Late Quaternary Megafaunal Extinctions in South America: Chronology, environmental changes and human impacts at regional scales.

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by

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Abstract

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By the end of the Pleistocene the world lost most of its species of large mammals in what is known as the Late Quaternary Extinction event. The debate about the possible causes of extinction revolves around the impacts caused by modern humans migrating around the world, the climate changes associated with the glacial-interglacial transition happening at the time of the extinction and combinations of both. South America was one of the most severely impacted continents losing over eighty percent of all its species of mammals with an average body weight exceeding forty four kilograms. In this continent, human arrival and late glacial climate changes were not far separated in time and previous analyses have shown interesting regional differences in the timing and pattern of extinction inside the continent.

A critical step to understand the extinction event at regional and continental scales is the development of robust radiocarbon-based chronologies of megafaunal presence and extinction which can be compared to the timing of arrival of humans and of environmental changes. This dissertation addresses the Late Quaternary Extinction event debate in South America by developing analyses of the extinction at regional scales, and improving the chronology of extinction for some regions of the continent by radiocarbon dating bone specimens of extinct megafauna following high standard procedures for radiocarbon dating bone.

Chapter one consists of a bestiary of the Pleistocene megafauna of South America. It describes each species and genera of megafauna giving details about their geographic distribution and general paleoecology. A final synthesis of the information shows regional differences in megafaunal diversity that can be explained by sampling bias. While regional differences in diversity persist in time when the Late Pleistocene is compared to the present, regions are today more similar than in the past, which suggests that a considerable amount of regional megafaunal endemism was lost during the Late Quaternary Extinction event.

Chapter two is a regional scale analysis of the megafaunal extinction in Southern Patagonia. Using published information it was possible to build a robust chronology of magefaunal extinction and human arrival into this region. When comparing these chronologies with the timing of major environmental changes it seems that a combination of human impacts and vegetation changes were behind most of the megafaunal extinctions.

Chapter three describes the process of radiocarbon dating bone specimens of extinct megafauna following high-standard procedures of bone treatment. It was possible to produce fifty four radiocarbon dates from which twenty seven are reported in this chapter. The new data improves the chronology of extinction for some areas, particularly for the Central Andes and for Southern Chile. These new chronologies of extinction showed that in the Central Andes extinct megafauna disappears at the time of human arrival while the megafauna present in Southern Chile coexisted with humans for thousands of years. In the second case the megafaunal extinction happens at a time of major environmental changes. These differences highlight the need of developing regional analyses, rather than continental-scale analyses, in order to have a more comprehensive understanding of the extinction event in South America.

“It is impossible to reflect on the changed state for the American continent without the deepest astonishment. Formerly it must have swarmed with great monsters: now we find mere pigmies, compared with the antecedent, allied races.”

Charles Darwin in the Voyage of the Beagle (1839)

Introduction

About 50 thousand years ago the world was inhabited by a great variety of big to very big forms of mammals that today do not exist anymore. This so called megafauna (term used to refer to terrestrial mammals weighing over 44 kg of body mass), was present in diverse forms in every continent of the earth. In Australia there were giant wombats of the size of a large pig and the giant kangaroo *Procoptodon* which weighed over 200 kg. Eurassia was inhabited by wolly mammoths, wholly rhinoceros and the giant Irish elk *Megaloceros* with antlers spanning over 3 meters in length. In North America saber tooth cats, short-faced bears and mastodonts were common. South Americas was characterized by giant gorund sloths, giant armadillo-like glyptodonts and by macrauchenias which were big camel-like ungulates with long necks and small trunks in their rostrum. By ten thousand years ago all the forms mentioned, along with many others, were gone from the face of the earth. This extinction phenomenon is known as the Late Quaternary Extinction event (LQE) (Martin and Klein 1984) during which over 90 genera of large mammals became extinct in the world. The LQE hit most parts of the world with the exception of Africa were a great diversity of large mammals still persists. A delayed extinction was observed in high latitude islands were large-sized mammals disappeared close to the mid-Holocene.

The magnitude and timing of the LQE differs among continents (Koch and Barnosky 2006), happening at different times during the last 50,000 years before present (yr BP). For more than five decades now, the discussion about the possible causes of extinction has revolved around the human impacts caused by modern humans moving out of Africa, climate changes associated with the glacial-interglacial transition or combinations of both (Martin and Steadman 1999).

South America was one of the most severely impacted continents, losing around 82% (53 genera) of all its large mammal species with average body mass exceeding 44 kg (Brook and Barnosky 2012). In South America, human arrival and late glacial climate changes occurred within a relatively short span of time (between 18-10 ky BP at a continental level), although marked regional differences are present in both the timing and direction of climate change, as well as in the timing of human arrival. These regional differences provide opportunities to test possible synergistic effects of these changes in driving the LQE (Barnosky and Lindsey 2010) and highlight the importance to realize detailed regional scale analyses in order to understand how the possible drivers of extinction operated in different circumstances.

A critical step to pursue any type of analysis of the LQE at regional or continental scales is the development of strong chronologies of extinction. With the advances and improvements of radiocarbon dating techniques (^{14}C dating), that started in 1940 with Libby's work, the construction of chronologies of extinction documenting the LQE have been developed for many places including Europe (i.e. Stuart et al., 2004, Stuart and Lister 2011, Stuart and Lister 2012), North America (i.e. Guthrie 2006, Faith and Surovell 2009) and South America (Borrero 2008, Borrero 2009, Barnosky and Lindsey 2010, Prado et al. 2016). Nevertheless more radiocarbon dates are always needed to make robust inferences, to use statistic tools in investigating extinction times and, to fill gaps in the information for some particular regions or particular taxa that have been under studied.

In this context, the present dissertation aims to accomplish the two following main objectives:

Objective 1: Understand the state of the knowledge about the Late Pleistocene diversity of Megafauna in South America and its implication with regards to the LQE in that continent.

Objective 2: To develop detailed regional analyses of the chronology of extinction of megafauna in relation to climate changes, environmental changes and human arrival.

Objective 3: To improve the chronology of extinction in South America by radiocarbon dating bone specimens of megafauna following high-standard procedures for the pre-treatment of bone samples for radiocarbon dating.

In order to fulfill the main objectives stated above, three chapters were developed:

Chapter 1: A Megafaunal Bestiary for the Pleistocene of South America

This chapter is an introduction to the Late Quaternary megafauna in South America. It consists of a review of the genera and species of the Pleistocene of South America according to the latest systematic revisions and includes notes about their paleoecology when available, as well as a brief summary of their geographic and stratigraphic distribution. The main goal of this chapter is to know how much is understood about the extinct megafauna in South America, what areas of the continent are well represented in the fossil record and from what areas we can extract meaningful information about the LQE in this continent.

Chapter 2: Extinction chronology of megafauna in relation to human arrival, climate change and environmental changes at regional scales: The case of Southern Patagonia

This work consisted of the detailed analyses of the megafaunal extinction in a particular region of Southern Patagonia. This area was chosen as the starting point to analyze the LQE in South America giving its rich record of radiocarbon dates on extinct megafauna, human arrival and complete late Pleistocene-early Holocene records of climate and vegetation changes.

Chapter 3: Radiocarbon dating of extinct South American Megafauna

This chapter summarizes the work done in processing bone samples of South American megafauna in order to get high-quality radiocarbon dates and improve the chronology of extinction for some areas of the continent in order to make similar analyses to the ones made in chapter 2.

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Chapter 1: A Megafaunal Bestiary for the Pleistocene of South America

Introduction

Much new research has recently become available to shed light on many aspects of the diversity of large-bodied mammals, so-called megamammals, which inhabited South America during the Pleistocene (last 2.6 millions of years). The recent work ranges from systematic to, evolutionary relationships of different groups, to the paleoecology and function of various organisms. These advancements make it possible to synthesize, based on increasingly robust data, the diversity of Late Quaternary mammals that lived on the continent. While some recent publications detail information on megamammals inhabiting different regions of South America (i.e. Labarca 2015), no up to date synthesis portrays key information about all megamammals of the continent. The most recent compilations of South American megafauna, while full of valuable information, have focused primarily on general aspects at the genus or family level, and take into account the more conspicuous taxa only (Fariña et al., 2013).

In this chapter I review the Pleistocene diversity of mega-mammals in South America at the species level, with a special emphasis on the taxa that inhabited the continent during the late Pleistocene and during the Pleistocene-Holocene transition (around 11.8 ka BP Fig. 1i). I reviewed the literature published through the first half of 2016 and compiled relevant information about of all megamammal species in South America (Fig. 2i) following the latest taxonomic updates for each group. For each genus and species, I mapped the reported localities, and summarized the paleoecology and the stratigraphic and geographic distribution. I also provided some brief notes on the taxonomic status when necessary, although reviewing details of taxonomy is beyond the scope of this report. When possible, I followed the most recent taxonomic assignments, with more detailed taxonomic discussions restricted to the more complex or controversial groups.

As historically defined megafauna are often considered to be animals weighing over ~44 kg (~100lb) (Martin and Klein 1985, Owen-Smith 1988). However, in this chapter I used a less stringent definition and consider all mammals weighing over ~40 kg as megafauna, plus some extinct taxa for which estimated body weight < 40 kg, if they are the biggest representatives of their particular ecological or taxonomic groups. Extant megafauna taxa that were also in South America during the Pleistocene are included as well.

Stratigraphic Terminology in South America

The Pleistocene Epoch spans the time period from 2.58- 0.00117 millions of years ago (Ma yr. BP) (Cohen et al., 2015), and is followed by the Holocene. The Holocene is formally recognized as persisting until today, although the hypothesis that the Anthropocene should be formally defined as beginning near the mid-20th century is currently under study (Waters et al., 2016).

Mammalian paleontology provides an alternative stratigraphic scale based on biostratigraphy, essentially the faunal successions observed in the fossil record of a particular region. These Land Mammal Ages are defined for each continent, with each age defined by the presence and/or absence of particular taxa (Flynn and Swisher 1995). Besides recording continental-level faunal turnovers, Land Mammal Ages can be essential in assigning ages to deposits when mammal fossils are present in the absence of materials amenable to radiometric dating.

Six different South American Land Mammals Ages (SALMAs) are recognized for the Pleistocene through Holocene of South America (Figure 1i). These biochronologic units can be correlated to the absolute time scale presented in the International Chronostratigraphic Chart in Figure 1i (Cione et al., 2015, Cohen et al., 2013). Throughout this chapter I primarily use the terms from the chronostratigraphic chart (i.e. Late Pleistocene, Pleistocene and Holocene); however, the SALMAs are are also mentioned in some cases, along with the radiometric-age time estimates.

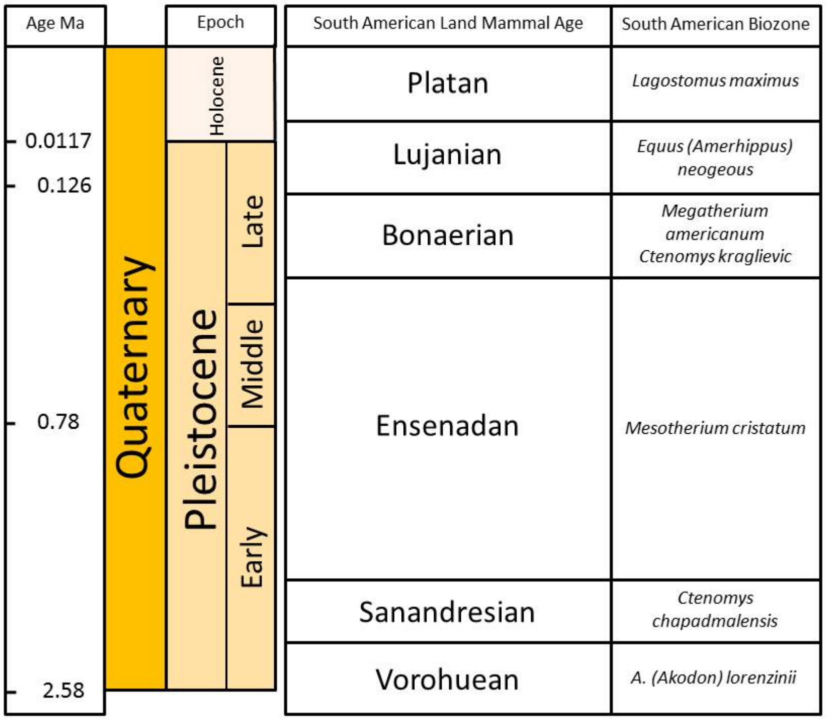

Figure 1i: Correlation of Pleistocene SALMAs with geological epochs and periods (Cione et al.,2015).

Figure 2i: Political divisions of South America (extracted from Google Earth 2016).

The South American Megafaunal Bestiary

The bestiary is organized taxonomically and hierarchically, by order, family, in some cases subfamily, genera and species. I summarize a parallel range of information for each species when possible, but in some cases no information other than the original description of a type specimen was found.

For each species and/or genus, I attempted to include the following subsections.

- **General Taxonomic Characters**
- **Body Size**
- **Diet**
- **General Ecology and/or Locomotion**
- **Confidence in Species Assignment**
- **Geographic and stratigraphic distribution**

If published pertaining to one of these subsections was unavailable for a given taxon, I did not include that subsection for the taxon.

Maps showing the geographic and stratigraphic distribution of each genus and species are included for each of the following time periods:

Pleistocene: includes all the localities dated to the Early Pleistocene, Middle Pleistocene and general Pleistocene. The SALMAs included are Sanandresian and Ensenadan (Figure 1i), shown as yellow/orange symbols on the maps.

Late Pleistocene: includes all the localities recorded as Late Pleistocene in age, SALMAs Bonaerian and Lujánian (Figure 1i), shown as blue symbols on the maps.

Holocene: includes all the localites dated as Holocene or Platan SALMA (Figure 1i), shown as green figures in the maps.

In the captions of the maps presented for the different mammalian genera the name of the sites displayed are listed and related to the country where they are located. Here, country names abbreviations are used according to the following: Argentina: AR, Bolivia: BO, Chile: CL, Colombia: CO, Ecuador: EC, Paraguay: PY, Peru: PE, Uruguay: UY, Venezuela: VE.
The distribution of the different mammalian genera displayed in the maps was taken from the Paleobiology Database (PBDB https://paleobiodb.org/#/) and complemented with geographic distribution information from the literature up to 2016.

Order ARTIODACTYLA Owen, 1848
(Even-toed Ungulates)

Artiodactyls (Table 1) include herbivorous forms such as camels, deer and peccaries (Eisenberg and Redford 1992). The order originated in the northern hemisphere, and members of it reached South America as part of the Great American Biotic Interchange (GABI) once the PanamaIsthmus was complete enough to allow fauna to migrate north and south (Woodburne 2010). One of the main characteristics of artiodactyls is that the first, second and fifth digits in the feet are reduced or lost and that the body weight is borne equally by the third and fourth toe.

The diet of modern artiodactyls varies greatly. They can forage on falling fruits and nuts, leaves and grasses. The check teeth can be high crowned in the taxa that mainly graze (Camelids) or low crowned in the more omnivorous forms that feed on fruits and softer leaves (peccaries, deer).

Table 1: South American Megafaunal Artiodactyla. † = extinct.

Family CAMELIDAE Gray, 1821
Tribe LAMINI Webb, 1965
Genus *EULAMAOPS* Ameghino, 1889 †
Eulamaops parallelus (Ameghino 1884) †
Genus *HEMIAUCHENIA* Gervais & Ameghino, 1880 †
Hemiauchenia paradoxa (Gervais & Ameghino, 1880) †
Genus *LAMA* Cuvier, 1800
Lama guanicoe (Muller 1776) *Lama glama* (Linnaeus 1758) (Llamas, domesticated form) *Lama castelnaudi* (Gervais 1855) †
Genus *PALAEOLAMA* Gervais, 1867 †
Paleolama weddelli (Gervais 1855) † *Paleolama major* (Liais 1872) † *Palaeolama hoffstetteri* (Guerin and Faure 1999) †
Genus *VICUGNA* Miller, 1924
Vicugna vicugna (Molina 1782) *Vicugna pacos* (Linnaeus 1758)(Alpaca, domesticated form) *Vicugna provicugna* (Boule and Thevenin 1920) †
Family CERVIDAE Goldfuss, 1820
Genus *AGALMACEROS* Hoffstetter, 1952 †
Agalmaceros blicki (Frick, 1937) †
Genus *ANTIFER* Ameghino, 1889 †
Antifer ensenadensis (Ameghino 1888) † *Antifer ultra* (Ameghino 1888) †

Genus *BLASTOCERUS* Illiger, 1815
Blastocerus dichotomus (Illiger 1815)
Genus *CHARITOCEROS* Hoffstetter, 1963 †
Charitoceros tarijensis (Hoffstetter 1963) †
Genus *EPIEURYCERUS* Ameghino, 1889 †
Epieurycerus truncus (Ameghino, 1889) † Subsp. *Epieurycerus truncus truncus* (Bagnalasta 1980) † Subsp. *Epieurycerus truncus scillatoi* (Bagnalasta 1980) † *Epieurycerus proximus* (Castellanos 1945) †
Genus *HIPPOCAMELUS* Leuckart, 1816
Hippocamelus antisensis (d'Orbigny, 1834) *Hippocamelus bisulcus* (Molina 1782) Genus *MORENOELAPHUS* (MORENELAPHUS) Carette, 1922 †
Morenoelaphus brachyceros (Gervais and Ameghino 1880) † *Morenoelaphus Lujánensis* (Ameghino 1888) †
Genus ODOCOILEUS Rafinesque 1832
Odocoileus virginatus (Zimmermann, 1780) *Odocoileus* salinae (Frick 1937) †
Genus *PARACEROS* Amgehino, 1888†
Paraceros fragilis (Amgehino 1888) †
Family TAYASSUIDAE Palmer, 1897
Genus *CATAGONUS* Ameghino, 1904
Catagonus metropolitanus (Ameghino 1904) † *Catagonus bonaerensis* (Ameghino 1904) † *Catagonus carlesi* (Rusconi 1930) † *Catagonus stenocephalus* (Lund in Reinhardt 1880) † *Catagonus wagneri* (Rusconi 1930)
Genus *PLATYGONUS* Le Conte, 1848 †
Platygonus cinctus (Ameghino 1886) †

1.1 Family CAMELIDAE Gray, 1821

These artiodactyls are characterized by selenodont dentition and by the retention of the upper incisors and canines (Eisenberg and Redford 1992). Some of the main characteristics observed in extant taxa are ruminant digestion with three-chambered stomachs, toes bearing nails instead of hooves and the absence of horn like structures on their heads. All South American camels belong to the tribe Lamini. According to the most recent anatomical and systematic revision of the tribe based on cranial and postcranial characters (Scherer 2009; 2013), 5 genera are valid for the Pleistocene of South America, with a total of 11 species, two of which were domesticated in prehistoric times around 6,000 years BP (Wheeler 1995). The valid genera (and species) are: *Palaeolama* (*P. weddellii*, *P. hoffstetteri*, *P. major*), *Hemiauchenia* (*H. paradoxa*), *Eulamaops* (*E. parallelus*), *Lama* (*L. guanicoe*, *L. glama*, *L. castelnaudi*) and *Vicugna* (*V. vicugna*, *V. provicugna*, *V. pacos*). I exclude the domestic species from further descriptions.

Genus *EULAMAOPS* Ameghino, 1889 †
(Map 1.1.1: Geographic distribution)

Eulamaops paralellus (Ameghino 1884) †

General Taxonomic Characters: *E. paralellus* is based fragmentary material from the skull which presents a palate morphology not found in any other member of the Lamini. Teeth are very similar to the extant *Lama guanicoe* (Scherer 2009 and references there).
Body Size: Body mass has been estimated around 150 kg (Fariña et al. 2013).
Confidence in Species Assignment: Valid according to Scherer (2009).
Geographic and stratigraphic distribution: Late Pleistocene of the Pampean region of Argentina (Luján, Buenos Aires province).

Map 1.1.1: Geographic distribution of genus *Eulamaops*. Referecences: Tonni and Prado 1985, Scherer 2009: Luján (AR).

Genus *HEMIAUCHENIA* Gervais & Ameghino, 1880 †
(Map 1.1.2: Geographic distribution)

According to Scherer (2009) there is only one valid species in South America for this genus: *Hemiauchenia paradoxa*.

Hemiauchenia paradoxa (Gervais & Ameghino, 1880: 585) †

General Taxonomic Characters: Elongated rostrum, elongated and graceful limbs, metapodials (tarsal and carpal bones) are long and epipodials (radio-ulna and tibia) are short when compared to *Palaeolama* (Scherer 2009), characteristics that have been associated to a cursorial habit in open environments (Webb and Stehli 1995).
Body Size: Large camelid, with a body mass estimated around 300 kg (Fariña et al., 2013).
Diet: Stable Isotope analyses on *Hemiauchenia* remains from Florida (USA) indicate a mixed diet with preference for trees and shrubs (Feranec 2003).
General Ecology and/or Locomotion: Scherer (2009) mentions that *Hemiauchenia* possibly lived in open environments with dominance of grasslands since it is characterized by strong incisors and more hypsodont molars, along with a thick layer of external cementum, which altogether indicates a mixed or grazing diet.
Confidence in Species Assignment: Valid according to Scherer (2009).
Comments: Scherer (2009) reports that *H. paradoxa* has a sympatric distribution with *Palaeolama weddelli* in sites from southern Bolivia, which challenges the view of *H. paradoxa* as a species adapted to open grasslands since *P. weddelli* shows limb proportion adapted to rocky environments with irregular ground. However, if these two species lived sympatrically, they could well have occupied different habitats consistent with their respective morphology.
Geographic and stratigraphic distribution: *Hemiauchenia* and *H. paradoxa* are found from the late Pliocene to the Late Pleistocene of Argentina (Buenos Aires, Entre Rios, Santa Fe and Córdoba provinces); Late Pleistocene of northern Uruguay (Artigas and Salto districts), southern Bolivia (Tarija and Chuquisaca districts), southern and northern Brazil (Amapá, Ceará and Rio Grande do Sul states) and southern Chile (Los Lagos region).

Map 1.1.2: Geographic distribution of the genus *Hemiauchenia*. References: Paula Couto 1980: Joao Cativo site 1 and 2 (BR), Curimatas (BR); Boule and Thevenin 1920: Tarija (BO); Zurita et al., 2009a: Río Bermejo (AR); Scherer et al., 2007: Hermenegildo beach (BR), Uruguaiana(BR), Salatiel II (BR); Alvargenga and Jones 2010: Casil Quarry (UY); Tonni and Prado 1985: Luján (AR); Zurita et al., 2007: San Francisco (AR); Deschamps and Borromei 1992: Bajo San José (AR); Scherer 2009: Olivos-Río de la Plata (AR), Río de la Plata (AR), Miramar (AR), Anchorena-Ciudad de Buenos Aires (AR), Playa Santa Elena (AR), Tandil (AR), Río Paraná (AR), Río Carcaraña (AR), Río Quequen Salado (AR), Arroyo Tapalque (AR), Monte Hermoso - Playa del Barco (AR), Río Arrecifes (AR), Ñuapua (BO), Arroio Touro Passo (BR), Itaqui (BR), Sanga da Cruz (BR), Arroyo Yucutujá (BR), Colonia de Artigas (UY), Río Quarai (UY), Localidad Pintado (UY), Río Arapey Grande (UY) Arroyo Sopas (UY), Paso Muñoz (UY), Río Quarai (UY), Piedra Pintada (UY), Arroyo Catalán Grande (UY), Urunbeba (UY), Arroyo Pelado (UY).

Genus *PALAEOLAMA* Gervais, 1867 †

(Map 1.1.3: Geographic distribution)

There are three species for this genus reported in South America: *Paleolama wedelli*, *Paleolama major* and *Palaeolama hoffstetteri* (Guerin and Faure 1999). The validity of *P. hoffstetteri* has been questioned (Scherer 2009).

General Taxonomic Characters: Extremities are short and robust; the rostrum is elongated (Scherer 2009). In general, the post cranial elements of *P. weddelli* are slightly smaller and more robust than *P. major* (Scherer 2009).
Body Size: Camelid of large size with a body mass estimated between 200-300 kg (Fariña et al. 2013).
Diet: The dental characters suggest a primarily browsing diet (Scherer 2009). Stable isotope analyses from one *Palaeolama* specimen from Arroyo Seco 2 in Argentina indicates a diet based on C3 plants (Domingo et al., 2012). Similarly, studies of plant composition in coprolites found in Bahia State in Brazil show a diet based on shrubs (C3 plants) (de Melo França et al., 2015).
General Ecology and/or Locomotion: It presents short and robust metapodials along with elongated epipodials (tibia and radio-ulna), which is interpreted as and adaptation to live in rough rocky environments and/or to escape from predators in forested environments (Scherer 2009).
Confidence in Species Assignment: Valid genus according to Scherer (2009).
Geographic and stratigraphic distribution: The genus *Palaeolama* is known in South America from the Late Pliocene to Early Pleistocene of coastal Peru; Middle to Late Pleistocene of southern Bolivia; Late Pleistocene of Ecuadorian and Peruvian Andes, southern coast of Ecuador and Northern Peru, Late Pleistocene of the Pampean region of Argentina and Uruguay, north and northeast Brazil, central-southern Chile and northern Venezuela.

Palaeolama major (Liais 1872) †

General Taxonomic Characters: Compared to *P. weddelli* this species seems to be bigger and more graceful. The gracility index calculated for carpal bones is between 0.15 and 0.18 for this species (Scherer 2009) indicating robust podials but still more gracile than in P. weddelli (Gracility index: 0.17-0.20).
Body Size: It is estimated around 250 kg (Fariña et al., 2013).
Confidence in Species Assignment: Valid according to Scherer (2009).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Amazonas, Piauí, Rio Grande do Norte, Bahia and Rio Grande do Sul, Mato Grosso do Sul states), Argentina (Buenos Aires province) and Uruguay (Artigas district), Ecuador (Santa Elena province), Peru (Piura district) and northern Venezuela (Falcon state).

Palaeolama weddelli (Gervais 1855) †

General Taxonomic Characters: It presents a higher gracility index (0.17-0.20) for its metapodials compared to other species (Scherer 2009) which possibly indicates a generaly robust built of the limbs.
Diet: According to stable isotope analyses it had a browsing diet (McFadden and Shockey 1997).
General Ecology and/or Locomotion: The sturdy character of its limbs indicates adaptation to rocky and mountainous environments (Scherer 2009).
Confidence in Species Assignment: Valid according to Scherer (2009).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of southern Bolivia (Tarija and Chuquisaca district), Late Pleistocene of the Ecuadorian Andes (Chimborazo and Pichincha districts).

Palaeolama hoffstetteri (Guerin and Faure 1999) †

General Taxonomic Characters: Large camelid, robust limb bones, proportions of tibia, astragalus and metacarpal bones are similar to those of *P. weddelli* but larger (Scherer 2009).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Dubious validity according to Scherer (2009).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of the Andean region of Bolivia (Tarija district).

Map 1.1.3: Geographic distribution of genus *Palaeolama*. Referecences: Czaplewski and Rincón 2005: Mene de Inciarte (VE); Boule and Thevenin 1920: Tarija (BO); Churcher 1959, Pujos and Salas 2004: La Brea Talara (PE); Coltorti et al., 2007: Montesur (BO); Hoffstetter 1952: La Carolina (EC), Punin-Chalan (EC), Quebrada Guaslan (EC), Calderon (EC), Río Chiche (EC); Hoffstetter 1968, Marshall and Sempere 1991: Ñuapua 1 and Ñuapua 2 (BO); Salles and Cartelle 2006: Japones Cave (BR); Hoffstetter 1978: General Bruguer/Riacho Negro (PY); Ubilla 1985: Piedra Pintada – Sopas (UY); Ubilla and Alberdi 1990: Pintado (UY); Lumley et al., 1987: Toca da Esperanca (BR); Garrincho Guerin 1991: Toca da Janela da Barra do Antoniao (BR); Porpino and Santos 2004: Lajedo de Soledade (BR); Reig 1957: Arroyo Loberia (AR); Salas et al., 2003: Site 596 (PE); Nuñez 1983: Quereo I (CL); Tonni 1970: Punta Hermengo (AR); Scherer 2009: Laguna Chascomus (AR), Luján (AR), Quequen Salado (AR), Río Juruá (BR), Toca dos Ossos (BR), Gruta dos Brejões (BR), Toca do Serrote do Artur (BR), Toca do Serrote das Moendas (BR), Toca da Janela da Barra do Antonião (BR), Toca De Cima dos Pilão (BR), Lagoa São Vitor (BR), Arroyo Valentines (AR), San Pedro-Tarija (BO), Santa Ana-Tarija (BO), Armados-Tarija (BO), Pueblo Viejo-Tarija (BO), Tolomosa-Tarija (BO), Quebrada Colorada (EC), Mañatul – Punin (EC), Quebrada Grande - Punin (EC) , Quebrada El Colegio - Punin (EC), Quebrada Bamante – Punin (EC)

Genus *LAMA* Cuvier, 1800

(Map 1.1.4: Geographic distribution)

This is an intermediate size member of the lamini tribe, with a body size between *Hemiauchenia*/*Paleolama* and *Vicugna*. Three species belong to this genus. One of them, *Lama glama*, is the domestic Llama (not described in this work). Some species previously classified under this genus (*Lama angustimaxilla*, *Lama owenii* and *Lama gracilis*) have been recently classified as belonging to other groups (Scherer 2009). In this new scenario *L. angustimaxilla* and *L. owenii* would be junior synonyms of *Palaeolama major* and *Hemiauchenia paradoxa* respectively, while *L. gracilis* is considered a junior synonym of *V. vicugna*.

Geographic and stratigraphic distribution of the genus: Late Pliocene to Late Pleistocene of the Pampean region of Argentina. Middle (?) to Late Pleistocene of the Bolivian Andes; Late Pleistocene of the Mesopotamic region of Argentina, southern and northeastern Brazil, northern Uruguay; Late Pleistocene, Holocene and present in Chile, Perú, Bolivia and northwestern Argentina.

Lama castelnaudi (Gervais, 1855) †

General Taxonomic Characters: Has elongated and graceful limbs (Scherer 2013). The radio-ulna and the metapodials are more elongated compared to *Lama guanicoe* (Scherer 2009).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid according to Scherer (2009).
Geographic and stratigraphic range: Middle to Late Pleistocene of southern Bolivia (Tarija district).

Lama guanicoe (Müller, 1776)
(Fig. 1.1.1)

General Taxonomic Characters: This is the biggest wild camelid in South America at present. It has a relatively short rorstrum and gracile limbs but more robust than the extant Vicugna.
Body Size: The measured body size in guanacos ranges between 121-118 kg (Redford and Eisenberg 1992).
Diet: Guanacos are intermediate selective foragers as they can browse and graze depending on the availability of different food sources (Raedeke and Simonetti 1988; Fraser 1998; Puig et al., 1997; Puig et al., 2001).
General Ecology and/or Locomotion: Guanacos can live in cold and warm grasslands and shrublands from sea level to 4,000 masl (Eisenberg and Redford 1992). They can survive long periods without drinking. In some habitats family groups exhibit seasonal migrations (Redford and Eisenberg 1992). The range of guanacos has been reduced due to habitat destruction, hunting and climate change. Guanacos are today common only in the Southern tip of the continent. Females usually have a single young per breeding season after a gestation of 11 months. The lactation period lasts between 11 and 15 months.
Confidence in Species Assignment: Valid extant species according to Marín et al., (*2013*).

Geographic and stratigraphic distribution: Historically, guanacos were found from southern Colombia to the southern tip of Chile and all throughout Argentina. Today they are found from Southern Perú along the Andean zone of Chile and northern Argentina, and all throughout the Argentinian and Chilean Patagonia, living even in Tierra del Fuego and Navarino Islands. The species is known from Ensenadan (Middle Pleistocene) of Argentina (Buenos Aires province) and from the Late Pleistocene of northeastern Brazil (Piauí and Bahía states), Argentina (Buenos Aires, Santa Fe, Coerrientes and Córdoba provinces), southern Peru and southern Patagonia

Map 1.1.4: Geographic distribution of genus *Lama*. References: Scherer 2009: Punta Hermengo (AR), Las Grutas Necochea (AR), Playa Santa Elena (AR), Camet Norte (AR), Chapadmalal (AR), Olivos (AR), Anchorena-Río de la Plata (AR), Arroyo Tapalque (AR), Río Quequen Salado-Paso del Medano (AR), Los Quirquinchos (AR), Miramar (AR), Tandil (AR), Río Salado (AR) , Cordoba (AR), La Plata (AR), Toca da Janela da Barra do Antonião (BR), Toca do Garrincho (BR), Olivera (AR), Luján (AR), Río Carcaraña-Cerca del Puente Carretero (AR), Playa del Barco (AR) , Loberia (AR), Arrecifes (AR), Arroio Touro Passo (BR), BalneáRío Hermenegildo (BR), Río Arapey Grande (UY), Río

Quarai (UY), Río Quarai - Localidad Paso de Leon (UY), Río Arapey Grande - Paso de Las Cadenas (UY), Arroyo Sopas Localidad Pipo (UY), Arroyo Sopas - Paso Muñoz (UY) , San Pedro 1 (BO), Pueblo Viejo (BO), Armados (BO), San Blas (BO), Tolomosa (BO), Huaico (BO), San Pedro 2 (BO), Ñuapua (BO), Cochabamba Sacaba (BO), Tarija (BO); Alberdi and Menegaz 1987: Los Toldos (CL), Cueva Fell (CL), Cerro Sota (CL), Pali Aike (CL), Cueva del Milodon (CL), Cueva de las Buitreras (CL) ; Mazzanti and Quintana 1997: Quequen Salado-Indio Rico (AR); Alberdi and Mengegaz 1989: Cueva Tixi (AR); Deschamps and Tonni 1992: Garcia del Río (AR), Bajo San José (AR), Puesto La Florida (AR) (Deschamps 2005); Arroyo Nepostá ; Aramayo 1985: Monte Hermoso (AR); Bargo et al., 1986: Arroyo Tapalque (AR); Prado et al., 1987: Paso Otero (AR); Prevosti et al., 2003: Cueva de los Chingues (CL); Rozzi et al., 2000: Piedra Museo (AR); Politis and Selemme 1980: La Moderna (AR); Reig 1957: Arroyo Loberia (AR); Tonni et al., 1987: Centinela del Mar (AR); Nuñez et al., 1983: Quereo (CL); Tonni and Prado 1985: Luján (AR); Lopez et al., 2010: Ojo Opache (CL); Fernandez et al., 1991: Barro Negro Stratum (AR); Boule and Thevenin 1920: Tarija (BO); Marshall and Sempere 1991: Upper Quebrada Tijascka (BO); Coltorti and Abbazzi 2007: Montesur (BO), Río Rujero (BO); Pujos and Salas 2004: Ayacucho Valley (PE), Huargo (PE); Cartelle and Hartwig 1996: Toca da Boa Vista (BR); Paula Couto 1980: Curimatas (BR), Joao Cativo-Site (BR).

Figure 1.1.1: *Lama guanicoe*: extant guanaco, Pali Aike National Park, Magallanes Region, Chile. Photo by N. Villavicencio.

Genus *VICUGNA* Miller, 1924

(Map 1.1.5: Geographic distribution)

Smallest of known lamini. It is represented by individuals with shorter rostrum compared to the other lamini. Two species are recognized for this genus: *Vicugna vicugna* and *Vicugna provicugna* (Scherer 2009).

Vicugna provicugna (Boule and Thevenin 1920) †

General Taxonomic Characters: *V. provicugna* differs from *Vicugna vicugna* in having more elongated metapodials and radioulna (Scherer 2009).
Body Size: It posses a body size larger than the extant *V. vicugna* and smaller than the extant *L. guanicoe.*
Diet: According to analyses of the degree of hypsodonty and of stable isotopes in this species a diet based on grasses and C4 plants can be inferred (MacFadden and Shockey 1997).
Confidence in Species Assignment: Valid species according to Scherer (2009).
Geographic and stratigraphic distribution: Middle (?) to Late Pleistocene southern Bolivia (Tarija district) and Late Pleistocene of northern Chile (Antofagasta region).

Vicugna vicugna (Molina, 1782)

General Taxonomic Characters: *V. vicugna*, commonly known as vicuña, has lower incisors with open roots; they are the only extant ungulate that presents continuously growing incisors. They are similar to guanacos but smaller in size (Redford and Eisenberg 1999).
Body Size: Body size of *V. vicugna* is between 45-55 kg (Redford and Eisenberg 1999).
Diet: Vicuñas are grazers and their continuously growing incisors may be an adaptation to crop small forbs and perennial grasses (Redford and Eisenberg 1999).
General Ecology and/or Locomotion: Vicuñas inhabit open areas, grasslands and bogs. They do not migrate as guanacos and defend permanent feeding territories. Females are seasonal breeders, only one young is born per pregnancy and lactation lasts between 6 to 8 months (Redford and Eisenberg 1999).
Confidence in Species Assignment: Valid extant species according to Miller (1924).
Geographic and stratigraphic distribution: Vicuñas are found only in the Andean altiplano over 3,500 masl, from southern Peru to Bolivia, northern Chile and northwestern Argentina (Redford and Eisenberg 1999). It is also fund in Late Pleistocene-Early Holocene of Argentina (Buenos Aires and Santa Cruz provinces), Uruguay (Artigas, Salto, and Colonia districts), Southern Brazil (Rio Grande do Sul state) and Chile (Antofagasta and Magallanes regions).

Map 1.1.5: Geographic distribution genus *Vicugna*. References: Marshall and Sempere 1991: Tarija (BO); Latorre 1998; Weinstock et al., 2009: Tres Arroyos (CL), Ultima Esperanza (CL), Piedra Museo (AR); Lopez et al., 2010: Ojo Opache (CL); Scherer 2009: Olivera (AR), Laguna Vitel (AR), Fontezuelas (AR), Paso Otero (AR), Centinela del Mar (AR), Arroyo Tapalque (AR), Río Arrecifes (AR), Las Flores (AR), Río Arrecifes (AR), Mar del Sur (AR), Playa Santa Elena (AR), Arroyo La Tapera (AR), La Plata (AR), Provincia de Buenos Aires (AR), Luján (AR), Río Salado (AR), Olivos (AR), Laguna Chascomus (AR), Río Quequen Grandes (AR), Laguna Chischis (AR), Arroio Touro Passo (BR), Balneario Hermenegildo (BR) , Río Arapey Grande (UY), Río Quarai - Piedra Pintada (UY), Arroyo Sopas (UY), Arroyo Arerunguá (UY), Arroyo Sopas - La Trocaza (UY), Arroyo Arapey Chico- Puente Buey Negro (UY), Arroyo Cañas (UY), Arroyo Sopas - Paso Muñoz (UY), Tarija (BO).

1.2 Family CERVIDAE Goldfuss, 1820

Living Cervidae are characterized by males possessing antlers, which are usually grown and lost annually. They lack upper incisors. Extant Cervidae are considered true ruminants, which after feeding eructate and re-masticate the content of the rumen cavity. Cervids possess a four chambered stomach and generally are considered browsers.
Seven extinct Pleistocene genera are recognized, plus six more extant genera, some of which have extinct species. The identification of the members of this family in the fossil record is usually based in the size and morphology of antlers.

Genus *AGALMACEROS* Hoffstetter, 1952 †

(Map 1.2.1: Geographic distribution)

Agalmaceros blicki (Frick, 1937) †

General Taxonomic Characters: This is the only species in the genus, and is a large-sized and robust cervid, characterized by by large antlers and short and sturdy metapodials (Hoffstetter 1952). Nevertheless, just a few remains exist in record for this taxon.
Body Size: Its body size is estimated around 60 kg (Smith et al., 2003).
Diet: Undetermined herbivore.
General Ecology and/or Locomotion: Sturdiness of the skeleton is interpreted as an adaptation to live in the high Andean mountains (Merino and Rossi 2010, Tomiati and Abbazzi 2002).
Confidence in Species Assignment: Valid according to Merino and Rossi (2010).
Geographic and strataigraphic range: Pleistocene of the Andes of Ecuador (Chimborazo and Pichincha district); Late Pleistocene to Early Holocene of the Andes of Peru (Junin district).

Map 1.2.1: Geographic distribution of genus *Agalmaceros*. References: Hoffstetter 1968b: Cueva Uchcumachay (PE), San Pedro de Cajas (PE); Hoffstetter 1952: Quebrada de Oton (EC), Alangasi (EC), Punin (EC), Chalan Puluxa (EC).

Genus *ANTIFER* Ameghino, 1889 †
(Map 1.2.2: Geographic distribution)

Two species in this genus are considered valid at present: *Antifer ensenadensis* (Ameghino 1888) and *Antifer ultra* (Ameghino 1888). *Antifer niemeyeri* (Casamiquela 1984) has been recently synonymized with *Antifer ultra* (Labarca and Alcaraz 2011). In the PBDB also reported is *Antifer crassus* from Villa Ballester, Provincia de Buenos Aires, Argentina, but other than the publication of Rusconi (1954), information about this taxon is unavailable.

General Taxonomic Characters: The different species have been classified mainly based on size and horn morphology, which has been questioned (Menegaz 2000). There are insufficient remains to undertake exhaustive and comparative work.
Body Size: The genus *Antifer* is a large-sized deer comparable to the extant *Blastocerus*, and then it would have had a size estimated between 100 and 150 kg, sensu Merino and Rossi (2010).
General Ecology and/or Locomotion: *Antifer* has been associated with open landscapes and bushy vegetation in the Pampean region of eastern South America (Menegaz y Ortiz-Jaureguizar, 1995). It has been associated with wet and warm conditions in the mesopotamic region of Argentina and to cooler and drier conditions in the Argentinian Pampas (Ortiz-Jaureguízar y Cladera 2006).
Confidence in Species Assignment: Valid according to Merino and Rossi (2010).
Geographic and stratigraphic distribution: Besides the specimens identified as *A. ultra* and *A. ensenadensis* (see below), the genus *Antifer* has been also reported from the late Pleistocene of El Chaco region of Argentina and from the late Pleistocene of southern Brazil.

Antifer ensenadensis (Ameghino 1888) †

General Taxonomic Characters: Identified based on the morphology of the antlers. *A. ensenadensis* is smaller than *A. ultra*, but otherwise both are similar (Kraglievic 1932) and of similar size to the extant *Blastocerus* (Merino and Rossi 2010)
Body Size: See descrciption for the genus.
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid according to Merino and Rossi (2010).
Geographic and stratigraphic distribution: Late Pliocene to the Middle Pleistocene of the Mesopotamian region of Argentina (Corrientes and Santa Fe provinces); possibly present during the Late Pleistocene.

Antifer ultra (Ameghino 1888) †

General Taxonomic Characters: Larger than *A. ensenadensis*, but similar on size to *Blastocerus* (Merino and Rossi 2010). Antlers are big, sturdy, with irregular and dichotomous bifurcation, and ventrolaterally compressed, with numerous grooves in both surfaces.
Body Size: See descrciption for the genus.

Diet: Undetermined herbivore.

General Ecology and/or Locomotion: In central Chile, at Tagua Tagua, the presence of this taxon occurs during times of warm climate and reduction of arboreal taxa (Heusser, 1983).

Confidence in Species Assignment: Valid according to Merino and Rossi (2010).

Geographic and stratigraphic distribution: Late Pleistocene of Chile (O´Higgins region), northern Uruguay (Artigas district) and Argentina (Buenos Aires, Corrientes and Entre Rios provinces); Middle Pleistocene of the Pampean region of Argentina.

Map 1.2.2: Geographic distribution of genus *Antifer*. References: Pereira et al., 2012: Chui Creek (BR); Ubilla and Alberdi 1990: Pintado (UY); Montané 1968, Labarca and Alcaraz 2011: Tagua Tagua (CL); Núñez et al., 1983, Núñez et al., 1994: Quereo (CL); Castellanos 1945: Provincia de Santa Fe (AR); Ferrero 2009: El Boyero (AR); Alcaraz and Zurita 2004: Río Pilcomayo (AR); Kerber and Olivera 2008: Ponte Velha I - Touro Passo (BR); Ameghino 1889: Laguna Adela (AR); Alcaraz et al., 2005: Arroyo Ensenada (AR); Alcaraz and Francia 2013: Lavalle (AR).

Genus *BLASTOCERUS* Gray, 1850

(Map 1.2.3: Pleistocene Geographic distribution)

Blastocerus dichotomus (Illiger, 1815)

General Taxonomic Characters: This is the only species known for the genus. It possesses an interdigital membrane and long limbs which are adaptations to inhabit flooded environments (Merino and Rossi 2010).
Body Size: The marsh deer is the largest cervid species of South America, with male animals reaching up to 150 kg and the females up to 100 kg (Duarte 1996).
Diet: Its diet is generally composed of grasses, reeds and aquatic plants, but may also include shrubs and vines during prolonged flooding (Nowak and Paradiso 1983).
General Ecology and/or Locomotion: Commonly known as marsh deer (ciervo de los pantanos in Spanish), this species is classified as Vulnerable (Duarte et al., 2016) and is found in the marshy habitats south of the Amazon River into northern Argentina (Pinder and Grosse 1991). The marsh deer is generally solitary or found in small groups of two or three individuals. Aggregations of up to six animals have been reported on islands during floods (Schaller and Vasconcelos 1978).
Confidence in Species Assignment: Valid extant species according to Illiger (1815).
Geographic and stratigraphic distribution: It now occurs in east-central and northeastern Argentina, west-central and southern Brazil, Paraguay, southeastern Peru, and eastern Bolivia. The species has been extirpated from Uruguay. Fossil specimens attributed to the genus *Blastocerus* have been found in the Late Pleistocene of Argentina (Provincia de Corrientes) and Brazil (Rio Grande do Sul) (Merino and Rossi 2010, Souza Cunha and Magalhaes 1981). *Blastocerus dichotomus* has been found in Pleistocene deposits in General Bruguer/Riacho Negro, Paraguay.

