation with Chron 24r (Thanetian-Ypresian) , i.e., a late Paleocene-early Eocene age (Sigé et al. 2004). This age matches with the last assignment of the Itaboraian SALMA previously mentioned (Gelfo and Sigé, 2011).

Finally two diverse fossil mammal assemblages have been found in the central Andean Main Range of Chile, in the upper course of the Tinguiririca river valley. The fossil bearing levels was referred to the Abanico Formation, a unit characterized by volcaniclastic sediments, ranging in color from brownish-red to violet, interbedded with flows and tuffs. The older Tapado Fauna includes didolodontid ‘condylarths’, and several notoungulates comparing closely to Casamayoran assemblages of Patagonia (Flynn *et al*., 1991; Wyss *et. al*., 1992; Flynn et al., 2005). The younger Chilean fauna permitted recognition of the Tinguiririca SALMA referred to the early Oligocene (Flynn et al., 2005).

3. PALEOCENE-EOCENE RECORD OF SANU

3.1. Notoungulata

The order Notoungulata constitutes the most successful group, is taxonomically and morphologically the most diverse and has the widest stratigraphic record within the SANU. This order includes herbivores of differing adaptive types, many of which are convergent on holarctic mammals. The earliest record of Notoungulata is a single molar from the early Paleocene of Bolivia (Muizon and Cifelli, 2000; Gelfo, 2006). The group's last record corresponds to *Toxodon* sp. exhumed in association with human remains, in sediments of 8.500 years old (Tonni et al., 1992).

Notoungulates reached their highest diversity (morphologically and taxonomically) during the Eocene-Oligocene. The notoungulate *Mixotodon*, the only native ungulate recorded outside South America, was recovered from the Pleistocene of Honduras and Nicaragua (Webb, 1985). The great diversity of notoungulates is reflected in the recognition of at least thirteen families, within three suborders (Notioprogonia, Typotheria and Toxodontia).

Notostylopidae and Henricosborniidae were grouped together in the Suborder Notioprogonia (Simpson, 1934). The Arctostylopidae, recorded in North America and Asia, were once referred to Notioprogonia (Simpson, 1934) but subsequently were placed with Condylarthra (McKenna and Bell, 1997) or their own order, Arctostylopida (Cifelli et al., 1989). Kodrashov and Lucas (2005) are the only authors who still consider them among notoungulates.

The oldest reported notoungulate is an isolated upper molar (M1 or M2) from the Santa Lucía Formation (early Paleocene) of Bolivia, referred to the Henricosborniidae or Oldfieldthomasiidae by Muizon (1991). This tooth is highly damaged, precluding a refined identification among both families.

Satshatemnus bonapartei Soria, from the Río Loro Formation is represented by a palatal fragment with broken premolars and molars. The upper molars bear a metaloph and possibly a crochet, allow this taxon to be considered a basal notoungulate with affinities to Notioprogonia, as originally proposed by Soria (1989c).

The henricosborniids have several generalized dental features that allow them to be placed in a basal position with respect to other notoungulates and nearly fulfilling all the theoretical requirements for a generalized type ancestral to all others known (Simpson, 1948:147). *Othnielmarshia pristina* Paula Couto is a henricosborniid from San José de Itaboraí (Itaboraian SALMA). Bond and López (2002) concluded that the type of this species species is not significantly differerent from *Itaboraitherium atavun* Paula Couto, a species recorded in Itaboraian levels of Brazil and Riochican levels of Patagonia (i.e., Gaiman and Bajo de la Palangana). *I. atavun* is closely related to *Paginula parca* Ameghino, from the Vacan of Patagonia and both species were considered as henricosborniids (Bond and López, 2002).

Simpsonotus praecursor Pascual et al., and *S. major* Pascual et al., were recovered from the Mealla Formation (Jujuy Province). These species present a combination of generalized features (e.g. premolar and molar design, auditory morphology) and derived features (e.g. third upper incisor enlarged, lower incisors reduced); were referred to the Henricosbornidae, suggesting a Riochican age for the assemblage (Pascual et al., 1978). From the overlay Maíz Gordo Formation a remain was exhumed with features more derived that Bond and Vucetich (1983) considered as *Simpsonotus* sp. I think it would be useful if a diagnosis for the Henricosbornidae were given: is it simply third upper incisor enlarged, lower incisors reduced? If so, how are isolated cheek teeth ever refered to the group? At the very least is would be useful to know what "premolar and molar design" features they retain.

Con formato: Resaltar

Acamana ambiguus Simpson et al., was established for a damaged cranial fragment with broken teeth from the Divisadero Largo Formation (Simpson et al.,1962). It was considered a henricosborniid closely related to *Simpsonotus* by Bond and Vucetich (1983) based on the small size of I1-2, the enlarged I3, and reduced canines. The type of *A. ambiguus* is Currently lost.

The Las Flores Formation of Chubut (Itaboraian SALMA) produces abundant isolated henricosborniid teeth (*e.g. Kibenikhoria* Simpson and ?*Peripantostylops* Ameghino).

Gelfo et al. (2010) reported isolated teeth of cf. *Peripantostylops* Ameghino, and cf. *Othnielmarshia* Paula Coutro (=*Itaboraitherium*) for post-Itaboraian levels of the locality Las Violetas (Chubut). Henricosborniids (*e.g. Henricosbornia*, *Peripantostylops*, *Itaboraitherium*), have been reported from several Riochican localities (*e.g.* Bajo de la Palangana, Pan de Azucar), making this family a distinctive element of this SALMA. Henricosborniids (referred to *Henricosbornia lophodonta* and *Othnielmarshia lacunifera* by Tejedor *et al.*, 2009) are abundant in both localities of Paso del Sapo . The assemblages of Paso del Sapo possibly represent a new biochronological unit between the Riochican and the Vacan subage of the Casamayoran (Tejedor *et al.*, 2009).

H. lophodonta Ameghino, *O. lacunifera* Ameghino, and *P. minutus* (Ameghino) are the henricosbornidos recorded at Cañadón Vaca (Cifelli, 1985b). The diversity and abundance of this family decreases in the Barrancan; only sparse remains of *Henricosbornia* sp. are reported at Gran Barranca (Gelfo *et al.* (2009).

Notostylopids are common and distinctive elements of Casamayoran assemblages. The group was never diverse; its members are rodent-like in appearance with stiliform incisors and large diastemata. Notostylopids are easily recognizable by the unique crochet of the upper molars and by the tricuspidate trigonid crests of the lower ones.

Isolated notostylopid remains collected from Itaboraian levels of the Las Flores Formation (Chubut) represent the FAD (First Appearnce Datum) for the family. *Seudenius cteronc* Simpson, from Cañadón Hondo (Itaboraian SALMA) was once referred to the Notostylopidae, but the molar occlusal design, especially the morphology of the protoloph, argues against this assignment and so, Bond (1986) argued that this taxon is not even a notoungulate. For the levels at Las Violetas locality Gelfo et al. (2010) reported the Casamayoran species *Homalostylops parvus* Ameghino, and, in the *Ernestokokenia chaishoer* biozone (= SALMA Riochiquense) from Bajo de la Palangana, remains of *Notostylops* sp were recorded.

Comentario [AW2]: Per haps a dental diagnosis of Notoungulata would be useful to your readers

Boreastylops lumbrerense Vucetich, a distinctive notostylopid, was described from the lower levels of the Lumbrera Formation (Salta Province); it is probably related to *Otronia muehlbergi* Roth, from Mustersan of Patagonia. notostylopids are abundant in both localities of Paso del Sapo including *Edvardotrouessartia sola* Ameghino, *Homalostylops parvus* and *Notostylops* sp. (Tejedor *et al*. 2009)

In the summer of 1895-96 Carlos Ameghino collected fossils from the Gran Barranca subsequently described by his brother Florentino as the "*Notostylops fauna*," due to the common occurrence of this taxon. The *Notostylops* fauna was the basis for the Casamayoran SALMA where *Edvardotrouessartia*, *Homalostylops* and *Notostylops* are characteristic forms. *Edvardotrouessartia sola* is recorded in the Vacan subage and at Laguna Fria (a locality of Paso del Sapo). Despite species recognized by Ameghino for *Homalostylops* came from Barrancan levels, this genus was also cited for Cañadon Vaca. Specimens of *Notostylops murinus* Ameghino, are very abundant in Barrancan localities, while *N. pendens* (Ameghino) occurs at Cañadon Vacan. Flynn et al. (2005) cited *Notostylops* sp. from the Casamayoran Tapado Fauna (Abanico Formation) from central Chile.

The diversity of notostylopids decreases in the Mustersan SALMA; only *Otronia muehlbergi* is represented in Patagonian assemblages (Cladera *et al*., 2004). Isolated upper molars, Notostylopidae gen et sp. indet (López (1997) have been recovered from the Geste Formation (Antofagasta de la Sierra, Catamarca) in northwest Argentina. In their degree of hypsodonty and general crown structure these teeth resemble those of the *Boreastylops-Otronia* group.

Olfieldthomasiids are notoungulates with a skull of generalized proto-toxodont aspect, dentition brachydont, in closed series and upper molar with complex oclusal surface (e.g. three constant fossettes, protocone and hypocone distinct but joined nearly to apices, strong parastyle and paracone folds on external wall and in some cases also distinct mesostyle, an uncommon cusp in notoungulates). The oldfieldthomasiids are characteristic of the Eocene of South America, and numerous species were referred to this family.

For the Paleocene levels from San José de Itaboraí in Brazil (Itaboraian SALMA), was described the oldfieldthomasiid *Colbertia magellanica* Paula Couto. Subsequently, *Colbertia lumbrerense* Bond, and *Dolichostylodon saltensis* García López and Powell were recognized from the Lumbrera Formation. *Kibenikhoria get* Simpson, was the name used for the middle biozone of the Riochican SALMA (Simpson, 1935b) and the record of this species in the Las Flores Formation allowed to confirmed the correlation of both units, as proposed by Legarreta and Uliana (1994). Undetermined olfieldthomasiids, still under study, were recovered in post-Itaboraian levels of the Las Violetas Locality (Gelfo et al., 2010) and from the Laguna Fria fauna of Paso del Sapo (Tejedor *et al.*, 2009).

In Cañadon Vaca only *Maxschlosseria consumata* (Ameghino) was mentioned by Cifelli (1985b). López and Bond reviewed the original remains considering that this species would be invalid, a nd the material recovered in this locality was referred to as the type of an unnamed new taxon (López and Bond, 2003). *Acoelodus connectus* Ameghino, was determined based on damaged mandibular fragments collected in Cañadon Vaca and considered by Simpson (1967b) as junior synonym of *Paginula parca* Ameghino. Nevertheless, López (2008) and López and Bond (2010) revalidated the status of this species and cited for Barrancan Subage the species *Oldfieldthomasia furcata* (Ameghino), *Ultrapithecus rutilans* Ameghino, and *"Acoelodus" oppositus* Ameghino.

Brachystephanus postremus Simpson et al; *Xenostephanus chiottii* Simpson et al., and *Allalmeia atalaensis* Rusconi, are the most abundant mammals in the Divisadero Largo Formation (Mendoza) and were considered by Simpson et al. (1962) as possible oldfieldthomasiids. Given that these species present a set of unusual features (e.g. brachyodont teeth, no incisors enlarged, upper premolars with two cuspids one inner and other outer; P4 not molarized; upper molar without mesostyles and with fossettes rapidly obliterated by wear; lower premolars not molarized), they were referred to a new suprageneric taxon different from oldfieldthomasiids López and Bond (2003).

From the Vaca Mahuida Formation (La Pampa Province) three damaged lower teeth that Montalvo and Bond (1998) considered as an undetermined oldfieldthomasiid were recovered. Traditionally, *Tsamnichoria cabrerai* Simpson is the oldfieldthomasiid recognized in Mustersan levels of Patagonia. However López (2008) and López and Bond (2010) considered that this species is a junior synonym of *Ultrapithecus rutilans* Ameghino. In the possibly Mustersan assemblage of the Geste Formation of Antofagasta de la Sierra (Catamarca Province), the oldfieldthomasiids are represented by *Suniodon catamarcensis* López, and ?*Colbertia* (López, 1995).