Map 1.2.3: Pleistocene Geographic distribution of genus *Blastocerus*. References: Alvarez 1974: Arroyo Toropi (AR); Hoffstetter 1978: General Bruguer/Riacho Negro (PR); Merino and Rossi 2010: Santa Vitoria do Palmar (BR).

Genus *CHARITOCEROS* Hoffstetter, 1963 †
(Map 1.2.4: Geographic distribution)

Charitoceros tarijensis (Hoffstetter 1963) †

General Taxonomic Characters: This is the only species known for this genus. Little information is available about the specimens on which it is based.
Body Size: According to Hoffstetter1963 it would have been of similar body size as the extant *Hipppcamelu*s, which body size varies between 45-100 kg (Redford and Eisenberg 1992).
Diet: Undeterminated herbivore.
Confidence in Species Assignment: Valid species according to Merino and Rossi (2010).
Geographic and stratigraphic distribution: Pleistocene of Bolivia (Tarija district) and Peru; Late Pleistocene of Peru (Puno district).

Map 1.2.4: Geographic distribution of genus *Charitoceros*. References: Marshall and Sempere 1991: Tarija (BO); Pujos et al., 2007: Casa del Diablo (PE); Hoffstetter 1963: Cuzco (PE).

Genus *EPIEURYCERUS* Ameghino, 1889 †
(Map 1.2.5: Geographic distribution)

E. truncus (Ameghino, 1889) and *E. proximus* (Castellanos 1945) are the two species included in this genus. Some authors have included this genus within the extant *Blastocerus* (McKenna and Bell 1998).

Epieurycerus truncus (Ameghino, 1889) †

General Taxonomic Characters: Antlers are palmate from the base and have 4 to 6 terminal points (Merino and Rossi 2010). Two subspecies have been recognized for *E. truncus*: *E. truncus truncus* † (Bagnalasta 1980) and *E. truncus scillatoi*† (Bagnalasta 1980).
Body Size: Very large deer, body size similar to the extant *Blastocerus* (100-150 kg) (Merino and Rossi 2010).
Diet: Undeterminated herbivore.
Confidence in Species Assignment: Valid species according to Merino and Rossi (2010).
Geographic and stratigraphic distribution: Late Pliocene to Middle Pleistocene (Ensenadan) of Argentina (Buenos Aires province).

Epieurycerus proximus (Castellanos 1945) †

General Taxonomic Characters: The main characteristic that putatively differentiates this species from *E. truncus* is that in *E. proximus*, the antlers arise from a well-developed pedicle, with defined concavity (Merino and Rossi 2010).
Body Size: As for *E. truncus*, body size similar to the extant *Blastocerus* (100-150 kg) (Merino and Rossi 2010).
Diet: Undeterminated herbivore.
General Ecology and/or Locomotion: The species is thought to have inhabited open shrubland and moist environments (Alcaraz and Zurita 2004).
Confidence in Species Assignment: Valid species according to Merino and Rossi (2010).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Argentina (Santa Fe and Corrientes provinces).

Map 1.2.5: Geographic distribution of genus *Epieurycerus*. References: Bagnalasta 1980: La Plata (AR); Cione and Tonni 1999: Santa Fe (AR); Alcaraz and Zurita 2004: Lavalle (AR).

Genus *HIPPOCAMELUS* Leukart, 1816

(Map 1.2.6: Pleistocene to early Holocene Geographic distribution)

This extant genus has two species. The genus is characterized by South American deer species with antlers that divide only once, near the base (Barrio 2016).

Pleistocene Geographic and stratigraphic distribution of the genus: Pleistocene of Bolivia (Tarija district); Late Pleistocene of Chile (O´Higgins, Metropolitana and Coquimbo regions), Argentina (Catamarca province), Peru (Junin district) and Brazil (Pernambuco state) and in Early Holocene archaeological sites in southern Chile (Magallanes region).

Hippocamelus antisensis (d´Orbigny 1834)

General Taxonomic Characters: Commonly called taruca, is a medium-sized cervid with characteristic facial markings (Barrio 2013). Compared to *H. bisulcus*, antler branching usually begins closer to the base of the antlers in tarucas (Barrio 2013).
Body Size: Body mass is between 45-65 kg, and they measure 80 cm at the shoulder (Regidor and Rosati 2001).
Diet: This species eats bushes, herbs and shurbs (Barrio 2013).
General Ecology and/or Locomotion: They prefer rocky areas of sparse vegetation with nearby water sources (Redford and Eisenberg 1992), but they have been observed in dense shrubbery near rivers (Barrio, in prep, International Union for Conservation of Nature Red list of Threatened species (IUCN Red List)). They socialize in groups of six on average (Redford and Eisenberg 1992).
Confidence in Species Assignment: Valid extant species according to Barrio (2013).
Comments: commonly called tarucas or huemul andino, this species is listed as vulnerable by the IUCN Red List.
Geographic and stratigraphic distribution: Tarucas inhabit in the Andes from Ecuador to northwestern Argentina and northern Chile at altitudes above 2,000 masl. There is no fossil record known for this species.

Hippocamelus bisulcus (Molina 1882)

General Taxonomic Characters: Sturdy body built. Only the males present antlres wich are shed every year. It differs from the taruca because is bigger and the coat is unirformily brown in color (Iriarte 2008).
Body Size: This is a robust deer with a body mass ranging between 60-100 kg and height at the shoulder of 80 to 100 cm (Serret 2001).
Diet: Herbivore, eats leaves and grasses and its diet varies depending on the environment where it lives (Iriarte 2008).
General Ecology and/or Locomotion: Their preferred habitat is rocky areas with abundant vegetation in the form of shrubs, but the species is also present in forest clearings (Redford and Eisenberg 1992).
Confidence in Species Assignment: Valid extant species (Iriarte 2008).

Comments: This species is commonly called huemul patagonico and is classified as Endangered by the IUCN Red List Red list.

Geographic and stratigraphic distribution: This species occurs in the Andes of southern Chile and Argentina. There are early Holocene findings of the species in archaeological sites in Southern Patagonia.

Map 1.2.6: Pleistocene to early Holocene geographic distribution of genus *Hippocamelus*. References: Frailey and Campbell 1980: Tarija (BO); Rolim 1974: Lage Grande (BR); Labarca and Alcaraz 2011: Las Pozas de Chacabuco (CL); Casamiquela 1968: Quereo (CL); Montané 1968: Tagua Tagua (CL); Sierpe et al., 2009: Alero Quemado (CL); Yacobaccio and Morales 2005: Hornillos 2 (AR); Tagle et al., 2008: Pataguilla (CL) ; Pires-Ferreira et al., 1977, Hoffstetter and 1986: Cueva Uchcumachay (PE).

Genus *MORENOELAPHUS* (MORENELAPHUS) Carette, 1922 †
(Map 1.2.7: Geographic distribution)

Historically (Gervais and Ameghino 1880, Ameghino 1888, Menegaz 2000), two species were recognized as belonging to the genus: *Morenoelaphus brachyceros* (Gervais and Ameghino 1880) and *Morenoelaphus lujanensis* (Ameghino 1888), as classified mainly on the basis of antler morphology. Recently, Pêgo (2014) suggested that characters from the antlers were not sufficient to suppport this classification and his analyses of dental morphology showed high similarity between specimens classified as *M. brachyceros* and *M. lujanensis*. Therefore, he synonymized *M. lujanensis* with *M. brachyceros,* which I follow here.

Morenoelaphus brachyceros (Gervais and Ameghino 1880) †
(Fig 1.2)

General Taxonomic Characters: This species is characterized by big antlers which are S-shaped (Merino and Rossi 2010).
Body Size: This is a deer of medium to small body size estimated around 50 kg (Fariña et al., 2013).
Diet: Undetermined herbivore.
General Ecology and/or Locomotion: The broad spectrum of deposits in which fossils are found suggests considerable plasticity in habitat preference. Not much is known about the paleoecology of this group; nevertheless it has been suggested they occupied open or partly open environments (Menegaz and Ortiz Jaureguizar 1995).
Confidence in Species Assignment: Valid species according to Merino and Rossi (2010).
Comments: An Electro Spin Resonance date from isolated teeth from Tocantins, Brazil, gave a date of 3.8 ± 0.5 kyr BP (Pêgo 2014).
Geographic and stratigraphic distribution: Middle Pleistocene to Late Pleistocene-Early Holocene of Argentina (Buenos Aires, Santa Fe, Corrientes and Formosa provinces), Uruguay (Artigas and Salto districts) and Paraguay (near Asuncion). It is also recorded from the Middle Holocene of Brazil (Ceará).

Map 1.2.7: Geographic distribution of genus *Morenoelaphus*. References: Deschamps and Borromei 1992: Bajo San José (AR), Río Carcaraña (AR); Tonni and Berman 1987 Centinela del Mar (AR); Tonni and Prado 1985: Luján (AR); Pereira and Lopes 2012: Chui Creek (BR); Ubilla and Alberdi 1990: Pintado (UY); Zurita and Carlini 2004: Barranqueras (AR); Hoffstetter 1978: General Bruguer/Riacho Negro (PY); Marshall and Sempere 1991, Hoffstetter 1968: Ñuapua (BO); Pêgo 2014: Janaúba (BR), Cascada de la Palaeolama (AR), Arroyo Cululú (AR), Salatiel II (BR), Gruta do Urso (BR), Banks of Río Bermejo near Villa Escolar (AR) , Santa Vitoria do Palmar (BR); Kerber and Oliveira 2008: Ponte Velha I (BR); Ameghino 1989: Mercedes (AR), Lobos (AR), El Monte (AR); Ferrero et al., 2007: El Boyero (AR); Alcaraz and Francia 2013: Arroyo Toropi (AR).

Figure 1.2.1: *Morenoelaphus* brachycerus. From Lydekker 1894.

Genus *ODOCOILEUS* Rafinesque, 1832
(Map 1.2.8 Pleistocene to early Holocene geographic distribution)

This genus consists of two extant species commonly called white-tailed deer (*Odocoileus virginianus*) and the mule deer (*Odocoileus hemionus*); only *O. virginatus* is present in South America. One fossil species, *O. salinae*, is also known in South America. Another fossil species that has been reported, *O. peruvianus*, is now considered a synonym of *O. virginatus* (Tomiati and Abbazzi 2002). The oldest fossils from the genus are reported as early Pliocene (Kurten and Anderson 1980).

Geographic and stratigraphic fossil distribution: Pleistocene findings of this genus are recorded in Ecuador (Pichincha and Chimborazo provinces), and Peru (Piura district).

Odocoileus virginianus (Zimmermann 1780)

General Taxonomic Characters: Medium sized deer. In South America, this species is characterized by a thick fur coat. Smith (1991) states that bigger forms of this species are found in higher latitudes and smaller ones near the equator, which would be the case of South American *O. virginatus*.
Body Size: Medium-sized cervid. Body mass varies between 50 and 120 kg (Eisenberg 2000) and body height is 95 cm at the shoulder (Silva and Downing 1995).
Diet: Herbivore. Its diet varies depending on the habitat where is living (Gallina and Lopez Arevalo 2016).
General Ecology and/or Locomotion: It inhabits a great variety of habitats but favors the interface between savanna and forests were deer can graze as well as browse (Redford and Eisenberg 1999).
Confidence in Species Assignment: Valid extant species (Gallina and Lopez Arevalo 2016).
Geographic and stratigraphic distribution: The species ranges from southern Canada to western Brazil and central Bolivia (Redford and Eisenberg 1999). It is also found in Holocene deposits in Venezuela and Pleistocene deposit of the Ecuadorian Andes (= *O. peruvianus*).

Odocoileus salinae (Frick 1937)

General Taxonomic Characters: The only known difference between this species and *O. virginianus* is that the antlers of *O. salinae* are more slender
Body Size: Its body size is estimated to be a 95% of *O. virginatus* (~52 kg, Tomiati and Abbazzi 2002).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid species according to Merino and Rossi (2010).
Geographic and stratigraphic fossil record: Late Pleistocene of coastal Ecuador (Santa Elena Peninsula) and Pleistocene of Colombia (Santander district).

Map 1.2.8 Pleistocene to early Holocene geographic distribution of genus *Odocoileus*. References: Czaplewski and Rincón. 2005: Mene de Inciarte (VE); Eisenberg 1979 et al.,: Fundo PecuaRío Masaguarai (VE); C. Villarroel and J. Brieva 1996: Nucleo Escolar La junta (CO); Churcher 1959, Lemon and Churcher 1961: Talara (PE); Hoffstetter 1952: Alangasi (EC), Punin Chalan (EC), La Carolina (EC).

Genus *PARACEROS* Ameghino, 1889 †
(Map 1.2.9: Geographic distribution)

Paraceros fragilis (Amgehino 1888) †

General Taxonomic Characters: Antlers are ~40 cm long, slender and lyre-shaped. The surface of the antlers is smooth with weak grooves (Merino and Rossi 2010).
Body Size: Small deer, similar to *Ozotoceros* (30 kg, Menegaz and Ortiz-Jaureguizar 1995).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid species according to Merino and Rossi 2010.
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Argentina (Buenos Aires provinces); Late Pleistocene of Uruguay (Artigas district).

Map 1.2.9: Geographic distribution of genus *Paraceros*. References: Prevosti and Vizcaíno 2006, Menegaz and Ortiz-Jaureguizar 1995: Río Arrecifes (AR); Ubilla et al., 2004: Sopas formation (UY).

Other South American Cervids

The genera *Ozotoceros* (Ameghino 1891), *Mazama* (Rafinesque 1817), and *Pudu* (Gray 1852) are represented by species of medium body size, under <40-44 kg which is the limit used here to refer to megafauna. For that reason they were not described in detail in this work. All of them are extant groups with no known Pleistocene extinct members.

1.3 Family TAYASSUIDAE Palmer, 1897

These are pig-like artiodactyls with low-crowned molars. They have four visible toes on the forefeet and three in the hind feet, but the weight of the body is supported by only two toes per foot. Extant peccaries have three chambered stomach but are not ruminant (Redford and Eisenberg 1999).

Genus *CATAGONUS* Ameghino, 1904
(Map 1.3.1: Geographic distribution)

Four extinct Pleistocene species and one extant species are recognized in South America.

Catagonus stenocephalus (Lund in Reinhardt 1880) †

General Taxonomic Characters: It presents an elongated rostrum, the profile of the rostrum considering only nasal bones is sharply convex. The profile of the skull at the level of the frontal bones is also convex. The dentition shows a general bunodont character and mesodont crowns with shapr cusps, canines are large and the “hypocone” is well developed in the PM3-4 (Gasparini 2007, Gasparini et al., 2009).
Body Size: Medium to large sized tayassuid (Avilla et al., 2013) but no quantitave body mass estimations are available.
Diet: The presence of bunodont dentition, with higher and sharper cusps than in typical bunodont forms, and with a mesodont crown height in species of the genus *Catagonus* supports the interpretation of an herbivorous and foraging diet (Menegaz & Ortiz Jaureguizar 1995, Gasparini 2007).
General Ecology and/or Locomotion: Some cranial features such as development of the sinus and nasal chambers, the position of the orbits and the elongation of the rostrum have been used to infer that this taxon was the most cursorial species of the genus, probably inhabiting dry and open environments and having an herbivorous and foraging diet (Gasparini et al., 2009).
Confidence in Species Assignment: Valid species according to Gasparini (2007).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Argentina (Buenos Aires province), Uruguay (Sopas formation) and Brazil (Rio Grande do Sul, Minas Gerais, Tocantins and Paraná states); Pleistocene of Bolivia (Tarija district).

Catagonus metropolitanus (Ameghino 1904) †

General Taxonomic Characters: Some of the characteristics of this species are the large body size and high degree of molarization of the premolars.
Body Size: Large tayassiudae, with a body mass estimated between 80-100 kg (Gasparini et al., 2010).
Diet: General herbivorous and foraging diet (Gasparini 2007). See description for *C. stenocephalus* for more details.

Confidence in Species Assignment: Valid species according to Gasparini (2007).
Geographic and stratigraphic distribution: Early to middle Pleistocene of the Buenos Aires Province, Argentina.

Catagonus bonaerensis (Ameghino 1904) †

General Taxonomic Characters: It was described by Ameghino based on isolated teeth and placed in the genus Catagonus by Rusconi (1930), based on tooth morphology. The characters used by Rusconi are also widespread among all Tayassuini taxa (Parisi-Dutra et al., 2016). There is no more information about the species in the published literature.
Body Size: Similar in size to *C. metrpolitanus*, with a body mass estimated between 80-100 kg (Gasparini et al., 2010).
Diet: General herbivorous and foraging diet (Gasparini 2007). See description for *C. stenocephalus* for more details.
Confidence in Species Assignment: Valid species according to Gasparini (2007).
Geographic and stratigraphic distribution: Late Pleistocene-early Holocene of the Buenos Aires province, Argentina; middle Pleistocene of Uruguay (Colonia district).

Catagonus carlesi (Rusconi 1930) †

General Taxonomic Characters: It was described by Rusconi (1930) based on an almost complete skull. In his description he notice the larger mandibles compared to the living *Tayassu*.
Diet: This taxon is thought to generally have an herbivorous and foraging diet (Gasparini 2007). See description for *C. stenocephalus* for more details.
Geographic and stratigraphic distribution: Middle Pleistocene of Santiago del Estero province, Argentina.

Catagonus wagneri (Rusconi 1930)

General Taxonomic Characters: This extant species is a medium-sized tayassuidae. According to Gasparini et al., 2013, the Chacoan Peccary in many aspects of the skeleton resembles extinct *Platygonus* than the other living peccaries. Some of these characteristics are: the orbits located in superior-posterior position behind the M3, which is due to elongation of the rostrum; it presents an great development of nasal sinuses and chambers; the infraorbital foramen located well anteriorly to the zygomatic arch; a distinct basicranial flexure; and the lateral digits in the limbs are reduced (Gasparini et al., 2013).
Body Size: Body size is of 35 kg on average (Eisenbergs and Redford 1992).
Diet: its diet is based mainly in eating tender parts of cacti, but it also eats roots, flowers and fruits (Gasparini et al., 2013).
General Ecology and/or Locomotion: They present a cursorial mode of life, inhabiting in open and dry xerophitic forests. Individuals can tolerate long periods of drought (Mayer and Brandt 1982).
Confidence in Species Assignment: Valid species according to Gasparini (2007).

Comments: Classified as an Endangered by the IUCN Red List.
Geographic and stratigraphic distribution: It is today endemic to the Gran Chaco region of Argentina, Paraguay, and Bolivia (Meyer and Wetzel 1989, Redford and Eisenberg 1992, Gasparini et al., 2006). It has been found in Late Pleistocene deposits of Uruguay (Artigas district) and in Holocene archaeological sites in Santiago del Estero Province, Argentina.

Map 1.3.1: Geographic distribution of genus *Catagonus*. References: Gasparini 2013: Arrecifes del Río de la Plata (AR), Colonia del Sacramento (AR), San Antonio de Areco (AR), NNE Mar del Plata (AR), Mercedes (AR), Malacra Stream-Gral. Alvarado (AR), Samborombon River (AR), Arroyo Cañas (UY), Uruguaiana (BR), Gruta Lapa da Escrivaninha N 11 (BR), Gruta dos Moura (BR), Gruta do Vale do Ribera (BR), Arrecifes del Río de la Plata (BR), Dulce river (AR), Capital federal (AR), Colonia del Sacramento (UY), Cureim river (UY); Gasparini et al., Soibelzon 2010: Tarija (BO), Arroyo de Las Limetas (UY); Avilla et al., 2013: Gruta dos Moura (BR); Parisi Dutra et al., 2016: Nascente do Formoso (BR), Caverna do Japonês (BR).

Genus *PLATYGONUS* Le Conte, 1848 †
(Map 1.3.2: Geographic distribution)

While there are five fossil species that have been defined for this genus, only one of them, *Platygonus cinctus*, occurs in Pleistocene sediments of South America (Gasparini 2007, Gasparini 2013, and thus is included in this treatment. The other four only occur in pre-Pleistocene sediments: *Platygonus marplatensis* (middle to late Pliocene of Buenos Aires Province, Argentina), *Platygonus chapadmalensis* (middle to late Pliocene of Buenos Aires province, Argentina), *Platygonus kraglievichi* (late Pliocene in the Jujuy Province, Argentina) and *Platygonus scagliai* (late Pliocene of Buenos Aires Province in Argentina).

Platygonus cinctus (Ameghino 1886) †

General Taxonomic Characters: As it was mention above, *P. cinctus* share several characteritics with the extant *C. wagneri*. It presents an elongated rostrum with the orbits located in superior–posterior position and behind the M3, a great development of nasal sinuses and, the infraorbital foramen located well anteriorly to the zygomatic arch; a distinct basicranial flexure, reduction of the lateral digits in the limbs (Gasparini et al., 2011).

Body Size: Body size of the genus *Platygonus* ranges from 30 and 70 kg (Soibelzon et al., 2008).

Diet: Herbivorous diet (Gasparini et al., 2011). Isotopic analysis and dental microwear examination on North American specimens of the genus *Platygonus* indicate a C3 browser to mixed-feeder diet which could include C4 grasses under special conditions (Feranec and MacFadden 2000; Feranec 2007; Schmidt 2008, from Gasparini et al., 2011).

General Ecology and/or Locomotion: Cursorial habit (Guilday et al., 1971, Gasparini et al., 2010). They were more adapted to open environments.

Confidence in Species Assignment: Valid species according to Gasparini (2007).

Comments: Estimations of body mass for older fossil species of *Platygonus* indicate that *Platygonus marplatensis* (Argentina middle to upper Pliocene) would have been the largest taxon with a body mass between 63–66 kg, and *Platygonus scagliai* (Argentina, upper Pliocene) the smallest weighing around 37 kg (Gasparini et al. 2010).

Geographic and stratigraphic distribution: Pleistocene of Argentina (Buenos Aires province), Bolivia (Tarija valley) and in Uruguay (Canelones district). *P. cinctus* has been found in Pleistocene deposits around La Plata River, Buenos Aires province in Argentina.

Map 1.3.2: Geographic distribution of genus *Platygonus*. References: Gasparini 2007, Gasparini 2013: Toscas del Río de la Plata (AR), Miramar (AR), Tarija (BO), Sauce (UY).

Other South American Tayassuid

The genus *Tayassu* (G. Fischer de Waldheim 1814) includes medium-sized extant species, *Tayassu pecari* Link 1795 (body size: 29-33 kg) and *Tayassu tajacu* Linnaeus, 1758 (body size: 19-22 kg). No further description of these species is given here because they are too small to be considered megafauna. However, both have been present in South America since the middle Pleistocene.

2. Order CARNIVORA Bowdich, 1821

The order Carnivora (Table 2) includes terrestrial mammals that are specialized in active predation of other vertebrates. This group includes cats, dogs, bears, foxes, wolves, and smaller carnivores such as raccoons and mustelids. Many members (e.g. foxes, bears, raccoons) are omnivores, subsisting on meat mixed with fruits, vegetables, and insects. The dental formula is somewhat variable but generally marked by the reduction of teeth and development of a carnassial. The canines are prominent and well developed. Modern carnivores (including late Pleistocene ones) are characterized by the carnassials, the upper fourth premolar and the lower first molar, which are specialized for shearing. The brain is relatively large and the tympanic bullae are usually enlarged. (Redford and Eisenberg 1999).

Table 2. South American Megafaunal Carnivora. † = extinct

Family CANIDAE Fischer, 1817
Genus *CANIS* Linnaeus, 1758
Canis dirus (Leidy, 1858) †
Genus *PROTOCYON* Giebel, 1855 †
Protocyon scagliarum (Kraglievich 1952) † *Protocyon tarijensis* (Ameghino, 1902) † *Protocyon troglodytes* (Lund 1838) †
Genus *THERIODICTIS* Mercerat, 1891 †
Theriodictis platensis (Mercerat 1891) †
Family FELIDAE Fischer, 1817
Genus *HOMOTHERIUM* Fabrini, 1890 †
Homotherium venezuelensis (Rincón et al., 2011) †
Genus *PANTHERA* Oken, 1816
Panthera onca (Linnaeus 1758) *Panthera onca mesembrina* (Cabrera 1934) †
Genus *PUMA* Jardine, 1834
Puma concolor (Linneaus 1771)
Genus SMILODON Lund, 1841 †
Smilodon fatalis (Leidy 1868) † *Smilodon populator* (Lund 1842) † *Smilodon gracilis* (Cope 1880) †
Family URSIDAE Gray, 1825
Genus *ARCTOTHERIUM* Brumeister, 1879 †
Arctotherium angustidens (Gervais & Ameghino 1880) † *Arctotherium wingei* (Ameghino 1902) † *Arctotherium vetustum* (Ameghino 1885) † *Arctotherium bonariense* (Gervais 1848-52) † *Arctotherium tarijense* (Ameghino 1902) †
Genus *TREMARCTOS* Gervais, 1855

Tremarctos ornatus (F. Cuvier 1825)

2.1 Family CANIDAE Fischer, 1817

This family includes dogs, wolves and foxes. Morphologically, they are characterized by long and prominent canines and an upper carnassial arrangements consisting of the m1 and P4 teeth that contains an expanded lingual surface. Members of this family tend to be adapted for cursorial lifestyles; they generally are digitigrade and have 5 toes on the forefoot and four in the hind foot. The claws in their feet are not retractable. Their diet can be hypercarnivorous or omnivorous. Strictly following the definition of megafauna used here (> 40 kg of body mass) would exclude all extant Canidae inhabiting South America (with the exception of some domestic breeds of dogs). The largest canid found today in the continent is *Chrysocyon brachyrus* (Illiger 1815), also known as lobo guara or maned wolf, with a body weight on average of around 24 kg (Redford and Eisenberg 1992). All other South American genera of foxes and dogs have body masses below 10 kg (Redford and Eisenberg 1992). However, some extinct canids were large enough to be considered megafauna.

Genus *CANIS* Linnaeus, 1758
(Map 2.1.1: Geographic distribution)

One species is recorded in South America.

Canis dirus (Leidy 1858) †

General Taxonomic Characters: Very similar to modern gray wolfs. Some specific characterirtics of the mandible and teeth separate this species from other forms of Canis. Some of these characteristics are a deepest and robust mandible, presence of accessory cuspids in p2 and enlarged premolars, among others (Hoddnet et al., 2009).
Body Size: Body size estimations for this specimen vary between 60-68 kg with differences among distinct geographic populations (Anyonge and Roman 2006). *C. dirus* was larger than modern *C. lupus* by 8-15% (Kurtén and Anderson 1980).
Diet: Carnivore. According to stable isotope analyses (Harris et al., 2003) *C. dirus* preferred preys such as *Bison*, but easily switched to other prey types. The minimum size of prey that *C. dirus* likely preferred varied between 100-600 kg (Van Valkenburgh and Koepfli 1993).
General Ecology and/or Locomotion: The fossil record of Rancho La Brea (California, US) suggests group-living (Merriam 1912, Stock and Harris 1992, Van Valkenburgh and Sacco 2002) and plausibly pack hunting.
Confidence in Species Assignment: Valid species present in South America according to Prevosti et al., (2009).

Comments: This species is very common in late Pleistocene deposits of North America, and inferences about its paleoecology come mainly from studies on specimens from that continent (Anyonge and Roman 2006).

Geographic and stratigraphic distribution: Late Pleistocene of Peru (Piura district), Bolivia (Tarija valley), and Venezuela (Muaco in Falcon state and Inciarte).

Map 2.1.1: Geographic distribution of genus *Canis*. References: Churcher 1959: Talara (PE); Marshall and Sempere 1991: Quebrada del Puente Alto- Tarija (BO); Prevosti and Rincón 2007: Inciarte asphalt (VE), Muaco (VE).

Genus *PROTOCYON* Giebel, 1855 †
(Map 2.1.2: Geographic distribution)

Three species are recognized for the Pleistocene of South America: *Protocyon scagliarum* (J. L. Kraglievich, 1952), *Protocyon tarijensis* (Ameghino, 1902), *Protocyon troglodytes* (Lund, 1838)

Estimates of body mass for the three species, ranging from 11-25 kg, fall below the megafauna limit (Prevosti et al., 2005), but some authors have suggest those body mass estimates are too low (Prevosti et al., 2005).

Along with *Theriodictis platensis*, the species of *Protocyon* formed the hypercarnivorous fossil guild of South America. With their extinction during the Pleistocene only one hypercarnivours canid, *Speothos venaticus* (Bush dog, Zorro vinagre) persists in South America. This extant taxon has a body size of only 5-8 kg, smaller than any of the *Protocyon* species. Therefore, the extinction of the genus *Protocyon* (along with *Theriodictis*) deleted all large canids from the hypercarnivorous South American guild. In addition it is worth mentioning that two of the three species, *P. troglodytes* and *P. tarijensis*, became extinct around the late Pleistocene-early Holocene transition (Prevosti et al., 2009). For this reason I include *Protocyon* in this discussion even though were not megafauna in the strict sense.

Protocyon scagliarum (Kraglievich 1952) †

General Taxonomic Characters: In this species, the cusps of P2-3 are more acute and less inclined posteriorly compared to other species in the genus. Also, the P2-3 has well developed posterior accessory cusps (Prevosti et al., 2009).
Body Size: Medium sized carnivore with a body mass estimated around 11 kg (Prevosti et al., 2005).
Diet: Hypercanivorous canid (Kraglievic 1952, Kraglievic 1928, Winge 1895). Diet is inferred to be more than 70% vertebrate meat (Van Valkenburgh 1991) for this and the other species in the genus.
General Ecology and/or Locomotion: According to the postacranial remains, *Protocyon* species were well adapted for running and probably inhabited open environments (Cartelle and Langguth 1999).
Confidence in Species Assignment: Valid species according to Prevosti (2006).
Geographic and stratigraphic distribution: Early to Middle Pleistocene of the Buenos Aires Province, Argentina.

Protocyon tarijensis (Ameghino, 1902) †

General Taxonomic Characters: Previously known as *Theriodictis tarijensis,* is now considered a member of the genus *Protocyon* following the most recent phylogenetic analysis (Prevosti 2006).
Diet: Hypercarnivore. Diet is inferred to be more than 70% vertebrate meat (Van Valkenburgh 1991) as for the other species in the genus.

General Ecology and/or Locomotion: According to the postacranial remains, *Protocyon* species were well adapted for running and probably inhabited open environments (Cartelle and Langguth 1999).
Confidence in Species Assignment: Valid species according to Prevosti (2006).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Tarija Valley, Bolivia.

Protocyon troglodytes (Lund 1838)

General Taxonomic Characters: It presents deep zygomata with wide masseteric scar alog with long palatines that extend beyond the toothrow; it has a wide palate bone. Some particular characteristics of the teeth are that the P4 protocone is very reduced, M1–2 with very reduced or absent hypocone, m1 lacking metaconid and entoconid and M2/m2 small relative to M1/m1 (Berta 1988; Cartelle and Langguth 1999, from Prevosti et al., 2005).
Body Size: It is estimated around 16 kg for *P. troglodytes* (25 kg for *P. orcesi=P. troglodytes*) (Prevosti et al., 2005).
Diet: Hypercanivorous canid (Kraglievic 1952, Kraglievic 1928, Winge 1895). Diet is inferred to be more than 70% vertebrate meat (Van Valkenburgh 1991). *P. troglodytes* is thought to have fed on medium size animals such as tayassuids, camelids, equids and cervids, but not on megamammals (Cartelle and Langguth 1999). According to stable isotope analyses on the specimen from Mercedes, Argentina, the diet may have consisted of *Equus neogeus*, *Hippidion principale*, *Notiomastodon platensis*, *Toxodon*, and *Megatherium americanum* (Prevosti and Schubert, 2013).
General Ecology and/or Locomotion: According to the postacranial remains, *Protocyon* species were well adapted for running and probably inhabited open environments (Cartelle and Langguth 1999).
Confidence in Species Assignment: Valid species according to Berta (1988).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Bolivia (Ñuapua and Tarija), Early to Middle Pleistocene of Argentina (Buenos Aires province) and Late Pleistocene-Early Holocene of Argentina (Buenos Aires and Formosa provinces); Late Pleistocene Ecuador (Andean and coastal regions); Late Pleistocene of Uruguay (Salto district), Brazil (Minas Gerais, Ceara, Bahia, Paraiba, Piau, Parana, Rio grande do Norte and Mato Grosso do Sul states) and Venezuela (Falcon state).

Map 2.1.2: Geographic and stratigraphic of genus *Protocyon*. References: Prevosti et al., 2009: Arroyo Santa Elena (AR), Tarija (BO), Camet norte (AR), Playa Quequén (AR) Ñuapua (BO) San Pedro II-Tarija (BO); Prevosti and Schubert 2013: Mercedes (AR); Prevosti and Ubilla 2009: Paso Muñoz (UY); Prevosti et al., 2005: Cliffs of the Bermejo river (AR); Hoffstetter 1986: Guamote-Chimborazo (EC); Berta 1988: Lagoa Santa (BR); Gomide 1989: Itapipoca (BR); Cartelle and Langguth 1999: Campo Formoso (BR), Toca da Boa Vista (BR); Bergqvist 1993: Curimatas (BR); Guerin 1991: Sao Raimundo Nonato (BR), Toca da Janela da Barra do Antoniao (BR) ; Born and Sedor 2001: Gruta Clarabela (BR); Porpino and Santos 2004: Lejado de Soledade (BR) ; Salles and Cartelle 2006: Japones Cave (BR); Hoffstetter 1952: La Carolina (EC); Prevosti and Rincón 2007: Inciarte (VE); Paula Couto 1980: Joao Cativo (BR).

Genus *THERIODICTIS* Mercerat, 1891 †
(Map 2.1.3 Geographic distribution)

A single species is recognized, *Theriodictis platensis*. Earlier classifications also recognized *Theriodictis tarijensis,* but that species is now assigned to the genus *Protocyon* (*P. tarijensis*), following the results of the most recent phylogenetic analysis (Prevosti et al. 2009, Prevosti 2010, Prevosti 2006). Like *Protocyon*, estimates of body size for this genus falls below the lower limit for the definition of megafauna used in this work (40 kg), but I include the genus here for the same reasons explained for *Protocyon*.

Theriodictis platensis (Mercerat 1891) †

General Taxonomic Characters: It presents a high zigomatic arch, pronounced masseter process, whide palate; M1-M2 with reduced hypocone, M2 with reduced metacone, m1 without metacone and presenting a small entocone and M2/m2 smaller compared to M1/m1, P4 medialy inclined (Berta 1988).
Body Size: Estimated body mass is around 37 kg according to craniodental measurements.
Diet: Hypercarnivorous canid as is evidenced by the presence of large carnassial teeth, wide palate and small postcarnassial molars, suggesting more than 70% of its diet represented was meat. Giving its size, the list of mammal species that could have been part of its diet are: cervids such as *Antifer* and *Epieurycerus*; equids like *Hippidion* and *Equus*; camels such as *Lama*; tayusids like *Catagonus*; mid-sized notoungulates such as *Mesotherium*; large rodents as *Neochoerus* and large armadillos like *Pampatherium*, *Eutatus seguini* and *Propraopus grandis*. (Prevosti and Palmqvist 2001).
General Ecology and/or Locomotion: Postcranial characteristics indicate they were probablu runners, occupying a similar ecological niche to the one occupied by small foxes today (Prevosti and Palmqvist 2001).
Confidence in Species Assignment: Valid species according to Berta (1988).
Geographic and stratigraphic distribution: Early to Middle Pleistocene of Argentina (Buenos Aires province); Late Pleistocene of Argentina (Corrientes province) and Brazil (Rio Grande do Sul state).

Map 2.1.3: Geographic distribution of genus *Theriodictis*. References: Prevosti et al., 2009: Arroyo Santa Elena (AR), Cantera Vialidad Nacional (AR), Ramallo (AR), Estación Retiro (AR); Drehmer and Ribeiro 1998: Mostardas (BR); Alvarez 1974: Arroyo Toropi- level 3 (UY); Rodrigues et al., 2004: Balneario Hermenegildo (BR).

2.2 Family FELIDAE Fischer, 1817
Cats

This family is characterized by an extremely modified tooth formula where the number of molars is reduced to just one upper and one lower molar. They possess a developed and inflated auditory bulla. The rostrum is short and the eyes are directed forward (Redford and Eisenberg 1992).

Genus *HOMOTHERIUM* Fabrini, 1890 †
(Map 2.2.1: Geographic distribution)

Only one species is recognized in South America: *Homotherium venezuelensis* (Rincón et al., 2011).

Homotherium venezuelensis (Rincón et al., 2011)

General Taxonomic Characters: Lion-sized saber-toothed cat with serrated canines. A good description of the skeleton of *Homotherium* has been published based on remains coming from Friesenhahn Cave in Texas, United States, identified as *H. serum*. The analyses of those fossils (an articulated skeleton and remains of more than 30 individuals) revealed that *H. serum* was a large and powerful animal but slender with strikingly elongated forelimbs and short tail. This anatomy is quite distinct from that of living cats and other fossil forms. The Venezuelan species is based on a complete and compressed skull (Rincón et al., 2011).
Body Size: Estimated body size is around 189 kg (Smith et al., 2013).
Diet: Carnivore. At the Texas site, it seems that *Homotherium* was feeding mostly on young mammoths (Rawn-Schatzinger 1992; Turner and Anton 1997).
Confidence in Species Assignment: Valid species according to Rincón et al., (2011).
Geographic and stratigraphic distribution: Early to Middle Pleistocene of Venezuela (Maturin District).

Map 2.2.1: Geographic distribution of genus *Homotherium*. References: Rincón et al., 2011: Breal del Orucual (VE).

Genus *PANTHERA* Oken, 1816
(Map 2.2.2: Pleistocene Geographic distribution)

The genus consists of one extant species, *Panthera onca* (Linnaeus 1758, jaguar) and one extinct subspecies present in South America: *Panthera onca mesembrina* (Cabrera 1934).
Panthera onca (Linnaeus 1758)

Panthera onca (Linnaeus 1758)

General Taxonomic Characters: The largest felid in the Americas at present, *P. onca* is characterized by a big head compared to the rest of the body, robust build and short tail.
Body Size: Body mass ranges between 60.5 and 119 kg and males are almost always larger than females (Redford and Eisenberg 1992).
Diet: Carnivore. *Panthera onca* preys on large to middle sized mammals (Redford and Eisenberg 1992) and its diet includes around 5% of small mammals of less than 1 kg, and 95% of mammals that are larger (Redford and Eisenberg 1992). Typical prey of jaguars include *Peccari tajacu* (19-30 kg), *Dasypus novemcintus* (3-4 kg) and *Hydrochaerus hydrochaerus* (63 kg); but they occasionally prey on larger mammals as *Tapirus terrestris* (177 kg) and cattle (361-500 kg) (Sunquist and Sunquist 2002).
General Ecology and/or Locomotion: Jaguars occur in a variety of environments ranging from the xeric Chaco in Paraguay and Argentina, as well as in tropical forest and the Pantanal region of Brazil. They need abundant cover, water, and sufficient prey. Prey selection and consumption varies depending on the region where the jaguar is living. (Sunquist and Sunquist 2002, Redford and Eisenberg 1992)
Confidence in Species Assignment: Species is Valid according to Linnaeus (1758).
Commetns: During the Pleistocene jaguars were all throughout the Americas, reaching north as far as what is today the states of Nebraska and Washington (PBDB 2016). The Pleistocene form is often larger than the extant one (Turner and Antón 1997), for example, the body mass of *Panthera onca* estimated using the late Pleistocene fossil record of the Pampean region of Argentina is between 95-137 kg (Prevosti and Vizcaíno 2006). Also in the Pampas region of Argentina, the typical minimum and maximum size of prey calculated for Pleistocene specimens of *Panthera* are 139 and 594 kg respectively, which is higher than the parameters observed for extant jaguars today and is in agreement with the greater body mass calculated for the Pleistocene form (Prevosti and Vizcaíno 2006).
Geographic and stratigraphic distribution: Historically, the species ranged from south Western United States (where still occurs close to the Mexican border) through the Amazon Basin to the Rio Negro in Argentina. Today it occurs in Mexico, through all Central America, in Venezuela, Colombia, the Amazonian forests of Ecuador, Peru, Bolivia, in Brazil, and the Chaco region of Paraguay and Argentina (IUCN Red List, 2016). In South America *P. onca* was present in the Late Pleistocene to Holocene of Argentina (Bueno Aires province); Early to late Pleistocene of Bolivia (Tarija, Chuquisaca and La Paz districts); Late Pleistocene to Holocene of Peru (Madre de Dios, Libertad and Piura districts); Pleistocene of Ecuadorian Andes (Pichincha and Chimborazo districts); early Pleistocene of Venezuela (Monagas state); late Pleistocene to Holocene of Brazil (Amazonas, Piauí, Bahía, Mato Grosso do Sul, Sao Paulo States).

Panthera onca mesembrina (Cabrera 1934) †

General Taxonomic Characters: Described by Cabrera in 1934, this is the largest subspecies of jaguar recorded in the fossil record and is restricted to austral South America. Generaly, is bigger than the extant form.
Body Size: Body mass for *P. onca mesembrina* has been estimated to be around 190 kg, based on specimens from the late Pleistocene to early Holocene of Ultima Esperanza and Tierra del Fuego, southern Chilean Patagonia (Prevosti and Martin 2013).
Diet: Carnivore. Typical and maximum prey size calculated for *P. onca mesembrina* from Última Esperanza and Tierra del Fuego are 404 and 913 kg respectively (Martin and Prevosti 2013). According to stable isotopes analyses in the same publication *P. onca mesembrina* may have consumed *Hippidion*, *Lama guanicoe*, *Lama gracilis* and possibly *Mylodon*.
Confidence in Species Assignment: Valid according to Cabrera (1934).
Geographic and stratigraphic distribution: Late Pleistocene to early Holocene of Southern Patagonia in Chile.

Map 2.2.2: Pleistocene Geographic distribution of genus *Panthera*. References: Marshall and Sempere 1991: Tarija (BO), Yaco-La Paz (BO); Hoffstetter 1968: Ñuaupua (BO); Terborgh 1990: Cocha-Cashu (PE); Pujos and Salas 2004: Celendin (PE), Talara (PE); Hoffstetter 1952: Punin-Chalan (EC); Lovejoy and Bierregaard 1990: Manaus (BR); Guerin 1991: Garrincho (BR); Cartelle and Hartwig 1996: Toca da Boa Vista; Lessa and Cartelle 1998: Toca dos Ossos (BR), Japones Cave (BR); Ameghino 1907: Iporanga (BR); Ghilardi and Fernandes 2011: Megafauna Upper Ribeira (BR); Prevosti and Martin 2013: Ultima Esperanza (CL); Prevosti et al., 2015: Lujan (AR); Carrion et al., 2012: Quito (EC).

Genus *PUMA* Jardine, 1834
(Map 2.2.3: Pleistocene-Holocene Geographic distribution)

Commonly called Puma, American Lion, or Leon Americano, this extant genus is represented by a single species in South America.

Puma concolor (Linneaus 1771)

General Taxonomic Characters: It is characterized by a lithe build, long tail and monocolored coat.
Body Size: Medium-sized felid with body size between 26 kg to 54 kg (Redford and Eisenberg 1992).
Diet: Carnivore. Eats small to medium sized mammals such as small deer, rodents, *Lama gunaicoe* and *Vicugna*, among others (Iriarte 2009).
General Ecology and/or Locomotion: Solitary animal, it occupies large territories where a male and several females can live but only gathering for mating season. It is a shy animal that avoids human contact. Litter size varies from 2 to 4 cubs (Iriarte 2009).
Confidence in Species Assignment: Valid species according to Johnson et al., (2006).
Geographic and stratigraphic distribution: Currently it ranges from northern Canada to southern Chile and Argentina. In South America it is most abundant in the southern cone, including Paraguay, Uruguay, as well as northern and central parts of Chile and Argentina. Fossil or sub-fossil remains are found in Late Pleistocene and Holocene deposits in South America, sometimes in the same context as some of the extinct felids. Fossils have been found in Holocene deposits of Venezuela and Peru (Madre de Dios district), from the Early Pleistocene of Bolivia (Tarija district), Late Pleistocene to Holocene of Brazil (Amazonas and Bahia states), Late Pleistocene of Uruguay (Artigas district), Late Pleistocene and Holocene of Argentina and, Late Pleistocene to Holocene of Chile (Magallanes region) (PBDB).

Map 2.2.3: Pleistocene-Holocene Geographic distribution of genus *Puma*. References: Eisenberg and O'Connell 1979: Fundo Pecuario Masaguaral (VE); Lovejoy and Bierregaard 1990: Manaus (BR); Terborgh 1970: Cocha-Cashu (PE); Marshall and Sempere 1991: Tarija (BO); Guerin 1991: Garrincho (BR), Toca da Janela do Barra do Antoniao (BR); Ubilla and Alberdi 1990: Pintado (UY); Mazzanti and Quintana 1997: Cueva Tixi (AR); Politis and Salemme 1990: La Moderna (AR); Cartelle and Hartwig 1996: Toca da Boa Vista (BR); Lessa and Cartelle 1998: Gruto dos Ossos (BR); Prevosti et al., 2003; Pujos and Salas 2004: Huargo (PE).

Genus SMILODON Lund, 1841 †

(Map 2.2.4: Geographic distribution)

Commonly known as saber-tooth cats, these were very large felids. The most distinctive feature is the presence of extremely long, flattened canines, hence the common name 'Saber-tooth cat.' The genus was present in North, Central and South America. In South America, where it was probably the top predator (Prevosti and Vizcaíno 2006), three different species have been recognized: *Smilodon populator* (Lund 1842), *Smilodon gracilis* (Cope 1880), and *Smilodon fatalis* (Leidy 1868) (Rincón et al., 2011; Bocherens et al., 2016; Kurten and Werdelin 1990).

Diet: Given the very large canines in *Smilodon* and other characteristics, this felid apparently consumed large prey, such as proboscideans and giant ground sloths (e.g. Meachen-Samuels and Van Valkenburgh 2010, Anderson and Werdelin 2011). Possible prey items included *Mesotherium*, *Scelidotherium* and *Neosclerocalyptus* (Bermann 1994, Early to Middle Pleistocene), and large camelids, equids and giant ground sloths (Prevosti and Martin 2013) in the Pampean Region. Likewise, in the late Pleistocene of Southern Patagonia *Smilodon´*s prey also included large camelids, equids and ground sloths (Prevosti and Martin 2013). Morphometric analysis of the craniomandibular morphology of *Smilodon* supports the proposition that they hunted big mammals (Prevosti et al., 2010). The inferred consumption of such large prey gave rise to the suggestions that *Smilodon* was social and hunted in packs (Bocherens et al., 2016).

Geographic and stratigraphic distribution: Besides the distributions reported for specimens placed within one of the three species, the genus *Smilodon* has been reported from the late Pleistocene of Uruguay, coastal and Andean Ecuador, and southern Patagonia in Chile.

For more details, see each species.

Smilodon fatalis (Leidy 1868) †

General Taxonomic Characters: Same as for the genus.

Body Size: Body mass for *Smilodon fatalis* has been estimated between 160-280 kg (Christiansen and Harris 2005).

Diet: Carnivore.

General Ecology and/or Locomotion: In addition to the characteristics mentioned for the genus, *S. fatalis* has pectoral and pelvic adaptations that indicate enhanced stalking abilities typical of an ambush predator (Naples 2014), leading to speculations that it lived in environments with vegetation cover adequate to hide, likely in dense vegetation or woody landscapes. The morphology of *Smilodon´*s forearm is similar to the one of extant forest felids (Meloro et al., 2013) which suggests that it was adapted for living in closed habitat.

Confidence in Species Assignment: Valid species according to Leidy (1868).

Geographic and stratigraphic distribution: Late Pleistocene of Peru (Piura district).

Smilodon populator (Lund 1842) †

General Taxonomic Characters: It differs from *S. fatalis* by a generally larger size, a nearly straight dorsal profile of the rostrum as the result of developing high nassals, narrower skull with cranial part elongated relative to facial part, marked angle between mastoid and occipital plane. The postcranial shows more graviportal limb bones and extremely massive metapodials (Kurten and Werdelin 1990).
Body Size: Largest *Smilodon* species known. Its body size is estimated to be between 220-360 kg, with individuals as large as 400 kg (Christiansen and Harris 2005).
Diet: Carnivore. Probably consumed *Macrauchenia*, giant ground sloths and glyptodonts, Altough, isotopic analysis of dental and bone remains suggests it consumed other mammals that lived in open environments (Bocherens et al., 2016).
General Ecology and/or Locomotion: Possible competition of *S. populator* and *Protocyon troglodites* has been suggested for the late Pleistocene-early Holocene of the Pampaen region, where they would have been preying on similar prey items such as *Macrauchenia*, giant ground sloths and glyptodonts (Bocherens et al., 2016).
Confidence in Species Assignment: Valid species according to Kurten and Werdelin (1990).
Geographic and stratigraphic distribution: Pleistocene and Late Pleistocene of Argentina (Buenos Aires, Cordoba, El Cacho provinces); Early to Middle Pleistocene of Bolivia (Tarija valley and Nuapua); Late Pleistocene to early Holocene of Brazil (Bahia, Rio Grande do Sul, Sao Paulo, Matto Grosso, Rio Grande do Norte, Piau states); Pleistocene and Late Pleistocene of Venezuela (Falcon state).

Smilodon gracilis (Cope 1880) †

General Taxonomic Characters: It appears to have been distinctly smaller than *S. fatalis* and *S. populator* (Kurten and Werdelin, 1990; Turner and Anton, 1997), comparable in size to extant leopards, pumas, and jaguars (Sunquist and Sunquist, 2002). The same authors observed that *S. gracilis* seems to have been less massive in overall built than *S. populator* and more similar to *S. fatalis*.
Body Size: Its body mass has been estimated around 55-100 kg (Christiansen and Harris 2005).
Diet: carnivore.
General Ecology and/or Locomotion: Stable isotope analyses have revealed that the growth of their canines would have taken 16 months (Feranec 2005).
Confidence in Species Assignment: Valid species in South America according to Rincón et al., (2011).
Comments: This species is commonly found in Late Pleistocene deposits in North America, especially in Florida.
Geographic and stratigraphic distribution: Early to Middle Pleistocene of el Breal de Orocual, Venezuela.

Map 2.2.4: Geographic distribution of genus *Smilodon*. References: Prevosti and Martin 2013: Ultima Esperanza (CL), Tres Arroyos (CL); Prado et al., 1987: Paso Otero (AR); Reig 1957: Arroyo Loberia (AR); Tonni and Prado 1985: Lujan (AR); Zurita and Gasparini 2007: San Frnacisco (AR); Ubilla and Alberdi 1990: Pintados (UY); Zurita and Carlini 2004: Barranqueras (AR); Marshall and Sempere 1991: Tarija (BO), Ñuapua (BO); Coltorti and Abbazzi: Montesur-Tarija (BO); Churcher 1967; Drehmer and Ribeiro 1998: Mostradas (BR); Ghilardi and Fernandes 2011: Upper Ribeira (BR); Castro and Langer 2008: Abismo Iguatemi (BR); Salles and Cartelle 2006: Japones cave (BR); Lessa and Cartelle 1998: Toca das Onças (BR), Toca dos Ossos (BR) ; Cartelle and Hartwig 1996: Toca da Boa Vista (BR); Porpino and Santos 2004: Lejado de Soledade (BR), Lejado de Escada (BR); Paula Couto 1980: Joao Cativo (BR); Guerin 1991: Garrincho (BR), Toca da Cima dos Pilaos (BR),Toca da Janela da Barra do Antoniao (BR); Balneário Hermenegildo (BR); Pujos and Salas 2004: Talara (PE); Hoffstetter 1952: La Carolina (EC), Punin-Chalan (EC); Rincón 2006: Mene de Inciarte (VE); Rincón et al., 2011: Breal de Orocual (VE).

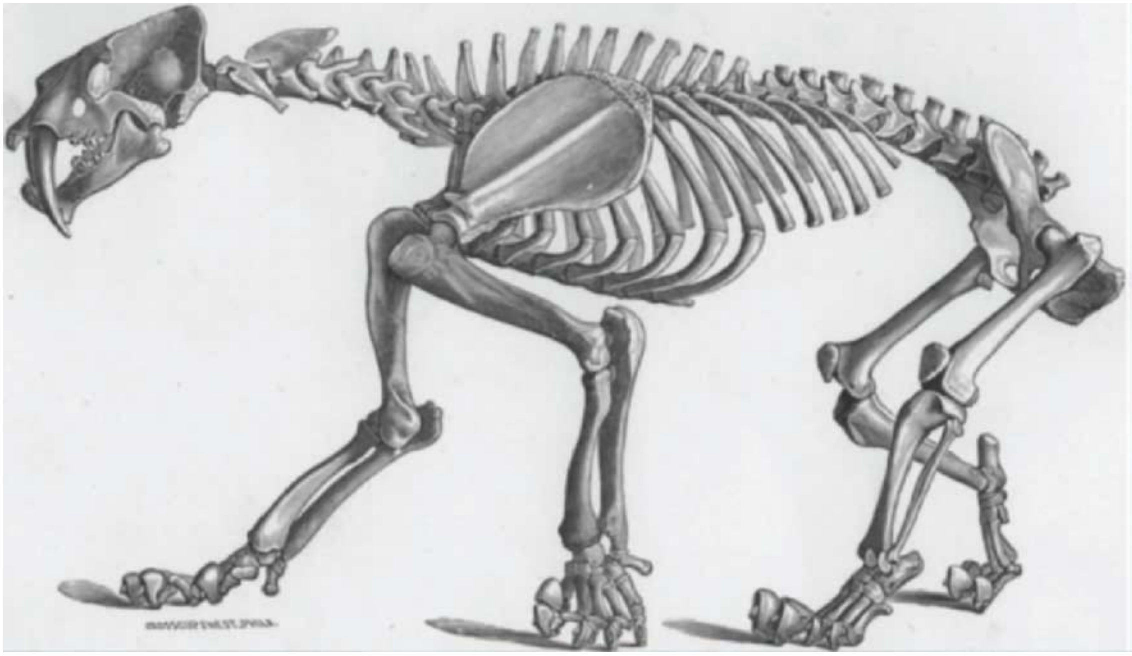

Figure 2.2.1: Skeleton of *Smilodon*. From Burmeister 1879.

2.3 Family URSIDAE Gray, 1825
Bears

Bears are medium to large carnivores, weighing up to 500 kg, with powerful build, short tail, and short ears. Among the skeletal features that differentiate them from other carnivores is a plantigrade posture where the weight is supported by the full sole of the foot. In diet, they are the most flexible Carnivora, being omnivorous but retaining morphological charcters that make them very efficient carnivores.

Today in South America only one genus and species of bear is present, the spectacled bear (*Tremarctos ornatus*). During the Pleistocene there were five additional species. Of these five, three were present in the Late Pleistocene.

Genus *ARCTOTHERIUM* Brumeister, 1879 †
(Map 2.3.1: Geographic distribution)

Five species are recognized in South America for this genus (Soibelzon 2004).

Arctotherium angustidens (Gervais & Ameghino 1880) †

General Taxonomic Characters: According to Soibelzon (2004) many cranial characters are usefull to diagnose this species, among these stand out a big skull with a very well developed saggital crest, pronounced zygomatic arches and flattened timpanic bullae. It presents a very well developed protocone in P4, and the paracone is higher than metacone in P4. (See Soibelzon 2004 for a more detailed diagnose of the species).
Body Size: This is the largest-sized bear with a calculated body mass that ranges between 412-1200 kg (Soibelzon and Tarantini 2009) and with some individuals weight up to ~2 tons (Soibelzon and Schubert 2011).
Diet: *A. angustidens* was probably omnivore, but with the morphological flexibility for eating meat when possible (Figueirido and Soibelzon 2010). Additional research based on morphology, biomechanics, dental pathology (breaking) and stable isotope analyses (from one individual from the Buenos Aires province) confirms the idea that *A. angustidens* was an omnivore that consumed a considerable amount of meat (Sobelzon et al., 2014). These authors proposed that meat was obtained through active hunting, fighting for prey captured by other predators and scavenging.
General Ecology and/or Locomotion: In size it was the biggest carnivore in the Ensenadan (Early to middle Pleistocene) of South America, only competing with *Smilodon populator*. It is likely that *A. angustidens* was one of the main predators of the carnivore guild of South America in the Ensenadan (Figueirido and Soibelzon 2010).
Confidence in Species Assignment: Valid species according to Soibelzon (2004).
Geographic and stratigraphic distribution: Early to middle Pleistocene (Ensenadan) in Argentina (Buenos Aires province) and Bolivia (Tarija District).

Arctotherium wingei (Ameghino 1902) †

General Taxonomic Characters: Small skull, timpanic bullae inflated. Messeteric crest is straight and perpendicular to the anterior axis of the mandible. The lingual cingulum is absent in P4 (Soibelzon 2004, see this reference for more details).
Body Size: This is the smallest representative of the group with a body mass estimated between 51-150 kg (Soibelzon and Tarantini 2009).
Diet: Based on the skull morphology of an immature individual of *A. wingei* it has been suggested that this was the most herbivorous species (if not exclusively so) of all the Pleistocene South American bears (Figueirido and Soibelzon 2010).
Confidence in Species Assignment: Valid species according to Soibelzon (2004).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Minas Gerais state); Pleistocene of Bolivia (Tarija district); Late Pleistocene-early Holocene of Venezuela (Falcon and Monagas states)

Arctotherium vetustum (Ameghino 1885) †

General Taxonomic Characters: Outstanding zigomatic arches with a pronounced posterior angle, inflated auditory bullae, P4 with paracone higher that the metacone (See Soibelzon 2004 for more details).
Body Size: *A. vetustum* has an estimated body mass between 102-300 kg (Soibelzon and Tarantini 2009).
Diet: The mandibular morphology suggests that it had an omnivorous diet with a high proportion of plant matter in it (Figueirido and Soibelzon 2010).
Confidence in Species Assignment: Valid species according to Soibelzon (2004).
Geographic and stratigraphic distribution: Middle Pleistocene of Argentina (Buenos Aires and Entre Rios province) and Pleistocene of Brazil (Minas Gerais).

Arctotherium bonariense (Gervais 1848-52) †
(Fig. 2.2.2)

General Taxonomic Characters: Inflated timpanic bulla, masseter crest is straight and perpendicular to the anterioposterior axis of the mandible. P4 without protocone, with paracone higher that the metacone (See Soibelzon 2004 for more details).
Body Size: Its body mass has been estimated between 171-500 kg (Soibelzon and Tarantini 2009).
Diet: The mandibular morphology of *A. vetustum* suggests an omnivorous diet with a high proportion of plant matter but with the possibility of ingesting meat and bones as well (Figueirido and Soibelzon 2010).
Confidence in Species Assignment: Valid species according to Soibelzon (2004).
Geographic and stratigraphic distribution: Middle to late Pleistocene of Argentina (Buenos Aires province).

Figure 2.2.2. *Archtotherium bonariense*. Located at the Natural History Museum of Denmark. Photo by N. Villavicencio.

Arctotherium tarijense (Ameghino 1902) †

General Taxonomic Characters: Timpanic bullae are inflated, masseter's crest is straight and perpendicular to the mesiodistal axis of the mandible, P4 presents a much higher protocone compared to the metacone (Soibelzon 2004, see reference for more details).
Body Size: Medium to large sized bear with a body mass ranging between 135-400 kg (Prevosti and Martin 2013).
Diet: The morphology of the masticatory apparatus suggests a high proportion of plant matter in its diet (Figueirido and Soibelzon 2010).
Confidence in Species Assignment: Valid species according to Soibelzon (2004).
Geographic and stratigraphic distribution: Middle Pleistocene to early Holocene of Argentina (Buenos Aires and Santa Fe provinces); early Holocene of Uruguay (Rio Negro district); Pleistocene of Bolivia (Tarija district); Late Pleistocene-early Holocene of Chile (Magallanes and Aysen regions).

Map 2.3.1: Geographic distribution of *Archtotherium*. References: Prevosti and Soibelzon 2003: Cueva de Los Chingues (CL); Ameghino 1904: Mercedes (AR); Berman 1994: Coronel Pringles (AR); Soibelzon et al., 1999: Arrecifes (AR), Minas Gerais (BR); Prevosti and Martin 2013: Cueva del Puma (AR); Soibelzon 2004: Buenos Aires city (AR); Mercedes (AR); Lujan (AR); Arrecifes (AR); Salto (AR); Camet (AR); Centinela del Mar (AR); Rios Salado (AR); Mar del Plata (AR); Toscas del Rio de la Plata (AR), La Plata (AR), Partido de Moreno (AR), Mar del Plata (AR), Ezeiza (AR), Ezpeleta (AR), Playa Camet (AR), Punta Hermengo (AR), Miramar (AR), Mar del Sur (AR) , Tarija (AR), Rio Quequen Salado (AR), Necocheea (AR), Roque Perez (AR), Olivos (AR), Martinez (AR), Punta Piedras (AR), Cueva del Guacharo (VE), Fauna Local El Muaco (VE); Cartelle and Hatwig 1996: Toca da Boa Vista (BR); Guerin and Faure 1991: Toca da Cima dos Pilao (BR); Trajano and Ferrarezzi 1995: Gruta do Urso Fosil (BR); López et al., 2015: Baño Nuevo (CL); Ubilla and Perea 1999: Arroyo Guitierres (UY); Cartelle 1998: Ubajara (BR); Lessa et al., 1998: Toca da Galameria (BR).

Genus *TREMARCTOS* Gervais, 1855

The genus *Tremactos* includes two species, *T. floridianus* from the Late Pliocene and Pleistocene of North America and the extant species *T. ornatus*, which is the only survivor of the subfamily Tremarctinae. *T. ornatos* has not been recorded as a fossil (Soibelzon et al., 2005).

Tremarctos ornatus (F. Cuvier 1825)

General Taxonomic Characters: The only extant species belonging to this genus and the only bear present in South America today.
Body Size: It is a medium-sized bear with a maximum weight of 200 kg (Redford and Eisenberg 1992).
Diet: Its diet is omnivorous, consisting of fruits, nuts and small vertebrae (Goldstein et al., 2008).
General Ecology and/or Locomotion: Inhabits mainly the foothills of the Andes Mountains, occupying a great variety of habitats from desert-scrub to forests to high altitude grasslands, ranging in elevation from 250 to 4,750 masl. Litter size is typically two cubs. (Redford and Eisenberg 1992, Goldstein et al., 2008).
Confidence in Species Assignment: Valid species according to Cuvier (1825).
Geographic and stratigraphic distribution: Presently it is found in Panama, Peru and Bolivia. Presumably it was also present through at least much of the Holocene although no fossils have been reported (Redford and Eisenberg 1992).

3. Order PROBOSCIDEA Illiger, 1811

This order includes extant elephants and extinct mammoths and mastodonts, very large-sized herbivores (over 2 tonnes) which are characterized by the presence of tusks and developed muscular trunks. No living member of this order persists today in South America.

Table 3. South American Megafaunal Proboscidea. † = extinct

Family GOMPHOTHERIIDAE Cabrera, 1929 †
Genus *CUVIERONIUS* Osborn, 1923 †
Cuvieronius hyodon (Fischer 1814) †
Genus *NOTIOMASTODON* Cabrera, 1929 †
Notiomastodon platensis (Ameghino 1888) †

3.1 Family GOMPHOTHERIIDAE Cabrera, 1929 †

Gomphotheres (Table 3) are the only Proboscidea recorded in the Pleistocene fossil record of South America. They are characterized by specialized dentition that consists of the two upper second incisors modified as tusks and six pairs of upper and lower molars with cusps arranged in a trefoil pattern. The skull and the jaw are short compared to other member of the order (Simpson and Paula-Couto 1957; Paula-Couto 1979; Prado et al. 2001; Ferretti 2008).

South American gomphotheres are derived from North American ancestors and have a set of unique morphological characteristics. For example they possess a higher cranium, wider forehead and relatively larger premaxillaries compared to North American gomphotheres (Ferretti 2008). Upper tusks are present in males and females. A longitudinal band of enamel occurs in juveniles and is lost during development through wear with the exception of the genus *Cuvieronius* where the band persists until adulthood (Ferretti 2008). Cheek teeth are bunodont but more hypsodont that in earlier gomphotheres (Ferretti 2008). The postcranial elements indicate that all South American gomphotheres were very massive and stout.

The taxonomy of South American gomphotheres has a complicated history and is still a matter of debate. According to the most recent publications (Mothe et al. 2011, 2012) only two genera are present in the Quaternary of South America: *Cuvierionus* (Osborn 1923) and *Notiomastodon* (Cabrera 1929). Previously, the presence of *Cuvieronius* along with the genus *Stegomastodon* (Pohlig 1912) was proposed (Alberdi y Prado 1995 and Prado *et al.* 2003, 2005, 2008) and the presence of a set of three genera: *Cuvireronius*, *Haplomastodon* (Hoffstetter 1950) and *Notiomastodon* was suggested based on morphological and phylogenetic analyses (Ferreti 2008, 2010). Here I follow the most recent publications of Mothe 2011 and Mothe 2012.

Genus *CUVIERONIUS* Osborn, 1923 †
(Map 3.1.1: Geographic distribution, Figure 3.1)

Cuvieronius hyodon (Fischer 1814) †

General Taxonomic Characters: The only recognized species of this genus is *C. hyodon*, which is the type species. It is different from *Notiomastodon* in having a lower cranium, by the persistence of a twisted enamel band along the upper tusks in adulthood and the occurrence of incisors in the mandible in some juvenile individuals (Ferretti 2008).
Body Size: Its body size is estimated around 5,000 kg (Smith et al., 2003).
Diet: Almost exclusively a mixed feeder (Prado et al., 2005). According to stable isotope analyses, *C. hyodon* had a broad and flexible diet consuming plant material from woodlands and mixed C3-C4 and C4 grasslands, but with some regional variation (Domingo et al. 2012). For example, *C. hyodon* from Ecuador shows δ^{13}C values typical of woodlands, C3 grasslands and mixed C3-C4 environments, while *C. hyodon* from Peru shows values typical of C4 grassland environments (Domingo et al. 2012, Sanchez et al. 2004).
General Ecology and/or Locomotion: It inhabited the Andean corridor of South America not occurring in the lowlands of eastern South America, possibli inhabiting in temperate-cold climate conditions (Prdao et al., 2005).
Confidence in Species Assignment: Valid species according to Prado et al., (2005).
Geographic and stratigraphic distribution: Pleistocene of Colombia, Ecuador, Bolivia, Peru and Chile.

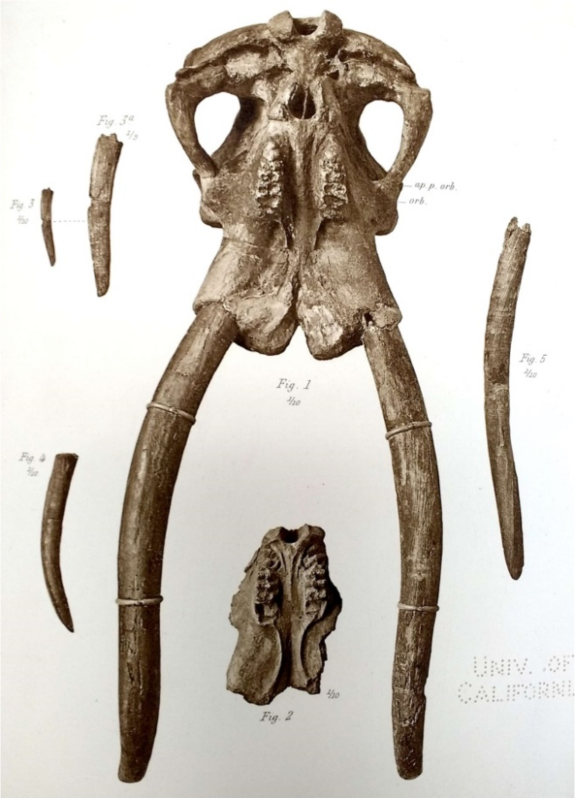

Figure 3.1.1: *Cuvieronius* from Tarija, Bolivia. From Boule and Thevenin 1920.

Map 3.1.1: Geographic distribution of genus *Cuvieronius*. References: Nuñez 1983: Quereo (CL); Boule and Thevenin 1920: Tarija (BO); Coltorti et al., 2007: Montesur-Tarija (BO), Rio Rujero (BO); Hoffstetter 1952: Cotocollao (EC), Malchingui (EC); Chavez-Aponte et al., 2008: La Colina (VE); Mothe et al., 2013: All other approximate locations.

Genus *NOTIOMASTODON* Cabrera, 1929 †
(Map 3.1.2: Geographic distribution)

Notiomastodon platensis (Ameghino 1888) †

General Taxonomic Characters: *Notiomastdon* differs from *Cuvieronius* by the absence of the spiraled torsion of the tusks and by lacking of the spiraled enamel band along the tusks (Ferretti 2008). It has a short but higher skull than *Cuvieronius* (Mothé et al 2011). The molars are more complex than in *Cuvieronius* and have a greater number of cones (Mothé et al 2011).
Body Size: Body mass has been calculated around 7,000 kg (Fariña et al. 2013).
Diet: Stable isotope analyses show that *Notiomastodon* inhabited a broad set on environments with δ^{13}C values typical of C3 woodlands, mixed C3-C4 environments and C4 grasslands (Domingo et al 2012). A stable isotope analysis from the intertropical region of Brazil during the late Pleistocene shows δ^{13}C values of a grazer on C4 grasses (Melo Franca 2014). Specimens from Ecuador have also been reported to have δ13C values showing a diet based exclusively in C4 plants (Sanchez et al. 2004).
General Ecology and/or Locomotion: It appears to have predominated in lower latitudes, and was better adapted to warm or temperate climatic conditions (Prado et al., 2005).
Confidence in Species Assignment: Valid species according to Mothé et al., (2012).
Geographic and stratigraphic distribution: Middle Pleistocene to early Holocene recorded in western and eastern South America (Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile, Brazil, Argentina).

Map 3.1.2: Geographic distribution of genus *Notiomastodon*. References: Guerin 1991: Toca da Janela da Barra do Antoniao (BR); Rolim 1974: Lage Grande (BR); Bryan et al., 1978: Taima Taima (VE); Alvarez 1974: Toropi (UY); Porta 1969: Curiti (BR); Hoffstetter 1978: General Bruguer (PY); Paula Couto 1978: Serro do Gronda (BR); Paula Couto 1980: Taperoa (BR); Tonni et al., 1985: Lujan (AR); Deschamps and Borromei 1992: Bajo San Jose (AR); Hoffstetter 1968: Nuapua (BO); Peyre et al., 1998: Garrincho (BR); Lemon and Churcher 1961: Talara (PE); Cruxent 1970: Cucuruchu (PE); Zurita et al., 2004: Avia Terai (AR), Barranqueras (AR), Charata (AR), Cateli (AR); Alvargenga et al., 2010: Casil Quarry (UY); Hoffstetter 1952: La Carolina (EC), Calderon (EC), Region de la Paz (EC), Alangasi (EC), Punin-Chalan (EC), Tumbaco (EC), Quebrada la Tola (EC), Checa (EC), Hacienda Pucara (EC); Alberdi et al., 2002: Gruta dos Brejoes (BR), Toca dos Ossos (BR), Janauba (BR), Gruta do Inga (BR), Bonito (BR), Pote (EC), Lapa do Caetano (EC); Alberdi et al., 2007: Campo Viñoles (UY); Tonni 1987: El Palmar (AR); Pujos and Salas 2004: Talara (PE), Celendin (PE); Villarroel and Clavijo 2005: Cantera Barrera (VE); Chavez-Aponte et al., 2008: LA Colina (CO); Villarroel et al., 2001: Nucleo Escolar LA Junta (CO); Costa Ribeiro and Souza Carvalho 2009: Lagoa do Rumo (BR); Dantas and Tasso 2007: Fazenda Caraiba (BR); Simpson and Paula Couto 1957: Aguas do Araxa (BR); Cantalamessa et al., 2001: Rio Canas (EC); Marshall and Sempere 1991: Tarija (BO); Mothe 2013: all other aproximate localities.

South American Native Ungulates

The following two orders of mammals, Litopterna and Notoungulata, are ungulates that evolved in South America before the Great American Biotic Interchange, at which time the ungulates from the northern Hemisphere (Perissodactyls and Artiodactyls) arrived. While there are 5 orders of South American native ungulates, only litopterns and notoungulates were present during the Pleistocene; they are now extinct.

4. Order LITOPTERNA Ameghino, 1889 †

Litopterns (Table 4) resemble camels and small horses. The clade was diverse, and was present in South America from the early Paleocene to the Late Pleistocene-Early Holocene, reaching their highest diversity in the Late Miocene (Bond 1999).

Table 4. South American Megafaunal Litopterna. † = extinct

Family MACRAUCHENIIDAE Gill, 1872 †
Genus *MACRAUCHENIA* Owen, 1838 †
Macrauchenia patachonica (Owen 1838) †
Genus MACRAUCHENOPSIS Paula Couto, 1945 †
Macrauchenopsis ensenadensis (Paula Couto 1945) †
Genus *WINDHAUSENIA* Kraglievich, 1930 †
Genus *XENORHINOTHERIUM* Cartelle and Lessa, 1998 †
Xenorhinotherium bahiense (Cartelle and Lessa 1998) †
Family PROTOTHERIIDAE (Ameghino 1887) †
Genus *NEOLICAPHRIUM* (Frenguelli 1921) †
Neolicaphrium recens (Frenguelli 1921) †

4.1 Family MACRAUCHENIIDAE Gill, 1872 †

Macraucheniids are large to very large herbivores with long necks and long limbs, with three digits on each foot. Their dentition was more hypsodont that in other litopterns, is complete and without a diastema. The most distinctive characteristic is the retraction of the nares, which migrated to a frontal position in the genus *Macrauchenia*. All were cursorial, and diet ranged from browsing to grazing (Bond et al., 1995; Bond 1999).

Genus *MACRAUCHENIA* Owen, 1838 †
(Map 4.1.1 Geographic distribution)

This genus is characteristic of the Lujanian (Late Pleistocene-early Holocene) of South America. Three species have been recognized: *M.* (*Pseudomacrauchenia*) *yepesi (*Kraglievich 1930), *M. ullomensis (*Sefve 1913) and *M. patachonica (Owen 1840)* (Guérin and Faure 2004, Paula Couto 1979). Some authors have postulated that *M. yepesi* is synonymous with *Promacrauchenia,* a Pliocene genus (Guérin and Faure 2004). The validity of *M. ullomensis* has also been questioned, as it may be a junior synonym of *M. patachonica* (Guérin and Faure 2004). For these reasons, recent work regards *Macrauchenia patachonica* as the only representative of the genus during the Pleistocene (e.g. Labarca 2015), a convention I follow here.

Macrauchenia patachonica (Owen 1838) †

General Taxonomic Characters: Elongated and stretch skull. The name *Macrauchenia* means "Long neck" which makes reference to that characteristic in this taxon. Distinctive features of the skull include elongation and especially the modified nasal region, which has reduced bones and nasal apertures that are located above the orbits and facing dorsally. This anatomical characteristic suggests the presence of a proboscis similar to that of tapirs; even the presence of a nasal blowhole like some cetaceans was suggested (Sefve 1925). The dental formula in *Macrauchenia* is complete with 44 low crowned teeth (MacFadden and Shockey 1997).
Body Size: Estimated body mass is around 1,100 kg (Fariña et al., 1998).
Diet: In general *Macrauchenia* is thought to have browsed on high plants (Scott 1913, Simpson 1980, Webb 1978). Recent analyses of the cranial morphology and reconstruction of the masticatory system of *Macrauchenia* also suggested a browsing feeding habit in open to mixed habitats (Varela and Fariña 2015). On the other hand, stable isotope analyses of *Macrauchenia* from Tarija, Bolivia, indicate a mixed diet with a combination of of c3 and c4 plants and possibly CAM plants as well (MacFadden and Shockey 1997). Another study using stable isotope analyses on a specimen from the Pampean region of Argentina also showed a mixed diet with δ^{13}C values typical of woody, more open C3 and C3-C4 environments (Domingo et al., 2012). A frugivorous diet has been inferred as well, based on cranio-dental measurements (Czerwonogora et al., 2003).
General Ecology and/or Locomotion: According to biomechanical and ecomorphological studies, it has been estimated that *M. patachonica* possibly reached running velocities of 50 km/h and was able to swerve and dodge in response to predator attacks (Fariña et al., 2005).
Confidence in Species Assignment: Valid species according to Lydekker (1894).
Geographic and stratigraphic distribution: Geographic and stratigraphic distribution: Late Pleistocene of Chile (Aysen and Antofagasta regions); Late Pleistocene of Argentina (Buenos Aires province); Middle to Late Pleistocene of Uruguay (Canelones district); Pleistocene of Paraguay (near Asunción); Early to Late Pleistocene of Bolivia (Tarija, Oruro, La Paz, Chuquisaca districts); Late Plesitocene of Perú; Pleistocene of Brazil (Pernambuco, Bahia, Rio Grande do Sul, Piaui States). The genus has also been reported in the late Pleistocene of Venezuela and in Southern Patagonia in Chile.

Map 4.1.1: Geographic distribution of genus *Macrauchenia*. References: Lopez et al., 2010: Baño Nuevo (CL); Labarca et al., 2008: Las Guanacas (CL); Labarca 2009: Kamac Mayu (CL); Deschamps and Tonni 1992: Arroyo Napostá Grande (AR); Aramayo 1985: Monte Hermoso Beach (AR); Prado et al., 1987: Paso Otero-Verde (AR); Bargo and Menegaz 1986: Arroyo Tapalque (AR); Tonni and Prado 1985: Lujan (AR), Indio Rico-Quequen Salado (AR); Ubilla and Alberdi 1990: Pintado (UY); Hoffstetter 1978: General Bruguer/Riacho Negro (PY); Marshall and Sempere 1991: Puchuni (BO), Tarija (BO), Ayo Ayo (BO); Boule and Thevenin 1920: Montesur (BO); Hoffstetter 1968: Ñuapua (BO); Frailey and Campbell 1980: Quebrada de Cachimayu (PE); Vidal 1955: Laje Grande (BR); Guerin 1991: Toca do Serrote do Artur (BR), Toca da Janela da Barra do Antoniao (BR), Lagoa Sao Vitor (BR), Toca da Cima dos Pilao (BR); Scherer and Pitana 2009: Sanga Borba Creek, Sanga da Cruz Creek (BR), Touro Passo creek (BR), Chui creek (BR), Hermenegildo beach (BR); Nordenskjöld 1900: Cueva del Milodon (CL); Labarca 2015: Quebrada de Tongoicillo (CL); Oliver Schenider 1935: Las Pozas (CL); Tonni 1970: Punta Hermengo (AR); Martinez and Jacay 2000: La Huaca (PE); Bryan et al., 1978: Taima Taima (VE); Paula Couto 1980: Curimatas (BR), Taperoa (BR); Alvargenga et al., 2010: Casil Quarry (UY).

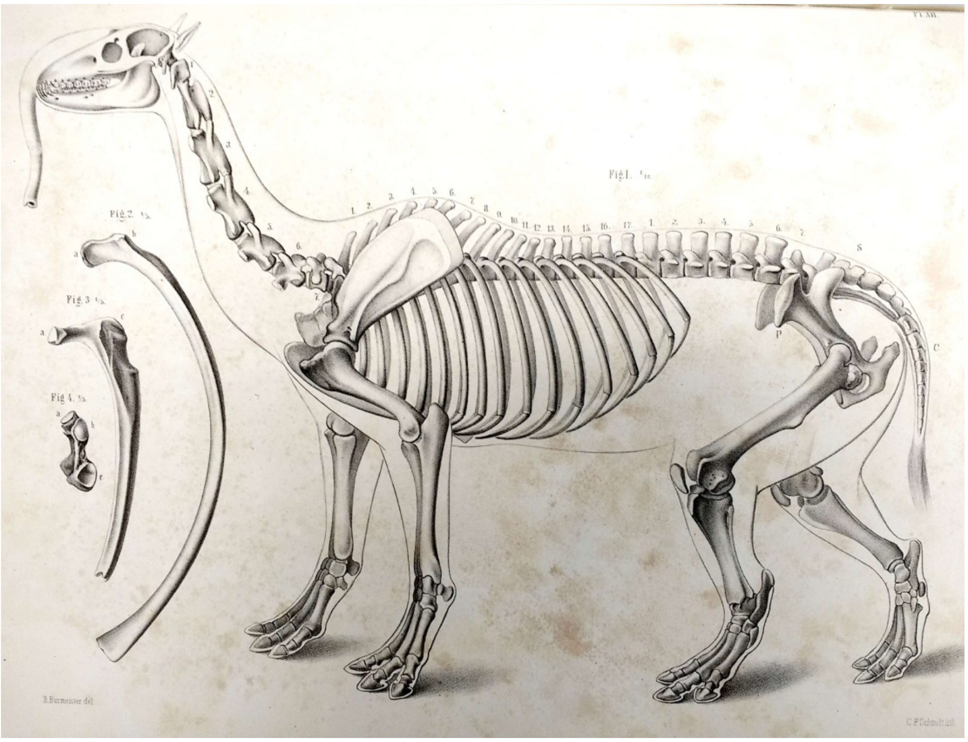

Figure 4.1.1: Skeleton of *Macrauchenia*. From Burmeister 1879.

Genus MACRAUCHENOPSIS Paula Couto, 1945 †
(Map 4.1.2: Geographic distribution)

Macrauchenopsis ensenadensis (Paula Couto 1945) †

This genus was described by Palula Couto in 1945 based on *Macrauchenia ensenadensis* (Ameghino, 1904) from the lower Pampean (Ensenadan, Middle Pleistocene), and possibly Lujánian (Pleistocene) (Soria 1987). Some authors have considered it as synonym with *Windhausenia* (Kraglievich 1950, Hofstetter and Paskoff 1966, Marshall et al., 1984), while is accepted as a valid taxon by others (Soria 1987, Cartelle and Lessa 1988, Bond et al., 1995).

General Taxonomic Characters: Only a few elements are known for this taxon including a calcaneus (holotype), the front half of a skull, a lower jaw and a mandible right half, teeth, a metatarsal and a proximal fragment of femur. The calcaneum and teeth are distinct from *Macrauchenia,* (Guerin and Feure 2005) supporting the hypothesis of a different genus.
Body Size: This is species is characterize by a bigger body compared to *Macrauchenia* (> 1,100 kg) (Guerin and Feure 2005).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid species according to Bond et al., (1995).
Geographic and stratigraphic distribution: Middle Pleistocene of Buenos Aires province of Argentina.

Map 4.1.2: Geographic distribution of genus *Macrauchenopsis*. Reference: Deschamps 2005: Bajo San Jose (AR).

Genus *WINDHAUSENIA* Kraglievich, 1930 †
(Map 4.1.3: Geographic distribution)

There is one species known for the late Pliocene of Uquia (*W. delacroixi*, Kraglievich, 1930). The genus is known from the Pleistocene of Argentina (Reig 1957). While some authors have proposed *Windhausenia* as a synonym of *Macraucheniopsis (*Marshall et al., 1984), the most recent phylogenetic analyses (Schmidt and Ferrero 2014) indicates that *Windhausenia* is more closely related to *Xenorhinotherium* than to *Macraucheniopsis*.

General Taxonomic Characters: The measurements presented by Kraglievich (1930) from the cranial material used to establish this new genus (Schmidt and Ferrero 2014) indicate that it was characterized by smaller body size than *Macrauchenia.*
Body Size: Its body size is estimated around 700 kg (Smith et al., 2003).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid according to Schmidt and Ferrero (2014).
Geographic and stratigraphic distribution: Pleistocene of the Buenos Aires Province in Argentina.

Map 4.1.3: Geographic distribution of genus *Windhausenia*. Reference: Reig 1957: Arroyo Loberia (AR).

Genus *XENORHINOTHERIUM* Cartelle and Lessa, 1998 †
(Map 4.1.4: Geographic distribution)

Xenorhinotherium bahiense (Cartelle and Lessa 1998)

General Taxonomic Characters: Several specific cranial characteristics and a more graceful skeleton, distinguish *Xenorhinotherium* from *Macrauchenia* (Cartelle and Lessa 1998, Guerin and Faure 2004)
Body Size: Body size is similar to *Macrauchenia* and probably around 1,100 kg (Cartelle and Lessa 1998, Guerin and Faure 2004).
Confidence in Species Assignment: The validity of this taxon is unclear. Guerin and Faure (2004) proposed that it is a junior synonym of *Macrauchenia patachonica* based on a study of dental and postcranial material of multiple specimens from the Sao Raimundo Nonato region in Brazil. Nevertheless, they did not make clear comparisons with the original material used by Cartelle and Lessa (1998) to erect the genus. More recent phylogenetic analyses of the Macraucheniidae do not support the synonym hypothesis (Correa et al., 2012), with *Xenorhinotherium* appearing as sister taxa of the group [*Macrauchenia* + *Machrauchenopsis*]. Most recent studies regard *X. bahiense* as a valid taxon (i.e.: Scherer 2009, Socorro 2006).
Geographic and stratigraphic distribution: Pleistocene of Venezuela (Falcon district); Pleistocene of the intertropical region of Brazil (Paraiba and Minas Gerais, Mato Grosso do Sul states).

Map 4.1.4: Geographic distribution of genus *Xenorhinotherium.* References: Salles and Cartelle 2006: Japones Cave (BR); Lessa and Cartelle 1998: Toca dos Ossos (BR); Porpino and Santos 2004: Lejado de Soledade (BR); Correa et al., 2012: Lagoa de Dentro (BR); de Melo et al., 2005: Araxa (BR); Socorro 2006: Falcon state (VE).

4.2 Family PROTOTHERIIDAE (Ameghino 1887) †

These small to medium –sized animals are characterized by brachydont to mesodont teeth and a marked trend towards monodactyly (like horses). Their skeleton resembles that of perissodactyls (horses and tapirs) but their dentition is characteristic of a litoptern (Bond, 1999; Bond *et al*., 2001).

Genus *NEOLICAPHRIUM* (Frenguelli 1921) †

(Map 4.2.1: Geographic distribution)

Neolicaphrium recens (Frenguelli 1921)

General Taxonomic Characters: Molariforms have a relatively high crown but retaining the mesodont character rather than hypsodont; p3-m3 present a very well developed entoconid; m3 has a rudimentary third lobe. At least p3-m3 present a well developed layer of cementum (Bond et al., 2001).
Body Size: This proterotheriid is medium to small in size, similar to the extant *Ozotoceros bezoarticus* (Pampas deer) which has a body mass of 35 kg.
Diet: Herbivore, possibly a mixed feeder given the mesodont dentitions present in this taxa.
General Ecology and/or Locomotion: The mesodont dentition suggests that they lived in environments similar to forested savannas (Bond et al., 2001).
Confidence in Species Assignment: Valid species according to Bond et al., (2001).
Geographic and stratigraphic distribution of the genus: Middle to Late Pleistocene of Argentina and Uruguay (Salto District); Late Plesitocene of Brazil (Rio Grande do Sul State).

Map 4.2.1 Geographic distribution of the genus *Neolicaphrium*. References: Bond et al., 2001: Toropi stream (AR), Cordoba province (AR); Ubilla et al., 1994: Sopas formation (UY).

5. Order NOTOUNGULATA Roth, 1903 †

The name Notoungulata means ¨Southern Ungulates¨. The order comprises two monophyletic groups, the Toxodontia which are large to very large animals that inhabited South America from the Paleocene to the late Pleistocene, and Typotheria, which were small to medium-sized forms resembling rodents. They also appeared in the Paleocene and persisted until the early Pleistocene (Ameghino 1907, Scott 1913, Bond et al., 1999).

Table 5. South American Megafaunal Notoungulata. † = extinct

Family TOXODONTIDAE Gervais, 1847 †
Genus *TOXODON* Owen, 1837 †
Toxodon platensis (Owen 1837) † *Toxodon ensenadensis* (Ameghino 1887) † *Toxodon gracilis* (Gervais and Ameghino 1880) † *Toxodon chapalmalensis* (Ameghino 1908) †
Genus TRIGODONOPS Kraglievich, 1930 †
Trigodonops lopesi (Roxo 1921) †
Genus *MIXOTOXODON* van Frank, 1957 †
Mixotoxodon larensis (van Frank 1957) †
Family MESOTRHERIIDAE Alston, 1876 †
Genus *MESOTHERIUM* (Serres 1867) †
Mesotherium cristatum (Serres 1867) †

5.1 Family TOXODONTIDAE Gervais, 1847 †

Genus *TOXODON* Owen, 1837 †
(Map 5.1.1: Geographic distribution. Fig. 5.1)

General Taxonomic Characters: The skull is big with short nasal bones and the limbs are short and robust, with three digits. Maxillaries are broad suggesting the presence of a prehensile lip. Teeth have continuous growth with lower incisors oriented forward while upper incisors are straight and vertical (Ubilla, 1985; Bond et al., 1995; Bond, 1999).
Body Size: *Toxodon* is characterized by a body mass estimated to be around 1791 kg (Elissamburu 2012) and a lengt of about 3.5 m.
Diet: Undetermined herbivore.
General Ecology and/or Locomotion: Biomechanical studies suggest an amphibious life style (Archuby, 1998). The morphology of the skull reveals the presence of a strong temporal muscle which indicates a great masticatory capacity. Orbits are slightly elevated as is the position of the auditory meatus. This last characteristic resembles the condition in *Hippopotamus* and is consistent with amphibious habits, (Paula Couto 1979) but it is also consistent with a grazing habit, as in modern Rhinoceros. According to the latest revision of *Toxodon* and its comparison

with modern rhinos and hippos (Santos 2012), the morphology of *Toxodon* seems to be more related to terrestrial habits and is more similar to modern rhinoceros. For example, the vertebral column in *Toxodon* is characterized by pronounced spiny process in the thoracic vertebra, related to musculature that sustains the head in an elevated position for long time, as in rhinos. Also, the hind limbs had great flexibility facilitating the support of the anterior part of the body.
Confidence in Species Assignment: Valid genus according to Owen (1837).
Comments: The species within *Toxodon* are differentiated mainly by specific differences in the cranium, differences in size and by difference in temporal occurrences.
Geographic and stratigraphic distribution: The genus *Toxodon* is known from the late Pliocene to the early Holocene in South America (Bond et al. 1995). Is known from Argentina (South of Buenos Aires province), Paraguay, Brazil, Bolivia and Venezuela.

Toxodon platensis (Owen 1837) †

General Taxonomic Characters: See description for the genus. *T. burmeisteri* is considered as a junior synonym of this species (Mendoça 2012).
Body Size: It has been estimated over 1600 kg (Fariña et al., 1998).
Diet: Stable isotope analyses on *Toxodon platensis* remains suggest a broad ecological flexibility, with preference for C3 forests in the Amazon; a C3 mixed diet in C3 grasslands and/or forested-grassland areas in Buenos Aires, Argentina and Bahia State, Brazil; and predominantly a C4 grass eater in northern Argentina and El Chaco of Bolivia (MacFadden 2005).
General Ecology and/or Locomotion: Same as for the genus.
Confidence in Species Assignment: Valid according to Santos (2012).
Geographic and stratigraphic distribution: Pleistocene of Bolivia (Tarija district) and southern Brazil (Matto Grosso state), Pleistocene and Late Pleistocene of the Pampas region (Argentina, Uruguay, and Rio Grande do Sul (Brazil).