The Interatheriidae includes small to moderate sized ungulates with an early tendency towards hypsodonty and a set of cranial features (*e.g*. anterior zygomatic root laterally expanded, with small ventral tubercle) that suggest an incipient rodent-like morphology. The oldest and most generalized members of the interatheriids (i.e. “notopithecines”) are recorded in Riochican levels of Bajo de la Palangana (i.e. *Ernestokokenia chaishoer* biozone) and the last record is in Tinguiririca*n* fauna of central Chile (Flynn *et al*., 2003). Among the Eocene faunal associations of Patagonia, the “notopithecines” are abundant and four genera are recognized: *Notopithecus* Ameghino for the Riochican and Casamayoran, and with some doubts for the Eocene of Bolivia; *Antepithecus* Ameghino and *Transpithecus* Ameghino from the Casamayoran, *Guiliermoscottia* Ameghino from the Mustersan. Outside of Patagonia other notopithecines are recognized. From levels of Geste Formation (Catamarca Province), probably Mustersan in age, the smallest *Punapithecus minor* López and Bond, was described (López and Bond, 1995). Two new basal interatheriids were reported in central Chile, *Ignigena minisculus* Hitz et al., known from the Tapado Fauna, estimated to be Casamayoran in age, and *Johnbell hatcheri* Hitz et al. from the Tinguiririca Fauna (Hitz et al. 2006). The presence of *Antepithecus brachystephanus* Ameghino was mentioned from levels of the Abanico Formation in the Azufre locality along the Rıo Azufre valley (Hitz et al., 2006).

The Archaeopithecidae includes small notoungulates with a combination of generalized (e.g. molar pattern) and derived (e.g. high crowned cheek teeth) traits. This family was proposed to embrace two species: *Acropithecus rigidus* Ameghino from the Cañadon Vaca and *Archaeopithecus rogeri* Ameghino of uncertain stratigraphic provenance, possibly from Barrancan levels. A broader systematic revision of this family is needed. *Acropithecus* cf. *A. rigidus* was recently reported for post-Itaboraian levels from Las Violetas locality (Gelfo et al., 2010). Remains of *Acropithecus* cf. *A. rigidus* were collected in the *Ernestokokenia chaishoer* biozone (Riochican SALMA) from Bajo de la Palangana (Chubut). The archaeopithecids are very abundant in the two localities from Paso del Sapo (Tejedor et al., 2009). material recovered in Mustersan levels of La Gran Hondonada (Chubut) was referred to *Archaeopithecus*? sp. nov. (Cladera et al., 2004).

The archaeohyracids are early notoungulates with accelerated hypsodonty not attaining continuous growth (Simpson, 1967 b), except in the Deseadan species. This group experienced a great radiation during the late Eocene or early Oligocene, evidenced by their high diversity in earliest Oligocene Tinguiririican faunas of Chile and Argentina (Croft et al., 2003; Reguero et al., 2003). Croft et al. (2003) and Reguero and Prevosti (2010) suggested that the “Archaeohyracidae” constitutes a paraphyletic group, being basal typotheres related to Hegetotheriidae and Mesotheriidae (Reguero and Castro, 2004).

Bond et al. (1995) mentioned the presence of *Eohyrax* sp. in the *Ernestokokenia chaishoer* biozone (Riochican SALMA) of Bajo de la Palangana, Chubut Province. However, this record is considered dubious and invalid since it is supported on two fragmentary remains, one likely referred to *Acropithecus* and the other to an undetermined notoungulate reference. The FAD of the Archaeohyracidae is well established, occurring in Barrancan horizons at several Patagonian localities (Reguero and Prevosti, 2010); two species *Eohyrax isotemnoides* Ameghino, and *E. praerusticus* Ameghino, are recognized for this age. Linares et al. (1961) reported the presence of *Eohyrax* in the Cosquín Formation, Córdoba Province referring this fossil-bearing levels to the Casamayoran SALMA. The Mustersan archaeohyracids are represented by *Pseudhyrax eutrachytheroides* Ameghino; *P. strangulatus* (Ameghino) and ?*Eohyrax*. *Punahyrax bondesioi* Reguero et al., of probable late Eocene age was described from the middle member of the Geste Formation of Catamarca and Salta Provinces. The Tinguiririican SALMA is remarkable for its abundant and diverse archaeohyracids, with six species recognized. The three large-bodied archaeohyracids are referred to *Archaeotypotherium* (*A. tinguiriricaense* and *A. pattersoni*) and *Pseudhyrax* cf. *P. eutrachytheroides* (Croft et al., 2003), and the three small-bodied forms to *Protarchaeohyrax gracilis*, *P. intermedius*, and *P. minor* (Reguero et al., 2003). Recently, Cerdeño et al. (2010) made a taxonomic reinterpretation of typothere from the early Oligocene of Cañadon Blanco, recognizing in this assemblage an unnamed archaeohyracid. They are last recorded in Deseadan faunas of Bolivia (Salla), Uruguay (Fray Bentos), and Argentina (Patagonia and Mendoza) (Billet et al., 2009; Reguero et al., 1998; Cerdeño et al., 2010).

The Isotemnidae is a native ungulate family of moderate to large size characterized by large canines associated to a brachyodont dentition, and a generalized molar pattern with respect to other Toxodontia. The oldest record of isotemnids is *Isotemnus ctalego* Simpson, from Itaboraian levels of Cañadón Hondo (*Kibenikhoria* biozone) and undetermined isolated teeth from the Las Flores Formation. Isolated upper molar referred to cf. *Isotemnus ctalego* were recorded in post-Itaboraian fauna of Las Violetas Gelfo et al. (2010).

Isotemnus and possibly *Pleurostylodon* occur in the *Ernestokokenia* biozone (Riochican SALMA) of Bajo de la Palangana. Tejedor et al. (2009) referred several maxillary and mandibular fragments from both faunas at Paso del Sapo to *Isotemnus*. isotemnids are diverse and common components of Casamayoran faunas; in Cañadon Vaca *Pleurostylodon similis* Ameghino, *Isotemnus primitivus* Ameghino, and *Thomashuxleya externa* Ameghino are recorded. Only *T. externa* is exclusive to the Vacan Subage. For Barrancan assemblages were cited *Pleurostylodon modicus* Ameghino, *Anisotemnus distentus* Ameghino, *Isotemnus primitivus* Ameghino, and *Thomashuxleya rostrata* Ameghino. *Pampatemnus infernalis* Vucetich and Bond and *P. deuteros* Vucetich and Bond were described from the lower third of the Lumbrera Formation and show generalized features with respect to the Barrancan species of Patagonia (Vucetich and Bond, 1982).

Isotemnids are diverse in the Mustersan SALMA; *Perisphragnis harmeri* Roth; *P. exauctus* (Ameghino); *Rhyphodon lankesteri* Roth, and *Distylophorus alouatinus* (Roth) are recorded from Patagonian localities. Fragmentary isotemnids remains were collected in Geste Formation of Antofagasta de la Sierra (Catamarca), tentatively assigned to the Mustersan SALMA (López, 1997). Among these remains one was referred to the same taxon described by Bond and López (1995) from the Casa Grande Formation in the Tres Cruces area, Jujuy Province.

The Notohippidae are medium-sized notoungulates, the oldest forms (Eocene) have brachydont to mesodont dentition while later forms attain hypsodonty and some taxa from the late Oligocene to middle Miocene display a thick layer of external cementum around the perimeter of the crown. The notohippids retain all upper incisors, never develop “tusk-like” I2 and I3, and their cheek tooth occlusal morphology is "toxodontoid" in pattern. Eocene notohippids are represented by *Pampahippus arenalesi* Bond y López, from the Lumbrera Formation (Salta) and Patagonian *Plexotemnus* Ameghino (Casamayoran), *Puelia* Roth and *Trimerostephanus* Ameghino (Mustersan) and *Eomorphippus* Ameghino of Tinguiririca levels (Gran Barranca, Cañadon Blanco, and Chile). Shockey (1997) questioned the inclusion of *Pampahippus, Plexotemnus* and *Puelia* in the Notohippidae. López et al. (2010) recently revised the notohippids of the Mustersan, Tinguiririca, pre-Deseadan and Colhuehuapian levels of Gran Barranca (Chubut).

Leontiniidae are endemic South American herbivores of medium to large size with distinctive brachydont to mesodont dentitions with either the first or second upper incisor and the third lower incisors enlarged into caniniform teeth with reduced or absent canines. Though the leontiniids are characteristic elements of Deseadan assemblages of Argentina, Brazil and Uruguay, they are recorded in the Colhuehuapian SALMA (late Oligocene) of Patagonia and the Laventan SALMA (middle Miocene) of Colombia. The FAD of this family is represented by *Martinmiguelia fernandezi* Bond and López from the Casa Grande Formation (Jujuy Province). A leontiniid related to *M. fernandezi* is *Coquenia bondi* Deraco et al., from upper levels of the Lumbrera Formation in Salta Province. Recently, Ribeiro et al. (2010) described the Deseadan and post-Deseadan leontiniids from of several levels of Gran Barranca.

Campanorcidae (Bond et al. (1984) is represented by a unique species, *Campanorco inauguralis* from the Lumbrera Formation, Salta Province. Peculiar features of the dentition, such as I1 enlarged and obliquely implanted, short pre and postcanine diastemas were considered precursors of the present condition seen in the basal mesotheres, and in general of all hypsodont rodent-like notoungulates, except Interatheriidae (Reguero et al., 1996). The validity of this taxon is pending a formal study and description. Nevertheless, it is important since it constitutes a key taxon within the hypsodont rodent-like notoungulate clade (Typotheria). According Reguero and Prevosti (2010) *Campanorco inauguralis* is a basal member of Typotherioidea (Reguero and Castro, 2004), and a sister group of the clade that includes "Archaeohyracidae" + Hegetotheriidae + Mesotheriidae. Recently, García López (2009) described new and more complete remains from the same horizon that were referred to *Campanorco* sp.

The FAD of the families Hegetotheriidae and Mesotheriidae were considered as Divisaderan SALMA because *Ethegotherium carettei* and *Trachytherus? mendocensis* were the two species supposedly recovered from the Divisadero Largo Formation. The sedimentary-petrographic study of the sediments bearing the type of *E. Carettei* (López and Manassero, 2008) and the discovery of remains closely related to *Trachytherus*? *mendocensis* in the Mariño Formation (Cerdeño et al., 2008) suggested that these two species came from the overlying Mariño Formation, that is to say, from a different stratigraphic level than the rest of the Dividaderan fauna (López, 2010).

3.2. Xenungulata

The Xenungulata are characterized by a bilophodont dentition, which was only shared with Pyrotheria among the native South American ungulates, but, in contrast, they retained more bunodont last molars. Even though two xenungulate families, Carodniidae and Etayoideae, were recognized, a full phylogenetic revision is still pending. The oldest known record belongs to *Carodnia feruglioi* Simpson, from the late Paleocene of Patagonia, which was found in outcrops from the Peñas Coloradas Formation (Rio Chico Group) at Bajo de la Palangana, Chubut Province (Simpson, 1935a). This taxon was the base of the "*Carodnia Zone*" (Simpson, 1935b), representing a still not well known span, between the Peligran and the Itaboraian SALMAs (Bonaparte et al., 1993; Gelfo et al., 2009a). The discovery of a xenungulate from the lower levels of Cerro Redondo which presents a more primitive pattern than *C. feruglioi* highlights previous observations from Simpson (1935b) that this outcrop could be older than those of "*Carodnia Zone*" at Bajo de la Palangana. The larger and more advanced *Carodnia vieirai* Paula Couto came from the Itaboraian SALMA at Sao José de Itaboraí, Brazil (Paula Couto, 1952a). *Etayoa bacatensis* Villarroel was described from the Bogota Formation, late Paleocene of Colombia and considered as a new xenungulate family, Etayoidae (Villarroel, 1987), since its dental pattern contrasts with those of the Carodniidae. These differences were reinforced with the southern record of *Notoetayoa gargantuai* Gelfo et al., which was recorded in association with *Carodnia cf. feruglioi* in Patagonia (Gelfo, et al., 2008).

3.3. Pyrotheria

Pyrotheria are medium to large elephant-like mammals with two pairs of upper and one pair of lower incisors specialized as tusks, associated with bilophodont cheek teeth. The configuration of the nasal region suggests the presence of a proboscis. Their column-like limbs were short and the hind foot had a serial tarsus. The pyrotheres were never diverse and the oldest is *Carolozittelia tapiroides* Ameghino, from Cañadón Vaca (Simpson, 1967b). The particularities of *C. tapiroides* led Simpson (1967b) to consider the possibility that it could be a xenungulate or even a new bilophodont group. Sallas et al., (2006) still consider it a pyrothere.

Propyrotherium saxeum Ameghino is the characteristic species from the Mustersan SALMA, recorded in Patagonia and Catamarca Province (Simpson, 1967b and López, 1997). A species closely related to *Propyrotherium* is *Griphodon peruvianus* Anthony, from the ?Eocene of Peru (Patterson, 1942) and it was considered by Lucas (1986) as junior synonym of *Propyrotherium*. Shockey and Anaya (2004) consider *Griphodon* as being generically distinct from *Propyrotherium* and suggest a heterochronic relationship. The specimen that formed the basis of *Colombitherium tolimense* Hoffstetter was recovered from an unnamed locality from the Gualanday Group in Colombia, supposedly Eocene in age. The holotype and only known specimen was interpreted as a right maxillary with P3-M3 (Hoffstetter, 1970; Kramarz and Bond, 2005), as a left lower jaw with p3-m3 (Avilla, 2005; Salas et al., 2006) and, recently, as a right maxilla with P2-M2 (Billet et al., 2010). Reference of this specimen to Pyrotheria was questioned by Billet et al. (2010).

Proticia venezuelensis Patterson is a controversial species from the Eocene or Miocene of Venezuela and, currently, is included in Colombitheriidae (Patterson 1977; McKenna and Bell 1997). However Sánchez-Villagra et al. (2000) revised the stratigraphic provenance suggesting that the holotype was collected in beds of the Castillo Formation (Miocene) instead of the Trujillo Formation (Eocene) and sirenian affinities were proposed.

Baguatherium jaureguii Salas et al. was described from the basal levels of the El Milagro Formation (late early Oligocene) of northern Peru (Salas et al. 2006). *Pyrotherium* Gaudry is the only well-known pyrothere and characterizes the Deseadan SALMA (late Oligocene in age) of Patagonia and Bolivia.

3.4. Astrapotheria

Astrapotheria represents an order of South American native ungulates, recorded in the Paleocene-middle Miocene interval and shows its highest diversity in the early Miocene (Kramarz and Bond, 2010). The early forms (e.g. *Trigonostylops* and *Eoastrapostylops*) included small to medium sized ungulates while the later ones (e.g. *Astrapotherium*) were very large and weighty animals with pillar-like legs that resemble modern-day tapirs or rhinos. Since many of the taxa show retracted nasal bones, a muscular trunk could have been present in life. The astrapotheres are characterized by several dental features. Even though upper incisors were absent, the lower ones were procumbent. Both upper and lower canines are enlarged as tusks and normally premolars are reduced, generating a diastema. The molars show some convergent similarities with notoungulate teeth, and with amynodontids perissodactyls of the Northern Hemisphere (Cifelli, 1985a).

Besides *Trigonostylops,* which is the only representative of the Trigonostylopidae, the other Itaboraian, Casamayoran and Mustersan astrapotherians, *Tetragonostylops*, *Scaglia*, *Albertogaudrya,* and *Astraponotus* have been considered as basal representatives of the astrapotherian family Astrapotheriidae (Carbajal et al., 1977; Soria, 1982).

The oldest record of astrapotherians is *Eoastrapostylops riolorensis* Soria and Powell from the Río Loro Formation, Paleocene of Tucumán, northwestern Argentina. It is a small form with many general characters. Soria and Powell (1981) even noted some similarities to the notioprogonians notoungulates. The type materials, skulls and mandibles, are incomplete, but a close inspection of the materials shows that, apparently, the premaxilla was reduced and, most probably, the upper incisors were much reduced or absent. A new study of the type specimens and the collection of new materials are needed, as well as a phylogenetic analysis to elucidate the relative position of the taxon relative to the other astrapotherians and other SANU. *Eoastrapostylops* is assigned to the family Eoastrapostylopidae, a group not recognized by all the authors (Cifelli, 1993). In addition, *Eoastrapostylops* is still considered as the most basal and generalized astrapotherian (Kramarz and Bond, 2009).

In the late Paleocene – early Eocene of Itaboraí, Brazil, the astrapotherians are represented by frequent remains of the Astrapotheriidae *Tetragonostylops apthomasi* (Price and Paula Couto) a taxon originally referred to the family Trigonostylopidae, but which Soria (1982) assigned to the Astrapotheria Astrapotheriidae. In the lower casamayoran levels (Vacan) of Cañadón Vaca, Chubut, Soria (1982) assigned an upper molar to aff. *Tetragonostylops apthomasi*. In Patagonia, Argentina, the late Paleocene – early Eocene astrapotherian remains are scarcer and fragmentary, and the earliest are recorded in the Las Flores Formation (Itaboraian SALMA). The Las Flores astrapotheres, represented by very fragmentary remains, indicate an astrapotherian of uncertain family position. In Cañadón Hondo, Chubut, with a fauna referred to the

Itaboraian SALMA, the astrapotherians are represented by *Shecenia ctirneru* Simpson, a taxon only known by a symphisis that also shows many similarities to *T. apthomasi* of Brazil. From the *Ernestokokenia chaishoer* Zone, in Bajo de la Palangana, Chubut, the astrapotherian are represented for a taxon referred to *Trigonostylops*.

Astrapotheres are farily common In the Eocene of Patagonia,. One of them is *Trigonostylops,* with the most common species *T. wortmani* Ameghino, characterized by its relatively simple molars and unretracted nasals. It is recorded in the Casamayoran (Vacan and Barrancan subages) up to the Mustersan SALMA in Patagonia, with *T. gegenbauri* (Roth), probably different from that of the Casamayoran. A new specimen from the Divisadero Largo Formation was considered as *Trigonostylops* sp. and constituted the first record of the Order Astrapotheria for this unit (López, 2009).

Other Eocene astrapotheres include *Scaglia kraglievichorum* Simpson from the Casamayoran (Vacan) of Patagonia. This astrapotherian of small size is known by a juvenile individual and shows more complex and lophodont molars than those of *Trigonostylops*, with the nasals not retracted. *Albertogaudrya unica* Ameghino was relatively common in the Casamayoran of Patagonia (Vacan and Barrancan), and probably also in the Mustersan. Its molars are less lophodont than those of *Scaglia*. A mandible referred to *Albertogaudrya? carahuasensis* was described from the Eocene levels of the Lumbrera Formation ("Faja Verde I") in Salta, northwestern Argentina (Carbajal *et al*. 1977). An isolated lower molar recovered from the Eocene levels of Laguna Fría, in Paso del Sapo (Chubut), was attributed to the Astrapotheria, however the family allocation was considered undetermined (Tejedor et al., 2009).

Some Eocene material of Astrapotheria has been discovered in the La Meseta Formation of Seymour Island, Antarctic Peninsula, that represents a new and endemic form most closely related to Albertogaudrya and Astraponotus (Bond et al., in press).

In the Mustersan SALMA of Patagonia, astrapotheres are represented by *Astraponotus assymmetrus* Ameghino, a larger form compared to Casamayoran astrapotheres. *Astraponotus* has more complex premolars and molars and reduced dental formula, with loss of the first upper and lower premolar. The skull of *Astraponotus* is very specialized, quite distinct from the Miocene *Astrapotherium*, with the nasal very retracted and reduced, and the maxillaries inflated (Kramarz et al., 2010). There are also fragmentary taxa known from the Mustersan and Tinguirirican (Cañadón Blanco fauna) of Patagonia, described as *Isolophodon* Roth. This indicates that the morphological diversity of the astrapotherians from the Eocene to the Eocene-Oligocene transition was greater than previously suspected.

A new astrapotheres, *Maddenia*, from the early Deseadan of Colhué Huapi, Chubut (Kramarz and Bond 2009), which is the sister group of all the other Deseadan and post-Deseadan astrapotherians, shows that the astrapotheres from the Itaboraian, Casamayoran and Mustersan represent basal lineages within the Astrapotheria, more related to the Astrapotheriidae than to the Trigonostylopidae.

Paleocene and Eocene astrapotheres show that the characters were not as lineal as was once thought, having in mind forms like the basal *Trigonostylops* and the terminal *Astrapotherium.*

3.5. Litopterna

Setting aside notoungulates, litopterns were the more diverse South American native ungulate group. Litopterns include ungulates with mesaxonic feet and a wide range of dental adaptations, from brachyodont and bunodont to bunoselenodont and lophodont check-teeth. They are usually considered as directly derived from didolodontid condylarths (Simpson, 1948) but their intraordinal taxonomy is debated, particularly for the Notonychopidae, Indalecidae and Amilnedwardsiidae, which are sometimes grouped in the order Notopterna, outside the litopterns (Soria, 1989a, b). Also, the Sparnotheriodontidae were considered as condylarths, more derived in their dental morphology than Didolodontidae (Cifelli, 1983a; 1993; Bergqvist, 2008). We follow here a conservative taxonomic arrangement, considering all of these groups to be litopterns. Nevertheless, it is important to highlight several alternative views. The status of Notopterna needs to be tested in a wide phylogenetic analysis including all litopterns representatives. Sparnotheriodontidae was considered as condylarths based on the association of isolated primitive postcranial remains to teeth (Cifelli, 1983a; Bergqvist, 2008). This interpretation was not followed by most authors and has been already criticized elsewhere (Soria, 2001; Gelfo, in this volume).

The Notonychopidae are only known from two species. *Requisia vidmari* Bonaparte and Morales was recorded in the middle Paleocene of Patagonia, at the BNI of the Salamanca Formation in the locality of Punta Peligro. *Notonychops powelli* Soria was found in the lower part of the Río Loro Formation in Tucumán Province, northwest Argentina (Soria, 1989b).

The Indaleciidae were little diverse in the fossil record but have a wide stratigraphic (Vacan-Deseadan) and geographic distribution (Patagonia and northwest

Argentina). *Indalecia grandensis* Bond and Vucetich was described from the Lumbrera Formation (Salta, Province), and originally referred as Adianthidae, Indaleciinae (Cifelli, 1983b; Cifelli and Soria, 1983). *Adiantoides leali* Simpson and Minoprio is from the middle section of the Divisadero Largo Formation at the Divisadero Largo Hills (Mendoza Province) and *A. magnus* from Cañadón Vaca (Chubut Province). *A. magnus* should be referred to a new genus owing to differences from the Divisadero Largo taxon. The affinities of these species have been controversial. Initially these taxa were considered a subfamily of Macraucheniidae (i.e. Adianthinae) by Simpson and Minoprio (1949); as a new family, Adianthidae (Simpson et al., 1962); as a subfamily of the Adianthidae (i.e., Indaleciinae) by Bond and Vucetich (1983) and Cifelli and Soria (1983); as a family, Indaleciidae, within Notopterna (Soria, 1989a; Bond, 1986) and as closely related to Sparnotheriodontidae (Cifelli, 1983b; 1993). Un-named taxa were mentioned from Tinguiririca fauna (Wyss et al., 1994) and Deseadan levels of Cabeza Blanca, Chubut (Soria et al., 1986).

Amilnedwardsidae were considered by Soria (1989a) where he included the Casamayoran (Eocene), *Amilnedwadsia, Rutimeyeria* and *Ernestohaeckelia.*

Sparnotheriodontidae are medium-sized (e.g. *Phoradiadius* and *Victorlemoinea*) to large-sized (e.g. *Sparnotheriodon*) litopterns, with complete and closed dental series, with brachyodont, lophobunoselenodont to lophoselenodont teeth. As previously stated, no associated postcranial remains have been described for sparnotheriodontids but some controversial elements were associated to them (see discussion in Gelfo, in this volume). They were one of the most widespread Paleocene-Eocene native ungulates groups, recorded from the Itaboraian levels of Río de Janeiro, several Patagonian localities, Divisadero Largo (Mendoza), and Antarctica. The oldest record is considered to be *Victorlemoinea prototypica* Paula Couto, from Itaboraí (Brazil) and two species of this genus (i.e. *V. labyrinthica* Ameghino and *V. emarginata* Ameghino) were recognized from Cañadón Vaca, where also was recorded a single jaw of *Sparnotheriodon epsilonoides* Soria. *Phoradiadius divortiensis* Simpson et al., from the Divisadero Largo (Mendoza), and *Notiolofos arquinotiensis* Bond et al., from Antarctica, are other taxa refered to Sparnotheriodontidae. *Heteroglyphis dewoletzky* Roth , a Mustersan taxon from Cerro Humo, Chubut, Argentina is doubtfully assigned to this family (Soria, 2001).