Toxodon ensenadensis (Ameghino 1887) †

General Taxonomic Characters: It is considered a differen species from *T. platensis* mainly because it occurs exclusively in Ensenadan (Middle Pleistocene) deposits (Santos 2012).
Body Size: This species is characterized by a bigger size compared to *T. platensis*.
Confidence in Species Assignment: Valid according to Santos (2012).
Geographic and stratigraphic distribution: Early to Middle Pleistocene (Ensenadan) of Buenos Aires province, Argentina.

Toxodon gracilis (Gervais and Ameghino 1880) †

General Taxonomic Characters: It differs from the other species mainly because of its smaller body size (Santos 2012).
Body Size: It is of smaller size than the other *Toxodon* species, being of similar size of extant pigmy hippos (180-275 kg) (Santos 2012).

Confidence in Species Assignment: The validity of this taxon remains uncertain according to Santos (2012).

Geographic and stratigraphic distribution: Middle to Late Pleistocene (Bonaerian) and Late Pleistocene to Early Holocene (Lujánian) of Argentina.

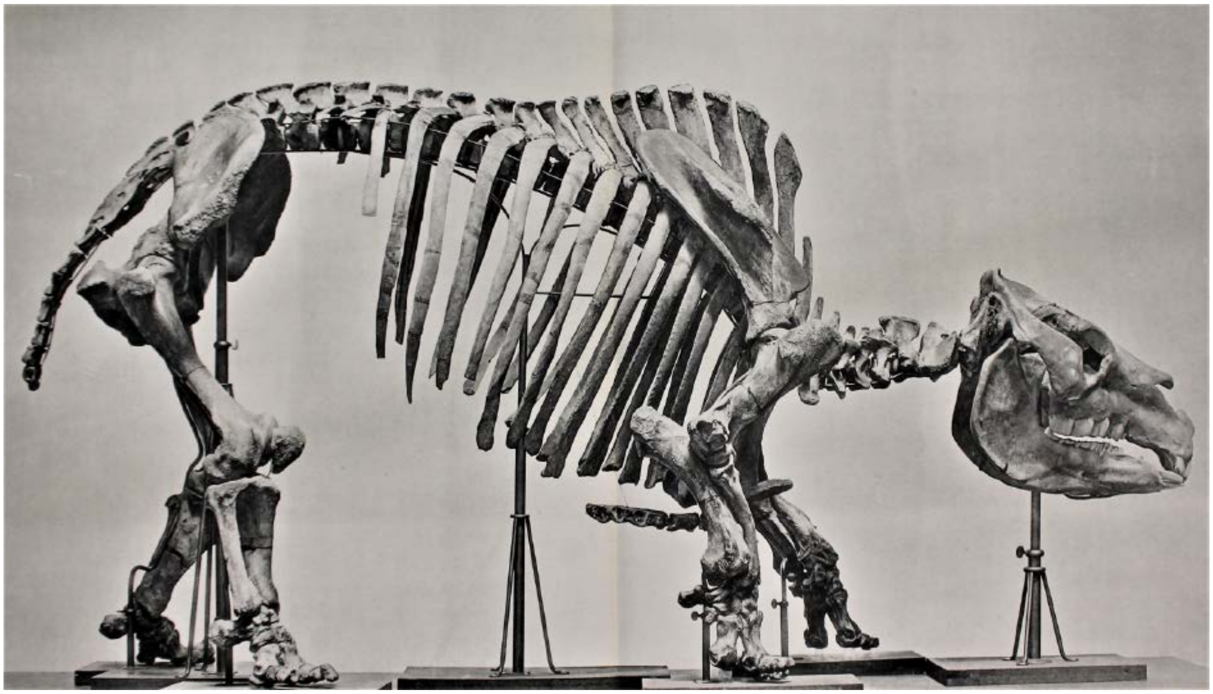

Figure 5.1.1: *Toxodon*, from Lyddeker 1894.

Map 5.1.1 Geographic distribution of the genus *Toxodon*. References: Alvargenga et al., 2010: Casil Quarry (UY); Aramayo 1985: Monte Hermoso (AR); Bargo and Menegaz 1986: Arroyo Tapalque (AR); Deschamps 2005: Bajo San Jose (AR); Deschamps and Borromei 1992: Bajo San Jose (AR); Prado and Menegaz 1987: Paso Otero (AR); Reig 1957: Arroyo Loberia (AR); Zurita and Gasparini 2007: San Francisco (AR); Ubilla 1985: Piedra Pintada (UY); Ubilla and Alberdi 1990: Pintado (UY); Paula Couto 1944: Rio Quarai (UY); Alvarez, 1974: Arroyo Toropi (AR); Zurita and Carlini 2004: Barramqueras (AR), Charata (AR), Avia Terai (AR), Presidencia Roque Saenz Peña (AR); Zurita and Miño-Boilini 2009: Rio Bermejo (AR); Patterson 1936: Quebrada Agua Blanca (AR); Hoffstetter 1978: General Bruguer (PY); Marshall and Sempere 1991: Tarija (BO); Hoffstetter 1968: Ñuapua (BO); Salles and Cartelle 2006: Japones Cave (BR); Ghilardi and Fernandez 2011: Upper Ribeira (BR); Baffa and Burnetti 2000: Ponta de Flecha (BR); Lessa and Cartelle 1998: Toca dos Ossos (BR); Paula Couto 1980: Lage Grande (BR), Curimatas (BR); Guerin 1991: Lagoa Sao Vitor (BR), Toca da Janela da Barra do Antoniao (BR), Garrincho (BR); Santo 2012: Morro da Chapéu (BR), Pesqueira (BR), Rio Carcarañá (AR), Santa Vitória do Palmar (BR), Touro Passo (BR), Pantano grande (BR), Rio Arrecifes (AR), Provincia de Corrientes (AR), Santiago del Estero (AR), Abismo da Ponta de Flecha (BR).

Genus TRIGODONOPS Kraglievich, 1930 †
(Map 5.1.2: Geographic distribution)

Trigodonops lopesi (Roxo 1921) †

General Taxonomic Characters: This genus differs from Toxodon and Mixotoxodon in characteristics of the skull. One of the main differences is tha rostral expansion and a palatine bone of triangular shape present in *Trigodonops*, contrary to the narrower character observed in *Toxodon* and *Mixotoxodon* (Santos 2012).
Body Size: Its body size is estimated aroun 1,600 kg (Lyons et al., 2016).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid according to Santos (2012).
Geographic and stratigraphic distribution: Pliocene? to late Pleistocene of northern Brazil.

Map 5.1.2 Geographic distribution of the genus *Trigodonops*. References: Santos 2012: Lage Grande (BR), Jurua River (BR).

Genus *MIXOTOXODON* van Frank, 1957 †
(Map 5.1.3: Geographic distribution)

Mixotoxodon larensis (van Frank 1957) †

General Taxonomic Characters: Similar to *Toxodon, M. larensis* differs only in some specific characteristics of the skull such as a more rounded mandible and molars without enamel in the lingual surface. As in *Toxodon,* it features high-crowned ever-growing teeth. (Santos 2012).
Body Size: It is characterized by a very large body size estimated to be ~3700 kg (Elissamburu 2012).
Diet: Stable isotopes analyses in *Mixotoxodon* from Honduras have shown a preference for mixed C3 forested grasslands in that area about 15,000 years BP (MacFadden 2005)
Confidence in Species Assignment: Valid species in South America according to Santos (2012).
Geographic and stratigraphic distribution: It was present in the Pleistocene of Central America, Venezuela (Falcon and Lara states), Bolivia (Beni district), Colombia (Magdalena district) and Argentina (Santiago del Estero province).

Map 5.1.3 Geographic distribution of the genus *Mixotoxodon*. References: Rincón 2003: Zumbador Cave (VE); Villarroel and Clavijo 2005: Chivolo (CO); Van Frank 1957: San Miguel (VE); Hoffstetter 1968: Cara Cara (BO); Chimento and Agnolin 2011: Santiago del Estero (AR).

5.2 Family MESOTHERIIDAE Alston, 1876 †

Genus *MESOTHERIUM* (Serres 1867) †

(Map 5.2.1: Geographic distribution)

Mesotherium cristatum (Serres 1867) †

General Taxonomic Characters: Upper and lower incisors were ever-growing. In body shape and general appearance it resembles a huge rodent.
Body Size: This medium-sized notoungulate had a body mass estimated to be ~138 kg (Elissamburu 2012) and a length of 1.5 m.
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid according to Serres (1867).
Geographic and stratigraphic distribution: This species is very abundant in Ensenadan deposits of the Buenos Aires Province, Argentina.

Map 5.2.1: Geographic distribution of the genus *Mesotherium*. References: Tonni 1970: Punta Hermengo (AR); Reig 1957: Arroyo Loberia (AR).

6. Order PERISSODACTYLA Owen, 1848
(Odd-toed ungulates)

In this group are extant horses, tapirs, rhinos and hippopotamus. The main characteristic is the enlarged middle digit in both hind and fore feet and a reduction of the other digits. The body weight falls in the middle digit (Redford and Eisenberg 1992).

Modern perissodactyls have an enlarged section of the cecum in the stomach, which serves as a fermentation chamber. Other than that, modifications to the digestive system are not evident (in contrast to multiple stomachs in artiodactyls). Horns occur in just a few extant forms (Rhinoceros) and are epidermal derivatives, situated in the midline of the nasal bones.
In present-day South America only members of the family Tapiridae (tapirs) are native on the continent. During the Pleistocene, horses (family Equidae) were also present and abundant (Table 6).

Table 6. South American Megafaunal Perissodactyla. † = extinct

Family EQUIDAE Gray, 1821
Genus *EQUUS* (*AMERHIPPUS*) Hoffstetter, 1950 †
Equus (Amerhippus) santaeelenae (Spillmann 1938) † *Equus (Amerhippus) andium* (Branco 1883) † *Equus (Amerhippus) neogeus* (Lund 1849) (=E. curvidens) † *Equus (Amerhippus) insulatus* (Ameghino 1904) † *Equus (Amerhippus) lasallei* (Daniel 1948) †
Genus HIPPIDION Owen, 1869 †
Hippidion principale (Lund 1845) † *Hippidion saldiasi* (Roth 1899) † *Hippidion devillei* (Gervais 1855) †
Family TAPIRIDAE Burnett, 1830
Genus *TAPIRUS* Brünnich, 1772
Tapirus critatellus (Winge 1906) † *Tapirus mesopotamicus* (Ferrero & Noriega, 2007) † *Tapirus rondoniensis* (Holanda Ferigolo & Ribeiro 2011) † *Tapirus rioplatensis* (Cattoi 1957) † *Tapirus tarijensis* (Ameghino 1902) † *Tapirus greslebini* (Rusconi 1934) † *Tapirus oliversai* (Ubilla 1983) † *Tapirus terrestris* (Linnaeus 1758) *Tapirus pinchaque* (Roulin 1829) *Tapirus bairdii* (Gill 1865) *Tapirus kabomani* (Couzzol et al., 2013)

6.1 Family EQUIDAE Gray, 1821

The clade Equidae has its origin in North America during the upper Eocene. The group experienced an adaptive radiation beginning in the Miocene, with evolutionary changes continuing into the Pleistocene, which is reflected in the morphology of the skull and limbs. The main distinguishing characteristic of the group is extreme reduction of the lateral digits, leaving only one digit functional (Redford and Eisenberg).

Two genera are recognized in the Pleistocene fossil record of South America: *Equus (Amerhippus)* and *Hippidion*. The presence of a third genus, *Onohippidium*, has been suggested by some authors (MacFadden 1997), based on differences in the rostrum, dental pattern and metatarsal proportions. This proposition has been questioned and considered as differences attributable to intraspecific variability (Alberdi y Prado 1993, 2004). Following Alberdi and Prado (2004), I consider that *Hippidion* and *Equus* are the only genera found in the fossil record of South America.

Genus *EQUUS* (*AMERHIPPUS*) Hoffstetter, 1950 †

(Map 6.1.1: Geographic distribution)

The subgenus *Equus* (*Amerhippus*) was erected by Hoffstetter in 1950 based on the absence of an infundibular mark on the surface of the upper incisors. This character is highly variable and probably related to dental wear (Alberdi 1974, Prado and Alberdi 1994); nevertheless, the validity of the subgenus has been maintained given the presence of other morphological characters, such as a common dental structure among the South American specimens, and a skull that is relatively large in relation to the body, giving a shorter and stockier character to this equid (Prado and Alberdi 1994). More recently, ancient mtDNA studies show a close relation between *Equus* (Amerhippus) and *Equus caballus* (Orlando et al. 2008) which suggests that *Equus (A.)* is aligned with *Equus caballus* and raises questions about the validity of the South American subgenus. Using a morphological species concept, five species of *Equus (Amerhippus)* are recognized in South America.

Equus (Amerhippus) andium (Branco 1883) †

(Fig. 6.1)

General Taxonomic Characters: A series of cranio-mandibular characteristics differentiate this species from the others of the group, for instance, a sharp and marked occipital crest (Alberdi and Prado 2004). Limbs are robust and short, specially the metapodials and the radius (Alberdi and Prado 2004).
Body Size: *Equus (Amerhippus) andium* is the smallest representative of the genus with an estimated body mass of 220 kg (Prado and Alberdi 1994).
Diet: Older literature suggested that the members of the subgenus *E. (Amerhippus)* are grazers, given the morphology of the teeth and the characteristics of the masticatory apparatus.

However, according to stable isotope analyses, *E. (A.) andium* utilized a mixed diet of both grazer and browser of plants (McFadden *et al.* 1999, Sánchez *et al.* 2006).
General Ecology and/or Locomotion: Present only in the Andean region of South America (See Map 6.1.1), which can suggest, along with the robust character of the limb bones, with inhabiting montanious environments.
Confidence in Species Assignment: Valid species according to Prado and Alberdi (1995).
Geographic and stratigraphic distribution: Late Pleistocene of Ecuador (Pichincha, Tungurahua and Chimborazo districts) and Chile (Coquimbo, Valparaiso and Los Lago regions).

Figure 6.1.1: *Equus (Amerhippus) andium*. Located at the American Museum of Natural History, New York. Picture by N. Villavicencio.

Equus (Amerhippus) santaeelenae (Spillmann 1938) †

General Taxonomic Characters: Similar to *E (A.) andium* in terms of postcranial morphology, this species differs in being larger and more robust. It has shorter metapodials with a ratio similar to what is observed in *E (A.) andium,* but the skeleton is in general more robust. The mandible is robust and similar to other *E. (Amerhippus)* species; the skull is similar to *E (A.) neogeus* but smaller.
Body Size: Its body mass is estimated around 350 kg (Alberdi et al., 1995).
Diet: undetermined herbivore.
General Ecology and/or Locomotion: This species has been found in deposits of coastal Ecuador, suggesting that it inhabited coastal plains with sandy soils, which ultimately may explain why it seems to be more robust than *E (A.) neogeous* taxon (Alberdi and Prado 1995).
Confidence in Species Assignment: Valid species according to Prado and Alberdi (1995).
Geographic and stratigraphic distribution: *Equus (Amerhippus) santaeelenae* has been reported only from the late Pleistocene of Península de Santa Elena in Ecuador and in Peru (Arequipa district).

Equus (Amerhippus) insulatus (Ameghino 1904) †

General Taxonomic Characters: This species has a bigger skull than *E (A.) andium*, but with otherwise similar morphology. Mandible is deep and massive, upper teeth show the typical *Equus* pattern but bigger in size. Limb bones are robust; the skull is very similar to *E (A.) neogeus* from Buenos Aires province in Argentina but with a relatively high and narrower rostrum (Prado and Alberdi 1994).
Body Size: The body size is similar to *E (A.) andium* and estimated around 350 kg (Alberdi et al., 1995).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid species according to Prado and Alberdi (1995).
Geographic and stratigraphic distribution: Middle Pleistocene of Bolivia (Tarija district).

Equus (Amerhippus) neogeus (Lund 1849) (=E. curvidens) †

General Taxonomic Characters: The skull is big and has an enlarged preorbital and nasal region. The limb bones are large, but less robust than in the other horse species from South America (Prado and Alberdi 1994).
Body Size: This species is one of the largest horse species of South America with a body size estimated around 370 kg (Alberdi et al., 1995).
Diet: Stable isotope analyses in fossils collected in the Pampean region of Argentina suggest adaptation to a mixed C3-C4 diet (Sanchez et al 2006).
General Ecology and/or Locomotion: The geographic and temporal range of this taxon indicates *E. (A.) neogeus* lived in the plains of the Argentinean pampa and Brazil at the end of the Pleistocene, where the conditions were probably dry and environments open, possibly like grasslands with compact soil (Marshall *et al.,* 1984; Webb, 1985). These conditions are consistent with the more slender morphology observed for this equidae.
Confidence in Species Assignment: Valid species according to Prado and Alberdi (1995).
Geographic and stratigraphic distribution: Late Pleistocene to Early Holocene of Argentina (Buenos Aires province) and Brazil (Rio Grande do Norte and Pernambuco states).

Equus (Amerhippus) lasallei (Daniel 1948) †

General Taxonomic Characters: This taxon is known only from skull remains. It has the largest skull among the South American equids; however, the analyzed skull belongs to an old animal. The skull is high and long, with a long diastema and a relatively slender rostrum (Prado and Alberdi 1994).
Body Size: Its body size is estimated around 350 kg (Prado and Alberdi 1994).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid species according to Prado and Alberdi (1995).
Geographic and stratigraphic distribution: Late Pleistocene to early Holocene of Colombia (Cerrogordo and Tibitó).

Map 6.1.1: Geographic distribution of genus *Equus* (Amerhippus). References: Labarca 2015: La Calera (CL), Valle del Elqui (CL), Recabarren et al., 2010: Pilauco (CL); Hoffstetter 1968; Hoffstetter 1952: Quebrada de Oton (EC), Calderon (EC), Llano Chico (EC), El Batan (EC), Alangasi (EC), Quebrada La Tola (EC), La Magdalena (EC), Rio Chiche (EC); Pujos and Salas 2004: Ayacucho (PE), Sacaco (PE); Lemon and Churcher 1961, Churcher 1959: Talara (PE); Ossa and Moseley 1971: La Cumbre (PE); Frailey and Campbell 1980: Quebrada de Cachimayu (PE); Coltorti and Abbazzi 2007: Montesur-Tarija (BO), Rio Rujero (BO); MacFadden and Azzaroli 1987: San Pedro-Tarija (BO); Boule and Thevenin 1920: Tarija (BO); Marshall and Sempere 1991: Ñuapua (BO); Patterson 1936: Quebrada Blanca (AR); Nuñez 1983: Quereo (CL); Schneider 1935: Las Pozas (CL); Zurita and Carlini 2004: General San Martin (AR), Barranqueras (AR); Alvarez 1974: Arroyo Toropi (AR); Zurita and Gasparini 2007: San Francisco (AR); Pereira and Lopez 2012: Santa Vitoria do Palmar (BR); Tonni and Prado 1985: Lujan (AR); Bargo and Menegaz 1986: Arroyo Tapalque (AR); Tonni 1970: Punta Hermengo (AR); Prado and Menegaz 1987: Paso Otero (AR); Alberdi et al., 1989: Quequen Salado (AR); Aramayo 1985: Monte Hermoso beach (AR); Deschamp and Tonni 1992: Arroyo Neposta (AR); Salles and Cartelle 2006: Japones Cave (BR); Guerin 1991: Toca do Serrote do Artur (BR), Toca da Janela da Barra do Antoniao (BR), Toca da Cima dos Pilao (BR); Paula Couto 1980: Lage Grande (BR), Joao Cativo Site (BR), Curimatas (BR); Porpino and Santos 2004: Lejado de Soledade (BR); Rincón et al., 2006: Taima Taima (VE); Correal Urrego 1981: Tibitó (CO) Porta 1960: Cerrogordo (CO).

Genus HIPPIDION Owen, 1869 †
(Map 6.1.2: Geographic distribution, Fig 6.2)

According to Alberdi 1987, this is the only hippidiform genus present in South America and includes three different species: *Hippidion devillei* (Lund 1846), *Hippidion principale* (Gervais 1855) and *Hippidion saldiasi* (Roth 1899). McFadden 1997 suggested that *H. deville* is actually a representative of the genus *Onohippidion* (*O. deville*) given certain differences in the development of the pre-orbital fossa in the skull. Nevertheless, this difference has been related to intraspecific variation according to other authors (Alberdi and Prado 1993, 2004). Ancient DNA analyses have revealed a close evolutionary relationship between *Hippidion* and *Equus* (Orlando et al 2009).

The genus is characterized by a retracted nasal notch at the level of M2 or behind M3. It has a primitive dentition similar to *Pliohippus*, the enamel configuration is simple, and teeth are somewhat brachyodont, suggesting a diet of less abrasive plant material. Limbs are monodactyl and robust (Alberdi and Prado 1994).

Figure 6.1.2: *Hippidion*. From Lydekker 1894

Hippidion principale (Lund 1845) †

General Taxonomic Characters: This is the largest and sturdiest of the South American hippidoforms. The nasal notch is quite retracted. The postcranial skeleton is large and bulky (Alberdi and Prado 1994).
Body Size: Body size has been estimated between 460 and 483 kg (Alberdi and Prado 1993, Fariña et al., 1998).
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid species according to Alberdi and Prado (1994).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Argentina (Buenos Aires province), Bolivia (Tarija district), Uruguay (Artigas district, Chile (Chacabuco province) and Brazil.

Hippidion saldiasi (Roth 1899) †

General Taxonomic Characters: The phalange and metapodials are more robust and short compared to the other species in the genus, with broad articular surface.
Body Size: This is the smallest of the species of Hippidion described for South America, the body size of *H. saldiasi* is estimated to be around 265 kg (Alberdi and Prado 1993).
Diet: stable isotope analyses from an individual from the Atacama Desert in northern Chile indicate a diet of C3 plants (Alberdi et al., 2007).
General Ecology and/or Locomotion: It has pronounced muscular attachment marks in the first phalanx, particularly in the proximal-posterior border, which has been related to adaptation to traverse long distances (Alberdi and Prado 2004).
Confidence in Species Assignment: Valid species according to Alberdi and Prado (1994).
Geographic and stratigraphic distribution: Late Pleistocene of Chile (Atacama and Magallanes region) and Argentina (Patagonia).

Hippidion devillei (Gervais 1855) †

General Taxonomic Characters: The skull is large compared to the rest of the body. The nasal notch is retracted at the level of the M^2. The main characteristic of the species is the molar series which is significantly shorter than in *H. principale* and longer than in *H. saldiasi*. The post cranial skeleton is short and stout, the limbs are robust. (Alberdi et al., 1995)
Body Size: this is a mid-sized *Hippidion*, intermediate in size between *H. saldiasi* and *H. principale*, with a slender body build and a body mass estimated to be 250 kg (Alberdi et al., 1995).
Diet: Undetermined herbivore.
General Ecology and/or Locomotion: The metapodial robusticity is greater in specimens from Tarija than in the ones from Buenos Aires in Argentina (Alberdi and Prado 1993), perhaps reflecting differences in populations living in montane vs. plains environments.
Confidence in Species Assignment: Valid species according to Alberdi and Prado (1994).
Geographic and stratigraphic distribution: Early to Late Pleistocene of Bolivia (Tarija and Ulloma), Argentina (Jujuy, San Luis and Buenos Aires provinces), Peru (Tirapata region).

Map 6.1.2: Geographic distribution of genus *Hippidion*. References: Bryan and Casamiquela 1978: Taima Taima (VE); Pujos and Salas 2004: Celendin (PE), Huargo (PE); De Iuliis 2006: Rio Desaguadero (BO); Lopez and Rojas 2010: Ojo Opache (CL), Kamac Mayu (CL); Hoffstetter 1968: Ñuapua (BO); Marshall and Sempere 1991: Tarija (BO); Fernandez and Markgraf 1991: Barro Negro (AR); Reguero and Candela 2007: Esquina Blanca (AR); Paula Couto 1980: Joao Cativo site (BR); Porpino and Santos 2004: Lejado de Soledade (BR); Guerin 1991: Garrincho (BR), Toca da Janela da Barra do Antoniao (BR), Toca da Cima dos Pilao (BR); Lumley et al., 1987: Toca da Esperanza (BR); Ghilardi and Fernandez 2011: Upper Ribeira (BR); Paula Couto 1944: Sr. Oscar Borba Ranch (BR); Ubilla and Alberdi 1990: Pintado (UY); Pereira and Lopes 2012: Santa Vitoria do Palmar (BR); Alvargenga and Jones 2010: Casil Quarry (UY); Reig 1957: Arroyo Loberia (AR); Deschamps 2005, Deschamps and Borromei 1992: Bajo San Jose (AR); Alberdi et al.,1987: Los Toldos (AR), Cueva Las Buitreras (AR), Cueva Fell (CL), Cueva Pali Aike (CL), Cerro Sota (AR), Ultima Esperanza (CL); Zarate 2000: Piedra Museo (AR); Prevosti and Soibelzon 2003: Cueva de Los Chingues (CL); Prado et al., 2011: Parana (AR), Arroyo Tapalque (AR), Rio Quequen (AR), Rio Salado (AR).

6.2 Family TAPIRIDAE Burnett, 1830

Among living members of this family the most distinctive characteristic is the presence of a proboscis formed from the nostrils and upper lip which overhangs the lower lip. The forefoot has four toes with a vestigial first digit, while hind foot has three toes.

Genus *TAPIRUS* Brünnich, 1772
(Map 6.2.1: Geographic distribution)

The genus is currently represented by five extant species, three of which occur in South America (Redford and Eisenberg 1992) and by seven recognized fossil species. The origin of the genus is Holarctic and the evidence suggests they entered South America as part of the Great American Biotic Interchange (Holanda and Ferrero 2013, Woodburne 2010). The oldest fossil record of the genus in South America is from the early Pleistocene (Tonni 1992).

Extant species of tapirs inhabit a variety of environments from tropical closed forest, to savannas and montane forests in the Andes. They are all browsers and frugivores (Redford and Eisenberg 1992).

Tapirus critatellus (Winge 1906) †

General Taxonomic Characters: This species is characterized by a larger skull and teeth than the extant *T. terrestris* (Winge 1906). According to Holanda et al. (2007) *T. critatellus* seems to be more similar to North American species and to the extant *T. pichanque* in the pattern of development of the saggital crests.
Body Size: Body size estimated around 616 kg (Lyons et al., 2016).
Confidence in Species Assignment: Valid species according to Holanda and Ferrero (2013).
Geographic and stratigraphic distribution: Late Pleistocene-Early Holocene of Brazil (Minas Gerais and Bahia states).

Tapirus mesopotamicus (Ferrero & Noriega, 2007) †

General Taxonomic Characters: This species has a robust and long skull compared to *T. terrestris*. Postcranial remains are restricted to foot bones, which are more robust than in *T. terrestris*.
Body Size: Body size estimated around 512 kg (Lyons et al., 2016).
Confidence in Species Assignment: Valid species according to Holanda and Ferrero (2013).
Geographic and stratigraphic distribution: Late Pleistocene of Argentina (District of Diamante, Buenos Aires province).

Tapirus rondoniensis (Holanda, Ferigolo & Ribeiro 2011) †

General Taxonomic Characters: *T. rondoniensis* differs from *T. terrestris* in a series of cranial features such as broad frontal bones with pneumatization extending from the frontoparietal bone, a high sagittal crest, and a weakly molarized P2. It has a mixture of derived and primitive characters. (Holanda, Ferigolo and Ribeiro, 2011)
Body Size: Body size estimated around 359 kg (Lyons et al., 2016).
Confidence in Species Assignment: Valid species according to Holanda, Ferigolo and Ribeiro (2011).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Rio Madeira formation in Rondonia State).

Tapirus rioplatensis (Cattoi, 1957) †

General Taxonomic Characters: This taxon is larger and more robust than any of the living and fossil species of the genus. The type specimen, a mandibular symphysis, has deciduous teeth still present, indicating a sub-adult age. No more information about this taxon is available. (Holanda and Ferrero 2013).
Confidence in Species Assignment: Valid species according to Holanda and Ferrero (2013).
Geographic and stratigraphic distribution: Early Pleistocene of the city of Buenos Aires, Argentina (Soibelzon 2008)

Tapirus tarijensis (Ameghino, 1902) †

General Taxonomic Characters: While this species was originally described as having larger tooth row compared to *T. terrestris* and a high dentary, these purportedly diagnostic characters are difficult to see in the type specimen (Holanda and Ferrero 2013). When tooth measurements are compared to other species, they seem larger than *T. terrestris* and are similar to North American species.
Confidence in Species Assignment: Given the fragmentary nature of the holotype, this is a dubious species (Holanda and Ferrero 2013), but I provisionally recognize it here in the absence of literature to the contrary.
Geographic and stratigraphic distribution: Late Pleistonece of Bolivia (Tarija district).

Tapirus greslebini (Rusconi, 1934) †

General Taxonomic Characters: This species was erected based on two upper molars. According to the measurements published by Rusconi (1934), they belonged to a tapir larger than *T. terrestris*, similar in size to the extinct North American *T. haysii*.
Confidence in Species Assignment: Given the fragmentary nature of the holotype, this too is a dubious species, but detailed systematic work remains to be done so here I provisionally recognize it.
Geographic and stratigraphic distribution: Pliocene to Pleistocene of Argentina (Villa Ballester, Buenos Aires Province).

Tapirus oliversai (Ubilla, 1983) †

General Taxonomic Characters: Based on a right dentary with m1-3, this species differs from *T. terrestris* only by being more robust and large, but it is smaller than *T. rioplatensis*, the largest Tapir known from the Pleistocene fossil record of South America (Holanda and Ferrero 2013).
Confidence in Species Assignment: Although the fragmentary nature of the material on which it is defined makes it a dubious species, it is recognized here in the absence of any detailed analyses that would synonomize it with another species.
Geographic and stratigraphic distribution: Early Pleistocene of Uruguay (Montevideo District).

Tapirus *terrestris* (Linnaeus 1758)

General Taxonomic Characters: The extant *Tapirus terrestris* (Linnaeus 1758) is the largest land mammal found in most tropical South America. It is characterized by a short but pronounced mane and by pronounced saggital crest in the skull (Redford and Esienberg 1992).
Body Size: It has a body mass of around 225 kg and a height of over a meter to the shoulder (Redford and Esienberg 1992).
Diet: they eat browse and fruits (Redford and Esienberg 1992).
General Ecology and/or Locomotion: It inhabits tropical forests, gallery forests and xeric environments of the Chaco region in northern Argentina and Paraguay.
Confidence in Species Assignment: Valid species according to Linnaeus (1758).
Comments: vulnerable according to UICN.
Geographic and stratigraphic distribution: It is currently found from Venezuela as far south as northern Argentina. It is known in the fossil record from the Late Pleistocene to Early – Holocene of Venezuela (Falcon State), Brazil (Sao Paulo and Bahia States) and Bolivia (Tarija State).

Tapirus pinchaque (Roulin, 1829)

General Taxonomic Characters: Known as the mountain tapir, this is one of the smallest species of tapirs known. It is distinguished by long brown hair and white lips (Redford and Esienberg 1992).
Body Size: Body mass is between 136 and 250 kg. Body length is 180 cm (from the nose to posterior part of the body) and height to the shoulder is 80 cm (Esienberg 1992).
Diet: as other tapirs, this species is a browser and also eats fruits (Esienberg 1992).
General Ecology and/or Locomotion: Inhabits the Andean area in four major habitat types: Paramo, Jalca and Tropical montane forest. It is found at elevations from 1,400 m to the snowline (Downer 1997).
Confidence in Species Assignment: Valid species according to Roulin (1829).
Comments: Endengared according to UICN.
Geographic and stratigraphic distribution: Presently this species inhabits moderate to high elevations in forested habitats in the Andes from Colombia, Ecuador and possibly Peru. The species is unknown in the fossil record.

Tapirus bairdii (Gill, 1865)

General Taxonomic Characters: Commonly called the Central American tapir, this is the biggest of the four species of extant tapirs found in South America. It is distinguished from other tapirs by the absence of a neck crest and by a uniformly short brown coat (Redford and Eisenberg 1992).
Body Size: its body mass is around 300 kg and has a height of 120 cm to the shoulder.
Diet: they are selective feeders eating a variety of leaves and fruits from different plant species (Redford and Eisenberg 1992).
General Ecology and/or Locomotion: It inhabits a variety of environments including evergreen tropical forests and dry deciduous forests (Redford and Eisenberg 1992).
Confidence in Species Assignment: Valid species according to Gill (1865).
Comments: endangered according to the UICN.
Geographic and stratigraphic distribution: This species inhabits the western part of the cordillera, from Veracruz in Mexico to Ecuador. The species is unknown in the fossil record.

Tapirus kabomani (Cozzuol et al., 2013)

General Taxonomic Characters: The smallest living tapir and a rencently named species. It differs from T. terrestris by its smaller size, darker hair and lower mane. It also has a broader forehead (Cozzuol et al., 2013).
Body Size: With total length 130 cm, height at shoulder 90 cm, and body mass estimated at about 110 kg (Cozzuol et al., 2013).
Confidence in Species Assignment: Valid species accorind to Cozzuol et al (2013).
Comments: Recently discovered species, reason why ir very little known.
Geographic and stratigraphic distribution: Brazil (Amazonas, Rondonia, and Mato Grosso states) and in Colombia (Amazonas District are) (Cozzuol et al 2013). The species is unknown in the fossil record.

Map 6.2.1: Geographic distribution of genus *Tapirus*. References: Ferrero and Noriega 2007: Diamante (AR); Holanda et al., 2011: Araras (BR); Pujos and Salas 2004: Talara (PE); Soibelzon 2008: Buenos Aires (AR); Holanda and Ferrero 2013: Tarija (BO); Rusconi 1954: Villa Ballester (AR); Ubilla 1983: Miguelete (UY); Holanda et al., 2007: Bahia state (BR), Minas Gerais state (BR); Ubilla and Alberdi 1990: Pintado (UY); Paula Couto 1980: Areia Preta (BR); Ghilardi and Fernandez 2011: Upper Ribeira (BR); Rio Garcia and Uchoa 1980: Piacaguera (BR); Salles and Cartelle 2006: Nascente do Formoso cave (BR), Japones cave (BR); Lessa and Cartelle 1998: Toca dos Ossos (BR); Lovejoy and Bierregaard 1990: Manaus (BR); Holanda and Rincón 2012: El Breal del Orucual (VE), Cueva del Zumbador (VE); Porta 1969: Curiti (CO); Terborgh 1990: Cocha-Cashu (PE).

7. Order RODENTIA Bowdich 1821

The main characteristics of the members of this group are found in their dentition. The dental formula consists of a pair of upper and a pair of lower incisors, no canines, and no more than two pairs of premolars and three molars per side. The incisors are ever-growing.

Table 7. South American Megafaunal Rodentia. † = extinct

Family CAVIIDAE Fischer von Waldheim, 1817
Subamily HYDROCHOERINAE Gray, 1825
Genus *HYDROCHOERUS* Brisson, 1762
Hydrochoerus ballesterensis (Rusconi 1934) † *Hydrochoerus isthmius* (Goodman 1912) *Hydrochoerus hydrochaeris* (Linnaeus 1766)
Genus *NEOCHOERUS* Hay, 1923 †
Neochoerus sulcidens (Lund 1839) † *Neochoerus tarijensis* (Ameghino 1902) † *Neochoerus fontanai* (Rusconi 1935) † *Neochoerus aesopi* (Leidy 1853) †

7.1 Family CAVIIDAE Fischer von Waldheim, 1817

Genus *HYDROCHOERUS* Brisson, 1762

(Map 7.1.1: Pleistocene-Holocene geographic distribution)

This group is composed of giant rodents with a semiaquatic habit (Mones & Ojasti, 1986). According to Mones 1991, three species lived in the Pleistocene of South America. One of them is extinct, and two remain extant.

Hydrochoerus ballesterensis (Rusconi 1934) †

General Taxonomic Characters: This species is differentiated from the other species in the genus by a several craniomandibular characters, including a straighter and more graceful mandible

Confidence in Species Assignment: Valid species according to Mones (1991).

Geographic and stratigraphic distribution: Early Pleistocene of Argentina (Buenos Aires Province).

Hydrochoerus hydrochaeris (Linnaeus 1766)

General Taxonomic Characters: Commonly known as capybaras, *H. hydrochaeris* is the biggest extant rodent in the world. It has a brown coat, body is massive and barrel shaped, limbs are

short. It differs from the other living species, the lesser capybara (*H. isthmius*) by the bigger proportions of the whole body and skeletal elements (Mones & Ojasti, 1986).
Body Size: Body mass of about 63 kg (Redford and Eisenberg 1992).
Diet: They are herbivorous eating grasses and aquatic vegetation.
General Ecology and/or Locomotion: They can be found in water holes, forming groups (Eisenberg and Redford 1992).
Confidence in Species Assignment: Valid species according to Linnaeus (1766).
Geographic and stratigraphic distribution: It can be found in Venezuela, Colombia, Ecuador, Perú, Bolivia, Guyana, Surinam, French Guayana, Brazil, Paraguay, Uruguay y north east of Argentina (Mones & Ojasti, 1986; Moreira et al., 2013). There are fossil record from the Late Pleistocene of Bolivia (Tarija and Nuapua districts), Brazil (Rio Grande do Sul, Sao Paulo and Bahia states) and from Holocene deposits in Peru and Venezuela.

Hydrochoerus isthmius (Goodman 1912)

Comments: This small Capybara (body size = 20 kg) is the only other species known for the genus. It is currently found in Colombia and in the Panama Isthmus (Delgado and Emmons 2016). There are no findings known from the fossil record. Not further described here as is not megafauna in the strickt sense.

Map 7.1.1: Pleistocene-Holocene geographic distribution of the genus *Hydrochoerus*. Reference: Mones 1991. Deschamps and Borromei 1992: Bajo San Jose (AR); Rusconi 1954: Villa Ballester (AR); Ubilla and Alberdi 1990: Pintado (UY); Kerber and Ribeiro 2011: Barranca Grande (BR), Ponte Velha (BR), Touro Passo (BR); Hoffstetter 1968: Nuapua (BO); Marshall and Sempere 1991: Tarija (BO); Terborg 1990: Chocha-Cashu (PE); Rio Garcia and Uvhoa 1980: Piacaguera (BR); Lessa and Cartelle 1998: Toca dos Ossos (BR); Porta 1969: Curiti (CO); Eisenberg and O' Connell 1979: Fundo Pecuario Masaguaral (VE).

Genus NEOCHOERUS Hay, 1923 †

(Map 7.1.2: Geographic distribution)

These are similar to the extant capybaras but up to twice as big. Body mass in the four extinct species has been estimated up to 200 kg (Ghizzoni 2014). The fossil remains are scarce, which is why not much is known about the paleoecology of species in this genus. According to the revision made by Mones 1991, four different species are recognized for the Pleistocene of South America.

Neochoerus sulcidens (Lund 1839) †

Body Size: This species is characterized by a body size in between *N. tarijensis* and *N. aesopi*, 40-50% bigger than the extant capybara which means a body size of about 90 kg.
Confidence in Species Assignment: Valid according to Mones (1991).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Minas Gerais).

Neochoerus tarijensis (Ameghino 1902) †

Body Size: This species is similar size to *N. sulcidens* (90 kg) (Mones 1991).
Confidence in Species Assignment: Valid according to Mones (1991).
Geographic and stratigraphic distribution: Middle Pleistocene of Bolivia (Tarija district).

Neochoerus fontanai (Rusconi 1935) †

Body Size: This species is similar in morphology to all other species in the genus. Its body size is 30% bigger than capybaras.
Confidence in Species Assignment: Valid according to Mones (1991).
Geographic and stratigraphic distribution: Early Pleistocene of Argentina (Buenos Aires province)

Neochoerus aesopi (Leidy 1853) †

Body Size: Body size is estimated around 200 kg (Mones 1991).
Confidence in Species Assignment: Valid according to Mones (1991).
Geographic and stratigraphic distribution: Late Pleistocene of southern North America, including the United States and Mexico; Late Pleistocene of Central America. In South America it is found in Venezuela, Ecuador (Santa Elena) and Peru.

Map 7.1.2: Geographic distribution of the genus *Neochoerus.* Reference: Mones 1991: Minas Gerais State (BR); Marshal and Sempere 1991: Tarija (BO); Deschamps 2005: Bajo San jose (AR); Tonni and Prado 1985: Lujan (AR); Rincón 2006: Zumbado cave (VE); Czaplewski and Rincón 2005: Mene de Inciarte (VE); Villarroel and Brieva 1996: Nucleo Escolar de Jutua (CO); Hoffstetter 1952: La Carolina (EC); Martinez and Jacay 2000: La Huaca (PE); Lemon and Churcher 1961: Talara (PE); Ubilla and Alberdi 1990: Pintado (UY).

Supeorder XENARTHRA Cope, 1889

The superorder Xenarthra includes several extinct taxa plus the extant tree sloths, armadillos and ant eaters. The name Xenarthra means “strange joints” and makes reference to the thoracic and lumbar vertebrae, which have an accessory articular process, a synapomorphy on of all the members of this group.

8. Order CINGULATA Illiger, 1811

This group includes all the armored armadillos and the extinct gliptodonts (Table 8).

Table 8. South American Megafaunal Cingulata. † = extinct

Family DASYPODIDAE Gray, 1821
Genus *EUTATUS* Gervais, 1867 †
Eutatus seguini (Gervais 1867) † *Eutatus pascuali* (Krmpotic et al., 2009) †
Genus *PACHYARMATHERIUM* Downing and White, 1995 †
Pachyarmatherium brasiliense (Poprino et al 2009) † *Pachyarmatherium tenebris* (Rincón and White 2008) †
Genus *PROPRAOPUS* Ameghino, 1881 †
Propraopus sulcatus (Lund 1842) †
Family PAMPATHERIIDAE Paula Couto, 1954 †
Genus *HOLMESINA* Simpson, 1930 †
Holmesina occidentalis (Hoffstetter 1952) † *Holmesina majus* (Lund 1842) † *Holmesina paulacoutoi* (Cartelle Guerra and Bohorquez Mahecha, 1985) † *Holmesina rondoniensis* (Góis et al. 2012) †
Genus *PAMPATHERIUM* Ameghino, 1891 †
Pampatherium humboldti (Lund 1841) † *Pampatherium typum* (Gervais and Ameghino 1880) †
Suborder GLYPTODONTIA Ameghino, 1889 †
Genus *HOPLOPHORUS* Lund, 1839 (=*SCLEROCALYPTUS* Ameghino, 1891) †
Hoplophorus euphractus (Lund, 1839) † *Hoplophorus echazui* (Hoffstetter 1964) †
Genus *NEURYURUS* Ameghino, 1889 †
Neuryurus trabeculatus (Zurita and Ferrero 2009) † *Neuryurus rudis* (Gervais 1878) †
Familia PANOCHTHIDAE Castellanos, 1927 †
Genus NEOSCLEROCALYPTUS Paula Couto, 1957 † (=SCLEROCALYPTUS Ameghino, 1891)

Neosclerocalyptus paskoensis (= Chacus paskoensis) † *Neosclerocalyptus gouldi (Zurita et al. 2008)* † *Neosclerocalyptus ornatus* (Owen 1845) † *Neosclerocalyptus pseudornatus* (Ameghino 1889) †
Genus *PANOCHTHUS* Burmeister, 1866 †
Panochthus tuberculatus (Owen 1845) † *Panochthus frenzelianus* (Ameghino 1889) † *Panochthus greslebini* (Castellanos 1942) † *Panochthus jaguaribensis* (Moreira 1965) † *Panochthus intermedius* (Lydekker 1895) † *Panochthus subintermedius* (Castellanos 1942) †
Family GLYPTODONTIDAE Gray, 1869 †
Genus *DOEDICURS* Burmesiter, 1874 †
Doedicurus clavicaudatus (Owen 1847) †
Genus *PLAXHAPLOUS* Ameghino, 1884 †
Plaxhaplous canaliculatus (Ameghino 1884) † *Plaxhaplous ensenadensis* (Ameghino 1904) †
Genus *DAEDICUROIDES* Burmeister, 1874 †
Daedicuroides eguiai (Ameghino 1891) †
Genus *GLYPTODON* Owen, 1838 †
Glyptodon clavipes (Owen 1839) † *Glyptodon reticulatus* (Owen 1838) † *Glyptodon elongatus* (Burmeister 1866) † *Glyptodon munizi* (Ameghino 1881) †
Genus *GLYPTOTHERIUM* Osborn, 1903 †

8.1 Family DASYPODIDAE Gray, 1821

The members of this family are characterized by the presence of many scutes made of dermal bone and arranged regularly over the trunk, head and tail of the body. The scutes form movable bands in the midsection of the body and immobile shields in the forequarters and hindquarters (Eisenberg & Redford 1992). The family is represented by living species (armadillos) and extinct ones. The extant species have epidermal scales covering the bony scutes and hair growing between the mobile bony bands and un-armored underside of the animal (Eisenberg & Redford 1992).

The biggest living representative of this family and of all the order Cingulata is *Priodontes maximus*, the giant armadillo. It is currently found east of the Andes from Colombia and Venezuela south to Paraguay and northern Argentina and can attain a body mass up to 32 kg (Eisenberg & Redford 1992).