The Anisolamdinae, considered part of the Proterotheridae (Cifelli, 1983b) or an independent family, Anisolambdidae, (Soria, 2001), embraced several poorly understood and primitive taxa from the Paleogene of Patagonia, most known from isolated teeth. *Wainka tshotshe* Simpson, represented by an isolated left upper molariform, comes from the Riochican levels of Cerro Redondo in Patagonia. The dentition of *Paranisolambda prodromus* Paula Couto from Itaboraí, is considered a structural ancestor of the sparnotheriodontid *Victorlemoinea* (Soria, 2001). As suggested by Simpson (1948), the genus *Anisolambda*, based on lower teeth, includes several synonyms including *Josepholeydia*, represented upper molars, and *Ricardolydekkeria*, known from P3-4. For now is represented by *Anisolambda fissidens* Ameghino, that came from the Casamayoran from Patagonia, and, *Anisolambda amel* Simpson, that came from the Vacan subage of the Casamayoran SALMA.

The Protolipternidae are characterized by the retention of a bunodont dentition as in didolodontid condylarths, but with a litoptern talus structure (Cifelli, 1983a). They are restricted to late Paleocene and early Eocene. They are fully discussed elsewhere in this volume and will not be considered here (Gelfo in this volume).

Polymorphis lechei Roth the oldest known Macracucheniidae, comes from the Mustersan SALMA of Patagonia, but its affinities with younger taxa are not yet well understood.

3.6. Similarity analysis of localities with a SANU record

A cluster analysis using Jaccard similarity and the single-linkage algorithm, was performed with PAST 1.97 software, considering a data matrix of 164 SANU taxa and 27 localities or levels in a specific locality in South America and Antarctica (Appendix 1). The taxonomic list was up-dated by personal observation of the authors and from the literature here mentioned, and the use of taxonomic hierarchical levels, genera, family, and order, is undertaken in order to account for the absence of common genera between some faunas. The distribution of taxa in each locality was scored as presence (1) or absence (0), without considering pseudo-extinctions. The localities include five levels from the Gran Barranca: GBV-3, GBV-4, GBV-19, GBV-60 and Simpson Y level (Ré etal., 2010). The inclusion of "Mustersan" refers to several localities. Most of the taxa here included were collected by George G. Simpson at "El Pajarito" and by Carlos Ameghino at Colhue Huapi Norte (also known as Cerro del Humo) (Simpson, 1948, 1967b). The fauna collected in these localities, as well as those taxa collected by Roth in the place he named "Cañadón Colorado", which has not been relocated, were the basis of the classic conception of Mustersan (Simpson, 1948, 1967b).

----------------- PLACE FIGURE 2 ABOUT HERE ---------------

Figure 2 shows the similarity relations of the localities or various levels of the same locality, based exclusively on SANU. The biochronological unit to which these localities have been assigned is indicated. The coefficient of correlation is 0.903. The highest levels of similarity are between the Paso del Sapo locality, and Riochican and Casamayoran units. The three Mustersan units join together, close to the Tinguiririca units. Antofagasta de la Sierra, GBV-19 and Sao Jose de Itaboraí, are close to this previous assemblage. All the previous localities mentioned, are joined together in a higher group, where SANU taxa explain well the similarities and is consistent with the known biochronological framework. The more distant relation between localities from NW Argentina and Patagonia, reflect the endemicity of taxa from lower latitudes. These faunas were assigned to Patagonian SALMAs since their family-level similarity and the interpretation of they represent the same evolutionary grade. Two geographically distant localities, Bajo Palangana lower levels (Patagonia) and Bogotá Formation (Colombia), are joined together due to the exclusive presence of xenungulates among their faunas. The group formed by La Meseta Formation and the Divisadero Largo, is not well explained according to the SANU record, and is the product of the presence of common higher taxa (*i.e.* Litopterna, Sparnotheriodontidae). The older faunas, such as Tiupampa and Punta Peligro, clearly show the lower levels of similarity relative to the rest of the Paleogene localities. In fact Tiupampa is characterized by a more laurasic fauna, while Punta Peligro reflects the mixture of Mesozoic Gondwanan lineages with a few SANU.

4. PHYLOGENETIC RELATIONSHIPS OF SANU

The knowledge of phylogenetic relationships of the earliest SANU, their link with non South American Eutheria and, their geographic origin are still matter of debate. The possible monophyly of the SANU has been discussed widely (*e.g.*: Ameghino, 1906; Simpson, 1948; Reig, 1981; Cifelli, 1993) but no consensus has been reached up to now. The first formal recognition for the possible common origin of SANU was proposed by McKenna (1975) under the term Meridiungulata. McKenna and Bell (1997) used Meridiungulata as a subdivision of Ungulata, together with Altoungulata (perissodactyls) and Eparctocyona (artiodactyls and ceteartiodactyls). Not only was Meridiungulata monophyly never tested, but this classification also suggested that some relationships were problematic, as for example that the Litopterna shared a closer common ancestor with Pyrotheria, than with didolodontids (Gelfo, 2006), which were placed among the artificial wastebasket taxon, “Condylarthra” (McKenna and Bell, 1997).

The incorporation of molecular characters in the phylogenetic analyses changed the traditional morphology-based classifications of Eutheria. As a consequence, the Ungulata clade, supposedly having originated from the stem-group Condylarthra, became polyphyletic (Murphy *et al.*, 2001), and the traditional ungulates have been split in two monophyletic groups, the Laurasiatheria and the Afrotheria (Murphy *et al.*, 2001). As a consequence various ungulates characters evolved independently among these groups. SANU were excluded from these analyses. They could represent, at least a third evolutionary experiment or be related to the Afrotheria or to the “true” ungulates, the Laurasiatheria.

Despite the formal proposal of Meridiungulata previously mentioned, several other interpretations have been proposed regarding in relation to the origin of SANU. Traditionally, it has been considered that notoungulates, litopterns (including notopterns), astrapotherians (including trigonostylopoids), pyrotheres and xenungulates evolved in South America, from an hypothetical Laurasian ancestor related to the “Condylarthra”, which is supposed to arrived during the Late Cretaceous or early Paleocene from North America (Simpson, 1948; Cifelli, 1983, 1985, 1993). This event was possible via the connections available between Laurasia and Gondwana, through the current Caribean area (Iturralde-Vinent and Macphee, 1999, Case *et al.*, 2004). The early Paleocene Tiupampan fossil record, particularly with the pantodont *Alcidedorbignya inopinata* and the Kollpaniinae condylarths, constituted a strong evidence for the relationships between Laurasian groups and at least the condylarths; with the SANU (Muizon and Cifelli, 2000; Gelfo, in this volume)

The proposal of Tong and Lucas (1982), and Lucas (1993) suggested for example that Pyrotheria, including there Xenungulata, were not Ungulata in the sense followed by McKenna and Bell (1997), and in contrast, were more related to Paleogene Dinocerata of Asia and North America. But, the only feature that links Xenungulata and Pyrotheria is bilophodonty, which is not necesary homologous in both groups (Gelfo et al., 2007a). The resemblance with dinoceratans could be based on homoplasic characters and so, would not represent true phylogenetic relationships (Cifelli, 1993).

The suggested link between Notoungulata and the Paleocene-Eocene Arctostylopidae from North America and Asia (Simpson, 1934, 1945), leads to a different hypothesis in relation to the origin and diversification patterns of these groups (Cifelli *et al.*, 1989 and literature therein). Several authors still consider arctostylopids as part of the Notoungulata (Kondrashov and Lucas, 2005), even though the more general opinions, which are followed here, suggest that probably this group probably shared a common unknown ancestor, but evolved independently from it (Cifelli, 1983; Soria, 1988, 2001; Cifelli *et al.*, 1989; Missiaen *et al.*, 2005).

Another alternative hypothesis for the Meridiungulata, was suggested by Soria (1989a) who identified two lineages derived from a common hypothetical ancestor. The first is represented by the Astrapotheria, Notoungulata, Xenungulata, Pyrotheria and, probably, Notopterna, and the other, by the Didolodontidae and Litopterna.

The Panameriungulata were created to include the Kollpaniinae, Didolodontidae and Litopterna (Muizon and Cifelli, 2000), but it should be noted that only Protolipternidae were included in the analysis, and they are not representative of litoptern diversity. The authors also suggested the possibility of a close link between these groups with Notoungulata, which was previously suggested by Cifelli (1993).

The relationships of the astrapotherians to the other groups of South American ungulates are not clear (see for example Cifelli, 1993). Ameghino (e.g. 1906) supported a relationship within in the Amblypoda which in this view, was very different from the concept of other authors (e.g. Gregory, 1910). According to Ameghino the astrapotherians were related not only to the Uintatheriidae, which were "classical" amblypods but also to the Amynodontida and Lophiodontida, which were extinct perissodactyls. Currently is well knowkn that the similarities between amynodontid rhinoceroses and astrapotheriids are only due to evolutionary convergence. Simpson (1967) noted some resemblances between the astrapotherians and the notoungulates and also between the astrapotheres and trigonostylopids to litopterns, but did not recognize any special relationship between the astrapotheres-trigonostylopids to the notoungulates or litopterns. Cifelli (1993) suggested the Xenungulata were a sister taxon to the Astrapotheria (including Trigonostylopida) and made no objections for the common origin of all the SANU.

The postcranial analysis of Horovitz (2004) which included some SANU, concluded that the Litopterna and Notoungulata were sister taxa, but the Astrapotheria were not related, and that was another point in favor of a polyphyletic origin of the

SANU.

Billet (2010) considered the Pyrotheria as within the Notoungulata, and the Astrapotheria as the sister group of the Notoungulata. The clustering of the Notoungulata-Pyrotheria and the Astrapotheria suggested a long isolated evolution of these ungulates in South America, similar to the history of the afrotherian mammals in Africa. Nevertheless is important to emphasize that these results did not include a consideration of the Xenungulata.

Notoungulates and astrapotherians were considered part of the afrotherian radiation (Agnolin and Chimento, 2011) but the arguments presented in support it are weak or wrong. Litopterna were not considered by Agnolin and Chimento (2011), suggesting that they were part of the mioclaenid radiation (Muizon and Cifelli, 2000), and independent from other SANU. This statement underestimated without comment, the possible relationships between the Panameriungulata and notoungulates (Muizon et al., 1998; Muizon and Cifelli, 2000). They also considered Didolodontidae as part of the Litopterna, but without any justification of this taxonomic decision. Litopterns where excluded from their analysis considering that they were related to Laurasian Mioclaenidae. In fact, the Panameriungulata group together the Kollpaniinae, Didolodotidae and Protolipternidae, the last one not representative of the diversity of the litopterns (see Gelfo in this volume). But already Muizon and Cifelli (2000) suggested the possibility that the Notoungulata could be part of the Panameriungulata, a statement which needs further discussion, particularly considering the basal taxa.

The main argument for considering Notoungulata and Astrapotheria as Afrotheria (Agnolin and Chimento, 2011) rests on a misconception of the synapomorphy concept, and the use of three morphological features. These characters, taken from the literature were the presence of more than 19 thoracolumbar vertebrae (Sánchez-Villagra et al., 2007), late eruption of permanent dentition (Asher and Lehmann, 2008) and the presence of an astragalar cotylar fossa (Tabuce et al., 2007). Agnolin and Chimento (2011) indicated their figure 5 is a cladogram showing the phylogenetic position of South American Ungulate clades. To the contrary there is no specification of the data matrix used or the steps followed to obtain this cladistic hypothesis, the number of trees obtained in the analysis and how was it accomplished, the level of support for, or the synapomorphies that defines the nodes. There is no evidence of why Notoungulata, Astrapotheria, Pyrotheria and Xenungulata are part of a polytomy in the afrotherian clade. Setting aside this methodological vacuum, there are also some objections to the identification of the three characters mentioned above.