Genus *EUTATUS* Gervais, 1867 †
(Map 8.1.1: Geographic distribution)

According to the latest revision (Krmpotic et al 2009) two species are recognized in the South American fossil record: *Eutatus pascuali* (Krmpotic et al 2009) present in Ensenadan stage (middle to late Pleistocene) and *Eutatus seguini* for the Bonaerian, Lujánian and Platan stages (Late Pleistocene-early Holocene).

Eutatus seguini (Gervais 1867) †

General Taxonomic Characters: External and internal surfaces of the osteoderms are made of compact bone and the osteoderms of the head shield are elevated centrally and are surrounded by peripheral tubercles. The species differs from *E. pascuali* mainly by characteristics of the osteoderms, for example the number of hair follicles in the osteoderms is usually 4 in *E. seguini* (5-6 in *E. pascuali*), and the central part of the osteoderms is narrower in *E. seguini*. Differences in the size of osteoderms can be seen in different areas of the body and also differ between *E. seguini* and *E. pascuali* (Krmpotic et al. 2009).
Body Size: This species is large, body size has been estimated around 50 kg (Vizcaíno et al., 2003).
Diet: Analyses of the masticatory apparatus of *Eutatus* indicate they had an herbivorous diet (Vizcaíno and Bargo 1998).
General Ecology and/or Locomotion: Limb bone proportions indicate digging behavior, similar to the fossorial activity seen in living armadillos, probably more for building burrows than for searching for food (Vizcaíno et al., 2003).
Confidence in Species Assignment: Valid species according to Krmpotic et al., (2009).
Geographic and stratigraphic distribution: Middle Pleistocene to Early Holocene of Argentina (Buenos Aires, Santa Fe and Entre Ríos provinces).

Eutatus pascuali (Krmpotic et al., 2009) †

General Taxonomic Characters: This species is very similar to *E. seguni*, but more robust; see description of *E. seguni* for some relevant comparisons.
Confidence in Species Assignment: Valid species according to Krmpotic et al., (2009).
Geographic and stratigraphic distribution: Late Pliocene to Middle Pleistocene Argentina (Buenos Aires province).

Map 8.1.1: Geographic distribution of the genus *Eutatus*. References: Deschamps and Borromei 1992: Bajo San Jose (AR); Mazzanti and Quintana 1997: Cueva Tixi (AR); Prado et al., 1987: Paso Otero (AR); Tonni and Berman 1987: Centinela del Mar (AR); Tonni and Fidalgo 1982: Punta Hermengo (AR); Krmpotic et al. 2009: Provincia de Santa Fe (AR), Provincia de Entre Rios (AR).

Genus *PACHYARMATHERIUM* Downing and White, 1995 †
(Map 8.1.2: Geographic distribution)

The main characteristic that differentiates this genus from other dasypodidae is greater thickness of the carapace osteoderms. The genus has been reported in the Quaternary sediments of Venezuela, Brazil, and Uruguay (Rincón and White 2008; Bostelman et al. 2008; Porpino et al. 2009; Oliveira and Pereira 2009). Two species have been proposed for South America: *Pachyarmatherium tenebris* (Rincón and White, 2008), found only in Venezuela, and *Pachyarmatherium brasiliense* (Porpino et al., 2009), found in Brazil. The description of both species is based on isolated osteoderms or carapace fragments; postcranial material elements have been described for the Brazilian taxon as well (Porpino et al., 2010). The genus has also been reported from Uruguay.

There has been some debate about the validity of both taxa with some authors (Martinez and Rincón 2010) suggesting that *P. brasiliense* is a junior synonym of *P. tenebris* leaving the second as the only valid taxon for South America. However, this suggestion has been questioned using morphological characteristics of the osteoderms as evidence (Oliveira et al 2013). For this reason I regard both taxa as valid for this revision, and await discovery and analysis of more complete material needed to resolve the debate.

Pachyarmatherium brasiliense (Poprino et al 2009) †

General Taxonomic Characters: This taxon differs from the North American *Pachyarmatherium leiseyi* (which size comparable to *Priodontes*, 26-32 kg) in being larger and in having osteoderms with heptagonal shape, main figure with oblong, subrounded -and polygonal outline (instead of only polygonal), and a larger number of peripheral structures (Porpino et al 2009). Some more specific differences of the osteoderms differentiate this taxon from the Venezuelan form, for example, the osteoderms of *P. brasiliense* has three to six peripheral structures, while *P. tenebris* has one to six peripheral structures (Rincón and White 2008).
Body Size: Body mass is estaimated aroun 106 kg (Lyons et al., 2016).
Confidence in Species Assignment: Valid species according to Poprino et al., (2009).
Geographic and stratigraphic distribution: Pleistocene of Brazil (Pernambuco and Rio Grande do Sul states).

Pachyarmatherium tenebris (Rincón and White 2008)

General Taxonomic Characters: This species was defined on the basis on isolated scutes from the carapace and the tail. Nor description of other elements is known. The species purportedly differs from *P. brasiliensis* by the presence of small complementary ornamentations in the buckler osteoderms and by differences in the microstructure of the bony scutes (Rincón and White 2008).
Confidence in Species Assignment: Valid species according to Rincón and White (2008).
Geographic and stratigraphic distribution: Pleistocene of Venezuela.

Map 8.1.2: Geographic distribution *Pachyarmatherium*. References: Porpino et al., 2009: Lajedo de Escada (BR) Fazenda Nova (BR); Rincón and White 2007: Cueva Zumbador (VE), Cueva el Miedo (VE).

Genus *PROPRAOPUS* Ameghino, 1881 †
(Map 8.1.3: Geographic distribution)

Propraopus sulcatus (Lund, 1842) †

General Taxonomic Characters: According to the latest taxonomic revision, this is the only species can be reliably defined for the Pleistocene of South America. As in all dasypodids its carapace is composed by both immobile and mobile bucklers. The immobile scapular shields have a sharp denticular border made of projecting osteoderms (Castro et al. 2013). Foramina are evident in the osteoderms (Castro et al., 2013), possibly indicative of hair growth.
Body Size: *Propraopus sulcatus* is a medium sized dasypodid, with estimated body mass around 50 kg (Fariña and Vizcaíno 1997).
Confidence in Species Assignment: Valid species according to Castro et al. (2013).
Geographic and stratigraphic distribution: Pleistocene to Early Holocene of Argentina (Buenos Aires and El Chaco provinces); Pleistocene of Brazil (Minas Gerais, Bahia, Rio Grande do Norte, Piaui, Rio Grande do Sul, and Mato Grosso states), Venezuela (Falcon and Zuila states), Colombia (Meta district), Ecuador (Chimborazo), Uruguay (Artigas and Durazno districts), and Bolivia (Tarija district).

Map 8.1.3: Geographic distribution of the genus *Propraopus*. References: Boule and Thevenin 1920: Tarija (BO), Deschamps 2005: Bajo San Jose (AR); Guerin 1991: Toca do Serrote do Artur (BR); Hoffstetter 1968: Ñuapua (BO); Hoffstetter 1952: Punin-Chalan (EC); Lumley et al., 1987: Toca da Esperanca (BR); Oliveira and Pereira 2009: Arroio Chui, Santa Vitoria do Palmar (BR), Ponte Velha (BR); Pitana and Ribeiro 2007: Balneario Hermenegildo (BR), Lagoa Mangueira (BR). Cerro da Tapera (BR), Fazenda Milton (BR), Sanga da Cruz (BR); Rincón et al., 2008; Rincón and White 2007: Cueva El Miedo (VE); Salles and Cartelle 2006: Japones cave (BR); Tonni and Berman 1987: Centinela del Mar (AR); Zurita and Carlini 2004: Castelli (AR); Czaplewski and Rincón 2005: Mene de Inciarte (VE); Faure et al., 1999: Piaui state (BR); Cartelle and Hirooka 2005: Mato Grosso state (BR); Porpino 1999: Rio Grande do Norte State (BR).

7.2 Family PAMPATHERIIDAE Paula Couto, 1954 †

Pampatheriidae are recorded in South America from the middle Miocene (Edmund & Theodor, 1997) to the early Holocene (Cartelle & Bohórquez, 1985; Cartelle, 1999; Scillato-Yané *et al*., 2005; Góis & Scillato-Yané, 2008). This family is shares traits with both the Dasypodidae and the Glyptodontidae, which has made it difficult to reach consensus about its taxonomic position. Some authors consider the contained species to belong to Glyptodontidae, others to Dasypodiidae, and still others regard Pamatheriidae to be valid family (See Gois et al. 2012 and references there), which I follow here. It is evident that taxa I include in Pampatheriidae and the validity of the family itself requires considerable study and potentially taxonomic revision (Edmund 1985, 1987, Downing & White 1995, Edmund & Theodor 1997 and, De Iuliis & Edmund 2002).

Pampatheres occur in both North and South America. They originated in South America and migrated north as part of the Great American Biotic Interchange (Woodburne 2010). According to Scillato-Yané et al. 2005, the members of this group are identifiable by the morphology of the osteoderms and by craniomandibular characteristics. Two genera comprise the family: *Holmesina* and *Pamapatherium*, the latter of which is the type genus.

Analyses of the morphology of the masticatory system of pampatheres indicate that they were grazing mammals with a well-developed masseter muscle consistent with processing tough vegetation (Vizcaíno et al. 1998). A main difference among the members of this group relates to their ability to process coarse vegetation (De Iuliis et al. 2000), which may suggest niche partitioning of sympatric species (De Iuliis et al. 2000).

Genus *HOLMESINA* Simpson, 1930 †
(Map 8.2.1: Geographic distribution)

Four species are recognized for the Pleistocene of South America. While it has been suggested that *H. majus* and *H. paulacoutoi* are synonyms (Edmund 1996), recent work supports retaining them as distinct species (Scillato-Yané et al. 2005).

Diet of the genus: Compared to *Pampatherium*, it was less adapted for chewing coarse tough vegetation, and possibly inhabited areas of that contained many low shrubs (De Iuliis et al., 2000). Unlike living armadillos, neither genus of pampathere shows adaptations to eating carrion, insects, or generally having an omnivorous diet (Edmund 1985).
General Ecology and/or Locomotion of the genus: *Holmesina* seems to have been more characteristic of warmer and wetter environments compared to *Pampatherium* (Vizcaíno *et al*., 1998; De Iuliis *et al*., 2000; Scillato-Yané *et al*., 2005).

Holmesina occidentalis (Hoffstetter 1952) †

General Taxonomic Characters: It is relatively smaller than the other two species. The

osteoderms are large but proportionally thin; the central figure in the osteaoderms is narrow and well defined with a more uniformly even surface than that of other species (Scillato-Yane´ et al., 2005).
Body Size: Body mass is estimated to be around 200 kg (De Iuliis et al. 2000).
Diet: Craniomandibular characteristics suggest this species was a grazer on relatively soft vegetation, with less capacity to utilize abrasive or tough vegetation with respect to most species of Pleistocene *Holmesina* (Vizcaíno *et al*. 1998; De Iuliis et al. 2000) except possibly *H. rondoniensis* (Góis et al. 2012); this inference requires further investigation.
General Ecology and/or Locomotion: The species it thought to have occupied open areas, at least in Ecuador (Hoffstetter 1952).
Confidence in Species Assignment: Valid species according to Scillato-Yane´ et al., (2005).
Geographic and stratigraphic distribution: Pleistocene of Colombia (Huila district) and Venezuela (Falcon state); Late Pleistocene of Ecuador (Santa Elena province) and Peru (Piura district).

Holmesina majus (Lund 1842) †

General Taxonomic Characters: This is the largest pampatherid but not the most robust according to linear measurements of long bones (Scillato-Yané et al. 2005). The surface of the osteoderms has a delicate punctuation and is rougher than the in osteoderms of *H. occidentalis,* but less than in *H. paulacouti*. The marginal area of the osteoderms is wide, the central figure is well defined, narrow and slightly depressed (Scillato-Yane et al. 2005).
Body Size: Its body mass is estimated around 200 kg, based on its similarity in size of skeletal elements to *H. septentrionalis* (McDonald 2005, Scillato-Yane et al., 2005).
Confidence in Species Assignment: Valid species according to Scillato-Yane et al., (2005).
Geographic and stratigraphic distribution: Late Pleistocene of Bazil (Minas Gerais and Ceará states) and Venezuela (Trinidad).

Holmesina paulacoutoi (Cartelle Guerra and Bohorquez Mahecha, 1985) †

General Taxonomic Characters: The carapace osteoderms are very large and exhibit a very rugose surface. The marginal area of the osteoderms is wideand low around an elevated central area (Scillato-Yane et al., 2005).
Body Size: this is the most robust species of the Pampatheriidae, with a body mass estimated to be approximately 125 kg (De Iuliis et al., 2000).
Diet: According to craniomandibular morphology, this species ate vegetation that somewhat more abrasive and toughter than that consumed by *H. occidentalis,* but still less abrasive than the vegetal material consumed by *Pampatherium* (De Iuliis et al., 2000).
Confidence in Species Assignment: Valid species according to Scillato-Yane et al., (2005).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Rio Grande do Sul, Rio Grande do Norte and Bahia states) and Argentina (Corrientes, Buenos Aires, Santa Fe, Formosa, Santiago del Estero and Entre Rios states).

Holmesina rondoniensis (Góis et al. 2012) †

General Taxonomic Characters: This taxon was recently erected based on skull morphology only, which seems to be less robuts than in *H. occidentalis*. It is so far the most graceful species of the genus (Góis et al. 2012).
Body Size: It is very similar to *H. occidentalis* but smaller and less robust (<200 kg).
Diet: Góis et al., (2012) suggest that *H. rondoniensis* possibly consumed less abrasive vegetal material than *H. paulacoutoi*.
Confidence in Species Assignment: Valid species according to Góis et al., (2012).
Geographic and stratigraphic distribution: Late Pleistocene-Holocene of Rio Madeira fm, Rondônia State, Brazil.

Map 8.2.1: Geographic distribution of the genus *Holmesina*. References: Rincón and White 2007: Zumbador cave (VE), Cueva El Miedo (VE); Edmund 1996: Villavieja (CO), Minas Gerais State (BR), Ceara State (BR), Rio Grande do Sul (BR); Oliveira and Pereira 2009: Trinidad (VE), Ponte Velha (BR); Cartelle 1999: Bahia state (BR); Oliveira 1999: Arroyo Chui (BR); Porpino and Santos 2004: Lajedo de Soledade (BR); Scillato-Yané et al. 2002: Rio Salado (AR), Arrecifed (AR), Arroyo Feliciano (AR); Rodríguez-Bualó *et al.*, 2009: Formosa (AR); Chimento and Agnolin 2011: Santiago del Estero (AR); Góis et al. 2012: Rio Madeira (BR); Pujos and Salas 2004: Talara (PE), Cuspinque (PE); Hoffstetter 1952: La Carolina (EC).

Genus *PAMPATHERIUM* Ameghino, 1891 †
(Map 8.2.2: Geographic distribution)

Included species are medium-sized and have been postulated to be responsible for some of the paleoburrows found in Mar del Plata (Vizcaíno et al. 2001, Dondas et al. 2009).

Diet: According to Vizcaíno et al,. (1998), De Iuliis et al., (2000) and Scillato-Yané et al., (2005), *Pampatherium* seems to have been adapted to eat more abrasive food compared to *Holmesina*, such as vegetation found in cold, arid climates, which has led to the idea that that pampatheres were inhabiting such places.

The genus is composed of two species during the Pleistocene of South America.

Pampatherium typum (Gervais and Ameghino 1880) †

General Taxonomic Characters: This species is the smallest and least robust of the Pampatheriidae. Osteoderms are even and lack of a central ornamentation (Scillati-Yane et al., 2005).
Body Size: Estimated size is around 95 kg (Abrantes et al., 2005), and their maximum transverse body diameter is estimated to be around 80 cm (Gervais and Ameghino 1880).
Diet: this species appears to have been a grazer on abrasive vegetation, and more specialized for eating abrasive vegetation than *P. humboldti* and species of *Holmesina* (De Iuliis et al., 2000).
Confidence in Species Assignment: Valid species according to Scillato-Yane et al., (2005).
Geographic and stratigraphic distribution: Late Pleistocene of Bolivia (Ñuapúa and Tarija Districts), Brazil (Rio Grande do Sul and Catarina states), Paraguay (near Asuncion), Argentina (Buenos Aires, Formosa and Corrientes provinces) and Uruguay (Canelones district).

Pampatherium humboldti (Lund 1841) †

General Taxonomic Characters: Osteoderms are slightly sculpted and have a central structure (Scillato-Yane 2005).
Body Size: The body mass of this species has been estimated around 94 kg (Abrantes and Avilla, 2005).
Diet: According to the characteristics of the masticatory apparatus, *P. humboldti* was adapted for grazing abrasive vegetation, but less so than *P. typum* (De Iuliis et al., 2000).
General Ecology and/or Locomotion: Biomechanical study of the limbs of this taxon suggest some degree of cursoriality, that is, an ability to movement fast and diminished or absent capability of digging (Abrantes and Avilla, 2005). This conclusion would dismiss the possibility of *P. humboldti* digging the paleoburrows found in Mar del Plata (Vizcaíno et al. 2001, Dondas et al. 2009). Some authors have suggested a nocturnal habit (Abrantes and Avilla 2005, mentioned in Rincón et al., 2008). Given its dietary adaptations, *P. humboldti* may have been inhabiting savanna environments (De Iuliis et al., 2000; Ranzi, 2000).
Confidence in Species Assignment: Valid species according to Scillato-Yane et al., (2005).

Geographic and stratigraphic distribution: Middle to Late Pleistocene of Brazil (Minas Gerais, Rio Grande do Sul, Ceara, Bahia, and Matto Grosso states), Uruguay (Artigas district) and Venezuela (Zuila state).

Map 8.2.2: Geographic distribution of the genus *Pampatherium*. References: Hoffstetter 1968: Ñuapúa (BO); Hoffstetter 1963: Tarija (BO); Paula Couto 1980: Santa Catarina state (BR); Oliveira *et al*., 2003: Arroio Chuí (BR); Carlini and Tonni 2000: Near Asuncion (PY); Scillato-Yané et al. 1995: Toscas del Rio de La Plata (AR); Bargo et al., 1986: Buenos Aires (AR), Centinela del Mar (AR), Quequen Grande (AR), Quequen Salado (AR); Tonni and Scillato-Yané, 1997: Pilcomayo River (AR); Rodríguez-Bualó *et al*. 2009: Fm Fortin Tres Pozos (AR); Scillato-Yané *et al*., 2005: Fm Toropi (AR); Ubilla et al. 2009: Dolores fm (UY); Cartelle 1999: Minas Gerais State (BR), Bahia State (BR); Edmund 1996: Rio Grande do Sul (BR), Ceara State (BR), Matto Grosso State (BR); Oliveira & Pereira, 2009: Ponte Velha I (BR); Rincón et al. 2008: Mene de Inciarte (VE).

Suborder GLYPTODONTIA Ameghino, 1889 †

Genus *HOPLOPHORUS* Lund, 1839 (=*SCLEROCALYPTUS* Ameghino, 1891) †
(Map 8.3.1: Geographic distribution)

Two species recognized for the Pleistocene of South America: *Hoplophorus euphractus* (Lund 1839) and *Hoplophorus echazui* (Hoffstetter 1964).

Hoplophorus euphractus (Lund 1839) †

General Taxonomic Characters: The most recent description of the genus is based on the description for this species (Porpino et al., 2010). In size species are larger than those in *Neosclerocalyptus* (Porpino et al., 2010). The carapace is thinner as compared to glyptodonts of similar size. The skull is more elongated and narrower and femur and humerus are more graceful than in *Neosclerocalyptus* (Paula Couto 1979). Caudal and carapace osteoderms present clearly demarcated ornamentation, with main and peripheral structures. The genus differs from *Panochthus* by having a central main structure in all its carapace osteoderms. Also, the osteoderms of the dorsal region of the carapace show two rows of peripheral ornamentation. Dermal ossicles more rounded in the dorsal section of the carapace and not hexagonal or pentagonal like in *Panochthus* and *Neosclerocalyptus* (Paula Couto 1979).
Body Size: body size has been estimated around 280 kg (Smith et al., 2003).
Confidence in Species Assignment: Valid species according to Porpino et al., (2010).
Geographic and stratigraphic distribution: Pleistocene of Brazil (Minas Gerais, Piaui, Acre states).

Hoplophorus echazui (Hoffstetter 1964) †

General Taxonomic Characters: It is based on only a few remains: The holotype which is a distal portion of the caudal armour, several dorsal carapace fragments and one caudal ring osteoderm (Zurita et al., 2009).
Body Size: Body size estimated around 280 kg (Smith et al., 2003).
Confidence in Species Assignment: The species was erected based on potentially non-diagnostic material, so its validity has been questioned (Zurita et al., 2009).
Geographic and stratigraphic distribution: Pleistocene of Bolivia (Tarija district).

Map 8.3.1: Geographic distribution of the genus *Hoplophorus*. References: Paula Couto 1979; Porpino et al 2010: Minas Gearis State (BR), Acre State (BR), Piaui State (BR); Paula Couto, 1983: Sao Paulo state (BR); Zurita et al 2009: Tarija (BO).

Genus *NEURYURUS* Ameghino, 1889 †
(Map 8.4.1: Geographic distribution)

The genus is characterized by thick osteoderms, rectangular in shape and loosely articulated. The osteoderms are not ornamented; they have rough aspect and are perforated in the entire surface in a uniform manner. The thicker osteoderms generally have 3 to 4 foramina in the center of the ventral surface (Pascual et al., 1966; Zurita and Ferrero, 2009). Only two species are recognized: *Neuryurus rudis* and *Neuryurus trabeculatus*.

Neuryurus trabeculatus (Zurita and Ferrero 2009) †

General Taxonomic Characters: This is a large glyptodont with very thick osteoderms (42 mm) in the dorsal and postero-dorsal region of the carapace, 30% thicker than in *N. rudis* (the other species of the genus). Osteoderms have a rougher and more sponge-like aspect than in *N. rudis*. The foramina in the ventral surface of the osteoderms are uniformily distributed, contrary to *N. rudis* in which they are all found in the central area. (Zurita and Ferrero 2009).
Body Size: Body mass estimated aroun 311 kg (Vizcaíno et al., 2006).
Confidence in Species Assignment: Valid species according to Zurita and Ferrero (2009).
Geographic and stratigraphic distribution: Pleistocene of Argentina (Entre Ríos province)

Neuryurus rudis (Gervais 1878) †

General Taxonomic Characters: This glyptodont also is large, comparable in size to *Panochthus*. The carapace is composed of large, thick osteoderms, with no evidence of ornamentation except they are uniformely perforated. The osteoderms of the caudal tube are similar to the ones from the carapace, loosely articulated. Lateral osteoderms of the caudal tube present a conical elevation in the central areas (Ameghino, 1889, 1895; Hoffsetter, 1958; Paula Couto, 1979).
Body Size: Body size estimated around 311 kg (Vizcaíno et al., 2006).
Confidence in Species Assignment: Valid species according to Soibelzon et al., (2010).
Geographic and stratigraphic distribution: Exclusively found in sediments from the Ensenadan of the Pamepan region of Argentina (Santa Fe and Buenos Aires provinces).

Map 8.4.1: Geographic distribution of the genus *Neuryurus*. References: Alvargenga et al., 2010: Casil Quarry (UY); Reguero et al., 2007: Esquina Blanca (AR); Zurita and Ferrero 2009: Arroyo Ensenada (AR); Zurita et al., 2009: Santa Fe (AR).

7.5 Familia PANOCHTHIDAE Castellanos, 1927 †

Genus *NEOSCLEROCALYPTUS* Paula Couto, 1957 † (=*SCLEROCALYPTUS* Ameghino, 1891)

(Map 8.5.1: Geographic distribution)

According to the most recent systematic and taxonomic revisions (Zurita 2007, Poprpino et al 2010, Fernicola et al 2008) *Neosclerocalyptus* includes taxa formerly referred to *Sclerocalyptus* from the Pampean region of Uruguay, Argentina and Southern Brazil, differentiating it from the intertropical form *Hoplophorus* that was once also included in the genus *Sclerocalyptus*.

General Taxonomic Characters: These are the smallest Pleistocene glyptdonts known (Carlini and Tonni 2000). The carapace is low, elongated, subcylindrical in shape, almost straight in the dorsal surface, and the anterior end margins are opened as wings. The margins are composed of very small hexagonal or pentagonal scutes. The osteoderms forming the carapace have rosette ornamentation with low elevation and the osteoderms of the dorsal region of the carapace show a single row of 7 to 10 peripheral figures (Porpino et al. 2010). The caudal tube consists of 4 to 5 caudal rings and is cylindrical and conical in shape, somewhat depressed dorsoventrally (Zurita *et al.*, 2005; Zurita, 2007). The main distinctive feature is the high degree of pneumatization of the rostral area, especially the fronto-nasal sinuses, a characteristic that no other glyptodont taxa have (Zurita *et al.*, 2009).

Body Size: At the generic level, the body size has been calculated to be between 380 and 600 kg (Vizcaíno et al. 2011).

Diet: According to ecomorphological analyses, *Neosclerocalyptus* probably was a bulk feeder of vegetation living in open environments (Vizcaíno et al., 2011).

General Ecology and/or Locomotion: The pneumatization in the rostrum becomes successively more evident in geologically younger species of the genus, with maximum expression in the late Pleistocene *N. paskoensis* (Zurita 2007; Zurita et al. 2009). This characteristic has been inferred to be an adaptation to cold and arid climates (see Tonni and Fidalgo 1979; Carlini and Scillato-Yané 1999; Zurita et al. 2005) and is used to tell apart the different species of the genus.

Comments: According to Zurita et al., (2011) there are four valid species for this genus, but only one of them is Late Pleistocene to Early Holocene in age.

Neosclerocalyptus paskoensis (= Chacus paskoensis) †

General Taxonomic Characters: The dorsal carapace is more elevated than in the other species of the genus (Zurita 2002).

Body Size: With a body size estimated at 574 kg (Vizcaíno et al. 2011), individuals in this species were on average larger than those belonging to other species of *Neosclerocalyptus*. The length of the dorsal carapace is around 130 cm and caudal tube length is between 45-49 cm.

Diet: Undetermined herbivore. See description for the genus.

General Ecology and/or Locomotion: This species seems to be exclusively adapted to open, dry and cold environments at least during the Pleistocene (Noriega et al., 2004).

Confidence in Species Assignment: Valid species according to Zurita (2011).

Geographic and stratigraphic distribution: Late Pleistocene of Argentina (Buenos Aires, La Pampa, Tucuman, Santa Fe, Chaco and Cordoba provinces).

Neosclerocalyptus gouldi (Zurita et al. 2008) †

General Taxonomic Characters: This species is similar to *N. paskoensis* but with a more robust, yet narrower and more elongated skull (Zurita et al. 2008).
Confidence in Species Assignment: Valid according to Zurita et al., (2008).
Geographic and stratigraphic distribution: Middle Pleistocene of Argentina (Buenos Aires Province, and in Cordoba provinces) (Luna et al 2012).

Neosclerocalyptus ornatus (Owen 1845) †
(Figure 8.5.1)

General Taxonomic Characters: It is characterized by greater development and pneumatization of the fronto-nasal sinuses (Zurita et al. 2009).
Body Size: Body size of this species has been estimated to be near 598 kg (Vizcaíno et al. 2011). The length of the dorsal carapace is around 124 cm and caudal tube length is 43 cm (Zurita et al 2008).
Confidence in Species Assignment: Valid species according to Zurita et al., (2008).
Geographic and stratigraphic distribution: Early to middle Pleistocene of Argentina (Buenos Aires, Santa Fe and Cordoba provinces).

Figure 8.5.1*:* Skull of *Neoscleroscalyptus ornatus*. From the collections of the Natural History Museum of Denmark. Photo by N. Villavicencio.

Neosclerocalyptus pseudornatus (Ameghino 1889) †

General Taxonomic Characters: Among other characters, *N. pseudornatus* is characterized by an incipient degree of development and pneumatization of the fronto-nasal sinuses (Zurita et al., 2011).The length of the dorsal carapace is around 110 cm and the length of the caudal tube is 44.5 cm (Zurita et al 2008).
Confidence in Species Assignment: Valid species according to Zurita et al., (2008).
Geographic and stratigraphic distribution: Early to Middle Pleistocene of Argentina (Buenos Aires province) (Zurita 2007).

Map 8.5.1: Geographic distribution of the genus *Neosclerocalyptus*. References: Deschamps and Borromei 1992: Bajo San Jose (AR); Politis and Messineo 2008: Campo Laborde (AR); Politis and Salemme 1990: La Moderna (AR); Tonni and Berman 1987: Centinela del Mar (AR); Zurita and Carlini 2008: San Andres de Giles (AR); Zurita and Gasparini 2007: San Francisco (AR); Zurita and Carlini 2004: Charata (AR), Avia Terai (AR); Alvarez 1974: Arroyo Toropi (AR); Zurita and Miño-Boilini 2009: Rio Bermejo (AR); Hoffstetter 1978: General Bruguer (PY); Marshall and Sempere 1991: Nuapua (BO), La Paz (BO); Luna et al., 2012, Luna and Cruz 2014: Cordoba province (AR).

Genus *PANOCHTHUS* Burmeister, 1866 †
(Map 8.5.2: Geographic distribution)

General Taxonomic Characters: In general, members of this genus are large and are characterized by having a highly domed carapace and caudal tube not expanded in the distal end. Molariform teeth are trilobated and as in all the members of the glyptodontidae, the tooth rows are displaced and located under the neurocranium. The cephalic shield is sub-circular and convex. The carapace and the cephalic shield are covered by ornamented osteoderms. The osteoderms in the cephalic shield have an enlarged central structure surrounded by rows of peripheral structures, going from one row to seven depending on the species. The carapace has thick osteoderms, which have a polygonal shaped surface with smaller polygonal, flat ornaments surrounding a central structure which is usually flattened. The caudal tube is cylindrical proximally, and becomes smaller towards the distal end, with its termination blunt or pointy. The caudal tube has elliptical rugged depressions along the sides, each of which has an elevated central segment. (Zamorano 2012).
Body Size: Body weight has been estimated to be over 1 tonne (Fariña et al. 1998).
Diet: *Panochthus* was an herbivore, non-selective feeder in open environments (Vizcaíno et al. 2011).
General Ecology and/or Locomotion: Specific characteristics of the skeleton of *Panochtus* and other glyptodonts, such as rigid carapace fused to the pelvic griddle, dorsal and lumbar vertebrae fused forming tubes and the fact that they lack of the appropriate adaptations in limbs and skull suggest that they were not suited for digging (Kraglievic 1934, Quintana 1992).
Comments: The most recent revision of the group was made by Zamorano 2012 (PhD dissertation). According to his work, from the 14 species previously known from the fossil record, only 9 are valid. Of these nine, four were recorded during the Late Pleistocene.

Panochthus tuberculatus (Owen 1845) †
(Fig. 8.5.2)

General Taxonomic Characters: This species is a large glyptodont, with a highly vaulted skull. The nasal cavity is highly pneumatized compared to *P. frenzelianus* and *P. subintermedius*, and even more so compared to *Panochthus* species from the Ensenadan (Zamorano et al., 2013). The femur is more graceful than in *P. subintermedius* and of similar robustness of *P. greslebini*. The head shield is nearly circular with osteoderms having a central figure with up to 5 rows of peripheral smaller figures surrounding it. Dorsal carapace is compressed and elevated. The tail is composed of 6 caudal rings followed by a caudal tube.
Body Size: Body size has been estimated to be between 1000-1300 kg (Fariña 1995, Fariña et al., 1995, Vizcaíno et al. 2011).
Diet: Undetermined herbivore. See description for the genus.
General Ecology and/or Locomotion: Studies of the proportions, function of limbs and distribution of body mass in *P. tuberculatus* have shown that it had the capability of adopt bipedal positions and possibly dig (Fariña et al., 1995).
Confidence in Species Assignment: Valid species according to Zamorano (2012).

Geographic and stratigraphic distribution: Middle to Late Pleistocene (Bonaerense-Lujánense) of Southern to north-central Argentina, of Uruguay, south central Bolivia and south east of Brazil.

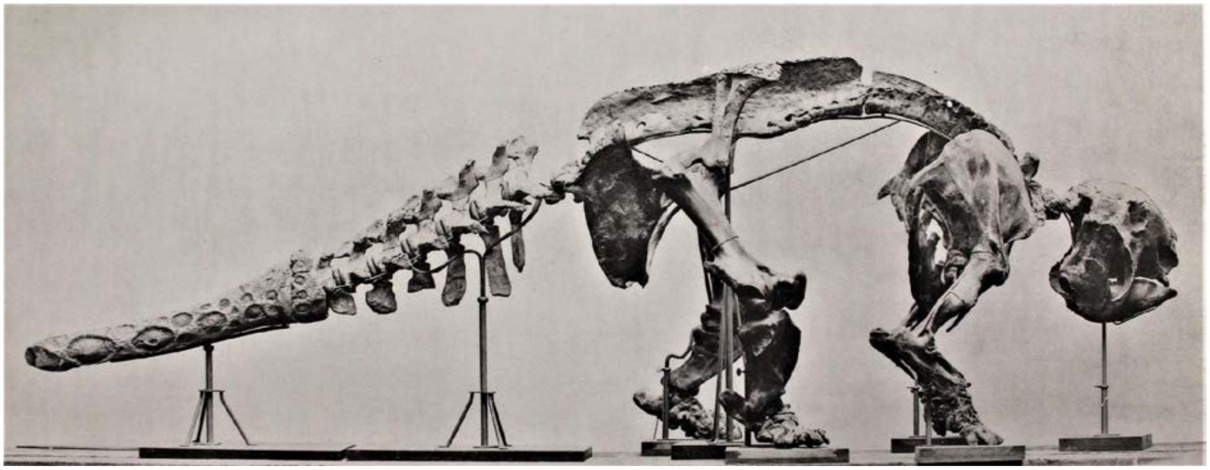

Figure 8.5.2 *Panochthus tuberculatus*, skeleton without carapace. From Lydekker 1894

Panochthus frenzelianus (Ameghino 1889) †
(Fig. 8.5.3)

General Taxonomic Characters: The skull size is similar to *P. tuberculatus*, but nasal pneumatization much less developed in this taxa. Head shield osteoderms are characterized by a central figure with two rows of peripheral smaller figures surrounding the central figure. Dorsal carapace is less compressed than in *P. tuberculatus* but of similar size, is slightly smaller than *P. subintermedius* and smaller than *P. intermedius*. Caudal tube is very similar to the one of *P. tuberculatus,* blunt at the end. Length of caudal tube is between 750-800 mm. (Zamorano 2012).
Body Size: Similar size to *P. tuberculatus* which is between 1,000-1,300 kg (Zamorano 2012).
Diet: Undetermined herbivore. See description for the genus.
Confidence in Species Assignment: Valid species according to Zamorano (2012).
Geographic and stratigraphic distribution: Middle to late Pleistocene of Argentina (Provincia de Buenos Aires) and Uruguay (near Montevideo).

Figure 8.5.3: *Panochthus frenzelianus*. Specimen in the exhibitions of the American Museum of Natural History in New York. Photo by N. Villavicencio.

Panochthus greslebini (Castellanos 1942) †

General Taxonomic Characters: The femur (529 mm in length) shorter and less robust than that of *P. tuberculatus*, but nevertheless, it is still more robust than in *Glyptodon clavipes*. Osteoderms lack a distinguishable central figure and no clearly delimitations are visible. The caudal tube is similar in size to that of *P. tuberculatus* (746 mm in length) and the distal end is less pointy than in *P. subintermedius*, although it is less blunt than in *P. tuberculatus*, *P. frenzelianus* and *P. jaguaribensis*. No complete carapace is known for this taxon.
Body Size: This species is characterized by a body size similar to P. tuberculatus (1,000-1,300 kg, Zamorano 2012).
Diet: Undetermined herbivore. See description for the genus.
Confidence in Species Assignment: Valid according to Zamorano (2012).
Geographic and stratigraphic distribution: Pleistocene of north eastern Brazil.

Panochthus jaguaribensis (Moreira 1965) †

General Taxonomic Characters: The osteoderms of the carapace have a central figure, well defined and surrounded by small polygonal ornamentations. The caudal tube is smaller and more graceful compared to other Argentinian Lujánian species of *Panochthus*. The distal end of the caudal tube is blunt (caudal tube length is 985 mm). No complete carapace is known for this taxon. (Zamorano 2012).
Diet: Undetermined herbivore. See description for the genus.
Confidence in Species Assignment: Valid species according to Zamorano (2012).
Geographic and stratigraphic distribution: Pleistocene of north eastern Brazil.

Panochthus intermedius (Lydekker 1895) †

General Taxonomic Characters: The carapace is the largest of all the species of *Panochthus*, with a sagittal contour length of 2 m, and is wide without anterior elevation or compression. The skull presents less degree of pneumatization compared to *P. tuberculatus*. The cephalic shield consists of big osteoderms with a central figure surrounded by 2 rows of smaller figures like in *P. frenzelianus*. The humerus and femur are more graceful compared to *P. tuberculatus*. The caudal tube is different compared to the ones of other species of *Panochthus*, with central figures in the dorsal and ventral side of the tube, each of them surrounded by one row of smaller figures. (Zamorano 2012).
Body Size: It seems to be of similar size to *P. tuberculatus* but the carapace is bigger (Zamorano 2012).
Diet: Undetermined herbivore. See description for the genus.
Confidence in Species Assignment: Valid species according to Zamorano (2012).
Geographic and stratigraphic distribution: Early to Middle Pleistocene of Argentina (Buenos Aires province) and Bolivia (Cochabamba).

Panochthus subintermedius (Castellanos 1942, stated as Castellanos 1936 by Cruz et al. 2010) †

General Taxonomic Characters: According to Cruz et al., (2010), it differs from other species in the genus by characteristics of the osteoderms, carapace and caudal tube. For example, *P. subintermedius* presents osteoderms without a central figure on the surface, contrary to what is seen in *P. intermedius*. Dorsal carapace is compressed and elevated with the mid-dorsal outline of the carapace presenting an elongated S-shape in lateral view, differing from *P. intermedius* and *P. frenzelianus*. The caudal tube has a strongly sharpened tip, unlike the shape of the caudal tube in *P. greslebini*, *P. tuberculatus* and *P. frenzelianus*. The caudal tube of the specimen analyzed in Cruz et al. (2010) was 96 cm long.
Body Size: This species is similar in size to *P. intermedius*.
Diet: Undetermined herbivore. See description for the genus.
Confidence in Species Assignment: Valid species according to Cruz et al., (2010).
Geographic and stratigraphic distribution: Early-middle Pleistocene of the Buenos Aires province in Argentina.

Map 8.5.2: Geographic distribution of the genus *Panochthus*. References: Zamorano 2010: Ceara State (BR), Paraiba State (BR), La Plata (AR); Aramayo 1985: Monte Hermoso Beach (AR); Deschamps and Borromei 1992: Bajo San Jose (AR); Bargo and Menegaz 1986: Arroyo Tapalque (AR); Prado and Menegaz 1987: Paso Otero (AR); Tonni and Berman 1987: Centinel del Mar (AR); Tonni and Prado 1985: Lujan (AR); Alvargenga and Jones 2010: Casil Quarry (UY); Ubilla and Alberdi 1990: Pintado (UY); Paula Couto 1944: Sr. Oscar Borba Ranch (BR); Alvarez 1974: Arroyo Toropi (AR); Zurita and Carlini 2004: La Tigra (AR), Avia Terai (AR); Hoffstetter 1978: General Bruguer (PY); Marshall and Sempere 1991: Tarija (BO), Betanzos (BO), Nuapua (BO); Zurita and Zamorano 2011: Cochabamba (BO); Costa Ribeiro and Souza Carvalho 2009: Lagoa do Rumo (BR); Guerin 1991: Toca da Janela da Barra do Antoniao (BR); Paula Couto 1980: Taperoa (BR); Porpino and Santos 2004: Lejado de Soledade (BR), Joao Cativo site (BR), Curimatas (BR).

8.6 Family GLYPTODONTIDAE Gray, 1869 †

Along with several Neogene taxa, a number of Pleistocene genera have been recognized (e.g. *Plaxhaplous* Ameghino, 1884; *Daedicuroides* and *Doedicurus* (Burmeister, 1874). Most have been erected on the basis of isolated osteoderms and are known only from dorsal dermal ossicles and carapace elements. The exception is *Doedicurus clavicaudatus*, which is also known from complete specimens (Zurita et al., 2014; Ameghino 1889; Castellanos 1940)

Genus *DOEDICURS* Burmesiter, 1874 †

(Map 8.6.1: Geographic distribution)

General Taxonomic Characters: This group is characterized by a flattened long tail that thickens at the distal end. The carapace is hemispherical, composed of big, thick, flattened dermal plates which may be slightly concave on the exposed surface (Paula Couto 1979). Burmeister classified this group as a different genus from *Glyptodon* based on the morphology of the osteoderms and the characteristics of the caudal tube. First, osteoderms on *Doedicurus* lack ornamentation and instead they present two or more perforations in the form of big holes. The tail is composed of a series of caudal rings in the proximal end and by a caudal tube at the distal end, which is formed by fused caudal rings. The tail is longer than in *Glyptodon*. The surface of the distal caudal tube is widened at the end and has several depressions that might be attachments for spike-like structures (Fariña et al. 2013).
Diet: According to ecomorphological studies, *Doedicurus* was a bulk feeder in open environments. It was highly hypsodont (Vizcaíno et al. 2011). Studies of limb function and center of gravity indicate *Doedicurus* would have had the capacity for bipedal stance (Vizcaíno et al. 2011 b).

Doedicurus clavicaudatus (Owen 1847) †

(Fig. 8.6.1)

General Taxonomic Characters: This species attained 3.6 m in length. Its caudal tube is ~1.30 m long and twice as wide at the distal end of the tail than at the base, with a maximum diameter of 0.35 m (Paula Couto 1979).
Body Size: Body size has been estimated 1900-2400 kg (Soibelzon et al. 2012)
Confidence in Species Assignment: Valid species according to Zurita et al., (2014).
Geographic and stratigraphic distribution: Late Pleistocene to Early Holocene (Lujánian) of the Pampean region of Argentina (Buenos Aires province), Uruguay (Canelones and Colonia district) and Brazil (Rio Grande do Sul state).

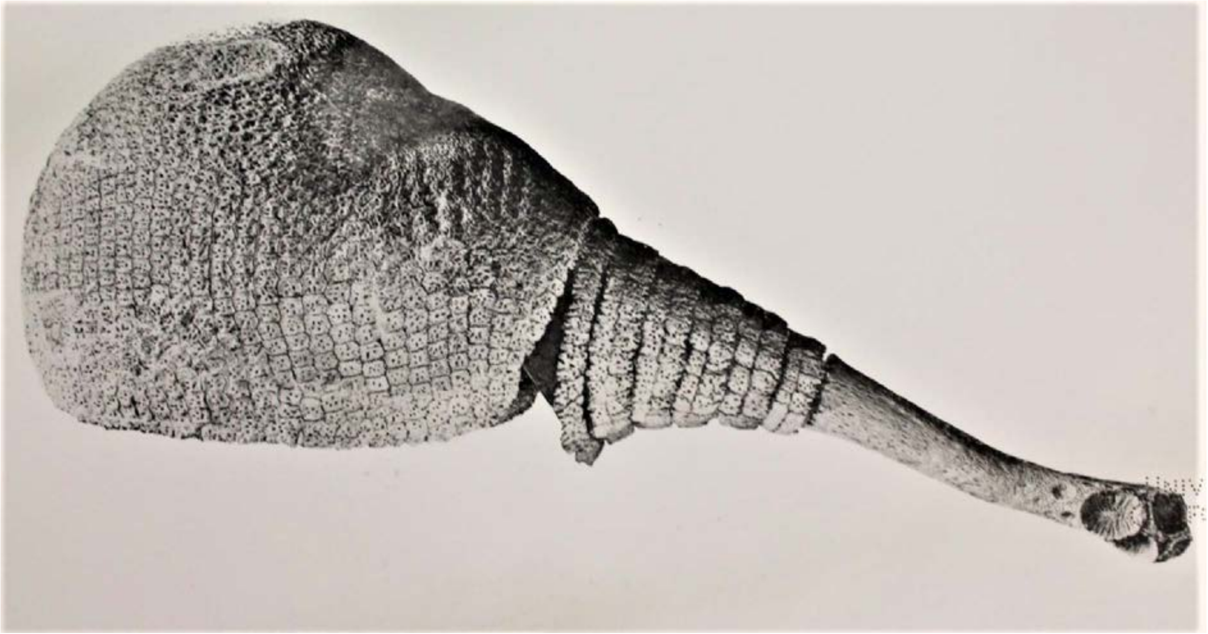

Figure 8.6.1: *Doedicurus clavicaudatus*, carapace and tail. From Lydekker 1894.

Map 8.6.1: Geographic distribution of the genus *Doedicurus*. References: Alvargenga and Jones 2010: Casil Quarry (UY); Aramayo 1985: Monte Hermoso Beach (AR); Bargo and Menegaz 1986: Arroyo Tapalque (AR); Deschamps 2005: Bajo San Jose (AR); Mones 1988: Arroyo Tararias (UY); Pereira and Lopes 2012: Chui Creek (BR); Politis and Salemme 1990: La Moderna (AR); Prado and Menegaz 1987: Paso Otero (AR); Tonni and Prado 1985: Lujan (AR).

Genus *PLAXHAPLOUS* Ameghino, 1884 †
(Map 8.6.2 Geographic distribution)

General comments: Two species are recognized for this genus: *Plaxhaplous canaliculatus* (Ameghino 1884) and *Plaxhaplous ensenadensis* (Ameghino 1904). The first one was erected by Ameghino based on carapace remains which cannot be located today (Rinderknecht 1999) and the second is based on a caudal tube. Both taxa are poorly known and have not been recently examined in the context of taxonomic revisions. The genus has been reported as Ensenadan (Early Pleistocene) in age.
Geographic and stratigraphic distribution: Pleistocene of the Pampean Region of Argentina and Uruguay (Playa del Balneario Arazatí in Departamento de San José).

Map 8.6.2 Geographic distribution of the genus *Plaxhaplous.* References: Rinderknecht 1999: Playa del Balneario Arazatí (UY), Pampas Region (AR).

Genus *DAEDICUROIDES* Burmeister, 1874 †
(Map 8.6.3: Geographic distribution)

Daedicuroides eguiai (Ameghino 1891) †

General comments: Little information exists for this taxon, other than being mentioned as being recovered from Middle to Late Pleistocene sediments of Mar del Plata in Argentina (Ameghino 1891).
Geographic and stratigraphic distribution: Middle to late Pleistocene (Ensendadan) of Mar del Plata in Argentina (Buenos Aires Province).

Map 8.6.3: Geographic distribution of the genus *Daedicuroides*. References: Ameghino 1891: Mar del Plata (AR).

Genus *GLYPTODON* Owen, 1838 †
(Map 8.6.4: Geographic distribution)

General Taxonomic Characters: The genus is characterized, among other things, by the presence of caudal rings and absence of caudal tube in the tail and by having five digits (Hoffstetter 1958). All molariform teeth are trilobulate except M1 (Soibelzon et al. 2006). The carapace is formed by thick osteoderms which are ornamented with a central figure surrounded by a row of 5 to 7 smaller figures (Ameghino, 1889). The genus includes large-sized species (see below).
Diet: The group has generally been described as mainly grazers, primarily because of the the stout architecture of the masticatory apparatus and the high degree of hypsodonty, along with teeth that bear ridges of hard dentine on the occlusal surface (Fidalgo y Tonni, 1983; Pérez *et.al*., 2000; Fariña and Vizcaíno 2001, Vizcaíno *et al.*, 2006). A more recent ecomorphofunctional analysis performed by Vizcaíno et al. 2011 suggested dietary alternatives for *Glyptodon* that ranged from selective feeders in relatively closed environments to browers on specific types of plants or parts of plants above ground. There also is evidence of powerful tongue musculature in *Glyptodon* (Perez et al, 2000), which may have well be an adaptation for food intake and oral processing.
Comments: Three well characterized Lujánian species are recognized (Zurita et al. 2011, Soibelzon et al 2006, Scillato-Yané *et al*., 1995; Carlini y Scillato-Yané, 1999). A fourth species*, G. perforatus (*Ameghino, 1882) may in fact be synonymous with G. clavipes or G. reticulatus (Zurita et al 2011).

*Glyptodon clavipes (*Owen 1839) †
(Fig. 8.6.2)

General Taxonomic Characters: This was the first species described for the genus by Richard Owen in 1839. The osteoderms of the carapace are thick (119-265 mm) but thinner than in *G. reticulatus*. Their shape is hexagonal or pentagonal, the dorsal surface is covered by a rosette pattern consisting of a central figure surrounded by a single row of 6 to 10 peripheral figures. The central figure can be equal in size or larger than the peripheral figures; they are separated by a relatively wide and shallow groove (Solorzano et al., 2015). The dorsal surface of the central and peripheral figures is flat. The plane of the surface of the central figure is slightly depressed below the plane of the peripheral ones (Rincón et al., 2008).
Body Size: Its body size has been estimated to be around 2,000 kg (Vizcaíno et al 2011)
Diet: Hervibore. See description for the genus.
General Ecology and/or Locomotion: Analyses of its athletic capabilities and center of gravity suggest it was able to sustain a bipedal posture (Fariña et al. 1995).
Confidence in Species Assignment: Valid species according to Zurita et al., (2011).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Argentina (Buenos Aires province), Uruguay (San Jose and Salto districts), Brazil (Sao Paulo, Sergipe and Bahia states), Paraguay (near Asuncion), Bolivia (Tarija district), Peru (Cuzco) and Venezuela.

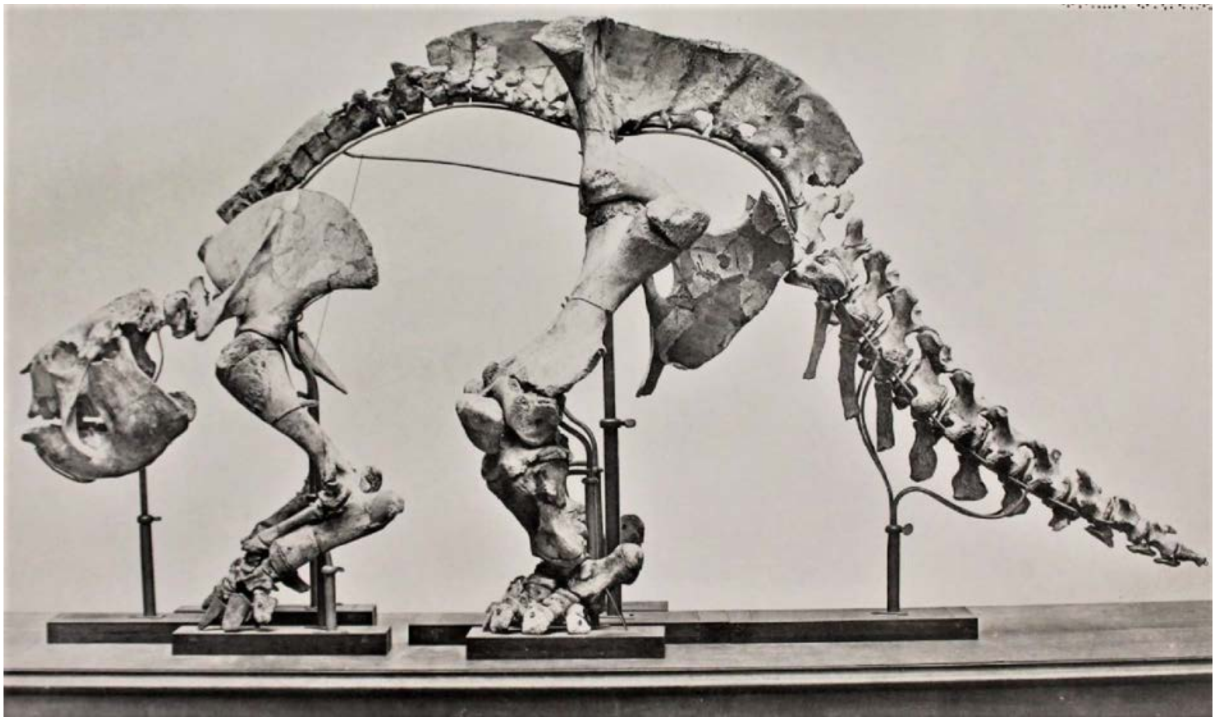

Figure 8.6.2: *Glyptodon clavipes*, skeleton without carapace. From Lydekker 1894.

Glyptodon reticulatus (Owen 1838) †

General Taxonomic Characters: Osteoderms are thicker (4 cm) and smaller in size than those of *G. clavipes*. The osteoderms are composed of a central figure surrounded by peripheral figures. In the osteoderms of the dorsal part of the carapace, the central figure is of the same size as the peripheral ones while, in the anterior part and in the margins of the carapace, the central figure is larger than the peripheral ones (Ameghino 1889, Duarte 1997). The dorsal surface of each osteoderm, central figure, and peripheral figures, is convex and in the same plane (Duarte, 1997; Rincón et al., 2008).
Body Size: Body size is stimated around 862 kg (Fariña et al. 1998). The maximum length of the carapace is about 170 cm and the total anterior posterior curvature length approximately 200 cm (Duarte 1997).
Diet: Herbivore. See description for the genus.
Confidence in Species Assignment: Valid species according to Zurita et al., (2011).
Geographic and stratigraphic distribution: Middle to Late Pleistocene of Argentina (Buenos Aires and Cordoba Provinces), Uruguay (Colonia district), Bolivia (Tarija district) and Brazil (Sao Paulo state).

Glyptodon elongatus (Burmeister 1866) †

General Taxonomic Characters: The main difference between the osteoderms of *G. elongatus* and the ones from the other two Late Pleistocene taxa is that the central figure is much bigger than the peripheral ones (Ameghino 1889).
Body Size: body size was similar to *G. clavipes*, calculated around 2000 kg (Soibelzon et al. 2012).
Diet: Herbivore. See descrciption for the genus.
Confidence in Species Assignment: Valid species according to Zurita et al., (2011).
Geographic and stratigraphic distribution: Late Pleistocene of Bolivia (Tarija district).

Glyptodon munizi (Ameghino 1881) †

General Taxonomic Characters: The postcranial elements are generally more robust and bigger compared to the Lujánian species of the genus (Soibelzon et al. 2006). Accesory osteoderms in the neck and in the area of the abdomen are present (Zurita et al., 2010).
Body Size: This species is larger than the Lujánian (Late Pleistocene-early Holocene) species. The skull is about 30% bigger than *G. clavipes* and more elongated and more robust (Soibelzon et al. 2006).
Diet: Herbivore. See description for the genus.
General Ecology and/or Locomotion: Accessory osteoderms in the neck and abdomen area of the carapace have been described for this taxon and could have served as protection from predators that arrived after the GABI (Zurita et al., 2010).
Confidence in Species Assignment: Valid species according to Zurita et al., (2011).
Geographic and stratigraphic distribution: Middle to Late Pleistocene (Ensenadan) of Argentina (Buenos Aires province).

Map 8.6.4: Geographic distribution of the genus *Glyptodon*. References: Aramayo 1985: Monte Hermoso beach (AR); Deschamps 2005: Bajo San Jose (AR); Forasiepi and Martinelli 2009: Power Line (AR); Bargo and Menegaz 1986: Arroyo Tapalque (AR); Prado and Menegaz 1987: Paso Otero (AR); Zurita and Soibelzon 2010: Baliza Chica (AR), Mercedes (AR); Politis and Salemme 1990: La Moderna (AR); Tonni and Berman 1987: Centinel del Mar (AR); Tonni 1981: Laguna Las Encadenadas (AR); Zurita and Gasparini 2007: San Francisco (AR); Zurita and Carlini 2004: Charata (AR), Avia Terai (AR); Reguero and Candela 2007: Esquina Blanca (AR); Zurita and Miño-Boilini 2009: Rio Bermejo (AR), Monte Cercado (BO); Ubilla and Alberdi 1990: Pintado (UY); Paula Couto 1944: Rio Quarai (UY), Sr. Oscar Borba Ranch (BR); Hoffstetter 1978: General Bruguer (PY); Coltorti et al., 2007: Montesur (BO); Boule and Thevenin 1920: Tarija (BO); Marshall and Sempere 1991: Nuapua (BO), Sucre basin (BO), Tijascka (BO), Sacaba-Cochabamba (BO); De Iuliis 2006: Rio Desaguadero (BO); Pujos and Salas 2004: Cuzco Valley (PE); Dantas 2009: Toca da Raposa (BR); Guerin 1991: Garrincho (BR), Toca do Serrote do Artur (BR), Toca da Janela da Barra do Antoniao (BR); Porpino et al., 2004: Lejado de Soledade (BR); Porpino and Fernicola 2009: Lejado de Escada (BR); Rincón and White 2007: Cueva El Miedo (VE); Rincón 2006: Zumbador Cave (VE); Bryan and Casamiquela 1978: Taima Taima (VE); Cruxent 1970: Cucuruchu (VE); Czaplewski and Rincón 2005: Mene de Inciarte (VE); Ghilardi et al., 2011: Upper Ribeira (BR).

Genus *GLYPTOTHERIUM* Osborn, 1903 †
(Map 8.6.5: Geographic distribution)

General Taxonomic Characters: Anatomically, the three Pleistocene species are different from older members of the genus in shortening of dorsal carapace, a very convex dorsal carapace from lateral view, an elongated rostrum and a more graceful mandible (Carlini et al 2008). Some of the main characteristics that differentiate *Glyptotherium* from *Glyptodon* are: the rostral area of the skull is narrower in *Glyptotherium*. The dorsal carapace has a convex profile from a lateral view and is more highly ached compared to *Glyptodon*; in *Glyptodon* the carapace is lower and more elongated. The posterior region of the carapace is re-curved upwards, a trait that is not seen in *Glyptodon*. The osteoderms of the carpace are less thick compared to *Glyptodon*. The central figures in osteoderms of *Glyptotherium* are concave or flat, while they are convex and surrounded by less developed peripheral figures in *Glyptodon* (Zurita et al 2008).
Body Size: *G. cylindricum* body mass is calculated to be around 562 kg (McDonald 2005). Carapaces of *G. floridanus* are about 1.5 m long and 1.2 m in height (Anderson 1984).
Confidence in Species Assignment: Valid in South America according to Zurita et al., (2012).
Geographic and stratigraphic distribution: The genus *Glyptotherium* is known from North and Central America. Only three species (*G. mexicanum*, *G.floridanum* and *G. cylindricum*) are restricted to the Rancholabrean stage (late Pleistocene). In South America the genus is found in the Late Pleistocene of Venezuela (*Glyptotherium* cf. *cylindricum*) and Brazil (Rio Grande do Norte, Pernambuco, Minas Gerais states).

Map 8.6.5: Geographic distribution of the genus *Glyptotherium*. References: Oliveria et al., 2010: Lago Santa (BR), Conceicao das Crioulas (BR), Lajedo da Escada (BR); Carlini and Zurita 2008: Quebrada Ocando (VE), Muaco (VE); Cruxent 1970: Cucuruchu (VE); Bryan and Casamiquela 1978: Taima Taima (VE).

9. Order TARDIGRADA (=Folivora) Latham & Davies in Forster, 1795

It includes the extant tree sloths found in the neotropics of South America and Central America and the extinct forms of giant ground sloths belong to this order (Table 9).

Table 9. South American Megafaunal Tardigrada. † = extinct

Family MYLODONTIDAE Gill, 1872 †
Subfamily LESTODONTINAE Ameghino, 1891 †
Genus *LESTODON* Gervais, 1855 †
Lestodon armatus (Gervais 1855) †
Genus *OCNOTHERIUM* Lund, 1842 †
Ocnotherium giganteum (Lund 1839) †
Subfamily SCELIDOTHERIINAE Ameghino, 1889 †
Genus *CATONYX* Ameghino, 1891 †
Catonyx tarijensis (Gervais and Ameghino 1880) † *Catonyx chiliensis* (Lydekker 1886) † *Catonyx cuvieri* (Lund 1839) †
Genus *SCELIDOTHERIUM* Owen, 1839 †
Scelidotherium leptocephalum (Owen 1839) † *Scelidotherium bravardi* (Lydekker 1886) †
Genus *VALGIPES* Gervais, 1874 †
Valgipes bucklandi (Lund 1839) †
Subfamily MYLODONTINAE Gill, 1872 †
Genus *GLOSSOTHERIUM* Owen, 1839 †
Glossotherium robustum (Owen 1842) † *Glossotherium lettsomi* (Gervais & Ameghino 1880) † *Glossotherium tropicorum* (Hoffstetter, 1952) † *Glossotherium wegneri* (Spillmann, 1931) †
Genus *MYLODON* Owen, 1839 †
Mylodon darwinii (Owen 1839) †
Genus *MYLODONOPSIS* Cartelle, 1991 †
Mylodonopsis ibsensi (Cartelle 1991) †
Family MEGATHERIIDAE Owen, 1843 †
Subfamily MEGATHERIINAE Gill, 1872 †
Genus *MEGATHERIUM* Cuvier, 1796 †
Subgenus *Megatherium* (*Megatherium*) (Cuvier 1796) †
Megatherium (M.) americanum (Cuvier 1796) † *Megatherium (M.) gallardoi* (C. Ameghino & Kraglievich, 1921) †
Subgenus *Megatherium* (*Pseudomegatherium*) (Kraglievic 1931) †

Megatherium (P.) celendinense (Pujos 2006) † *Megatherium (P.) medinae* (Philippi 1893) † *Megatherium (P.) sundti* (Philippi 1893) † *Megatherium (P.) tarijense* (Gervais and Ameghino 1880) † *Megatherium (P.) urbinai* (Pujos and Salas 2004) † *Megatherium (P.) elenense* (Hoffstetter 1949) †
Genus *EREMOTHERIUM* Spillmann, 1948 †
Eremotherium laurillardi (Lund 1842) † *Eremotherium sefve* (De iuliis and Saint-Andre 1997) †
Subfamily NOTHROTHERINAE Ameghino, 1920 †
Genus *NOTHROPUS* Burmeister, 1882 †
Nothropus priscus (Burmeister 1882) † *Nothropus tarijensis* (Burmeister 1887) † *Nothropus carcaranensis* (Bordas 1942) †
Genus *NOTHROTHERIUM* Lydekker, 1889 †
Nothrotherium maquinense (Lund 1839) † *Nothrotherium escrivanense* (Reinhardt 1878) †
Family MEGALOCHYNIDAE Gervais, 1855
Genus *AHYTHERIUM* Cartelle, De Iuliis, and Pujos, 2008 †
Ahytherium aureum (Cartelle, De Iuliis, and Pujos, 2008) †
Genus *AUSTRALONYX* De Iuliis, Pujos, and Cartelle, 2009 †
Australonyx aquae (De Iuliis, Pujos, and Cartelle, 2009) †
Genus *DIABOLOTHERIUM* Pujos et al., 2007 †
Diabolotherium nordenskioldi (Kraglievich 1926) †

Family MYLODONTIDAE Gill, 1872 †

9.1 Subfamily LESTODONTINAE Ameghino, 1891 †

Genus *LESTODON* Gervais, 1855 †

(Map 9.1.1: Geographic distribution)

Only one Pleistocene species is recognized for the genus, restricted to Late Pleistocene: *Lestodon armatus* (Czerwonogora and Fariña 2013).

Lestodon armatus (Gervais 1855)

General Taxonomic Characters: One of the main characteristics of the skull is the presence of a caniniform tooth displaced forward in the jaw (Czerwonogora et al., 2011).
Body Size: Calculations of body size for many individuals exceed than 3 tonnes (Fariña et al., 1998, Czerwonogora and Fariña 2013), up to as much as 4,100 kg (Bargo et al., 2000).

Diet: *Lestodon* has a wide muzzle and the reconstruction of the musculature of the mouth points to the presence of a square, non-prehensile upper lip, which suggests they were bulk feeders and that the lips and tongue were used to pull plant material from the ground (Bargo et al. 2006). Stable isotopes analyses of $\delta^{15}N$ point to a non-ruminant herbivorous physiology (or to colder and drier climate) while $\delta^{13}C$ results indicate a preference for C3 vegetation in open environments (Czerwonogora et al. 2011).

General Ecology and/or Locomotion: Ear morphology suggests *L. armatus* had the capability of hearing low frequency sound, similar to elephants, which could mean that this species used long range communication (Blanco and Rinderknecht 2008). Limb bone studies have suggested the capacity to dig, although to a lesser degree compared to other mylodontids (Bargo et al 2000).

Confidence in Species Assignment: Valid species according to Czerwonogora et al., (2011).

Geographic and stratigraphic distribution: Pleistocene (Ensenadan and Lujánian) of Argentina (Buenos Aires, Corrientes, Entre Rios, Chaco, San Luis provinces), Pleistocene of Paraguay (General Bruguer/Riacho Negro), Pleistocene and Late Pleistocene of Brazil (Sao Paulo and Minas Gerais states), Late Pleistocene of Uruguay, Late Pleistocene of Bolivia (Tarija district).

Map 9.1.1: Geographic distribution of the genus *Lestodon*. References: Deschamps and Borromei 1992: Bajo San Jose (AR); Bargo and Menegaz 1986: Arroyo Tapalque (AR); Miño-Boilini et al. 2012: Arroyo Toropi (AR); Brunetto et al. 2015: Ensenada Creek (AR); Tonni and Prado 1985: Lujan (AR); Martinez et al., 2013: Paso Otero (AR); Miño-Boilini et al., 2012: Corrientes (AR); Czerwonogora et al., 2011: El Caño (AR); Zurita et al., 2010: Laguna Blanca (AR); Alberdi et al., 1989: Quequén Salado (AR); Bargo et al., 2000: San Antonio de Areco (AR); Czerwonogora et al., 2011: San Luis (AR); Hoffstetter 1978: General Bruguer/Riacho Negro (PY); Pitana et al., 2013: Chuí Creek (BR); Paula Couto 1944: Sr. Oscar Borba Ranch (BR); Ghilardi et al., 2011: Upper Ribeira (BR); Fariña et al., 2014: Arroyo del Vizcaíno (UY); Alvarenga et al. 2010: Pintado (UY); Ubilla and Alberdi 1990: Casil Quarry (UY); Boule and Thevenin 1920: Tarija (BO); Coltorti et al. 2007: Montesur (BO), Tarija (BO).

Genus *OCNOTHERIUM* Lund, 1842 †
(Map 9.1.2: Geographic distribution)

Ocnotherium giganteum (Lund 1839) †

General Taxonomic Characters: this genus and species is described on only two teeth from Lagoa Santa Brazil (Winge 1915).
Confidence in Species Assignment: Despite some controversy about its validity (it was assigned to *Glossotherium* by Hoffstetter 1954 and Kraglievich 1921), Cartelle 1992 considers it as a valid species based on dental characters that seem unique among edentates (Cartelle 1999). No further specimens or information about this species are available.
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Minas Gerais state).

Map 9.1.2: Geographic distribution of the genus *Ocnotherium*. References: Araújo-Júnior et al. 2013: Jirau (BR); Cartelle 1995: Toca dos Ossos (BR); Dantas et al., 2016: Paraiba State (BR), Lagoa Santa State (BR).

8.2. Subfamily SCELIDOTHERIINAE Ameghino, 1889 †

This subfamily comprises middle-sized ground sloths, with a narrow and laterally compressed skull and mandible (Corona et al. 2013).

Genus *CATONYX* Ameghino, 1891 †
(Map 9.2.1: Geographic distribution)

This genus has an elongated and high skull. Three species are known from the Quaternary of South America: *C. (=S.) tarijensis*, *C. (=S.) chiliensis*, *C. cuvieri*. Sexual dimorphism has been suggested as all three species in the genus include specimens that differ by the presence and absence of a pronounced sagittal crest in the skull (Miño-Boilini and Zurita 2015).

Catonyx (= Scelidodon) tarijensis (Gervais and Ameghino 1880)

General Taxonomic Characters: The skull is characterized by temporal ridges and a well-developed sagittal crest, more evident than in *C. chiliensis* and *C. cuvieri*. The mandible is robust. Postcranial elements are in general more robust than in *C. chiliensis* and *C. cuvieri*. The degree of hypsodonty is similar to that of *Scelidotherium bravardi* but less high than in *Scelidotherium leptocephalum* (C. tarijensis Hypsodonty Index=0.76, Miño-Boilini 2012).
Body Size: This is the largest species of the genus. De Esteban-Trivigno et al., (2008) estimated the body mass being between 1,400 and 1,800 kg.
Diet: undetermined herbivore.
Confidence in Species Assignment: Valid species according to Miño-Boilini (2012).
Geographic and stratigraphic distribution: Pliocene to Late Pleistocene of Argentina (Buenos Aires, Corrientes, Córdoba, and Salta provinces, Late Pleistocene of Bolivia(Tarija district) and Uruguay (San Jose District).

Catonyx (= *Scelidodon*) *chiliensis* (Lydekker 1886) †

General Taxonomic Characters: There are subtle differences that separate this species from *C. tarijensis*, such as smaller body size. Dermal ossicles have been reported (Romero-Pittman 2001; Pujos y Salas 2004; Cartelle et al., 2009).
Body Size: Body size is 30% smaller than *C. tarijensis*; therefore, the body mass of *C. chiliensis* is likely around 980-1,200 kg.
Diet: Herbivore. Stable isotope values of $\delta^{13}C$ from a specimen collected in the Pampas region showed C3 plants from a wooded environment as part of its diet (Domingo et al.,2012).
Confidence in Species Assignment: Valid species according to Miño-Boilini (2012).
Geographic and stratigraphic distribution: Late Pleistocene of Argentina (San Luis and Tucuman provinces). Late Pleistocene of Chile (Metropolitana and Tarapaca regions), Bolivia (Tarija district), Peru (Cupisnique desert) y Ecuador (Guayas district).

Catonyx cuvieri (Lund 1839) †

General Taxonomic Characters: Type species of the genus. Skull is more tubular than in *Valgipes bucklandi*. It is the least hypsodont species in the genus (Miño-Boilini 2012).
Body Size: Estimated body size is around 1,600 kg (Lyons et al., 2016).
Diet: undetermined herbivore.
Confidence in Species Assignment: Valid species according to Miño-Boilini (2012).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Minas Gerais, Río Grande do Sul, Iporanga, Sergipe, São Paulo states) and possibly Uruguay (Canelones district).

Map 9.2.1: Geographic distribution of the genus *Catonyx*. References: Soibelzon et al. 2008: Toscas del Rio de la Plata (AR); Miño-Boilini 2012: Mar del Plata (AR), Miramar (AR), Olavarria (AR), Quequen Salado (AR), Lavalle (AR), Guachipas (AR), Necochea (AR), Puerto Arazati (UY), Padcaya (BO), Turamoyo (BO), Pasos Malos (AR), Pampa del Tamarugal (CL), San Bernardo (CL), Salinas (EC), La Carolina (EC), Gruta do Túnel (BR), Iraquara (BR), Toca dos Ossos (BR), Gruta de Itacarambi (BR), Saõ Joaõ das Missões (BR), Saõ Joaõ das Missões (BR), Departamento de Canelones (UY); Casamiquela 1967: Conchali (CL); Pujos 2000: Pampa de Los Fósiles (PE), Talara (PE).

Genus *SCELIDOTHERIUM* Owen, 1839 †
(Map 9.2.2: Geographic distribution)

This genus is endemic to the Quaternary of Argentina and Uruguay. Two species have been recognized: *S. leptocephalum* (Owen 1839) and *S. bravardi* (Lydekker, 1886). Contrary to what has been suggested for the other genera of the scelidotherinae subfamily, the two species in *Scelidotherium* do not show evidence of sexual dimorphism (Miño-Boilini and Zurita 2015).

Scelidotherium leptocephalum (Owen 1839) †
(Fig. 9.2.1)

General Taxonomic Characters: It is the biggest species of the genus. *S. leptocephalum* has the highest hypsodonty index among mylodontids (0.91, Bargo et al., 2006). Some of the charactritic features are: Skull is elongated, low and narrow; the dorsal profile of the braincase is flat; the frontonasal region is narrow; premaxillaries are very developed; The molariforms (M1-5) are simple-crowned, subcylindrical; the mandible is more gracefull; in the foot, finger I is atrophied withour ungula phalanx. (Miño-Boilini and Carlino 2009).
Body Size: this medium-sized ground sloth with a body mass estimated between 600-1,000 kg (Fariña et al., 1998, Bargo et al., 2000).
Diet: It has been classified as a mixed to selective feeder. Its narrow muzzle and other features are consistent with a prehensile lip that was used to select particular plants; the muzzle may also have been used to take roots and tubers from the ground (Bargo and Vizcaíno 2008). Mixed feeding is supported by stable isotope studies (Melo Franca et al., 2015). More recent studies using geometric morphometric methods postulate that *Scelidotherium* sp. was omnivore-frugivore (De Esteban-Trivigno 2014). As in other extinct sloths, *S. leptocephalum* has a small dental occlusal surface area, which is translated into low capacity for oral processing of food (Vizcaíno et al. 2006). From this evidence it has been suggested that *Scelidotherium* could have had a digestive system adapted to efficient nutrient absorption and/or very low metabolic rates. Both characteristics have been observed in modern tree sloths (Britton 1941, McNab 1985).
General Ecology and/or Locomotion: According to biomechanical analyses of the limbs *Scelidotherium* had the appropriate anatomy for digging (Bargo et al. 2000); therefore, it has been considered as one of the diggers of the paleo-burrows found in Mar del Plata, Argentina (Dondas et al. 2009). Scelidotheriinae in general seemed to have had quadrupedal locomotion (Trevigno y Casabán, 2000).
Confidence in Species Assignment: Valid species according to Miño-Boilini and Carlino (2009).
Geographic and stratigraphic distribution: Middle to late Pleistocene of Argentina (Buenos Aires, Cordoba, Corrientes, Salta, Formosa and Santa Fe Provinces.). Late Pleistocene of Uruguay (Soriano district).

Figure 9.2.1: *Scelidotherium leptocephalum*. From Lydekker 1894.

Scelidotherium bravardi (Lydekker 1886) †

General Taxonomic Characters: Morphology is similar to *S. leptocephalum* but of smaller size. The skull is narrower compared with *S. leptocephalum* (Miño-Boilini 2012). The postcranium is more gracile as well. The hypsodonty index is lower than *S. leptocephalum* (Hypsodonty Index: 0.75, Miño-Boilini 2012)
Diet: Undetermined herbivore.
Confidence in Species Assignment: Valid species according to Miño-Boilini (2012).
Geographic and stratigraphic distribution: Early to Middle Pleistocene (Ensenadan) of the Provincia de Buenos Aires and the Pleistocene of the Provincia de San Luis, Argentina.

Map 9.2.2: Geographic distribution of the genus *Scelidotherium*. References: Miño-Boilini 2012: San Pedro (AR), Laguna Vital (AR), Necochea (AR), Mar del Plata (AR), Centinela del Mar (AR), La Plata (AR), Playa del Barco (AR), Olavarria (AR), Río Quequén (AR), Alvear (AR) Villa Escolar (AR), Toscas del Rio de la Plata (AR), Punta Hermengo (AR), La Plata (AR); Corona et al., 2013: Santa Clara (AR); Cruz et al., 2010: Provincia de Cordoba (AR); Esteban et al., 1992: Rosario de la Frontera (AR); Corona and Perea 2010: Soriano (UY).

Genus *VALGIPES* Gervais, 1874 †

(Map 9.2.3: Geographic distribution)

Valgipes bucklandi (Lund, 1839) †

General Taxonomic Characters: Triangular shape of the skull in dorsal view, limb bones are more gracile than in *C. cuvieri* (Miño-Boilini 2012). Individuals possessed osteoderms in the skin (Cartelle et al. 2009).
Body Size: Body size is similar to that of *Catonyx cuvieri*, but limb bones are more elongated and gracile (Cartelle 2009).
Diet: Stable isotope analyses on one individual from Rio Grande do Norte state in Brazil indicate a browsing habit, with leaves, shoots, roots, and fruits as part of the diet, and with preference for relatively closed environments (dos Santos Pereira et al. 2013).
General Ecology and/or Locomotion: Study of craniomandibular characters suggests the presence of sexual dimorphism (Miño-Boilini and Zurita 2015).
Confidence in Species Assignment: Valid species according to Cartelle (2009).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Minas Gerais, Bahia y Piauí States).

Map 9.2.3: Geographic distribution of the genus *Valgipes*. References: Miño-Boilini 2012: Serra do Ramallo (BR); Hubbe et al. 2009: Cuvieri cave (BR); Cartelle et al. 2009: Saõ Joaõ das Missões (BR), Coronel José Dias (BR), Iraquara (BR), Nova Redenção (BR); Santos Pereira et al. 2013: Descoberta cave (BR).

8.3 Subfamily MYLODONTINAE Gill, 1872 †

Genus *GLOSSOTHERIUM* Owen, 1839 †

(Map 9.3.1: Geographic distribution)

Species in this genus are somewhat similar to those in *Mylodon* but are somewhat bigger and with a shorter rostrum. The genus was erected base on remains collected by Darwin in Rio Negro, Uruguay. Owen described the fossil and gave this sloth the name of *Glossotherium*, which means 'tongue beast', given his analyses of the skull morphology that made him realize that this animal probably had an enormous tongue.

Historically, several species have been named under this genus. In a revision made by Esteban 1996, many of these species were synonymized and only two species were considered as valid: *G. chapadmalensis* (Pliocene) and G. robustum for the Pleistocene. Nevertheless, more recent publications (Pitana et al., 2013) still consider at least four species as possibly valid for the Pleistocene of South America: *Glossotherium robustum* (Owen 1842), the most widely distributed; *Glossotherium lettsomi* (Gervais & Ameghino, 1880); *Glossotherium wegneri* (Spillman 1931) and *Glossotherium tropicorum* (Hoffstetter 1852). All these species are distinguishable by subtle differences in size and by geographic location (Pitana 2011). Studies comparing the morphological characteristics of *Glossotherium* specimens from Brazil, the Argentinian Pampas and Uruguay have shown important differences between tropical specimens and subtropical ones suggesting different species or at least very different phenotypes inhabited these two areas (Pitana et al., 2013).

Glossotherium robustum (Owen 1842) †

The most widely distributed species, *G.robustum is* found in Argentina, Uruguay, Bolivia, Brazil and Peru.

General Taxonomic Characters: Elongated and tubular skull but without prenasal arch; long palate; dental formula is 5/5 with C1 always present. *Glossotherium tarijensis* (Ameghino 1902) is considered as a junior synonym of this species. (Esteban 1996).
Body Size: Body size is estimated around 1,200 kg (Prevosti and Vizcaíno 2006).
Diet: *Glossotherium robustum* has been identified as a wide-muzzled sloth, likely behaving as a bulk feeder, using its lips coupled with the tongue to pull out grass and herbaceous plants (Bargo et al. 2006, Bargo and Vizcaíno 2008). Analyses of dental occlusal surface area in *G. robustum* have shown values that indicate a low capacity of oral processing of food (Vizcaíno et al. 2006). This might indicate the presence of a digestive tract capable of more efficient digestion (fermentation) and/or very low metabolic rates in this species, both of which have been observed in extant tree sloths (Britton 1941, McNab 1985).
General Ecology and/or Locomotion: Analysis of the limb morphology and biomechanics have shown that *G. robustum* had the anatomical capabilities for digging and it is proposed, along with *Scleidotherium leptocepahlum*, as one of the possible diggers of the paleo-borrows found in Mar del Plata, Argentina (Bargo et al. 2000). At the same time, Bargo et al., (2000) concluded

that *G. robustum* had a hind limb capable to support a bipedal stance and a fossorial habit. It has not as hypsodont teeth as other sloths in the Tardigrada (Bargo et al 2006).
Confidence in Species Assignment: Valid species according to Esteban (1996).
Geographic and stratigraphic distribution: Late Pleistocene of Argentina (Buenos Aires, Entre Rios, Catamarca Provinces), Uruguay (Colonia, Soriano, Artigas and Tacuarembó districts), Brazil (Rio Grande do Sul), Peru (Piura district) and Bolivia (Tarija district). Possibly present in Paraguay.

Glossotherium lettsomi (Gervais & Ameghino 1880) †

General Taxonomic Characters: The species was erected based on cranial material. It diffes from other species of *Glossotherium*, and particularly from *Glossotherium robustum*, by the smallersize of the skull and wear pattern observed on the teeth (Pitana 2011).
Confidence in Species Assignment: A recent revision of the genus (Pitana 2011) suggests it is possible that this taxon is synonym of *G. robustum*.
Geographic and stratigraphic distribution: Late Pleistocene of Argentina (Santa Fe province), Uruguay (Rio Negro district) and southern Chile (Araucania region)

Glossotherium tropicorum (Hoffstetter, 1952) †

General Taxonomic Characters: This species was erected based on very few elements (Maxillary bone, mandible and isolated molariform teeth). Its classification was mainly supported by the geographic location of the specimens, all of them found in the Ecuadorian coast (Pitana 2011).
Confidence in Species Assignment: Valid species according to Pitana (2011).
Geographic and stratigraphic distribution: Coastal Ecuador

Glossotherium wegneri (Hoffstetter 1948) †

General Taxonomic Characters: The species was based on fairly complete cranial material. It differs from other species in the genus by the presence of an inter-nasal bone; nasal bones are elongated (Pitana 2011).
Confidence in Species Assignment: Valid species according to Pitana (2011).
Geographic and stratigraphic distribution: Pleistocene of the Ecuadorian Andes.

Map 9.3.1: Geographic distribution of the genus *Glossotherium.* References: Bargo et al. 1986: Arroyo Ensenada (AR); Noriega et al. 2003: Arroyo el Espinillo (AR); Czerwonogora and Fariña 2013: Arroyo el Chileno (UY); Mones and Francis 1973: El Cano (UY), Arroyo Vera (UY), Perico Flaco (UY), Las Maulas (UY), Juncal (UY), Arachichú (UY), Chileno (UY), La Palma (UY); Ubilla et al. 2004: Urumbeba (UY); Ubilla and Perea 1999: Piedra Pintada (UY), Arroyo Yucutuja (UY); Alfaro et al. 2002: Arroyo Caraguata (UY); Pitana 2013: Sanga da Cruz (BR), Arroio Garupa (BR), Arroio Chui (BR), Santa Elina (BR), Poco Redondo (BR), Gruta dos Brejoes (BR); Casamiquela 1968: Lonquimay (CL); Bryan and Casamiquela 1978: Taima Taima (VE); ; Hoffstetter 1952: Region La Paz (EC), Quebrada de Oton (EC), Calderon (EC), Llano Chico (EC), Cotocollao (EC), Quebrada de San Antonio de Monteserin (EC), El Batan (EC), Alangasi (EC), Conocoto (EC), Cusubamba (EC), Calhua (EC), Paramo de Sisgun (EC), Punin-Chalan (EC), Puluxa (EC), La Carolina (EC); Pujos and Salas 2004: Talara (PE), Sacado (PE); Marshal and Sempere 1991: Charana (BO), Tarija (BO); Paula Couto 1980: Joao Cativo (BR), Taperoa (BR), Curimatas (BR); Hoffstetter 1954: Lagoa Santa (BR); Rolim 1974: Lage Grande (BR); Salles and Cartelle 2006: Japones Cave (BR); Hoffstetter 1978: General Bruguer (PY); Ubilla and Alberdi 1990: Pintado (UY); Tonni and Prado 1985: Lujan (AR); Moreno and Mercerat 1891: olivera (AR); Deschamp 2005: Bajo San Jose (AR), Balneario Saldungaray (AR); Esteban 1988: Agua de las Palomas (AR); Hoffstetter 1963: Ayo Ayo (BO); Marshal et al. 1984: Savana de Bogota (CO); Román-Carrión 2008: Quito (EC).

Genus *MYLODON* Owen, 1839 †

(Map 9.3.2: Geographic distribution)

Four species have been proposed for the Pleistocene of South America: *M. darwini (*Owen 1839), *M. zeballozi (*H. Gervais and Ameghino 1880), *M. listai (*Ameghino 1898), and *M. insigne* (Kraglievich 1928). The validity of most of these species is considered questionable and *Mylodon darwini*, the type species of the genus, is recognized as the only valid species (see Kraglievich, 1934; Esteban, 1996; Tonni et al., 2003).

Mylodon darwinii (Owen 1839) †

(Fig. 9.3.1)

General Taxonomic Characters: Skull is long. The pre-orbital process is more developed than in other mylodontids. The rostrum is long and the lateral margins of it are parallel. The braincase is flat. The premaxilary bone presenta ans asecndent process that fuses with the nasal bones forming a bony arch (see Brandoni *et al.* 2010 for more details).

Body Size: Body size has been estimated around 1,600 kg, based on measurements of specimens from the Pampas region of Argentina (Fariña et al. 1998).

Diet: *Mylodon darwini* had a narrow-muzzle, with a cone-shaped and prehensile lip that was used to select particular plants or parts of plants (Bargo et al. 2006), indicating that *M. darwinii* was a mixed or selective feeder. It is plausible that *M. darwini* used the stoutly built muzzles to look for food (Bargo and Vizcaíno 2008). Analyses of the dental occlusal surface indicates that teeth were used mainly for crushing and grinding turgid and fibrous items respectively, but the capacity for oral processing of food was low (Vizcaíno et al. 2006). Low occlusal surface area values have been associated with low metabolic requirements and or low quality food (Bargo and Vizcaíno 2008). Layers of *Mylodon* dung are well preserved in Mylodon Cave, Ultima Esperanza, Chile. In this dung grasses and sedges have been identified as the dominant plant types (Moore, 1978).

General Ecology and/or Locomotion: Along with dung, exceptionally well preserved skin of *M. darwinii* was also found in this cave. The skin has dermal osscicles embedded and thick red hair. Large body size and low thermal conductance found in the skin-hair would have allowed *M. darwinii* to inhabit places at high latitudes (McNab 1985). Analyses of the skeleton have suggested that *Mylodon* walked using its four limbs and that the hind limbs had the necessary strength to support and bipedal stance aided by the tail (Fariña and Vizcaíno 1999).

Confidence in Species Assignment: Valid species according to Brandoni et al., (2010) and Esteban (1996).

Geographic and stratigraphic distribution: Pleistocene of Bolivia (Chuquisaca district), Late Pleistocene of Argentina (Buenos Aires, Cordoba, San Luis and Santa Cruz provinces), Uruguay (Soriano and Canelones district), Brazil (Rio Grande do Sul state) and Chile (Magallanes and Aysen regions).

Map 9.3.2: Geographic distribution of the genus *Mylodon.* References: Fariña et al., 2014: Arroyo Vizcaíno (UY); Perea 1998: Arroyo Gutierrez (UY); Pitana et al., 2013: Chui Creek (BR); Martinez et al., 2013: Paso Otero (AR); Brandoni et al. 2010: El Palmar (AR); Long et al., 1998: Gruta del Indio (AR); Alberdi et al., 1987: Las Buitreras (AR); Alberdi et al 2001: Piedra Museo (AR); Tauber and Di ronco 2003: Rio Anisacate (AR); Cruz et al. 2007: Departamento Rio Cuarto (AR); Borrero and Martin 2008: Cueva Condor (CL); Martin et al., 2013: Cueva Chica (CL); Prevosti et al., 2003: Cueva de Los Chingues (CL); Steele and Politis 2009: Lago Sofia 4 (CL); Nami and Nakamura 1995: Cueva del Medio (CL); Jackson 2003: El Membrillo (CL); Alberdi et al. 1987: Cerro Sota (AR); Bird 1988: Pali Aike (AR), Cueva Fell (CL); Martin 2008: Cueva del Puma (CL); Prieto 1991: Cueva Lago Sofia 1 (CL); Labarca et al., 2008: Cueva Las Guancas (CL); Lopez 2009: Bano Nuevo (CL); Latorre 1998: Tres Arroyos (CL), Cueva del Milodon (CL); Bargo and Deschamp 1996: Olavarria (AR), Punta Alta (AR), Miramar (AR), Carcarañá River (AR); Kraglievic 1928: Tandil (AR); Bargo and Deschamp 1996: Faro Segunda Barranca (AR); Brandoni et al. 2010: San Alberto (AR), Calamuchita (AR), Rio Tercero (AR), Santa Maria (AR), San Pedro (AR), Salto (AR), Necochea (AR), Santa Clara (AR), Mojotorillo (BO); Hoffstetter 1968: Ñuapua (BO); Carlini and Tonni 2000: General Bruguer (PY).

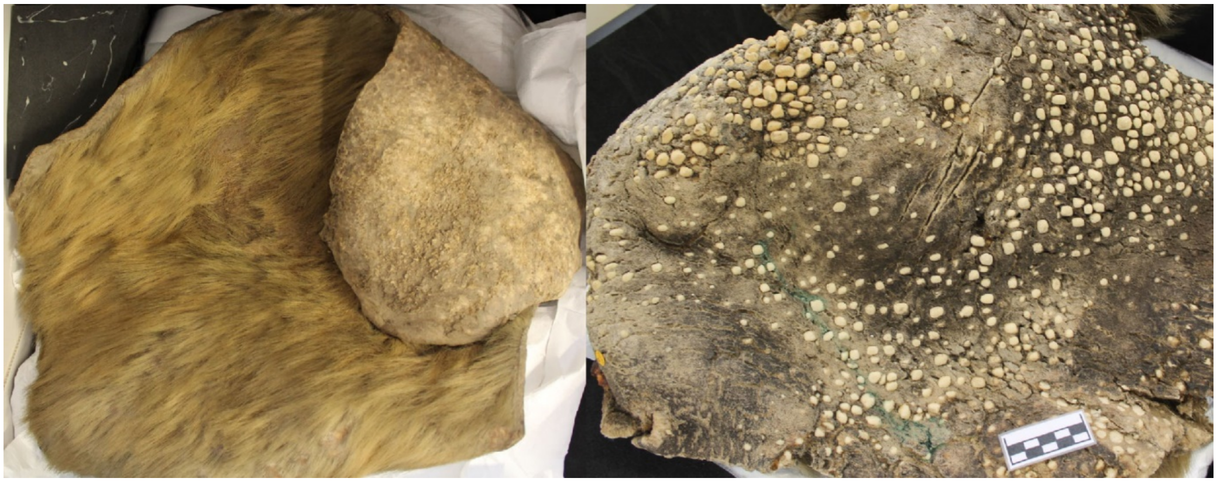

Figure 9.3.1: *Mylodon darwini*, skin. Right image shows the hair, left image is the underside of the same sample, showin the incrusted dermal ossicles. Specimen located at the Natural History Museum in London. Photo by N. Villavicencio.

Genus *MYLODONOPSIS* Cartelle, 1991 †
(Map 9.3.3: Geographic distribution)

Mylodonopsis ibsensi (Cartelle 1991) †

General Taxonomic Characters: Described by the first time from Bahia, Brazil (Cartelle 1991), this species is very similar to *Mylodon darwini*, which is why it the generic name is *Mylodonopsis*. The main characteristic that separates this genus from *Mylodon* is that the first superior molariform tooth is still present (but atrophied), while it is absent in *Mylodon* (Cartelle 1999).
Body Size: Body size is similar to *Mylodon* but bigger than *Glossotherium*, in comparison with which it also has more slender bones (Cartelle 1991)
Confidence in Species Assignment: Valid species according to Cartelle (1999).
Comments: Specimens referred to *Glossotherium giganteum* found in Brazil have recently been referred to *Mylodonopsis ibsensi* (Cartelle 1991, Pitana, 2011).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Pernambuco, Paraiba, Piaui, Minas Gerais, Sao Paulo and Matto Grosso states).