Asher and Lehmann (2008) state that in afrotherians, permanent cheek teeth finish erupting only after they have reached adult body size, and Agnolin and Chimento (2011) argue that this character is present in notoungulates, astrapotherians and pyrotherians. But, Billet and Thomas (2011) criticized the bivariate analysis of Agnolin and Chimento (2011) to justify the interpretation of delayed dental eruption in notoungulates, highlighting also that the references used (e.g., Roth 1903, 1927; Scott 1912) to reinforce their interpretation could not be found in most cases. Billet and Thomas (2011) analyzed the pattern of dental eruption relative to skull growth in the notoungulates *Notostylops, Santiagorothia, Trachyterus, Adinotherium*, *Nesodon* and *Protypotherium*, and concluded that normal, rather than delayed, eruption represents the ancestral state for this group. Regarding astrapotherians, Agnolin and Chimento (2011) suggest that the deciduous teeth are retained into the adult and senile stage, and that most putative juvenile specimens of Astrapotheria are indistinguishable from those of adult or senile individuals, showing a rather similar body size and tooth proportions. We could not find any evidence in support of these statements among astrapotherians and, in contrast, it should be mentioned that the deciduous cheek-teeth are clearly different from the replacing teeth, and that adult specimens show an already replaced dentition (Kramarz and Bond, 2010). Also, Agnolin and Chimento (2011) state that *Parastrapotherium* has a dental formula of five cheek-teeth, of which Dp1-Dp3 are still retained in the adult and senile specimens. It should be pointed out, that this statement suggests that *Parastrapotherium* only has the first two molars, which is not accurate (Kramarz and Bond, 2008). In fact this taxon retains only two upper and lower premolars which are fully replaced in the adult stage and correspond to P3-P4 and p3-p4. There are no astrapotherians in which the P1 and p1 were ratained since the Middle-Upper Eocene. Among Pyrotheria, base in the only known specimen of *Griphodon peruvianus* which shows a dp4 and a well erupted m1, with p4 still at the base of the mandible, Agnolin and Chimento (2011) inferred that the Pyrotheria also exhibited a delayed tooth replacement. We disagree that the presence of dp4-m1 supports this inference. Particularly since other teeth are missing and below the dp4 the replacing p3 and p4 are quite formed, so this is not proof of any delayed replacement. Also from what is known of *Pyrotherium* (see Gaudry, 1901) apparently there is no evidence of delayed replacement. No inferences can be made about this character in the carodniid or etayoid xenungulates, due to the rarity of the complete specimens.

In sum, there is no clear evidence that the ancestral state for SANU was the eruption of permanent cheek teeth after the attainment of adult size. The possible exception of the notoungulate *Protypotherium* seems to be a derived and exceptional state among Typotheria (see Billet and Thomas, 2011).

The presence of more than 19 thoracolumbar vertebrae was considered as another possible link of astrapotherians, notoungulates and afrotherians (Agnolin and Chimento, 2011). But a thoracolumbar formula greater than 19 is also observed in non-afrotherian mammals (*e.g.* Murinae and Bathyergidae (Rodentia), Soricidae (Eulipotypla), Tayasuidae, several Bovidae (Ceteartiodactyla) (Narita and Kuratani, 2005; Sanchez Villagra et al., 2007) and, among the SANU excluded from the Agnolin and Chimento (2011) analysis, at least the litoptern *Macrauchenia patachonica* (MLP12-1424) has 20 thoracolumbar vertebrae (15 thoracic plus 5 lumbar). This character has to be examined in more detail prior to offering a generalized statement for any SANU group and analyzed in the context of a cladistic analysis before being considered as a derived character.

The third argument used by Agnolin and Chimento (2011) to link Afrotheria with SANU (except Litopterna) was the presence of a cotylar fossa. This character was observed in stem members of Hyracoidea, Proboscidea, Tubulidentata and Macroscelidea, and considered as a reliable afrotherian synapomorphy (Tabuce et al., 2007). However, living golden moles and tenrecs, both crown members of Afrotheria, do not show this tarsal evidence (Salton and Szalay 2004) and other non-afrotherians mammals show this character (Tabuce et al., 2007). There are two principal problems with this argument by Agnolin and Chimento (2011). The first is the misinterpretation of the cotylar fossa, which was defined by them as a deep concavity located at the medial margin of the medial rim of the astragalar throclea to receive the medial malleolus of the distal tibia, citing Szalay (1977) as the source, and Ameghino (1905) as the first who noticed the cotylar fossa among SANU. We could not find any comparable statement in Szalay (1977) or in Ameghino (1905) to support their argument. In fact, Ameghino (1905) only described a concavity on the facet for the medial malleolus of the tibia in *Orycteropus*, and it was MacPhee (1994), who first described it as a “cotylar fossa” defined as an anterior extension of the medial malleolar facet of the astragalus that deepens into a cup and receives the condylar articular surface developed on the medial malleolus. So, not every lateral concavity present on the medial side of the talus is in fact a cotylar fossa, but those receiving the condylar articular surface of the medial malleolus of the tibia. There is a difficulty in some cases to determinate a “clear cut” presence of a cotylar fossa as seen in *Orycteropus* and several depressions find over the medial side of the talus in isolated SANU fossils, particularly when no tibial remains are available to analyze the expression of the malleolus.

The second argument against the Agnolin and Chimento (2011) proposal concerns the incorrect identification of the characters among SANU. They mentioned a well developed cotylar fossa in early notoungulates *Colbertia, Itaboraitherium, Camargomendesia* and cited Cifelli (1993) as source. However, in this last paper, Cifelli specifies three states for the astragalar medial malleolar facet, vertical, restricted to the side of the body, or with a strong anterior stop. But in the three species mentioned above, the state for this character is indeterminate (Cifelli, 1993). Agnolín and Chimento (2011) said that the presence of a deep and concave cotylar fossa is shown in all known notoungulates, but in fact this character is extremely variable among them. The talus of *Nesodon* (MLP 12-90) has a well developed maleolar facet, which extends over the head, forming a cotylar fossa. But, in the right talus of *Homalodotherium* (MLP 67-VIII-15-1) and *Toxodon* (MLP 12-1125 and 1126) there is a brief and flat tibial malleolar facet not a concave depression to receive the medial malleolous of the tibia. Particularly there is no cotylar fossa in basal isotemnids, as for example, the specimen AMNH 28690 considered possibly near *Pleurostylodon similis* (see description in Shockey and Flynn, 2007). The talus of basal isotemnids resembles those of phenacodontid archaic ungulates, and probably is morphologically close to the unknown talus of the first notoungulates.

Agnolin and Chimento (2011) consider that the presence of the medial side of the astragalus of *Pyrotherium* could not be properly observed due to the modification of the bones, and considered the presence of cotylar fossa as uncertain. However an observation of a right talus of *Pyrotherium* (MLP 79-XII-18-29) shows the presence of a long and thin medial facet for the tibial malleolus, without a cotylar fossa, similar to what was described for *Pyroterium macfaddeni* (Shockey and Anaya, 2004). Something similar could be identified in Astrapotheriidae (MLP 95-III-10-30) where the fibular facet is larger and convex, and the medial malleolus facet is mostly restricted to the smooth medial surface of the medial trochlear crest. They also considered this character as present among xenungulates, in *Carodnia* but in fact the talus of this taxon shows a prominent posteromedial protuberance probably related to the medial collateral ligaments (Cifelli, 1983b) and a broad and flat head, somewhat medially oriented, which together form a medial groove in the talus. Probably this entrance was interpreted as a cotylar fossa by Agnolin and Chimento (2011), but it should be noted that the medial crest of the trochlea is very short and the medial malleolar facet seems to be restricted to it. Tibial remains of *Carodnia vierai* lack the distal end to check the presence of the condylar articular surface of the medial malleolus in order to analyze the contact between the tibia and talus.

In sum, most of the SANU mentioned by Agnolin and Chimento (2011) lack a cotylar fossa which seems to represent the ancestral state for them. Still, it is important to highlight that the cotylar fossa is in fact present in the malleolar facet of some derived taxa (*e.g*. *Nesodon* among notonugulates). Another important point is that this structure is in fact present in the talus associated with didolodontids of the Itaboraian fauna (Cifelli, 1983b, Bergqvist, 1996, 2007 but see Gelfo in this volume). In these taxa, the medial malleolar facet is extended far anteriorly on to the neck and nearly to the head of the astragalus, where it curves abruptly medially, a character that was considered as synapomorphic for the Didolodontidae (Cifelli, 1983b, Bergqvist, 1996; 2007) a group considered not related to afrotherians *sensu* Agnolin and Chimento (2011). Tabuce et al.(2007) point that the cotylar fossa as a character also present in other non related groups, as for example Primates, and we must add also the primitive “archaic ungulates” such as *Meniscotherium* (see MacPhee, 1994). It is also worth mentioning that a cotylar fossa in the astragalus is present in some dinocerates such as *Probathyopsis* (see Thewisen & Gingerich, 1987).

In summary, the phylogenetic relations of SANU, the dominant components in the Paleocene and Eocene South American faunas, are still controversial and debated. A recent and attractive proposal argued for affinities between afrotherians and some of them (notoungulates and astrapotherians). However as mentioned above, this relationshipships were established without a proper analysis, particularly methodological, and utilized misconceived morphological features. Therefore the clarification of the origin and the phylogeny of SANU, in higher levels and also in alpha taxonomy, is an unresolved but desired issue, in order to understand the biotic history of South America. The precise definition of morphological terms, homologies, the establishment of their variation in the different lineages, and the application of rigorous phylogenetic and paleobiogeographical methods, undoubtedly will result in a new and encouraging starting point.

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------------------ PLACE APPENDIX 1 TO THE END ----------------

REFERENCES

Agnolin, F.L., Chimento, N.R., 2011. Afrotherian affinities for endemic South American "ungulates" Mammalian Biology 76, 101-108.

Ameghino, F., 1901. Notices préliminaires sur des ongulés nouveaux des terrains crétacés de Patagonie. Boletín de la Academia Nacional de Ciencias de Córdoba, 16, 349-426.

Ameghino, F., 1905. La perforación astragaliana en el Orycteropus y el origen de los Orycteropidae. Anales del Museo Nacional de Buenos Aires 6, 59–95.

Ameghino, F., 1906. Les formations sedimentaires du cretace superieur et du tertiaire de Patagonie avec un parallele entre leurs faunes mammalogiques et celles de l'ancien continent. Anales del Museo Nacional de Buenos Aires 15 (8),1-568.

Andreis, R., 1977. Geología del área de Cañadón Hondo, Depto. Escalante, Provincia del Chubut, República Argentina. Obra del Centenario del Museo de La Plata, 4: 77-102.

Andreis, R., Mazzoni, M., Spalletti, L., 1975. Estudio estratigráfico y paleoambiental de las sedimentitas terciarias entre Pico Salamanca y Bahia Bustamante, Provincia. de Chubut, República Argentina. Revista de la Asociación geológica Argentina 30 (1), 85-103.

Asher R.J., Lehmann, T., 2008. Dental eruption in afrotherian mammals. BMC Biology 6:14

Avilla, L.S., 2005. A revision of *Colombitherium tolimense* Hoffstetter (Pyrotheria: Mammalia) and its significance on Pyrotheria relationships. Ameghiniana 42(4R), 60R.

Baez, A.M., Pugener L.A., 1998. A new Paleogene pipid frog from northwestern Patagonia. Journal of Vertebrate Paleontology 18, 511–524.

Bellosi, E.S., 2010. Physical stratigraphy of the Sarmiento Formation (middle Eocene - lower Miocene) at Gran Barranca, central Patagonia. In: Madden, R.H., Carlini, A.A., Vucetich, M.G. (Eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, 19-31.

Bellosi, E.S., Madden, R.H., 2005. Estratigrafía física preliminar de las secuencias piroclásticas terrestres de la Formación Sarmiento (Eoceno-Mioceno) en la Gran Barranca, Chubut. In: Cabaleri N., Cingolani, C.A., Linares, E., López de Luchi, M.G., Ostera, H.A. y Panarello, H.O. (Eds.), XVI Congreso Geológico Argentino, Actas (4), pp. 427-432.

Bergqvist, L.P., 2008. Postcranial Skeleton of the Upper Paleocene (Itaboraian) "Condylarthra" (Mammalia) of Itaboraí Basin, Brazil. In: Sargis, E.J., Dagosto, M. (Eds.), Mammalian Evolutionary Morphology. A tribute to Frederik S. Szalay. Springer-Verlag New York, pp. 107-133.