Map 9.3.3: Geographic distribution of the genus *Mylodonopsis*. References: Cartelle 1991: Gruta dos Brejões (BR), Gruta dos Ossos (BR), Grutas Lagoa Santa (BR); Salles and Cartelle 2006: Japones Cave (BR); Silva, 2009; Da Silva et al., 2010: Lagoa Tanque (BR).

Family MEGATHERIIDAE Owen, 1843 †

The largest of the extinct sloths (*Megatherium* and *Eremotherium*) belong to this group, and have body masses comparable to extant elephants. They are characterized by a bilophodont dentition, with no modification of the anterior teeth into caniniforms. The dental series are continuous without a diastema. The humerus lacks an entepicondylar foramen. The tibia and fibula tend to fuse in this group but not in other sloths.

9.4 Subfamily MEGATHERIINAE Gill, 1872 †

Genus *MEGATHERIUM* Cuvier, 1796 †
Subgenus *Megatherium* (*Megatherium*) Cuvier 1796 †
Subgenus *Megatherium* (*Pseudomegatherium*) Kraglievic 1931 †
(Map 9.4.1: Geographic distribution. Fig. 8.4.1)

The genus *Megatherium* is recorded in South America from the Middle Pliocene to the Late Pleistocene. Two subgenera are recognized: *Megatherium* and *Pseudomegatherium*. *Megatherium* (*Megatherium*) is composed of *M. (M.) americanum* and *M. (M.) altiplanicum*. *Megatherium (Pseudomegatherium)* (Kraglievic 1931) consists of *M. (P). sundti*, *M. (P). urbinai*, *M. (P). celendinense*, *M. (P). tarijense*, *M. (P). mediane*, (De Iuliis 1996, Pujos 2006, 2008). The species *M. elenense* (Hoffstetter 1949) and *M. nazarrei* (Kraglievic 1925) may be valid but remains are too fragmentary and further analyses about its taxonomic need to be done (Pujos 2006, De Iuliis 1996).

Megatherium (Megatherium) exhibits high hypsodonty compared to *Megatherium (Pseudomegatherium)* species and also compared to the genus *Eremotherium* (Bargo et al. 2006). This characteristic is consistent with the consumption of more abrasive plants in open habitats such as the ones from the Pampas region where *M. americanum* is commonly found. Hypsodonty also is consistent with the vegetation present in the high Andes region where *M. altiplanicum* was present; however, *M. americanum* in the Tarija basin, Bolivia, probably lived in habitats with less abrasive vegetation (De Iuliis 1996).

Megatherium (Pseudomegatherium) species exhibit intermediate hypsodonty between *M. (M.) americanum* and *Eremotherium*. All Andean forms of *M. pseudomegatherium*, with the exception of *M. (P). celendinense*, show a reduction in size compared to *M. americanum* (20%-60% smaller). All Andean *Megatherium* exhibit a short rostrum (Pujos 2008) and a more quadrupedal stance than specimens recovered elsewhere (Pujos et al., 2002).

Megatherium (M.) americanum (Cuvier 1796) †

General Taxonomic Characters: This species was the first extinct giant ground sloth discovered and described. It had a small head compared to the robust body; the skull presents a short and narrow snout; the zigomatic arch has a developed ascendent process that joints the skull at the level of the cheeck; it presents 5 upper molariforms and 4 lower each of which has transversal crests; the forelimbs are larger that the hind limbs; digit I in the hand is vestigial while the digit II presents a predominant ungual phalanx; in the foot, digits II and I are reduced while digit III presents a well-developed ungual phalanx. (Forasiepi et al., 2007).

Body Size: It has the largest body size of all giant ground sloths, with an estimated mass between 3-6 tonnes (Casinos 1996, Fariña et al., 1998).

Diet: With regards to its feeding habits, cranio-mandibular analyses suggest a browsing diet in open habitats, with the potential to feed on moderate to tough food, including fruits (Bargo 2001). The plants consumed by *M. americanum* would have been of low to moderate toughness according to microwear analyses (Green and Kalthoff 2015). The teeth of *M. americanum* are extremely hypselodont and bilophodont, which suggests they were used mainly for cutting food rather than for crushing and grinding (Bargo 2001). According to dental occlusal surface area analyses, *M. americanum* would have performed high oral food processing and maybe exhibited a low fermentation capacity and/or high metabolic requirements (Vizcaíno et al. 2006) when compared with other sloths and ungulates. Through analyses of the biomechanics of the limbs in *M. americanum*, it has been suggested that this animal might have been a scavenger or possibly and active predator (Fariña and Blanco 1996). The capacity of eating flesh is not discarded by cranio-dental and cranio-mandibular analyses (Vizcaíno et al 2006), although most authors consider it to be herbivorous. A coprolite attributed to *M. americanum* contained mainly woody plants (Carretero et al. 2004).

General Ecology and/or Locomotion: It has been suggested that *M. americanum* was hairless given its body size and the climatic conditions inferred for the late Pleistocene of its geographic distribution (Fariña 2002). Studies of footprints found in Pehuen-co, Argentina (Blanco and Czerwonogora 2003) concluded that *Megatherium* was walking in a bipedal stand when the footprints where made. The possibility of bipedalism in this giant sloth was proposed previously based on biomechanical analyses (Casinos 1996). It has been estimated that *M. americanum* could reach average speeds of 1.21 m per second (Blanco and Czerwonogora 2003).

Confidence in Species Assignment: Valid species according to De Iuliis (1996).

Geographic and stratigraphic distribution: Late Pleistocene to Early Holocene of Argentina (Buenos Aires province), Uruguay (Artigas district), Brazil (Rio Grande Do Sul, Sao Paulo and Bahia states); Pleistocene of Bolivia (Oruro, Chuquisaca and Tarija provinces), Paraguay (near Asuncion), and Peru (Cuzco and Cachimayu).

Figure 9.4.1: *Megatherium americanum* on the exhibitions of the Natural Hitory Museum in London. Photo by N. Villavicencio.

Megatherium (M.) gallardoi (C. Ameghino & Kraglievich, 1921) †

General Taxonomic Characters: Very similar in size and morphology to *M. (M.) americanum* and *M. (M.) altiplanicum*. Some differences in the cranium and postcranium support its status as a valid species (Brandoni et al., 2008).
Body Size: Large megatheriidae, similar in size to *M. (M.) americanum*.
Diet: Herbivore. See description for the genus.
Confidence in Species Assignment: Valid species according to Brandoni et al., (2008).
Geographic and stratigraphic distribution: Early to Middle Pleistocene of Argentina (Buenos Aires province).

Megatherium (Pseudomegatherium) celendinense (Pujos 2006) †

General Taxonomic Characters: This species was the largest Andean megatheriine, comparable in size to *M. americanum*, *Eremotherium laurillardi* and *Eremotherium eomigrans*. It had a short rostrum and a moderate degree of hypsodonty. (Pujos 2006)
Diet: The Andean lineage of *Megatherium* may have been more of a grazer than browser (Pujos and Salas 2004).

General Ecology and/or Locomotion: it had a quadrupedal stance as other Andean megatheriidae (Pujos 2006).
Confidence in Species Assignment: Valid species according to Pujos (2006).
Geographic and stratigraphic distribution: Late Pleistocene of Peru (Cajamarca district).

Megatherium (Pseudomegatherium) medinae (Philippi 1893) †

General Taxonomic Characters: A megatheriid of medium size, this species was similar to *M. sundti* and *M. tarijense*, smaller than *M. americanum* and bigger than *M. altiplanicum*.
Confidence in Species Assignment: Valid species according to Pujos and Salas (2004).
Geographic and stratigraphic distribution: Late Pleistocene of Chile (Antofagasta, Tarapaca, Metropolitana regions).

Megatherium (Pseudomegatherium) sundti (Philippi 1893)

General Taxonomic Characters: This medium-size megatheriine was very similar in linear dimensions to *M. (P.) medinae* and M. (P.) tarijense; larger than *M. altiplanicum* and *Eremotherium sefvei*; and smaller than *M. americanum* (De Iuliis 2006). While is very similar to *M. (P.) mediane*, particular characteristics of the femur, which seems more similar to *M. (M.) americanum*, support that it is a different species (De Iuliis 2006).
Confidence in Species Assignment: Valid species according to Pujos and Salas (2004).
Geographic and stratigraphic distribution: Late Pleistocene of Bolivia (Oruro district).

Megatherium (Pseudomegatherium) tarijense (Gervais and Ameghino 1880) †

General Taxonomic Characters: This medium-sized megatheriine is smaller than *M. (M.) americanum*, *M. (P.) celendinense*, *Eremotherium laurillardi*, and *Eremotherium eomigrans*, but with linear dimensions overlapping the lower end of ranges of these species. It is similar in size to *M. (P.) medinae*, *M. (P.) urbinai* and *M. (P.) sundti*, and larger than *M. (M.) altiplanicum*.
Diet: It belongs to the Andean linage of *Megatherium*, which as noted above is believed to be more of a grazer than a browser (Pujos and Salas 2004).
Confidence in Species Assignment: Valid species according to Pujos and Salas 2004.
Geographic and stratigraphic distribution: Late Pleistocene or Peru (Ayacucho and Cuzco provinces) and Bolivia (Tarija district).

Megatherium (Pseudomegatherium) urbinai (Pujos and Salas 2004) †

General Taxonomic Characters: Some 35% smaller that *M. americanum* and 5% larger than *M. altiplanicum* (which is the smallest *Megatherium*), M. (P.) urbinai is a medium-sized, relatively gracefully built megatheriid.
Body Size: Body size can be estimated aroun 2,600 kg (Pujos and Salas 2004).
General Ecology and/or Locomotion: Probably it had a quadrupedal habit but perhaps used a bipedal stance occassionally (Pujos and Salas 2004).
Confidence in Species Assignment: Valid species according to Pujos and Salas (2004).

Comments: Two specimens have been found, one from the coast and one from the Andean region. The size of the Andean specimen is 18% greater than the coastal one, showing intraspecific variation (Pujos and Salas 2004).
Geographic and stratigraphic distribution: Pleistocene to Late Pleistocene of Peru (Arequipa, Lima, Ica districts).

Megatherium (Pseudomegatherium) elenense (Hoffstetter 1949) †

General Taxonomic Characters: This small-sized temperate-latitude megathere was approximately half the size of *Eremotherium laurillardi*. It belongs to the Andean linage of *Megatherium*.
Diet: This species, like other members of the Andean lineage of *Megatherium*, may have been more of a grazer than browser (Pujos and Salas 2004).
Confidence in Species Assignment: Valid species according to Pujos and Salas (2004).
Geographic and stratigraphic distribution: Late Pleistocene of Ecuador (Santa Elena Peninsula) and Peru (Piura and Pasco districts)

Map 9.4.1: Geographic distribution of the subgenera *Megatherium (Megatherium)* and *Megatherium (Pseudomegatherium)*. References: Tonni 1970: Punta Hermengo (AR); Reigh 1957: Arroyo Loberia (AR); Rusconi 1954: Villa Ballester (AR); Alvarez 1974: Arroyo Toropi (AR); Zurita and Carlini 2004: General San Martin (AR), General Roca (AR); Zurita and Miño-Bolini 2009: Rio Bermejo (AR); Paula Couto 1944: Rio Quarai (BR); Marshall and Sempere 1991: Umala (BO), Quebrada Tijascka (BO); Pujos and de Iuliis 2007: Casa del Diablo (PE); Pujos and Salas 2004: Ayacucho-Pikimachay (PE), Celendin (PE), Talara (PE), Cuzco (PE), Quebrada Cachimayu (PE), Quebrada El Jahuay (PE), Tres Ventanas (PE), Uyujalla (PE); Bargo et al. 1986: Arroyo Tapalque (AR); Prado et al. 1987: Paso Otero (AR); Tonni et al. 1985: Lujan (AR); Tonni et al. 1987 Centinela del Mar (AR); Politis and Messineo 2008: Campo Laborde (AR); de Iuliis 2006: Rio Desaguadero (BO); Marshall and Sempere 1991: Nuapua (BO); Boule and Thevenin 1920: Tarija (BO); Hoffstetter 1978: General Bruguer (PY); Ubilla and Alberdi 1990: Pintado (UY); Oliveira and Lindner 2002: Passo do Megatherio (BR); Brandoni et al., 2008: Cuidad Autonoma de Buenos Aires (AR); Pujos 2006: Santa Rosa cave (PE); Moreno et al., 1991: Chiu-Chiu (CL); Labarca 2015: Lo Hermida (CL); Casamiquela 1969: Las Pozas-Chacabuco (CL), Cumiñalla (CL), Pampa del Tamarugal (CL), Salar de Pintados (CL); Lopez et al., 2010: Jalquincha (CL); De Iuliis 2009: Padcaya (BO), Yantac (PE); Coltorti and Abbazzi 2007: Montesur (BO); Hoffstetter 1968: Ayacucho (PE); Pujos 2004: Cerro Pasco (PE).

Genus *EREMOTHERIUM* Spillmann, 1948 †

(Map 9.4.2: Geographic distribution)

According to Cartelle and De Iuliis (1995) only one species is recognized for the late Pleistocene of South America, Central America and Southern North America, including southern parts of the United States: *Eremotherium laurillardi* (Lund 1842). Guerin and Faure (2000) and Faure et al., (2014) have postulated the presence of a dwarf species of *Eremotherium* in intertropical Brazil, the validity of which has been questioned using arguments about the ontogeny of the specimen studied and the intraspecific variation that has been found in large scale studies of *E. laurillardi* specimens (De Iuliis and Cartele 2006; Cartelle et al. 2014). Another Pleistocene species has been proposed based on a femur found in Ulloma, Bolivia: *Eremotherium sefvei* (De Iuliis and Saint-Andre 1997).

The members of this genus are very similar in size to *Megatherium*. They differ from the last by presenting longer limbs, having only three digits on their hands (opposed to the 4 seen in *Megatherium*) and by having a slender skull (Fariña et al., 2013).

Eremotherium laurillardi (Lund 1842) †

General Taxonomic Characters: it differs from *Megatherium* by differences in the skull, molariforms and manus. The premaxillae are small and triangular in shape. The zigomatic arch and orbit are located in a more ventral positions compared to Megatherium. With regards to the molariforms, the pulp cavity is shorter in Eremotherium compared to Megatherium. The manus of Eremotherium is characterized by retaining digits III and IV, both of wich present well developed ungula phalange. (Cartelle and De Iuliis 1995).

Body Size: *E. laurillardi* is equal or greater in size than *Megatherium americanum*, with an estimated body mass of about 4 tonnes (Fariña, 2013) and with some specimens reaching 6 m in length (Dantas & Cozzuol 2016).

Diet: Herbivore. The masticatory apparatus of *Eremotherium* reveals that it had great oral capacity for processing food which could suggest low digestive efficiency. On the other hand, some authors have suggested that even if the masticatory apparatus efficiency was maximized, it would have not been enough to maintain such body size and therefore *Eremotherium* probably had the stomach capacity for fermenting plant tissue as is seen in modern tree sloths (Naples and McAfee 2011). The biomechanics of its bite shows that it had the capacity for processing soft and fibrous types of food (Bargo et al., 2006). Carbon stable isotope studies from individuals found in Rio Grande do Norte, Alagoas, Sergipe and Bahia states in northern Brazil indicate that these animals had a mixed diet composed of C3 and C4 plants, mixing grass, herbs leaves and fruits (Viana et al., 2011; de Melo Franca et al., 2014; Dantas et al. 2013). Large nasals compared to *Megatherium* could be related to food selection (Naples and McAfee 2011).

General Ecology and/or Locomotion: Variation in size among adult and young individuals has been found, and the possibility of sexual dimorphism is suggested as an explanation for this (Cartelle and De Iuliis 1995).

Confidence in Species Assignment: Valid according to Cartelle and De Iuliis (1995).

Geographic and stratigraphic distribution: Plio-Pleistocene of tropical South America (Peru, Brazil, Colombia, Ecuador, Bolivia, Venezuela), Central America, North America including south Eastern United States.

Eremotherium sefve (De iuliis and Saint-Andre 1997) †

General Taxonomic Characters: This species is the smallest post-Miocene megatheriinae known. The description of this species is based on an isolated femur found in Bolivia (De iuliis and Saint-Andre 1997). The size of the femur is about 40% smaller than for the homologous bone in *Eremotherium laurillardi*.
Confidence in Species Assignment: Valid species according to De iuliis and Saint-Andre (1997).
Geographic and stratigraphic distribution: Pleistocene of Bolivia (Ulloma, Chuquisaca district).

Map 9.4.2: Geographic distribution of the genus *Eremotherium*. References: Pereira and Lopes 2012: Chui creek (BR); Oliveira and Dutra 2002: Passo do Megaterio (BR); Ghilardi and Fernandez 2011: Upper Ribiera (BR); Martinelli and Fonseca 2012: Uberaba (BR); Hoffstetter 1954: Lago Santa (BR); Paula Couto 1978: Cerro do Gronda (BR); Dantas and Tasso 2007: Fazenda Suse (BR); Lumley and Lumley 1987: Toca da Esperanca (BR); Lessa and Cartelle 1998 (Toca dos Ossos (BR); Ribeiro and Carvalho 2009: Lagoa do Rumo (BR); Dantas and Zucon 2007: Fazenda Caraiba (BR); Paula Couto 1980: Lage Grande (BR), Taperoa (BR), Joao Cativo site (BR), Curimatas (BR); Guerin 1991: Toca da Janela da Barra do Antoniao (BR), Lagoa Sao Vitor (BR), Lagoa do Ipu (BR); Porpino and Santos 2004: Lejado de Soledade (BR), Lejado de Escada (BR); Pujos and Salas 2004: Miramar (PE); Hoffstetter 1952: Engabao de Chanduy (EC), La Carolina (EC); Cantalamessa and Di Celma 2001: Rio Caña (EC); Cruxent 1970: Cucuruchu (VE); Rincón et al., 2006: Zumbador Cave (VE); De Iuliis 1995: Fusagasuga (CO), Huila (CO), Norte de Santander (CO); Salles and Cartelle 2006: Japones Cave (BR); Simpson and Paula Couto 1981: Pedra Preta (BR); Pujos and Salas 2004: Talara (PE); Czaplewski and Rincón 2005: Mene de Inciarte (VE); De Iuliis and Saint-Andre 1997: Rio Desaguadero (BO).

9.5 Subfamily NOTHROTHERIINAE Ameghino, 1920

Genus *NOTHROPUS* Burmeister, 1882 †
(Map 9.5.1: Geographic distribution)

Currently, three species are recognized for this genus, all of them erected based on craniomandibular characters with no associated postcranial elements.

Nothropus species are characterized by bilophodont and rectangular molariform teeth, in which shape and occlusal surface is very similar to that in *Nothrotherium* and *Nothrotheriops* (North America).

No information about the body size of *Nothropus* or other paleoecological characteristics has been reported, given the scarce material upon it has been described.

Nothropus priscus (Burmeister, 1882) †

General Taxonomic Characters: This species was erected based on an isolated mandible with teeth from the Pleistocene of Argentina. It is possible to observe an alveolus for a small anterior caniniform tooth, separated by a diastema from the three posterior molariforms (Brandoni and McDonald 2015).
Confidence in Species Assignment: Valid species according to Brandoni and McDonald (2015).
Geographic and stratigraphic distribution: Late Pleistocene of Argentina (Santa Fe province).

Nothropus tarijensis (Burmeister, 1887) †

General Taxonomic Characters: This species was erected based on a partial dentary from the Pleistocene of Bolivia. As in the case of *N. priscus*, it is also possible to observe the place for a small anterior caniniform tooth, separated by a diastema from the three posterior molariforms (Brandoni and McDonald 2015).
Confidence in Species Assignment: Valid species according to Brandoni and McDonald (2015).
Geographic and stratigraphic distribution: Pleistocene of Bolivia (Tarija district).

Nothropus carcaranensis (Bordas, 1942) †

General Taxonomic Characters: This species was erected based on a partial dentary from the Pleistocene of Santa Fe Province, Argentina, which lacks evidence for the caniniform, unlike the condition in the other two species of *Nothropus*. Analysis of postcranial elements associated with this dentary have shown considerable similarity to the skeleton of the North American *Nothrotheriops*, raising doubt about the validity of this species, and the possibility of *Nothrotheriops* occurring in South America (Brandoni and McDonald 2015)
Confidence in Species Assignment: Valid species according to Brandoni and McDonald (2015).
Geographic and stratigraphic distribution: Late Pleistocene of Argentina (Santa Fe province).

Map 9.5.1: Geographic distribution of the genus *Nothropus*. References: Paula Couto 1979: Santa Fe (AR); Marshall and Sempere 1991: Tarija (BO); Brandoni and McDonald 2015: Carcarañá river (AR).

Genus *NOTHROTHERIUM* Lydekker, 1889 †
(Map 9.5.2: Geographic distribution)

These are small-sized ground sloths that are differentiated from other Norhotheriinae by the absence of the caniniform (Paula Couto 1979, Brandoni and McDonald 2015, Pujos 2001). Two species are recognized for the Pleistocene of South America, differentiated by dental characters: *N. maquinenese* and *N. escrivanense*. These two species were described based on cranial and postcranial elements found in Brazil at the sites of Lapa nova de Maquiné and Lapa de Escrivania n° 5, respectively. All elements were collected by the Danish paleontologist and father of Brasialian paleontology, P. W. Lund.

Nothrotherium maquinense (Lund 1839) †

General Taxonomic Characters: Based on materials collected by P.W. Lund in Cavernas de Maquiné, Brazil, the species is characterized by its slenderness and relatively small size, similar to the extant Tapir. The claws were very narrow (Paula Couto 1979).
Body Size: Estimated around 150-300 kg based on *Tapir terrestris*, sensu Paula Couto 1979.
Confidence in Species Assignment: Valid species according to Paula Couto (1979).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Minas Gerais and Bahia States)

Nothrotherium escrivanense (Reinhardt, 1878) †

General Taxonomic Characters: The validity of this species is questionable because it is based on remains of a young adult; however, the skeleton is almost complete. According to Pujos (2001) *N. escrivanense* is valid and differs from *N. maquinenese* by dental characters as well as in characteristics of the manus and pes. At the same time, the postcranial elements in *N. ecrivanense* are longer and more gracile compared to *N. maquinense.*
Confidence in Species Assignment: Valid species according to Pujos (2001)
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Minas Gerais state).

Map 9.5.2: Geographic distribution of the genus *Nothrotherium*. References: Ameghino 1907: Iporanga (BR); Cartelle and Hartwig 1996: Toca da Boa Vista (BR); Ghilardi et al., 2011: Upper Ribeira (BR); Hoffstetter 1954: Lagoa Santa (BR); Pujos et al., 2001: Minas Gerais State (BR).

9.6 Family MEGALOCHYNIDAE Gervais, 1855

Several morphological traits separate this group from other families of sloths. The main characteristic is a modification in the anterior-most upper and lower teeth into either caniniforms or incisiforms separated from the molariforms by a diastema. The shape of the caniniforms varies among different genera of the family, which includes extant genus *Choloepus* (two-toed sloth).

For the late Pleistocene of South America four species have been recently described based on fairly complete remains. These are: *Diabolotherium nordenskioldi* (Pujos, De Iuliis, Argot, and Werdelin, 2007), *Ahytherium aureum* (Cartelle, De Iuliis, and Pujos, 2008), *Australonyx aquae* (De Iuliis, Pujos, and Cartelle, 2009) and *Megistonyx oreobios* (McDonald, Rincón and Gaudin 2013). Also described previously are *Megalonychops primigenius*, *Megalonychops carlesi* and *Megalonychops fontanai* (Kraglievich, 1926), all of which are poorly known and based on incomplete long bones and some teeth (Paula Couto 1977, Pascual et al. 1967, Paula Couto 1979). *M. carlesi* and *M. fontanai* have been considered Miocene in age by some authors (Mones 1986). The presence of the North American genus *Megalonyx* was documented for Acre State in Brazil (Simpson and Paula Couto 1981), which is questioned by some authors since it has not been documented in any other part of South and Central America (De Iuliis et al. 2009).

Genus *AHYTHERIUM* Cartelle, De Iuliis, and Pujos, 2008 †
(Map 9.6.1: Geographic distribution)

Ahytherium aureum (Cartelle, De Iuliis, and Pujos, 2008) †

General Taxonomic Characters: Members of this genus are more graceful and smaller than *Megalonyx jeffersonii.* It had a short and wide rostrum (Cartelle, De Iuliis, and Pujos, 2008).
Body Size: Estimated around 1,200 kg (Lyons et al., 2016).
Confidence in Species Assignment: Valid species according to Cartelle, De Iuliis, and Pujos (2008).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Poço Azul, a submerged cave near Nova Redenção, Bahia Iporanga, São Paulo).

Map 9.6.1: Geographic distribution of the genus *Ahytherium.* References: De Iuliis et al., 2009: Poço Azul (BR).

Genus *AUSTRALONYX* De Iuliis, Pujos, and Cartelle, 2009 †
(Map 9.6.2: Geographic distribution)

Australonyx aquae (De Iuliis, Pujos, and Cartelle, 2009) †

General Taxonomic Characters: Compared to *Ahytherium aureum*, this species seems stockier and more robust, but with smaller and more graceful manus and pes. The built of the body and the short morphology of the metacarpus, metatarsus, and phalanges suggest that arboreal habits were improbable.
Body Size: Body mass is estimated around 1,150 kg (Lyons et al., 2016).
Confidence in Species Assignment: Valid species according to Cartelle, De Iuliis, and Pujos (2009).
Geographic and stratigraphic distribution: Late Pleistocene of Brazil (Sao Paulo state)

Map 9.6.2: Geographic distribution of the genus *Australonyx.* References: Cartelle et al., 2008: Nova Redenção (BR).

Genus *DIABOLOTHERIUM* Pujos et al., 2007 †
(Map 9.6.3: Geographic distribution)

Diabolotherium nordenskioldi (Kraglievich 1926) †

General Taxonomic Characters: Relatively small sloth, it presented long and slender bones and highly movile joints in the elbow, hip and ankle. It is characterized by a morphology that suggest climbing capabilities (Pujos et al., 2007).
Body Size: Estimated around 93 kg, based on half of the size of the North American Megalonychidae sensu Pujos et al., 2007.
General Ecology and/or Locomotion: A series of skeletal features described in Pujos et al. 2007, including a highly mobile elbow, hip, ankle joints, well developed pronator and flexor muscles, and a wide range of digital flexion, suggest good climbing capabilities. The poorly stabilized articulations suggest that it was slow moving. Most of the fossil findings of these taxa come from caves, which suggest that it was a rock climber.
Confidence in Species Assignment: Valid according to Pujos et al., (2007).
Geographic and stratigraphic distribution: Late Pleistocene of the Peruvian Andes (Casa del Diablo, Piedra Escrita, Jatun Uchco, Trigo Jirka caves), of Chilean and Argentinian Patagonia (Aysen region in Chile) and in the Atacama desert in Chile (Atacama Region).

Map 9.6.3: Geographic distribution of the genus *Diabolotherium.* References: Pujos et al. 2007: Casa del Diablo (PE); Bostelmann et al. 2011: Baño Nuevo (CL), Pampa del Tamarugal (CL); Shockey et al. 2009: Jatun Uchco (PE), Cueva Rosello (PE), Trigo Jirka (PE).

10. South American Bestiary - Synthesis

The information presented above allows for some new insights about the regional biogeographic and stratigraphic patterning of biodiversity and extinction of South American megafauna.

I divided South America in 10 different regions (Figure 10.1) considering the distribution of fossil sites (Figure 10.2), taking into account major geographic features (i.e. the Andes) and the present distribution of major biomes (such as the Amazon basin and coastal and high Andean deserts). This last consideration assumes a high probability that the present day biomes were identifiable biotic units during the Late Pleistocene-Holocene of South America as well.

The 10 geographic regions are:

1. Tropical Northern South America: this region includes the highlands, lowlands and coastal areas of Colombia, Ecuador and Venezuela, excluding the lowlands that are part of the Amazon basin. The region also includes the rich fossil sites in the region of Piura, the northernmost part of Peru.
2. Amazon basin: this region includes what is today the Amazon rainforest, corresponding to southern Venezuela, southeast Colombia, eastern Ecuador and Peru, northeastern Bolivia, and northwestern Brazil.
3. Northeastern Brazil: this region includes the Brazilian States of Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia.
4. Coastal and Andean arid to semi-arid regions and High Andean Altiplano: this area includes the Andean region and eastern Peru (excluding Pirua Region), Andean Bolivia, northwestern Argentina, and northern Chile. The region includes the rich Pleistocene fossil site of Tarija in Bolivia, located at ~2,000 masl.
5. Central and Southern Brazil: this region includes fossil sites coming from the States of Minas Gerais, Matto Grosso do Sul, São Paulo, Paraná and the northern part of the State of Rio Grande do Sul.
6. North-central Chile: this region includes sites coming from the semiarid north of Chile and central Chile. The political regions included are: Coquimbo, Valparaiso, Metropolitana, and O'Higgins region.
7. El Gran Chaco and North-western Patagonia: this region includes a small portion of south-east Bolivia, sites in Paraguay, sites in the Argentinian provinces of Formosa, Chaco, Corrientes, and part of Cordoba and Santa Fe provinces. Includes the Bolivian fossil site of Ñuapua.
8. Pampas: this area includes the grasslands of southernmost Brazil (Southern parts of Rio Grande do Sul State), Uruguay, and the areas around Rio de la Plata in eastern Argentina.
9. Western Northern Patagonia: this region includes sites from southern Chile between 37° and 42° latitude, in the western side of the Andes.
10. Southern Patagonia: This region includes all the fossil sites found in the southern tip of South America, from 44° latitude southward.

For each of these regions I compiled species lists that show the stratigraphic range associated with each taxon (Appendix-Chapter 1: Tables A1 to A10). In addition, Table A11 lists all taxa from all regions in South America from the Pleistocene to the present, a total of 134 species and 60 genera of megafauna. From these, 91 species and 56 genera were present during the Late Pleistocene and 85 species and 46 genera became extinct during the LQE. This table also includes the estimated body mass for extinct species and the measured body mass for extant species.

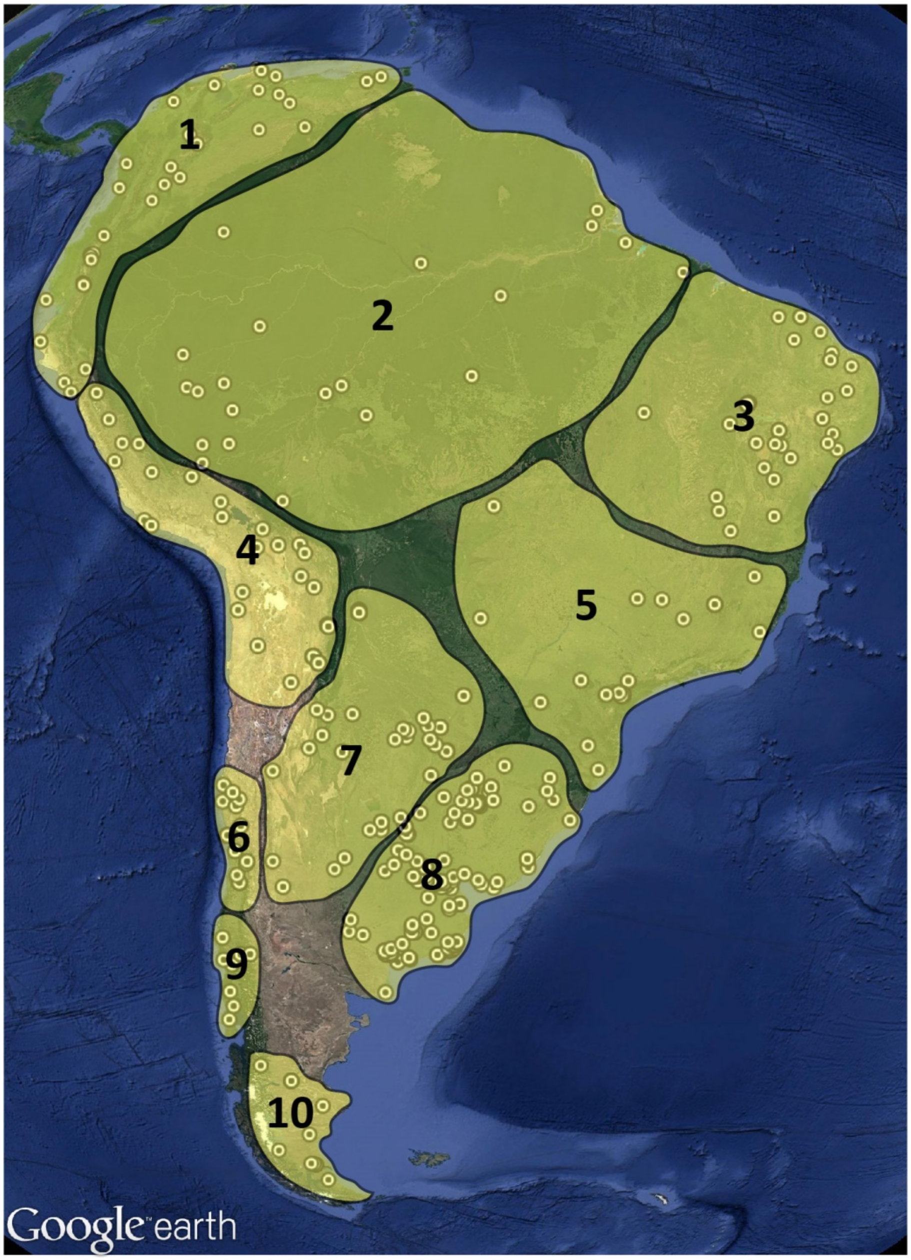

Figure 10.1: Map of the different regions used in to develop analyses and discussion in the synthesis.

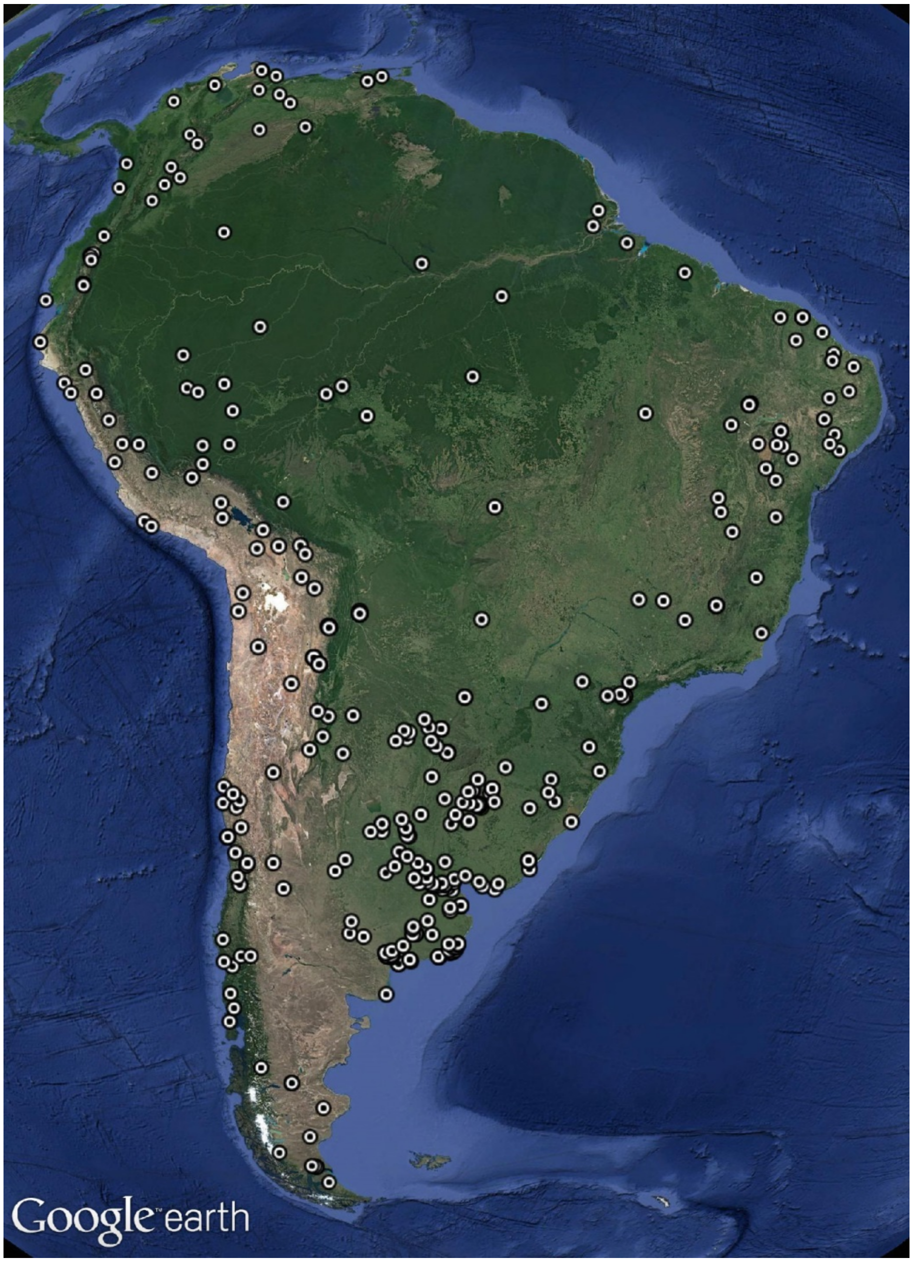

Figure 10.2: Geographis distribution of the sites where Late Pleistocene Megafauna has been found. This map was built based on the geographic information specified for each taxon along the bestiary.

Taxonomic Richness and Intensity of the LQE

From the information in Tables A1 to A10, I calculated species and generic richness for the Late Pleistocene, as well as the precentage of taxa lost during the LQE. In calculating the percentage of taxa lost, I included the taxa present in the Late Pleistocene and the taxa that survived until today. If a taxon has not been recorded from Late Pleistocene deposits but is present today (i.e. *Tapirus kabomami*, *Tremarctos ornatus*) it was not counted as a late Pleistocene taxon; the net effect of this would be to make the extinction magnitude appear larger than it is, if indeed all present taxa also extended back into the late Pleistocene. Taxa showing Holocene occurrences are scant, so data from this period was not use to calculate the extinction patterns and changes in biodiversity patterns; it was simply assumed that if a taxon is in a region presently, it was also present earlier in the Holocene. Counts of species extracted from Tables A1 to A11 are summarized below (table 10.1). In addition, I included in this table the number of highly ranked radiocarbon dates on megafauna that exist for each region, following the ranking system from Barnosky and Lindsey 2010. The numbers of radiocarbon dates for each region were calculated using the radiocarbon date lists presented in Barnosky and Lindsey 2010 (and references therein), Villavicencio et al., 2016 (and references therein), Meltcalf et al., 2016, Martin et al., 2015, Shockey et al., 2009, Dantas et al., 2013, Hubbe et al., 2013, Prado et al., 2016 and Pino et al., 2015.

Table 10.1: Summary of species counts and related information for each of the regions highlighted in Map 10.2. Number of Late Pleistocene fossil sites (# sites) Number of species present during the Late Pleistocene (#LPS), number of genera present during the Late Pleistocene (#LPG), number of extinct species (#ES), number of extinct genera (#EG), percentage species that went extinct (%ES) during the LQE, percentage of genera that went extinct during the LQE (%EG), number of radiocarbon dates on megafauna (# 14C) per region.

	# sites	# LPS	# LPG	# ES	# EG	% ES	% EG	# ^{14}C
Region 1: Tropical Northern South America	56	30	25	27	21	90	84	7
Region 2: Amazon basin	21	8	8	5	4	63	50	2
Region 3: North eastern Brazil	36	28	26	25	23	89	88	4
Region 4: Coastal and Andean arid to semi-arid regions, High Andean Altiplano	60	26	19	23	14	88	73	6
Region 5: Central and Southern Brazil	27	20	19	20	18	100	95	15
Region 6: North-central Chile	12	8	8	6	6	75	75	2
Region 7: El Gran Chaco and North-east Patagonia	57	25	25	22	21	88	84	1
Region 8: Pampas	130	45	36	40	30	90	84	34
Region 9: Western Northern Patagonia	9	4	4	4	4	100	100	9
Region 10: Southern Patagonia	15	10	10	7	7	70	70	95

Table 10.1 suggests that the faunally most rich region during the Late Pleistocene (at species and genera level), in terms of megafauna, was the Pampas (region 8). However, Pleistocene fossil sites are also most common in this area, so this is probably simply a function of sampling bias (Fig. 10.3).

It has been proposed that the Pampas had the capability of supporting many large herbivores in the Late Pleistocene, which remained latent after the LQE and made possible the introduction and support of large numbers of cattle by Europeans in historical times (Brailovsky 1990, Bengoa 2005). This may well be true, but Fig. 10.3 suggests that the Pampas was not necessarily capable of supporting more taxa than other regions, once the sampling issues are accounted for.

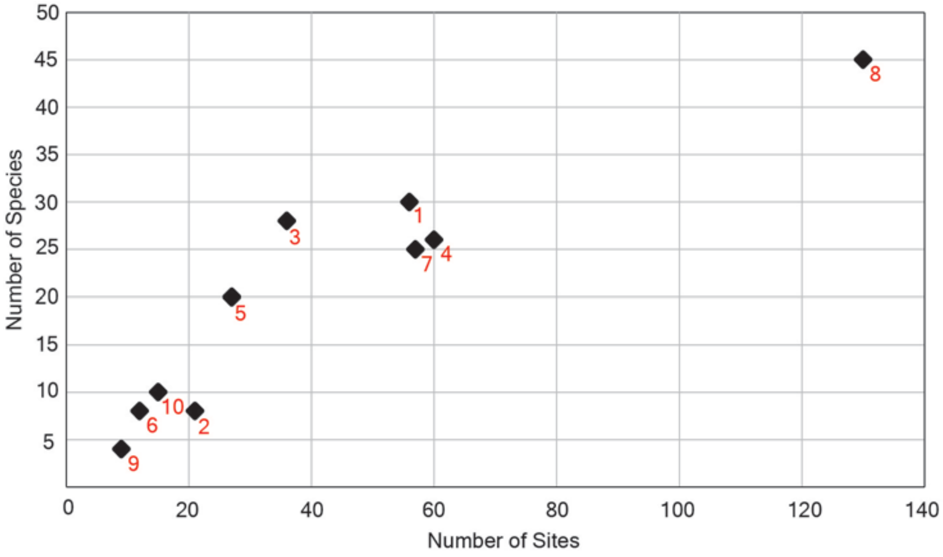

Figure 10.3. Comparison of numbers of sites versus number of taxa. The numerals indicate the region number.

The pattern of more species correlating with greater numbers of known sites generally holds for all of the regions except Region 2 (the Amazon basin), potentially Region 4 (Coastal and Andean arid regions and High Andean Altiplano), and Region 7 (El Gran Chaco and Northeast Patagonia), all of which appear depauperate in megafauna relative to the number of sites. The relatively low number of species with respect to localities in Region 7 may reflect biological reality, given that Region 7 contains the Bolivian site of Ñuapua, which has offered abundant records of Late Pleistocene extinct fauna (Coltorti et al., 2012, Marshall and Sempere 1991). Despite the richest fossil record found in region 7, only 1 radiocarbon date on an extinct species is reported for this area (Cruz et al., 2010) plus several dates on dung from Gruta del Indio (AR) which I did not include in my total counts of ^{14}C dates for this region as they are reported as coming from an undetermined sloth xenarthran (Steadman et al., 2005).

Even when sampling issues are taken into account (Fig. 10.3), a general pattern of higher taxonomic richness in lower latitudes (Regions 1, 3, 4, 5) compared to higher latitudes (Regions 6, 9 and possibly 10) can be observed, which would be in agreement with the pattern of higher biodiversity of megafuana found at lower latitudes seen in modern biota (Rosenzweig, M. 1995). An exeception to this biogepgraphic pattern is Region 2 which comprises to what is today the Amazon Basin. This region shows very low richness compared to neighbouring areas (Table 10.1), possibly attributable to the poor fossil preservation typical of tropical (wet) regions. The low taxonomic richness observed for regions 6 and 9 is probably due to a combination of their mid-latitude, the small geographic area they cover on the western side of the Andes, and the relatively few fossil sites present. Region 10 shows a slightly more diverse fauna compared to regions 6 and 9, despite the fact of being the more austral area. This high species richness probably is best explained by more exhaustive research, with multiple stratigraphic levels (in effect, sublocalities) in some of the sites, and more exhaustive excavation of most of the Pleistocene sites compared to those in regions 6 and 9 (See Chapter 2).

With respect to the magnitude of extinction calculated as percentage of taxa lost (Table 10.1), all areas lost more than 70% of the megafauna present during the Late Pleistocene with the most affected areas being north-western Patagonia (region 9) and north tropical South America (region 1). An exception to this pattern in the region of the Amazon basin (region 2) which lost between 50% and 60% of its taxa. At a continental level, the proportion of genera lost is 82% according to the information in table A11, which is 1% lower than values recently published (Brook and Barnosky 2012). This minor difference is probably due to my including mammals over 40 kg in my calculations whereas previous authors generally considered only those over 44 kg.