Billet, G., 2010. New observations on the Skull of *Pyrotherium* (Pyrotheria, Mammalia) and new Phylogenetic Hypotheses on South American Ungulates. Journal of Mammalian Evolution, 17: 21-59.

Billet, G., Orliac, M., Antoine, P.O., Jaramillo, C., 2010. New observations and reinterpretation on the enigmatic taxon *Colombitherium* (?Pyrotheria, Mammaia) from Colombia. Palaeontology 53, 319-325.

Billet, G., Patterson, B., Muizon, C. de., 2009. Craniodental anatomy of late Oligocene archaeohyracids (Notoungulata, Mammalia) from Bolivia and Argentina and new phylogenetic hypotheses. Zoological Journal of the Linnean Society 155, 458–509.

Billet, G., Thomas, M., 2011. No evidence for an afrotherian-like delayed dental eruption in South American notoungulates. Naturwissenschaften 1-9.

Bonaparte, J.F., Van Valen, L., Kramartz, A., 1993. La fauna local de Punta Peligro, Paleoceno inferior, de la provincia de Chubut, Patagonia, Argentina. Evolutionary Monograph 14, 3-61.

Bond, M., 1986. Ungulados fósiles de Argentina: evolución y paleoambientes. In Simposio de Evolución de los Vertebrados Cenozoicos. Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía 2, 173-185.

Bond, M., 1991. Sobre las capas de supuesta Edad Divisaderense en los "Estratos de Salla", Bolivia. In: Suarez-Soruco, R. (Ed.), Fósiles y Facies de Bolivia vol. 1 (Vertebrados). Revista Técnica de YPFB 12 (3-4), pp. 701-705.

Bond, M., Carlini, A.A., Goin, F.J., Legarreta, L., Ortíz Jaureguizar, E., Pascual, R., Uliana, M.A., 1995. Episodes in South American Land Mammal evolution and sedimentation: testing their apparent concurrence in Palaeocene succession from central Patagonia. Actas del VI Congreso Argentino de Paleontología y bioestratigrafía, 47-58.

Bond, M., Kramarz, A., Mac Phee, R.D.E., Reguero, M.A., In press. New astrapothere (Mammalia, Meridiungulata) from La Meseta Formation, Seymour (Marambio) Island, and a reassessment of previous records of Antarctic astrapotheres. American Museum Novitates.

Bond, M., López, G.M., 1995. Los Mamíferos de la Formación Casa Grande de La Provincia de Jujuy, Argentina. Ameghiniana 32 (3), 301-309.

Bond, M. and López, G.M., 2002. Consideraciones sistemáticas de *Paginula parca* Ameghino, 1901 y otros Notoungulata (Mammalia) del Paleogeno de Argentina y Brasil. XVIII Jornadas Argentinas de Paleontología de Vertebrados. Ameghiniana 39 (4) suplemento, 6 R.

Bond, M., Reguero, M.A., Vizcaíno, S.F., Marenssi, S.A., 2006. A new “South American Ungulate” (Mammalia: Litopterna) from the Eocene of the Antarctic Peninsula. In: Francis, J.E., Pirrie D., Crame, J.A. (Eds.), Cretaceous-Tertiary High-Latitude Palaeoenvironments, James Ross Basin, Antarctica. Geological Society, London, Special Publications 258, pp. 163-176.

Bond, M., Vucetich, M.G., 1983. *Indalecia grandensis* gen. et sp. nov. de Eoceno temprano del Noroeste argentino, tipo de una nueva subfamilia de los Adiantidae (Mammalia, Litopterna). Revista de la Asociación Geológica Argentina 38 (1), 107-117.

Bond, M., Vucetich, M.G., Pascual, R., 1984. Un nuevo Notoungulata de la Formación Lumbrera (Eoceno) de la provincia de Salta, Argentina. I Jornadas Argentinas de Paleontología Vertebrados, resúmenes, 20.

Carbajal, E., Pascual, R., Pinedo, R., Salfity, J.A., Vucetich, M.G., 1977. Un nuevo mamífero de la Formación Lumbrera (Grupo Salta) de la comarca de Carahuasi (Salta, Argentina). Edad y Correlaciones. Publicaciones de Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" 2 (7), 148-163.

Case, J.A., Goin, F.J., Woodburne, M.O., 2004. South American Marsupials from the Late Cretaceous of North America and the Origin of Marsupial Cohorts. Journal of Mammalian Evolution 11 (3-4), 223-255.

Cerdeño, E., López, G.M., Reguero, M.A., 2008. Biostratigraphical considerations on the Divisaderan faunal assemblage. Journal Vertebrate Paleontology 28 (2), 574-577.

Cerdeño, E., Reguero, M.A., Vera, B., 2010. Deseadan Archaeohyracidae (Notoungulata) from Quebrada Fiera (Mendoza, Argentina) in the paleobiogeographic context of the South American late Oligocene. Journal of Paleontology 84 (6), 1177–1187.

Cifelli, R.L., 1983a. Eutherian tarsals from the late Paleocene of Brazil. American Museum Novitates, 2761: 1-31.

Cifelli, R.L., 1983b. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). American Museum Novitates 2772, 1-49.

Cifelli, R.L., 1985a. South American ungulate evolution and extinction. In Stehli, F., Webb, S.D. (Eds.), The Great American Biotic Interchange, Plenum Press, New York, pp. 249-266.

Cifelli, R.L., 1985b. Biostratigraphy of the Casamayoran, early Eocene, of Patagonia. American Museum Novitates 2820, 1-26.

Cifelli, R.L., 1993. The Phylogeny of the Native South American Ungulates. In: Szalay, F.S. Novacek M.J., McKenna M.C. (Eds.), Mammal Phylogeny (2 vols.), Springer Verlag, vol. 1 pp. 195-216.

Cifelli, R.L., Schaff, C.R., McKenna, M.C., 1989. The relationships of the Arctostylopidae (Mammalia): new data and interpretation. Bulletin of the Museum of Comparative Zoology 152 (1), 1-44.

Cifelli, R.L., Soria, M.F., 1983. Systematics of the Adianthidae (Litopterna, Mammalia). American Museum Novitates 2771, 1-25.

Cladera, G., Ruigomez, E., Ortiz Jaureguizar, E., Bond, M., López, G.M., 2004. Tafonomía de la Gran Hondonada (Formación Sarmiento, Edad-mamífero Mustersense, Eoceno Medio) Chubut, Argentina. Ameghiniana 41 (3), 315-330.

Croft, D.A., Bond, M., Flynn, J.J., Reguero, M.A., Wyss, A. E., 2003. Large Archaeohyracids (Typotheria, Notoungulata) from Central Chile and Patagonia, Including a Revision of *Archaeotypotherium*. Fieldiana Geology, (NS), 49, 1-38.

DeCelles, P.G., Carrapa, B., Gehrels, G.E., 2007. Detrital zircon U-Pb ages provide provenance and chronostratigraphic information from Eocene synorogenic deposits in northwestern Argentina. Geology 35 (4), 323-326.

Del Papa, C.E., 1999. Sedimentation on a ramp type lake margin: Paleocene-Eocene Maiz Gordo, Northewest Argentina. Journal of South American Earth Sciences 12, 389-400.

Del Papa, C.E., García, V., Quattrocchio, M., 2002. Sedimentary facies and palynofacies assemblage in Eocene perennial lake, Lumbrera Formation, northwest Argentina. Journal of South American Earth Sciences 15, 553-569.

Deraco, M. V., Powell, J. E. y López, G. M., 2008. Primer leontínido (Mammalia, Notoungulata) de la Formación Lumbrera (Subgrupo Santa Bárbara, Grupo Salta– Paleógeno) del Noroeste Argentino. *Ameghiniana* 45 (1): 83-91.

Feruglio, E., 1938. Nomenclatura estratigráfica de la Patagonia y Tierra del Fuego. In: Fossa Mancini, E., Feruglio E., Justen, J.C. (Eds.), Una reunión de geólogos de YPF y el problema de la terminiología estratigráfica. Boletín de Informaciones petroleras 171, 54-67.

Flynn, J.J., Norell, M.A., Swisher, C.C.III, Wyss, A.R., 1991. Predeseadan, post-Mustersan mammals from central Chile: an update. Journal Vertebrate Paleontology 11, supplement to n° 3, 29A.

Flynn, J.J., Croft, D., Hitz, R., Wyss, A., 2005. The tapado fauna (?Casamayoran SALMA), Abanico Formation, Tinguiririca Valley, central Chile. Journal Vertebrate Paleontology 25, supplement to n° 3, 57A.

Flynn, J.J., Swisher, C.C.III., 1995. Cenozoic South American Land Mammal Ages: correlation to global geochronologies. In: Berggren, W., Kent, D., Aubry, M. P., Hardenbol, J. (Eds.), Geochronology Times Scales and Global Stratigraphic Correlation, SEPM Special Publication 54 pp. 317-333.

Flynn, J.J., Wyss, A., Croft, D., Charrier, R., 2003. The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogegrphy, and a new earliest Oligocene South American Land Mammal "Age". Palaeogeography, Palaeoclimatology Palaeoecology 195, 229-259.

García López, D.A., 2009. Notoungulados del Paleógeno del Noroeste Argentino: morfología y evolución. Ph.D. Dissertation, Facultad de Ciencias Naturales e Instituto Miguel Lillo. Universidad Nacional de Tucumán.

García López D.A. and Powell J. E. 2009. Un nuevo Oldfieldthomasiidae (Mammalia: Notoungulata) del Paleógeno de la provincia de Salta, Argentina. *Ameghiniana* 46(1): 153-164.

Gelfo, J.N., 2006. Los Didolodontidae (Mammalia, Ungulatomorpha) del Terciario Sudamericano. Sistemática, Origen y evolución. Ph.D. Dissertation, Facultad de Ciencias Naturales y Museo. Universidad Nacional de La Plata.

Gelfo J.N. (in this volume). The evolution of native South American bunodont ungulates.

Gelfo, J.N., Chornogubsky, L., López, G.M., Goin, F.J., Bond, M., Ciancio, M.R., Carlini, A.A., Raigemborn, M.S., 2010. La fauna paleógena de Las Violetas, Provincia del Chubut, Argentina. XXV Jornadas Argentinas de Paleontología de Vertebrados (San Luís) resúmenes, 18.

Gelfo, J.N., Goin F.J., Woodburne, M., Muizon, C. de., 2009a. Biochronological relationships of the earliest South American Paleogene mammalian faunas. *Palaeontology* 52, 251-269.

Gelfo, J.N., Reguero, M.A., López, G.M., Carlini, A.A., Ciancio, M.R., Chornogubsky, L., Bond, M., Goin, F.J., Tejedor, M., 2009b. Eocene mammals and continental strata from Patagonia and Antarctic Peninsula. In: Albright, L. B. III (Ed.), Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin 65 pp. 567-592.

Gelfo, J.N., López, G.M., Bond, M., 2008. A new Xenungulata (Mammalia) from the Paleocene of Patagonia, Argentina. Journal of Paleontology 82 (2), 329-335.

Gelfo, J.N. and Sigé, B., 2011. A new didolodontid mammal from the late Paleocene–earliest Eocene of Laguna Umayo, Perú. *Acta Palaeontologica Polonica* 56 (4): 665–678.

Gregory, W.K., 1910. The orders of mammals. Bulletin American Museum of Natural History 27,1-524.

Hitz, R.B., Flynn, J.J., Wyss, A.R., 2006. New Basal Interatheriidae (Typotheria, Notoungulata, Mammalia) from the Paleogene of Central Chile. American Museum Novitates 3520, 1-32.

Hoffstetter, R., 1970. *Colombitherium tolimense* pyrothérien nouveau de la Formation Gualanday (Colombie). Annales de Paléontologie 56, 149-171.

Horovitz, I., 2004. Eutherian mammal systematics and the origin of South American ungulates as based on postcranial osteology. Bulletin of the Carnegie Museum of Natural History, 36: 63-79.

Iturralde-Vinet, M.A., Macphee, R.D., 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. Bulletin American Museum of Natural History 238, 1-95.

Ivany, L.C. 2007. Contributions to the Eocene climatic record of the Antarctic Peninsula. U.S. Geological Survey and the National Academies, Extended Abstracts : 68.

Kramarz, A.G, Bond, M. 2005. Criticisms to the re-interpretation of the holotype of *Colombitherium tolimense* Hoffstetter (Mammalia: Pyrotheria) and its implication on the Pyrotheria–Notoungulata relationships. Ameghiniana 42(4R), 16R.

Kramarz, A.G, Bond, M. 2008. Revision of *Parastrapotherium* (Mammalia, Astrapotheria) and other Deseadan astrapotheres of Patagonia. Ameghiniana 45 (3), 537-551.

Kramarz, A.G., Bond, M., 2009. A new Oligocene astrapothere (Mammalia) from Patagonia and a new appraisal of astrapothere phylogeny. Journal of Systematic Palaeontology 7 (1), 117-128.

Kramarz, A.G., Bond, M., 2010. Colhuehuapian Astrapotheriids (Mammalia, Astrapotheria) from Gran Barranca Sur of Lake Colhué Huapí, Chubut, Argentina. In: Madden, R.H., Carlini, A.A., Vucetich, M.G. (Eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, 182-192.

Kramarz, A.G., Bond, M., Forasiepi. A.M., 2010. New remains of *Astraponotus* (Mammalia, Astrapotheria) and considerations on the Astrapothere cranial evolution. Paläontologische Zeitschrift, Springer Verlag 85 (2), 185-200.

Kodrashov, P.E., Lucas, S.G., 2005. South American Mammals in the Paleocene of Asia or Asian Paleocene Mammals in South America?. Boletin de Rusmos II Congreso Latinoamericano de Paleontología de Vertebrados, 144.

Legarrreta, L., Uliana, M.A., 1994. Asociaciones de fósiles y hiatos en el Supracretácico-Neógeno de Patagonia: Una perspectiva estratigráfico-secuencial. Ameghiniana 31(3), 257-281.

Linares, E., Timonieri, A.J., Pascual, R., 1961. La Edad de los sedimentos Terciarios del Valle de Punilla, provincia de Córdoba y la presencia de *Eohyrax rusticus*, Ameghino en los mismos. Revista de la Asociación Geológica Argentina 15 (3-4), 191-210.

López, G.M., 1995. *Suniodon catamarcensis gen. et sp. nov.* y otros Oldfieldthomasiidae (Notoungulata, Typotheria) del Eoceno de Antofagasta de la Sierra, Catamarca, Argentina. Actas VI Congreso Argentino de Paleontología y Bioestratigrafía, 167-172.

López, G.M., 1997. Paleogene Faunal assemblage from Antofagasta de la Sierra (Catamarca Province, Argentina). Palaeovertebrata 26(1-4), 61-81.

Eliminado: Province

López, G.M., 2008. Los ungulados de la Formación Divisadero Largo (Eoceno superior-Oligoceno inferior?) de la provincia de Mendoza, Argentina: sistematica y consideraciones bioestratigraficas. Ph.D. Dissertation, Facultad Ciencias Naturales y Museo. Universidad Nacional de La Plata.

López, G.M., 2009. Primer registro del Orden Astrapotheria en la Formación Divisadero Largo (Mendoza, Argentina). Aportes a la antigüedad de la fauna Divisaderense. (Nota Paleontológica). Ameghiniana 46 (1), 189-192.

López, G.M., 2010. Divisaderan: Land Mammal Age or Local Fauna?. In: Madden, R.H., Carlini, A.A., Vucetich, M.G. (Eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, 410-420.

López, G.M., Bond, M., 1995. Un nuevo Notopithecinae (Notoungulata, Typotheria) del Terciario inferior de la Puna Argentina. Stvdia Geológica Salamanticensia 31, 87-99.

López, G.M., Bond, M., 2003. Una nueva familia de ungulados (Mammalia, Notoungulata) del Paleógeno sudamericano. XIX Jornadas Argentinas de Paleontología de Vertebrados (Bs. As.). Ameghiniana 40 (4) suplemento, 60 R.

López, G.M., Bond, M., 2010. Revisión sistemática de los Oldfieldthomasiidae (Mammalia, Notoungulata) del Paleógeno de América del Sur. Actas X Congreso Argentino de Paleontología y Bioestratigrafía y VII Congreso Latinoamericano de Paleontología, 64.

López, G.M., Bond, M., Reguero, M.A., Gelfo, J.N., Kramarz, A., 2005. Los ungulados del Eoceno-Oligoceno de la Gran Barranca, Chubut. In: Cabaleri N., Cingolani, C.A., Linares, E., López de Luchi, M.G., Ostera, H.A. y Panarello, H.O. (Eds.), XVI Congreso Geológico Argentino, Actas (4), pp. 415-418.

López, G.M., Manassero, M., 2008. Revision of the stratigraphic provenance of *Ethegotherium carettei* (Notoungulata, Hegetotheriidae) by sedimentary petrography. Neues Jahrbuch für Geologie und Paläontologie 248 (1), 1-9.

López, G.M., Ribeiro, A.M., Bond, M., 2010. The Notohippidae (Mammalia, Notoungulata) from Gran Barranca, Sarmiento Formation, Chubut Province, Argentina: preliminary considerations. In: Madden, R.H., Carlini, A.A., Vucetich, M.G. (Eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, 143-151.

Lucas, S.G., 1986. Pyrothere systematics and a Caribbean route for land-mammal dispersal during the Paleocene. Revista Geológica de América Central 5, 1-35.

Lucas, S., 1993. Pantodonts, Tillodonts, Uintatheres, and Pyrotheres are not Ungulates. In: Szalay, F.S., Novacek, M.J., McKenna M.C. (Eds.), Mammal Phylogeny, Springer Verlag, New York II, 182-194.

Marshall, L.G., 1985. Geochronology and Land-Mammal Biochronology of the Transamerican Faunal Interchange. In: Stehli, F.G., Webb, S.D. (Eds.), The Great American Biotic Interchange, Plenum Press pp. 49-85.

Marshall, L.G., Hoffstetter, R., Pascual, R., 1983. Geochronology of the continental mammal-bearing Tertiary of South America. Paleovertebrata, mémoire extraordianire, 1-93.

Marshall, L.G., Muizon, C. De, Sigé, B., 1983. *Perutherium altiplanense*, un Notoungulé du Crétacé supérieur du Pérou. Palaeovertebrata 13 (4), 145-155.

Marshall, L.G., Sempere, T., Butler, R.F., 1997. Chronostratigraphy of the Mammal-bearing Paleocene of South America. Journal of South American Earth Science 10 (1), 49-70.

McPhee, R.D.E., 1994. Morphology, adaptations, and relationships of Plesiorycteropus, and a diagnosis of a new order of eutherian mammals. Bulletin American Museum of Natural History 220, 1-214.

Eliminado: province

McKenna, M.C., 1975. Toward a phylogenetic classification of the Mammalia. In: Luckett, W.P., Szalay, F.S. (Eds.), Phylogeny of the Primates, a Multidisciplinary approach, Plenum Press, 21-46.

McKenna, M.C., Bell, S.K., 1997. *The Classification of Mammals. Above species level.* Columbia University Press.

Missiaen, P., Guo, D., Smith, T., 2005. On foot (bones): the late paleocene asian Arctostylopid mamal *Plaeostylops* and its llaison with the South American Ungulates. II Congresso Latino-Americano de Paleontología de Vertebrados Río de Janeiro, Brasil, 172-173.

Montalvo, C., Bond, M., 1998. Un notoungulata de la Formación Vaca Mahuida (Eoceno), provincia de La Pampa, Argentina. Asociación Paleontológica Argentina Publicación especial n^o 5. Paleógeno de América del Sur y de la Península Antártica, 55-60.

Muizon, C. de., 1991. Fauna de mamíferos de Tiupampa (Paleoceno inferior, Formación Santa Lucía), Bolivia. In: Suarez-Soruco, R. (Ed.), Fósiles y Facies de Bolivia vol. 1 (Vertebrados). Revista Técnica de YPFB 12 (3-4), pp. 575-624.

Muizon, C. de, Cifelli, R.L., 2000. The “Condylarths” (archaic Ungulata, Mammalia) from early Palaeocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. Geodiversitas 22 (1), 47-150.

Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang, Y.P., Ryder, O.A., O'Brien, S.J., 2001. Molecular phylogenetics and the origins of placental mammals. Nature 409, 614-618.

Narita. Y., Kuratani, S., 2005. Evolution of the Vertebral Formulae in Mammals: A Perspective on Developmental Constraints. Journal of Experimental Zoology (Molecular development evolution) 304B, 91-106.

Ortíz Jaureguizar, E., Pascual, R., 1989. South American Land-Mammal faunas during the Cretaceous-Tertiary transition: evolutionary biogeography. In: Spalletti, L. (Ed.) Contribuciones de los Simposios sobre el Cretácico de América Latina. Parte A: Eventos y registro sedimentario pp. 231-251.

Pascual, R., Bond, M., Vucetich, M.G., 1981. El Subgrupo Santa Bárbara (Grupo Salta) y sus vertebrados. Cronología, paleoambientes y paleobiogeografía. Actas del VIII Congreso Geológico Argentino (3), 743-758.

Pascual, R., Ortega Hinojosa, E.J. Gondar, D., Tonni, E.P., 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquéllas del territorio bonaerense. Anales de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires 6, 165-193.

Pascual, R., Ortíz Jaureguizar, E., 1990. Evolving climates and mammal fauna in Cenozoic South America. Journal of Human Evolution 19, 23-60.

Pascual, R., Ortíz Jaureguizar, E., 1991. El ciclo faunístico Cochabambiano (Paleoceno temprano): su incidencia en la historia biogeográfica de los mamíferos sudamericanos. In:

Suarez-Soruco, R. (Ed.), Fósiles y Facies de Bolivia vol. 1 (Vertebrados). Revista Técnica de YPFB 12 (3-4), pp. 559-574.

Pascual, R., Ortíz 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 (2), 75-137.

Pascual, R., Vucetich, M.G., Fernandez, J., 1978. Los primeros mamíferos (Notoungulata, Henricosborniidae) de la Formación Mealla (Grupo Salta, Subgrupo Santa Bárbara). Sus implicancias filogenéticas, taxonómicas y cronológicas. Ameghiniana XV (3-4), 366-390.

Patterson, B., 1942. Two Tertiary mammals from northern South America. American Museum Novitates 1173, 1-7.

Patterson, B., 1977. A primitive pyrothere (Mammalia, Notoungulata) from the Early tertiary of Northwestern Venezuela. Fieldiana Geology, N.S. 33, 397-421.

Paula Couto, C. De., 1952. Fossil mammals from the beginning of the Cenozoic in Brazil. Condylarthra, Litopterna, Xenungulata and Astrapotheria. Bulletin of American Museum of Natural History 99, 355-394.

Paula Couto, C. De., 1978. Ungulados fósseis do Riochiquense de Itaboraí, Estado de Río de Janeiro, Brasil. III - Notoungulata e Trigonostylopoidea. Anais Academia Brasileira de Ciências 50 (2), 219-226.

Powell, J.E., Palma, R.M., 1981. Primer hallazgo de mamíferos en la Formación Río Loro, provincia de Tucumán y su significado cronológico. Revista de la Asociación Geológica Argentina 36 (2), 208-212.

Raigemborn, M.S., 2008. Estudio estratigráfico, sedimentológico y composicional de las sedimentitas del Terciario inferior (Grupo Río Chico) en el sector sudoriental del Chubut extraandino. Ph.D. Dissertation, Facultad Ciencias Naturales y Museo. Universidad Nacional de La Plata.

Ré, G.H., Bellosi, E.S., Heizler, M., Vilas, J.F., Madden, R.H., Carlini, A.A., Kay, R.F., Vucetich, M.G., 2010. A geochronology for the Sarmiento Formation at Gran Barranca. In: Madden, R.H., Carlini, A.A., Vucetich, M.G. (Eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, 46-58.

Reguero, M.A., Bond, M., López, G.M., 1996. *Campanorco inauguralis* (Typotheria, Notoungulata): an approach to the phylogeny of the Typotheria. Journal of Vertebrate Paleontology, 16 (3), 59A.

Reguero, M.A., Castro, P.V., 2004. Un nuevo Trachytheriinae (Mammalia, Notoungulata, Mesotheriidae) del Deseadense (Oligoceno tardío) de Cabeza Blanca, Chubut, Argentina. Importancia bioestratigráfica y filogenética del género *Trachytherus*. Revista Geológica de Chile 31(1), 45-64.

Reguero, M.A., Croft, D.A., Flynn, J.J., Wyss A.R., 2003. Small archaeohyracids (Typotheria, Notoungulata) from Chubut Province, Argentina, and central Chile: Implications for trans-Andean temporal correlation. Fieldiana Geology, N.S. 48, 1-17.

Eliminado: Province

Reguero, M.A., Marenssi, S., Santillana, S., 2002. Antartic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. Palaeogeography, Palaeoclimatology, Palaeoecology 179, 189-210.

Reguero, M.A., Prevosti, F.J., 2010. Rodent-like notoungulates (Typotheria) from Gran Barranca, Chubut Province, Argentina. In: Madden, R.H., Carlini, A.A., Vucetich, M.G. (Eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, 152-169.

Eliminado: Province

Reguero, M.A., Ubilla, M., Perea, D., 1998. A new species of Archaeohyracidae (Mammalia, Notoungulata) from Fray Bentos Formation (Deseadan) of Uruguay. Acta Geológica Lilloana 18, 178-179.

Reig, O.A., 1981. Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. Monographiae Naturae. Publicación del Museo de Ciencias Naturales y Tradicionales de Mar del Plata 1, 1-162.

Ribeiro, A.M., López, G.M., Bond, M., 2010. The Leontiniidae (Mammalia, Notoungulata) from the Sarmiento Formation at Gran Barranca, Chubut Province, Argentina. In: Madden, R.H., Carlini, A.A., Vucetich, M.G. (Eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia. Cambridge University Press, 170-181.

Eliminado: province

Roth, S., 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretáceo superior y Terciario inferior de la Patagonia. Revista del Museo de La Plata 11, 135-158.

Roth, S., 1927. La diferenciaci6n del sistema dentario en los ungulados, notoungulados, y primates. Revista del Museo de La Plata 30, 172-255.

Salas, R., Sánchez, J., Chacaltana, C., 2006. A new Pre-Deseadan Pyrothere (Mammalia) from northern Peru and the wear facets of molariform teeth of Pyrotheria. Journal of Vertebrate Paleontology 26, 760–769.

Salton, J.A., Szalay, F.S., 2004. The tarsal complex of Afro-Malagasy Tenrecoidea: a search for phylogenetically meaningful characters. Journal Mammalian Evolution 11, 73-104.

Sánchez-Villagra, M.R., Burnham, R.J., Campbell, D.C., Feldmann, R.M., Gaffney, E.S., Kay, R.F., Lozsán, R., Purdy, R., Thewissen, J.G., 2000. A new near-shore marine fauna and flora from the Early Neogene of Northwestern Venezuela. Journal of Paleontology 74, 957-968.

Sánchez-Villagra MR, Narita Y., Kuratani, S., 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Systematic and Biodiversity 5 (1), 1-7.

Scott, W.B., 1912. Toxodonta and Entelonychia of the Santa Cruz beds. In: Scott, W.B (Ed.), Reports of the Princeton University Expeditions to Patagonia, 1896-1899. Princeton, New Jersey, Princeton University, 6 (2-3), 111-300.

Shockey, B.J., 1997. Two new notoungulates (Family Notohippidae) from the Salla Beds of Bolivia (Deseadan: Late Oligocene): systematics and functional morphology. Journal of Vertebrate Paleontology 17 (3), 584-599.

Shockey, B.J., Anaya, F., 2004. *Pyrotherium macfaddeni*, sp. nov. (late Oligocene, Bolivia) and the pedal morphology of pyrotheres. Journal of Vertebrate Paleontology 24, 481–488.

Shockey, B.J., Flynn, J.J., 2007. Morphological Diversity in the Postcranial Skeleton of Casamayoran (?Middle to Late Eocene) Notoungulata and Foot Posture in Notoungulates. American Museum Novitates 3601, 1-26.

Sigé, B., Sempere, T., Butler, R., Marshall, L.G., Crochet, J.Y., 2004. Age and stratigraphic reassessment of the fossilbearing Laguna Umayo red mudstone unit, SE Peru, from regional stratigraphy, fossil record, and paleomagnetism. Geobios 37, 771–794.

Simpson, G.G., 1934. Provisional classification of extinct South American hoofed mammals. American Museum Novitates 750, 1-21.

Simpson, G.G., 1935a. Descriptions of the oldest known South American mammals, from the Rio Chico Formation. American Museum Novitates 793, 1-25.

Simpson, G.G., 1935b. Occurrence and relationships of Rio Chico fauna of Patagonia. American Museum Novitates 818, 1-21.

Simpson, G.G., 1948. The beginning of the Age of the Mammals in South America. Part I. Bulletin of the American Museum of Natural History 91, 1-232.

Simpson, G.G., 1967a. The Ameghino's localities for Early Cenozoic mammals in Patagonia. Bulletin of Museum of Comparative Zoology 136 (9), 63-76.

Simpson, G.G., 1967b. The beginning of the Age of the Mammal in South America. Part II. Bulletin of the American Museum of Natural History 137, 1-259.

Simpson, G.G., 1980. *Splendid Isolation. The curious history of South American Mammals*. Yale University Press, New Haven.

Simpson, G.G., Minoprio, J.L., 1949. A new adianthine litoptern and associated mammals from a deseadan faunule in Mendoza, Argentina. American Museum Novitates 1434, 1-27.

Simpson, G.G., Minoprio, J.L., Patterson, B., 1962. The mammalian fauna of the Divisadero Largo Formation. Mendoza, Argentina. Bulletin of the Museum of Comparative Zoology 127 (4), 239-293.

Soria, M.F., 1982. *Tetragonostylops apthomasi* (Price y Paula Couto, 1950): su asignación a Astrapotheria. Ameghiniana 19 (3-4), 234-238.

Soria, M.F., 1987. Estudios sobre los Astrapotheria (Mammalia) del Paleoceno y Eoceno. Parte I: descripción de *Eoastrapostylops riolorense* Soria y Powell, 1982. Ameghiniana 24 (1-2), 21-34.

Soria, M.F., 1989a. Notopterna: un nuevo orden de mamíferos ungulados Eógenos de América del Sur. Parte I. Los Amilnedwardsidae. Ameghiniana 25 (3), 245-258.

Soria, M.F., 1989b. Notopterna: un nuevo orden de mamíferos ungulados Eógenos de América del Sur. Parte II. *Notonychops powelli* gen. et sp. nov. (Notonychopidae nov.) de la Formación Río Loro (Paleoceno medio) provincia de Tucumán, Argentina. Ameghiniana 25 (3), 259-272.

Soria, M.F., 1989c. El primer Notoungulata de la Formación Río Loro (Paleoceno medio) de la provincia de Tucumán, República Argentina. Ameghiniana 26 (3-4), 145-151.

Soria, M.F., 2001. Los Proterotheriidae (Litopterna, Mammalia), sistemática, origen y filogenia. Monografías del Museo Argentino de Ciencias Naturales 1, 1-167.

Soria, M.F., Escribano, V., Abril, M., 1986. Sobre el primer Indalecidae (Mammalia) de Edad Deseadense, Cabeza Blanca, provincia del Chubut, República Argentina. III Jornadas Argentinas de Paleontología de Vertebrados. Resúmenes, 7.

Soria, M.F., Powell, J. E., 1981. Un primitivo Astrapotheria (Mammalia) y la edad de la Formación Río Loro, provincia de Tucumán, República Argentina. Ameghiniana 18 (3-4), 155-168.

Szalay, F.S., 1977. Phylogenetic relationships and a classification of eutherian mammals. In: Hecht, M.K., Goody, P.C., Hecht, B.M. (Eds.), Major Patterns in Vertebrate Evolution, Nato Advanced Study Institute, Plenum Publishing, New York, 14, 315-374.

Tabuce, R., Marivaux, L., Adaci, M., Bensalah, M., Hartengerger, J.L., Mahnboubi, M., Mébrouk, F., Tafforeau, P., Jaeger, J.J., 2007. Early tertiary mammals from North Africa reinforce the molecular Afrotheria clade. Proceding Royal Society of London 274, 1159-1166.

Tambussi, C.P., Noriega, J.I., 1998. Registro de Presbiornitidos (Aves, Anseriformes) en sedimentitas de la Formación Vaca Mahuida, La Pampa, Argentina. Asociación Paleontológica Argentina Publicación especial nº 5. Paleógeno de América del Sur y de la Península Antártica, 51-54.

Tejedor, M., Goin, F., Gelfo, J.N, López, G.M., Bond, M., Carlini, A.A., Scillato-Yané, G.J., Woodburne, M., Chornogubsky, L., Aragón, E., Reguero, M.A, Czaplewski, N., Vicon, S., Martin, G., Ciancio, M., 2009. New Early Eocene mammalian fauna from western Patagonia, Argentina American Museum Novitates 3638, 1-43.

Thewissen, J.G., Gingerich, P.D., 1987. Systematics and evolution of Probathyopsis from the late Paleocene and early Eocene of western North America. Contributions from the Museum of Paleontology, University of Michigan 27, 195-219

Tong, Y., Lucas, S. G., 1982. A review of chinese uintatheres and the origin of the Dinocerata (Mammalia, Eutheria). Proceding Third North America Paleontology Convention 2, 551-556.

Tonni, E.P., Alberdi, M.T., Prado, J.L., Bargo, M.S., Cione, A.L., 1992. Changes on mammal assemblages in the pampean region (Argentina) and their relation with the Plio-Pleistocene boundary. Palaeogeography, Palaeoclimatology, Palaoecology 95, 179-194.

Villarroel, C.A., 1987. Características y afinidades de *Etayoa* n. gen., tipo de una nueva familia de Xenungulata (Mammalia) del Paleoceno medio (?) de Colombia. Comunicaciones Paleontológicas del Museo de Historia Naturual de Montevideo 19 (1), 241-253.

Vucetich, M.G., Bond, M., 1982. Los primeros Isotemnidae (Mammalia, Notoungulata) registrados en la Formación Lumbrera (Grupo Salta), del Noroeste argentina. Ameghiniana 19 (1-2), 7-18.

Webb, S.D., 1985. Late Cenozoic mammal dispersals between the Americas. In: Stehli, F.G., Webb, S.D. (Eds.), The Great American Biotic Interchange. Plenum Press pp. 357-384.

Wyss, A.R., Flynn, J.J., Norell, M.A., Swisher, C.C.III, Novacek, M.J., McKenna, M.C., Charrier, R., 1994. Paleogene mammals from the Andes of Central Chile: A preliminary taxonomic, bioestratigraphic, and Geochronologic assessment. American Museum Novitates 3098, 1-31.

Wyss, A.R., Norell, M.A., Novacek, M.J., Flynn, J.J., 1992. New ?early Tertiary mammal localities from the Chilean Andes. Journal Vertebrate Paleontology 12, supplement to n° 3, 61A.

FIGURE CAPTIONS

FIGURE 1: Map showing the Paleocene-Eocene localities of the South American mentioned in the text. 1- Paso del Sapo; 2- Cerro Redondo; 3- Cañadón Hondo; 4- Cañadón Vaca; 5- Gran Barranca; 6- Valle Hermoso; 7- Cañadón Tourmouer; 8 - Cerro de Humo; 9- Laguna de la Bombilla; 10- Cerro Blanco; 11- Laguna del Mate; 12- Bajo de la Palangana; 13- Pan de Azúcar; 14- Las Flores; 15- Las Violetas; 16- Punta Peligro; 17- La Gran Hondonada; 18- Cañadón Blanco; 19- Tinguiririca; 20- Divisadero Largo; 21- Antofagasta de la Sierra; 22- Río Loro; 23-Tres Cruces; 24- Pampa Grande; 25- Pozuelos; 26- Cerro El Fresco; 27- Valle de Punilla; 28- Tiupampa; 29- Sao José de Itaboraí; 30- Laguna Umayo; 31- Bagua (Milagro Formation); 32- Bogotá (Bogotá Formation); 33- Unnamed locality were of Gualanday Group outcrop; 34- Seymour Island.

FIGURE 2: Cluster análisis of South American and Antarctic Paleocene-Eocene terrestrial mammal-bearing localities discussed in the text.

APPENDIX 1

Data matriz of 164 taxa of SANU and 27 localities or levels in a specific locality in South America and Antarctica.