The number of radiocarbon dates (^{14}C) existing for each region (Table 10.1) reflects that there are only two areas with a meaningful amount of radiocarbon dates on megafauna (regions 8 and 10, with 34 and 95 dates, respectively), followed by north-eastern Brazil (region 3) with 15 ^{14}C dates. The remaining regions have less than 10 ^{14}C dates each, indicating that much more work needs to be done in those regions before extinction chronologies can be reliably assessed.

I calculated Jaccard similarity indices using presence-absence data at the species and genus level in order to evaluate faunal similarity among the different regions in the Late Pleistocene. Using the results of the Jaccard index (Appendix-Chapter 1, Tables A12 and A13) a simple cluster analyses was performed (Figure 10.4) to compare similarity among regions. The same Jaccard similarity index and cluster analyses using the modern megafauna of each region provided a basis of comparison between present-day and past similarity patterns (Table A14 and A15).

Regions 6 and 9, 7 and 8, and regions 3 and 5 are clustered together at both genus and species level, meaning they are more similar to each other than to any other region in the continent. At species level, regions 4 and 10 cluster together but the pattern does not hold at genus level. The regions that are clustered together in pairs correspond mainly to adjoining regions as expected. Nevertheless, the values of the Jaccard index show that none of the 10 regions used in the analyses have more than a 60% of similarity at both species and genus level (tables A12 and A13), supporting the contention that they were discrete faunal provinces in the past, as they are today. The similiarity indices also provide a basis for potentially recognizing broadly defined biogeographic provinces that can be subdivided into more resolved provinces. For example, regions 5 and 3 have a degree of similarity of over 50% at species and genus levels, and on that basis might be considered to comprise a biogeographic region characterized by the presence of *Xenorhinotherium bahiense* †, *Ocnotherium giganteum* †, *Nothrotherium maquinese* †, *Aytherium aureum*† and *Hoplophorus euphractus*†, all of which do not occur in any other region of South America; nevertheless, they differ by the presence and absence of two different species of *Holmesina* (present in region 3 but not in 5), and several species of camels and cervids. The same occurs with regions 8 and 7, which are a 34% similar at the species level and a 54% similar at the genus level (table A12), and regions 9 and 6 that share 33% similarity in species they have and a 20% in the genera. The clustering of regions 4 and 10 at species level is because, while they show only 20% similarity of taxa (at species level), the species present in region 10 correspond almost totally to a subset of those present in region 4, which in addition has many other species. Region 1 is dissimilar to other tropical regions (regions 2, 3, 4 and 5), with similarity index in the neighborhood of 30%. The difference arises from the presence of Andean taxa (i.e. some species of *Megatherium*† and the genus *Cuvieronius*†), tropical taxa (i.e. *Holmesina majus*† and *Holmesina occidentalis*†), plus the presence of North American elements like the genus *Odocoileus.*

The results from the cluster analyses using extant megafauna (Figure 10.5) species and genera present in each region demonstrate that most of the regions that cluster together in pairs show more than 60% similarity at species and genus level, except by regions 1 and 4 that show a similarity below 40% at the species level and somewhat higher at the genus level. It is interesting to note that, for the cluster analysis using extant taxa, the tropical regions (1,2,3,4,5) are grouped together while subtropical ones form another independent cluster, evidencing two main biogeograohic regions at present. This holds for both the species and genus level.

It is important to note that of the taxa used in the cluster analyses for present-day megafauna species, only half of them have a fossil record going back to the Late Pleistocene. However, from the data available, it appears that there is higher Jaccard similarity among regions today than there it was during the Late Pleistocene (Tables A12 to A14). The fact that regions are more similar today possibly indicates the presences of more regional endemism during the Late Pleistocene.

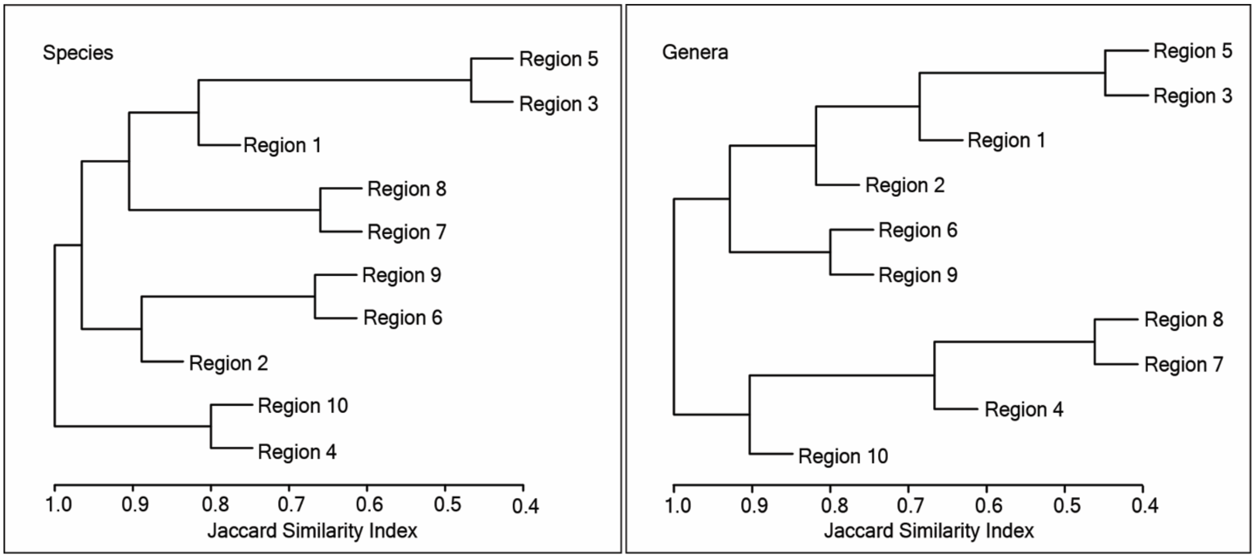

Figure 10.4: Simple cluster analyses using the different regions from map 10.2 and presence/absence data for megafauna species (left) and genera (right). Jaccard Similarity index: 0.0= 0% dissimilar, 1.0= 100% dissimilar.

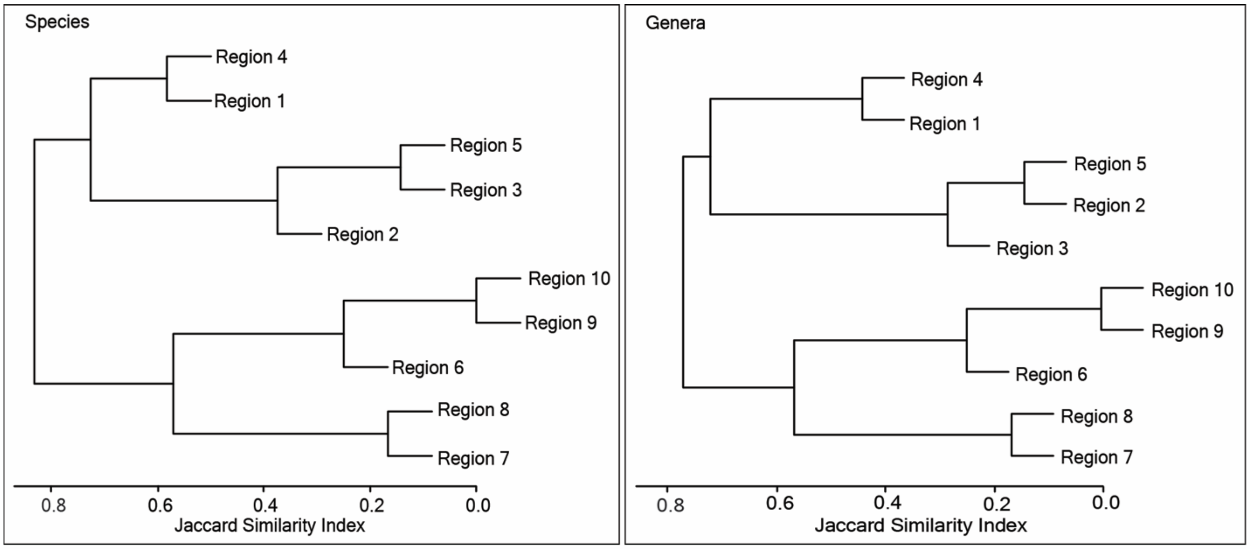

Figure 10.5: Simple cluster analysys using the different regions from map 10.2 and presence/absence data for extant megafauna species (left) and genera (right), at present time. Jaccard Similarity index: 0.0= 0% dissimilar, 1.0= 100% dissimilar.

Chapter 2: Megafaunal extinction chronology in relation to human arrival, climate change and environmental changes at regional scales: The case of Southern Patagonia

Introduction

Analyses of the chronology of megafaunal extinction in South America in relation to human arrival and climate changes during the Pleistocene-Holocene show different patterns of extinction in the different eco-regions of the continent (Barnosky and Lindsey 2010), highlighting the need to develop regional scale analyses of the extinction event in order to understand the nuances behind the process and its possible causes.

Southern Patagonia is an ideal starting place to develop this type of analyses since it presents one of the most complete chronologies of megafaunal extinction in the South American continent in terms of the number of radiocarbon dates existing for extinct fauna, along with archaeological information documenting the arrival/occupation of humans in the area. These data are the result of more than a century of archaeological, zooarchaeological and paleontological work in the area that started as early as 1897 with exploration by Francisco P. Moreno and Rodolfo Hauthal. The first formal excavation was done by the Swedish ethnographer Erland Nordenskiöld in Cueva del Milodón (Chile) in 1899 (Nordenskiöld 1899, Martinic 1994). The area has also been the subject of intense paleoecological and paleoclimatological research and dozens of scientific articles have been published recording climatic changes, glacial history, vegetation changes and changes in fire frequency since the last glacial maximum to the present (Killian and Lamy 2012 and references therein).

The main objective of this chapter is to assess megafaunal extinctions at a regional scale for Southern Patagonia in Chile. The chapter consists of one published article (Villavicencio et al., 2016) that focuses on the megafaunal extinction in the area of Cerro Benitez and Lago Sofía, Última Esperanza province, Chile. The article is based on a compilation of published radiocarbon dates on extinct megafauna and on evidence of humans, the combination of which provided the opportunity to build strong chronologies of megafaunal extinction compared to human arrival into the area. These chronologies are compared to the timing of major changes in vegetation and climate reported in the published literature. As a supplement to this published article (Villavicencio et al. 2016) I also include an update based on the addition to our dataset of 42 new radiocarbon dates on extinct megafauna that were recently published (Martin et al., 2015, Metcalf et al., 2016).

Here I also acknowledge the many scientists who, through a century of research have gathered the information used to make this analysis possible, including Francisco P. Moreno, Rodolfo Hauthal, and Erland Nordenskiöld, who were the first to systematically work and make collections in the area of Última Esperanza between 1897-1900. Santiago Roth and Roberto Lehmann-Nitsche made some of the earliest inferences about the faunas found in Cueva del Milodon between 1899-1900. Junius Bird made important discoveries about the first humans and their relation to extinct faunas during several years of work in the Magallanes region (1936-1937, 1969-1970)(Bird 1988); some of the first radiocarbon dates reported by Libby came from materials collected by Bird in Pali Aike (Bird 1988). The French ethnographer Joseph Emperaire and the archaeologist Annette Laming excavated Cueva del Milodón in Última Esperanza, Fell's cave in Pali Aike and explored the Magallanes region in several expeditions (1952, 1953, 1958, 1959)(Emperaire and Laming 1954). The archaeologist Earl Saxon explored and excavated several sites in Última Esperanza during 1976 (Saxon 1976). The botanist David Moore, who performed pioneer work in paleobotanical analyses from mylodon dung collected in Cueva del Milodón in 1978 (Moore 1978).

Since the decade of the 1980, many Argentine and Chilean archaeologists have taken the lead in the exploration of Última Esperanza. Among those whose work has been most influential are: Luis Alberto Borrero, who is one of the co-authors in the published article included here and who has done extensive work in the area since the late 1970s to the present; Mario Massone, Alfredo Prieto, Pedro Cárdenas, Hugo Nami, Fabiana Martin (also a coauthor in the first article), Rafael Labarca and Victor Sierpe, all of whom have explored, excavated and analyzed archaeological and paleontological remains from caves in the area—the use of the published data has been instrumental in the compilations and analyses presented here (Prieto 1991, Nami and Menegaz 1991, Martin 2008, Massone and Prieto 2004, Sierpe et al., 2009, Labarca et al., 2009). Also since 1980, paleoeclimatological and paleoecological work has flourished in the area. Pioneer work was done by Calvin Heusser, Vera Markgraf and John Mercer (Mercer 1965, Markgraph 1985, Heusser 1995). More recently, Patricio Moreno (coauthor in the published article presented here), Rodrigo Villa-Martinez, Charles Stern, Macarena Cárdenas and Esteban Sagredo published work in reconstructing the climate (Villa-Martínez et al., 2007) Moreno et al., 2012), glacial morphology (Sagredo 2007, Stern et al., 2011) and vegetation (Cardenas 2006) in the area of Última Esperanza and surroundings, which provided the necessary environmental framework to compare with the megafaunal extinction dynamics.

Combination of humans, climate, and vegetation change triggered Late Quaternary megafauna extinction in the Última Esperanza region, southern Patagonia, Chile.

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Abstract

South America lost around 52 genera of mammals during a worldwide event known as the Late Quaternary Extinction episode. More than 80% of South American mammals weighing >44 kg succumbed. Analysis of the megafaunal extinction chronology in relation to human arrival and major climate changes have revealed slightly different extinction patterns in different eco-regions of the continent, highlighting the importance of detailed regional analysis in order to understand how the possible drivers of extinction operated. Here we present an analysis of the megafaunal extinction in the Última Esperanza (UE) area of southwestern Patagonia, Chile. We have compiled a comprehensive chronology of megafaunal extinctions and earliest human occupation between 18-7 cal ka BP, based on radiocarbon dates from published literature. We calculated confidence intervals using the GRIWM method to estimate the times of human arrival and megafaunal local extinctions, and then compared these events to the timing of major climate and vegetation changes, fire frequency increase, and the Reclús volcanic eruption. Our results suggest that a combination of human impacts and climate-vegetation change drove megafaunal extinctions in the UE area, with the balance of factors being taxon specific; the volcanic eruption does not seem to have exacerbated extinctions. Competition between humans and mega-carnivores seems to be the most plausible cause for the extinction of the mega-carnivores. Coexistence of humans with extinct horses, extinct camels, and mylodonts for several thousand years rules out a scenario of blitzkrieg overkill of megafauna by humans. The transition of vegetation from cold grasslands to *Nothofagus* forests corresponds with the disappearance of *Hippidion saldiasi* and *Lama* cf. *owenii*. The later full establishment of *Nothofagus* forests and an increasing fire frequency coincided with the disappearance of

mylodonts. A climate-driven reduction of open environments plausibly reduced herbivore's populations making them susceptible to local extinction.

Introduction

By the end of the Pleistocene, the world lost about half of its terrestrial megafaunal species (average body weight exceeding 44 kg) in an event known as the Late Quaternary Extinction episode (LQE) (Martin 1967; Martin 1990; Martin and Steadman 1999; Martin and Klein 1984; Barnosky et al. 2004; Koch and Barnosky 2006). In sheer numbers, South America lost more genera (52) and species (~66) than any other continent (Brook and Barnosky, 2012). As on other continents, the primary debates about the causal mechanism of the LQE in South America revolve around the relative importance of humans, environmental change, and interactions between the two (Martin and Steadman 1999; Cione et al. 2003; Barnosky and Lindsey 2010). Nevertheless, the resolution of these debates is difficult without detailed chronologies and sound mechanistic underpinnings. In South America, the general picture has suggested that the chronology of extinction roughly coincided with major climatic changes that occurred during the Pleistocene-Holocene transition and also with the first arrival of humans into the South American continent (Koch and Barnosky 2006). However, recent work that synthesizes information from many investigators suggests somewhat different extinction chronologies in different eco-regions of the continent, that taken at face value suggest that extinction may have started in the north before human arrival and occurred later in higher latitudes, after humans were present and where climate changes were more severe (Barnosky and Lindsey 2010). The apparent differences in different regions emphasizes the need for highly resolved chronologies that compare the timing of megafaunal extinction, human arrival and population growth, and environmental change at the local and regional scale. Here, we attempt this for the Última Esperanza area, south western Patagonia, Chile (Fig. 1), with the goal of better understanding the relative roles of humans versus environmental change as a driver of the extinction of several species of large mammals that disappeared from this region.

Located between 51° 29’ - 51° 40’S and 72 ° 28’ - 72 ° 43’W, the Última Esperanza region has been the focus of intense archaeological and paleontological research since the discovery of Cueva del Milodón (Mylodon Cave) in 1895 (Martinic 1996), research that also includes some of the earliest insights into the causes of the local megafaunal extinction (Borrero 1977). As a result, the region now offers what is one of the most comprehensive chronologies of megafaunal occupation for the South American continent, along with some of the earliest archaeological sites. In addition, a wealth of paleoenvironmental proxies have become available in the form of pollen data, charcoal records, isotopic studies, glacial data, and geomorphic and geological information. The sensitivity of these paleoenvironmental proxies is enhanced by Última Esperanza’s location at the southern edge of the Southern Westerly Winds (SWW), a climatic boundary that can produce marked regional and zonal effects as it shifts slightly north and south in response to global forcings.

These data revealed a relatively detailed history of the Última Esperanza area from the Last Glacial Maximum (LGM) to the Holocene. In general terms, the area changed from a completely glaciated landscape to one dominated by cold grasslands that were rapidly colonized by a dozen megafaunal taxa and by humans as the LGM gave way to the Holocene (see sections 4, 6, and 8). A massive volcanic eruption from the Reclús Volcano (50° 57′ S/73° 35′ W) also occurred near the LGM-Holocene transition (see section 5). By the early Holocene most of the megafaunal taxa had disappeared, humans persisted, the landscape became dominated by *Nothofagus* forests, and fire frequency increased (see sections 6, 7, 9, and 10). In this study we examined in detail the timing of these dramatic changes in order to cast light on the most important drivers of megafaunal disappearance in the Última Esperanza region. We present a comprehensive compilation of radiocarbon dates on extinct fauna and on early human occupation in the region, all of them vetted from published literature, and used statistical techniques to place likely temporal bounds on the earliest occurrence of humans and latest occurrence of other megafauna. We then compared the arrival and extinction chronologies to the timing of major climate changes, vegetation changes, fire frequency, and volcanic activity gleaned from highly resolved paleoenvironmental proxies. Finally, we used this integrated information, along with inferences about the biology of affected megafaunal species, to draw conclusions about the relative roles of humans versus environmental perturbations in triggering the local collapse of the megafauna in Última Esperanza.

1. Study area

Our study area is located ~ 20 km north of Puerto Natales, with the paleontological, archaeological, and paleoenvironmental proxy localities distributed on and near the slopes of Cerro Benítez (~520 m.a.s.l.) and Cerro Señoret (~372 m.a.s.l) (Fig. 1). Both of these high hills are located in the lee side of the Andes, 10 km inland from the east coast of the Última Esperanza sound (Fig. 1A and 1B). A glacial valley running east-west separates Cerro Benítez and Cerro Señoret and is today partially occupied by Lago Sofía. Most of the sites lie topographically above a late Pleistocene lake terrace developed on the flanks of Cerro Benítez and Cerro Señoret (see section 4). The paleontological and archaeological material typically comes from caves and rock shelters (see Table 1 for complete list and descriptions of localities), most of which are wave-cut excavations in the bedrock that resulted from erosion along the shores of the pro-glacial lake that existed at the time (Sagredo et al. 2011, Stern et al. 2011).

2. Modern climate, vegetation and fauna

The climate of Patagonia is largely controlled by the Southern Westerly Winds (SWW), which deliver abundant precipitation derived from the Southeast Pacific Ocean. The Andes cordillera presents a significant barrier to the low level wind circulation, with an orographic or “rain shadow” effect that results in high precipitation on the western side of the Andes, and dry conditions on the east, in Argentine Patagonia (Carrasco et al. 2002, Garreaud et al. 2013). The amount of precipitation generally increases with altitude on the western side of the mountains and decreases down the lee eastern side. Annual precipitation at sea level can be as high as

~4,400 mm/yr (Faro Evangelista 52° 24’ S, 75° 06’ W), and increases to ~ 10,000 mm/yr in higher parts of the Western Andes (Paso Galería 52° 45’ S, 73° 01’ W, 383 m.a.s.l.), decreasing to ~ 505 mm/yr on the lee side (Punta Arenas, 53° 08’ S, 70° 53’ W, 6 m.a.s.l.) (measurements taken between 1999 and 2002, Schneider et al. 2003). The Última Esperanza area is located between the hyper-humid climate of the western side of the Andes and the drier, more continental climates of the Argentine steppe. The closest meteorological measurements have been recorded in Puerto Natales (51° 44’ S, 72° 31’ W, 2 m.a.s.l., Fig. 1A), with mean annual precipitation values of 513 mm. Precipitation is fairly evenly distributed through the whole year, with slight maxima in March, April, August, and November. The mean annual temperature at the same station is between 6° and 7° C with an annual range of 9°-10° C (Dirección Meteorológica de Chile <www.meteochile.gob.cl?inicio.php>).

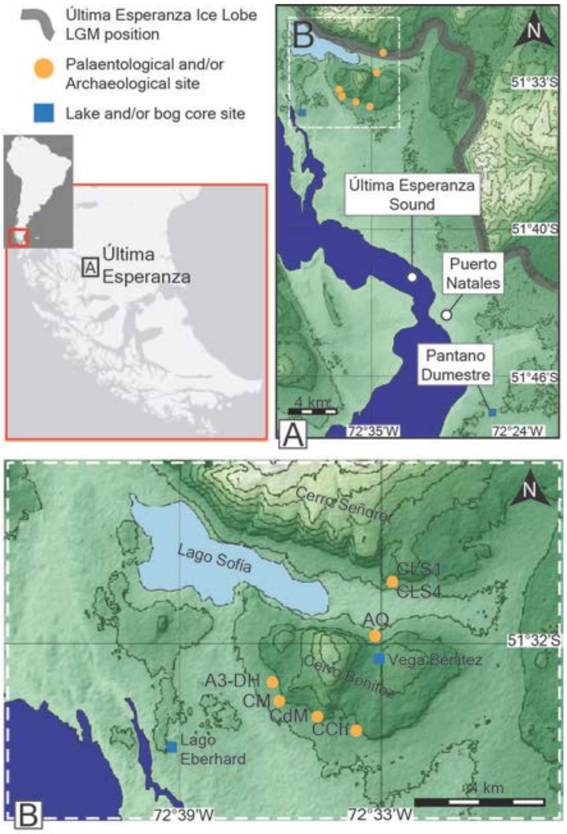

Figure 1. Study area. A: General view if the Última Esperanza area. The location of the bog and lake records discussed in the text (blue rectangles) and the Last Glacial Maximum (LGM) extension of the Última Esperanza Ice Lobe estimated by Sagredo et al., 2011 (dark transparent thick line) are shown. B: Closer view of the Cerro Benítez, Cerro Señoret, and Lago Sofía area. The distribution of the sites discussed in the text is shown. Abbreviations are: CLS1=Cueva Lago Sofía 1; CLS4=Cueva Lago Sofía 4; AQ= Alero Quemado; A3-DH= Alero 3 Dos Herraduras; CM= Cueva del Milodón; CDM= Cueva del Medio; CCh= Cueva Chica.

The general climate patterns described above result in different vegetation communities as one proceeds from west to east across southern Patagonia: the Magellanic moorland, Magellanic evergreen forest, Magellanic deciduous forest, and the Patagonian steppe. The steep precipitation gradient produces forests primarily on the west side of the Andes, but lack of moisture limits penetration of forests eastward and results in a distinct forest-steppe ecotone that is characteristic on the east side of the Andes (Villa-Martinez and Moreno 2007, Moreno et al. 2009). On the west side, the forests change with increasing altitude: the Magellanic evergreen forest gives way to deciduous forests at mid elevations, which are better able to resist low temperatures and prolonged snow cover (Lara et al. 2001). Above tree line the Andean desert dominates, which consists of a sparsely vegetated subnival alpine community

Table 1. Description of the sites discussed in this study.

Site Name	**Geographic coordinates**	**Altitude (m.a.s.l.)**	**General description and size**	**Interpretation**	**Taxon radiocarbon dates**	**Archaeological radiocarbon dates**
Cueva del Milodón	51° 33' 54'' S 72° 37' 13'' W	150	Large cave: ~250 m long, ~140 m wide, 30 m high in the entrance and 10 m high close to the back of the cave (Hauthal 1899, Borrero and Martin 2012).	Mainly paleontological. Middle to Early Holocene archaeological deposits have been described (Nordenskioöld 1900, Saxon 1976). Evidence of Hippidion saldiasi exploitation by humans has been found (Martin 2010, Prevosti and Martin 2013).	*Smilodon: 2* *Mylodon: 23* *M. darwini: 1* *Mylodontidae: 5* *Lama guanicoe: 1*	Charcoal: 4
Cueva del Medio	51° 34' 09'' S 72° 36' 12'' W	150	Cave, 90 m long, 40 m wide and 6 m high (Nami 1986).	Archeological site. It has a late-Pleistocene human occupation with evidence of extinct fauna and modern fauna utilization. There are faunal remains with evidence of carnivore consumption (Nami and Menegaz 1991, Nami a Nakamura 1995).	*H. saldiasi: 2* *L. cf. L. owenii: 4* *L. guanicoe: 3* *Mylodon: 1* *Mylodontidae: 2*	Charcoal: 7 Non-human bone: 12
Cueva Chica	51° 34' 23'' S 72° 35' 10'' W	160-165	Consist of a main chaber and two inner dark chambers. In general, is about 70 m long and 17 m wide (Martin et al., 2012).	Paleontological site, carnivore den (Martin et al., 2012).	L. gracilis: 1 P. onca mesembrina: 1 Panthera: 2 Mylodontidae: 3	None
Alero 3 - Dos Herraduras	51° 33' 35'' S 72° 37' 25'' W	150	One of three exposed rockshelters under the name of Dos Herraduras. The R1 tephra is present (Borrero and Massone 1994).	Mainly archaeological. Mylodon has been found but association with archaeological evidences has been discarded (Borrero and Massone 1994).	Mylodontidae: 2	None*
Alero Quemado	51° 54' 79'' S 72° 57' 64'' W	150	Rockshelter. Eight meters long, 3 m wide, 3 m high (Sierpe et al., 2009).	Mid-Holocene Archaeological site. Incursion of terretrial hunter gatherers to the coast. It has evidemce of use of modern faunas (Sierpe et al., 2009)	None	Charcoal: 1

Cueva Lago Sofia 1	51° 31' 54'' S 72° 34' 12'' W	150	30 m long, 8 m wide and 5 m high. It has evidence of ashed in its deposits (Prieto 1991).	Lower level is paleontological. Late Pleistocene occupation in upper levels (Prieto 1991, Massone and Prieto 2004, Jackson and Prieto 2005, Steele and Politis, 2009).	*H. saldiasi :2* *L. guanicoe: 1* *M. darwinii: 3*	Charcoal: 1 Bone: 4
Cueva Lago Sofia 4	51° 31' 54'' S 72° 34' 12'' W	150	Dark chamber, 6 m long, 2.5 m wide and 1.5 m high (Prieto 1991).	Carnivore den (Prieto 1991, Borrero et al., 1997).	*Mylodon: 1* *V. vicugna: 3* *Mylodontidae: 2*	None

Only three megafaunal species (mammals >44 kg) can be found in the region today: the guanaco *Lama guanicoe* (Camelidae), the South Andean deer or huemul *Hippocamelus bisulcus* (Cervidae), and the puma *Puma concolor* (Felidae). Other common mammal taxa are the foxes *Pseudalopex culpaeus* and *Pseudalopex griseus*, Humboldt's Hog-nosed Skunk *Conepatus humboldtii* (Mustelidae), and a variety of rodents mainly from the families Muridae, Caviidae, Chinchillidae, and Ctenomydae. Historical introductions of Leporidae include *Oryctolagus cuniculus* (European rabbit) and *Lepus capensis* (Cape hare), both of which are now broadly distributed and commonly found in the area. Among the most common large herbivores there is the ñandu, *Rhea pennata* (Aves) which weighs ~ 25 kg.

3. Late Pleistocene-Holocene climate

Kilian and Lamy (2012) summarized key features of the climate change chronology in southern Patagonia, and we review the salient information here. Land surface temperature estimations inferred from the EPICA Dome C (EDC) from East Antarctica show that by the LGM, between 20-18 ka BP, 100-yr mean surface temperatures over Antarctica were ~ 10.3° C colder than the mean of the last millennium. (Note that 'ka' indicates dates surmised from counting ice accumulation layers, and 'cal ka' indicates radiocarbon dates that have been calibrated to calendar years). A warming event of ~ 6.5° C is recorded between 18-14.5 ka BP, which was followed by the Antarctic Cold Reversal (ACR), a rapid cooling event that dropped the 100-yr mean temperature ~ 2° C between 14.5-13 ka BP. The ACR was initially characterized by a rapid decrease in temperatures of ~ 1.5° C that took place over the first ~500 yrs of its onset. After 13 ka BP, warming once again commenced, with 100-yr mean temperature eventually rising ~ 4° C by ~11.9 ka BP (Jouzel et al. 2007). This post-ACR warming is contemporaneous with the Younger Dryas cooling recognized in the northern hemisphere. Coeval with the Antarctic record of surface temperature, glaciers began to retreat in southwestern Patagonia during the first warming event recorded in the EDC. South of the Última Esperanza area, major ice lobes located over the Strait of Magellan (53° 04' S, 70° 38' W) and Skyring sound (52° 37' S, 71° 50' W) were already receding from their LGM maximum advance by ~17.3 cal ka BP and ~18 cal ka BP respectively (McCulloch and Davis 2001, Kilian et al. 2007). Near our study sites, the retreat of the Última Esperanza ice lobe started at ~17.5 cal ka BP (Sagredo et al. 2011; see section 4 for more details).

Warming beginning ca. 18 ka BP seems characteristic of most of the southern part of the South American continent, the southern Pacific Ocean, and Antarctica, as indicated by concordance of several paleoclimate records, although the signal for the ACR is somewhat variable. Sediment analyses on the MD07/3128 marine core retrieved offshore of the Strait of Magellan (52° 40' S/ 75° 34' W) shows a warming over the Pacific Ocean at about the same time as the first warming event indicated in the EDC ice core, but starting slightly earlier, between 18-19 cal ka BP, and followed by a plateau of relatively stable temperatures coincident in time with the ACR (Caniupán et al. 2011). This same pattern is seen in the ODP1233 marine core extracted further north (41° 00'S/ 74° 27'W, Lamy et al. 2007). During the ACR, glacial re-advances are reported in the Strait of Magellan (53° 03'S/70° 37'W) (Sugden et al. 2005), Torres del Paine (50° 50'S/72° 49'W) (Moreno et al. 2009), and further north in the Lago Argentino area (50° 35' S/72° 55'W) located in the lee side of the Andes (Ackert et al. 2008, Kaplan et al. 2011, Strelin et al. 2014). Also coincident with the ACR, glaciers re-advanced in a proglacial lake environment in the Última Esperanza area between 14.8 and 12.8 cal ka BP (Sagredo et al. 2011).

Lake and bog cores from Lago Eberhard and Pantano Dumestre, both sites located close to the Última Esperanza area, provide records of vegetation and climate changes in the region during the Late Pleistocene-Holocene transition (Moreno et al. 2012, Cárdenas 2006). Positive water balance associated with stronger Southern Westerly Winds occurred between 14.6 and 11.8 cal ka BP, and especially between 13.6-12.6 cal ka BP, at Pantano Dumestre as is inferred from the low percentage or organic matter accumulation that is related to subaqueous deposition at the site (Fig. 2B). Between 14.6 and 11.8 cal ka BP the area was probably cooler than present as inferred by a dominance of cold-resistant herbs in the pollen record (see section 6). Beginning at ca. 11.8 cal ka BP, negative water balance is inferred at these sites implying a decline in the influence of the SWW and a subsequent decline in precipitation in the area (Fig. 2A and 2B). In addition, the expansion of *Nothofagus* trees indicates an increase in temperature during this time.

4. Glacial history and Puerto Consuelo pro-glacial lake

During the LGM, Andean glaciers formed a continuous ice cover in western Patagonia (38°-55° S); south of 43° S, the ice sheet reached the Pacific Ocean to the west and formed outlet glaciers over the Patagonian plains to the east (Holling and Schilling 1981). In the Última Esperanza region, outlet glaciers from the Patagonian Ice Sheet coalesced and formed the Última Esperanza Ice Lobe (UEIL) (Quensel 1910, Caldenius 1932, Meglioli 1992, Sagredo et al. 2011). By the last glacial termination (T1), the northern end of this lobe covered much of our study area (Fig. 1A). As temperatures started to rise near ~18 ka BP, the UEIL thinned and began to recede. The minimum age for local ice free conditions, at least in the Cerro Benítez area, is estimated to be ~17.6 cal ka BP derived from the most basal organic layer of the Vega Benítez bog core (Fig. 1A) (Sagredo et al. 2011). However, a date of ~18 cal ka BP (14,870 ± 70 ^{14}C yrs) obtained from a *Lama gracilis* bone found at Cueva Chica (165 m.a.s.l.) (Martin et al. 2013, Table 2), just south of Vega Benítez, may indicate slightly earlier ice-free conditions for the Cerro Benítez area, although there is considerable overlap in the probability distributions of the two dates.

As the UEIL retreated, the Puerto Consuelo pro-glacial lake developed in sectors at elevations below the spillways or meltwater channels associated with the LGM moraines (Sagredo et al. 2011). A series of erosional lake terraces, paleo-shoreline caves, and bog and lake deposits containing clay-rich pebbly muds are evidence for the presence of this lake (Stern et al. 2011). In the Cerro Benítez and Cerro Señoret area, a terrace is prominent at 150 m.a.s.l, and above it are located wave-cut caves where most of the megafauna and human remains we discuss here were found. These caves would have been on an island when the lake level was at 150 m.a.s.l.

(Sagredo 2007); the water level had to drop at least below 120 m.a.s.l to connect the cave-bearing island fully to the mainland (Stern et al. 2011). A *Mylodon* bone found in Cueva del Milodón produced a date of ~16.4 cal ka BP, indicating that by that time the lake level must have been below 150 m.a.s.l. A *Lama gracilis* bone from Cueva Chica (165 m.a.s.l.) produced a somewhat earlier date, ~18 cal ka BP, suggesting either that some of the caves may have been connected to mainland by land bridges before the lake level dropped <120 m.a.s.l. and after the area was ice free, or that animals swam to the island. The presence of the R1 derived tephra (see section 5) in some of the caves at Cerro Benítez (Alero Quemado, Alero Dos Herraduras, and Cueva de la Ventana) suggests that by ~14.9 cal ka BP the lake level must have been lower than 150 m.a.s.l. (Stern et al. 2011).

The transition from glacio-lacustrine sedimentation to organic sedimentation seen in cores from Pantano Dumestre and Lago Eberhard between ~15.4-12.8 cal ka BP indicates that the lake level was between 70-80 m.a.s.l. by that time. Prior to ~10.3 cal ka BP, the pro-glacial lake that had previously covered the Última Esperanza area was gone (Sagredo et al. 2011).

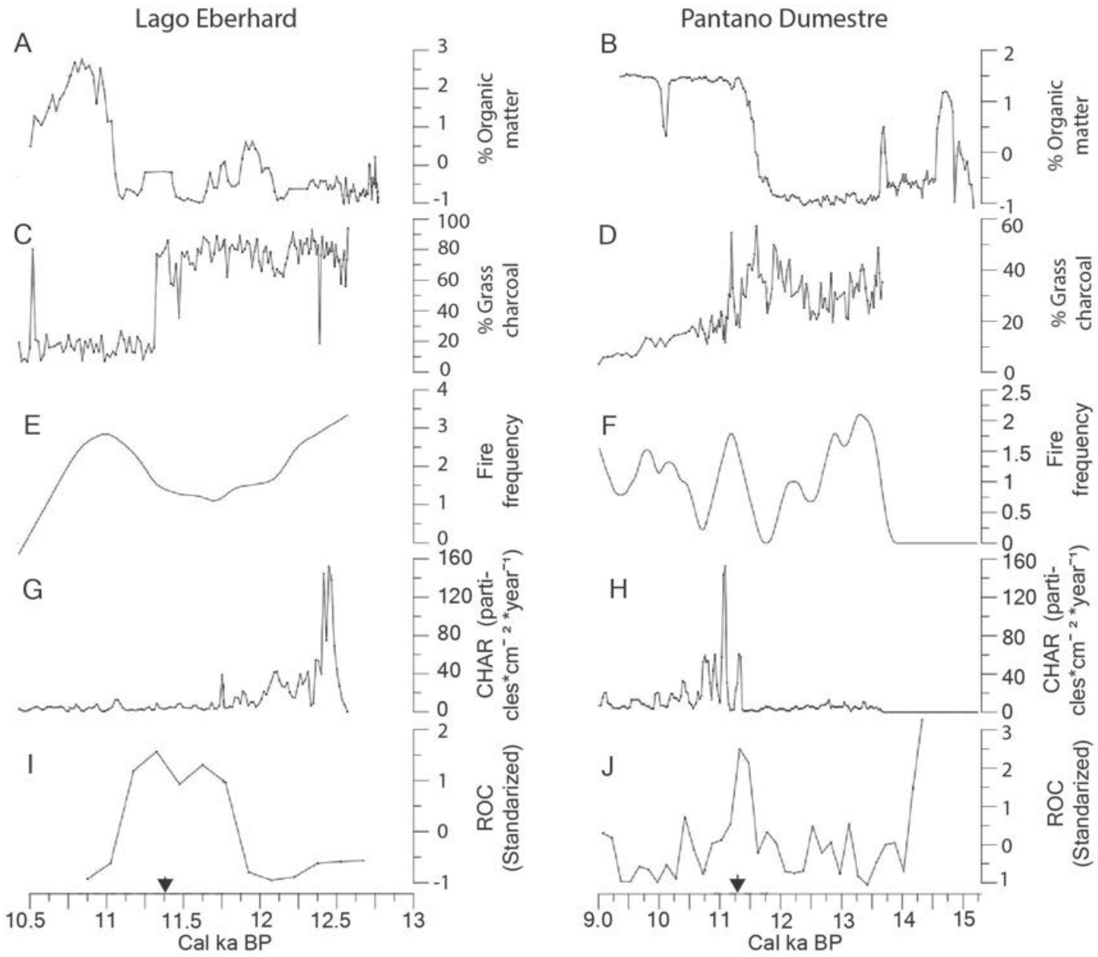

Figure 2. Comparison of the records of Lago Eberhard and Pantano Dumestre. A-B: % of organic matter through time, C-D: % of grass charcoal, E-F: Fire frequency, measured as fire events/500 yr, G-H: Charcoal Accumulation Rates analyses (CHAR), I-J: Rates of Change analyses (ROC) in the pollen records. Information extracted and

modified from Moreno et al., 2012. Black triangles show the timing of the onset in the increase of *Nothofagus* for each site

5. Reclús Volcano

The Reclús Volcano is located in the western side of the Southern Patagonian Ice Field at ~50° 57' S, 73° 35' W (Harambour 1988), within 100 km to the north-west of Última Esperanza. The volcano erupted near the end of the Pleistocene (R1), sending out a tephra plume which produced distinctive ash deposits in several different environments in southwestern Patagonia. More than twenty radiocarbon dates on sediments below and above the tephra layer have dated the Reclús eruption at ~14.9 cal ka BP (12,685 ± 260 ^{14}C yr) (Stern 2008, Stern et al. 2011). The eruption produced a volume of >5 km^3 of volcanic debris, (Stern et al. 2011) making it the largest eruption recorded during the Late Pleistocene-Holocene in the Austral Volcanic Zone (Stern 2008). Samples of R1 tephra can even be found in deposits located in Tierra del Fuego, more than 400 km south east of the Reclús Volcano location (Stern 2008).

A younger, thinner, and less spatially ubiquitous tephra from the Reclús volcano has been identified, which dates back to the early Holocene between 10.2-10.6 cal ka BP (AMS dates in Villa-Martinez and Moreno 2007).

6. Vegetation Changes (Fig. 2I and J and Fig. 3)

Early attempts to reconstruct the late glacial vegetation of the Última Esperanza region relied primarily on the analyses of plant remains in *Mylodon* dung and sediments from Cueva del Milodón (Salmi 1955, Moore 1978, Markgraf 1985, Heusser et al. 1992). These studies suggested dominance of grasses and herbs reflecting the presence of grasslands or a cold tundra-like landscape during the deglaciation, changing to a shrub land during the early part of the Holocene and becoming dominated by evergreen *Nothofagus* forests during the early to middle Holocene.

More recently, detailed records of late Pleistocene through Holocene vegetation changes have been obtained from bog and lake cores in the region. Most relevant for this study are cores obtained from Pantano Dumestre and Lago Eberhard (Fig. 3).

Lago Eberhard (51° 34'S, 72° 40'W; 68 m.a.s.l.; Fig. 1A) is the pollen site closest to Cerro Benítez, Lago Sofía, and Cerro Señoret. Lake and bog cores from this site record the vegetation and glaciolacustrine history of the area between ~12.8-10.4 cal ka BP. The pollen analyses reveal a dominance of cold-resistant herbs (Poaceae, *Acaena*, Asteraceae subfamily Asteroidea) between ~12.8 and 11.6 cal ka BP, deposited in a deep lake environment. Increase in *Nothofagus dombeyi* type pollen was prominent at ~11.2 cal ka BP, accompanied by an increase of the fern spore *Blechnum* (Not shown in Fig. 3). Both taxa began their rise to high abundance by ~11.6 cal ka BP reaching a peak between ~11.1-10.8 cal ka BP. This maximum in *N. dombeyi* type pollen is accompanied by markedly increasing abundance of the *Nothofagus* parasite taxon *Misodendrum*, indicating the establishment of a closed-canopy *Nothofagus* forest with an understory of ferns. As discussed by Moreno et al. (2012), the establishment of *Nothofagus* at this time is probably related to an increase in temperature rather than to an increase in moisture since it occurred at a time of decreasing precipitation inferred from the apparent decrease in lake levels noted in the Pantano Dumestre sediment record. This is consistent with studies that identify temperature as exerting greater control on the distribution of *Nothofagus pumilio* in the Chilean Andes (Lara et al. 2005).

Thirty km to the south east of Lago Eberhard is Pantano Dumestre. The pollen analyses from cores recovered from this bog have revealed dominance of cold-resistant herbs (*Acaena*, Poaceae, Asteraceae subfamiliy Asteroidea, *Galium* type) between ~14.6 and ~11.5 cal ka BP, similar to what is seen at the beginning of the record from Lago Eberhard. This cold-resistant herb component is accompanied by small amounts of *Nothofagus dombeyi* type pollen at the beginning of the Pantano Dumestre record. Percentages of *Nothofagus dombeyi* type pollen start to increase, then oscillate near ~13.0 cal ka BP, followed by a marked decrease, then a more pronounced, sustained increase at ~11.4 cal ka BP.   At this time there is also an increase in *Misodendrum* pollen, which marks the establishment of *Nothofagus* forests in the area. Poaceae pollen rapidly increases at the same time, peaking in abundance at ~11.6 cal ka BP and declining soon after that (Poaceae is not shown in Fig. 3). This increase in Poaceae has been interpreted as rapid colonization by grasses of the local area of Pantano Dumestre after the establishment of a more terrestrial bog environment and not as a regional signal for the establishment of grasslands in the area (Moreno et al. 2012).

In summary, both records -- Pantano Dumestre and Lago Eberhard -- suggest a landscape dominated by cold resistant herbs during the late glacial and the beginning of the Holocene (~12.8-11 cal ka for Lago Eberhard, ~14.6-11.5 cal ka for Pantano Dumestre), followed by a marked increase in *Nothofagus dombeyi* type (~12.2 for Lago Eberhard site and ~13 cal ka BP for Pantano Dumestre), culminating in the establishment of *Nothofagus* forests during the early Holocene (~11.1-10.8 cal ka BP for Lago Eberhard and ~11.4 cal ka BP for Pantano Dumestre). The offsets in timing of the changes among the two sites has been partially ascribed to edaphic factors, that is, the Lago Eberhard core is from a deep part of the lake and reflects a regional pollen signal, whereas the Pantano Dumestre record is from a bog site that reflects a more local signal. The overall rates of vegetation change (ROC) in the pollen records (Fig. 2I and 2J) are high between ~11.8-11.2 cal ka BP in Lago Eberhard and ~11.5 cal ka BP in Pantano Dumestre, coincident with the time intervals where the percentages of cold resistant herbs are dropping and the ones of *Nothofagus* are increasing, as the vegetation is changing from a cold grassland to a *Nothofagus* forest. This reflects the high rates of change of the vegetation in the landscape during these times.

At a regional scale (50°-54° S) vegetation changes inferred from pollen and bog records are consistent with the two described above in the sense that they show the presence of an open treeless landscape dominated by cold-resistant herbs and grasses during the deglaciation, followed by colonization by *Nothofagus* as temperature increases. Nevertheless, there are some differences in the vegetation structure evident from different areas, and more notably, in the details of timing of the vegetation changes. For example, sites located between (50°-53° S) show that the expansion of *Nothofagus* occurs ca. 16 and 11 cal ka BP (Mancini et al. 2005, Heusser 1995, Villa-Martinez and Moreno 2007, Huber et al. 2004), while sites in the southern extreme of Southern Patagonia (53°-54° S) show that the transition occurred much later and more abruptly between 11-9 cal ka BP. (McCulloch and Davies 2001, Huber et al. 2004, Markgraf 1993, Ponce et al. 2011).

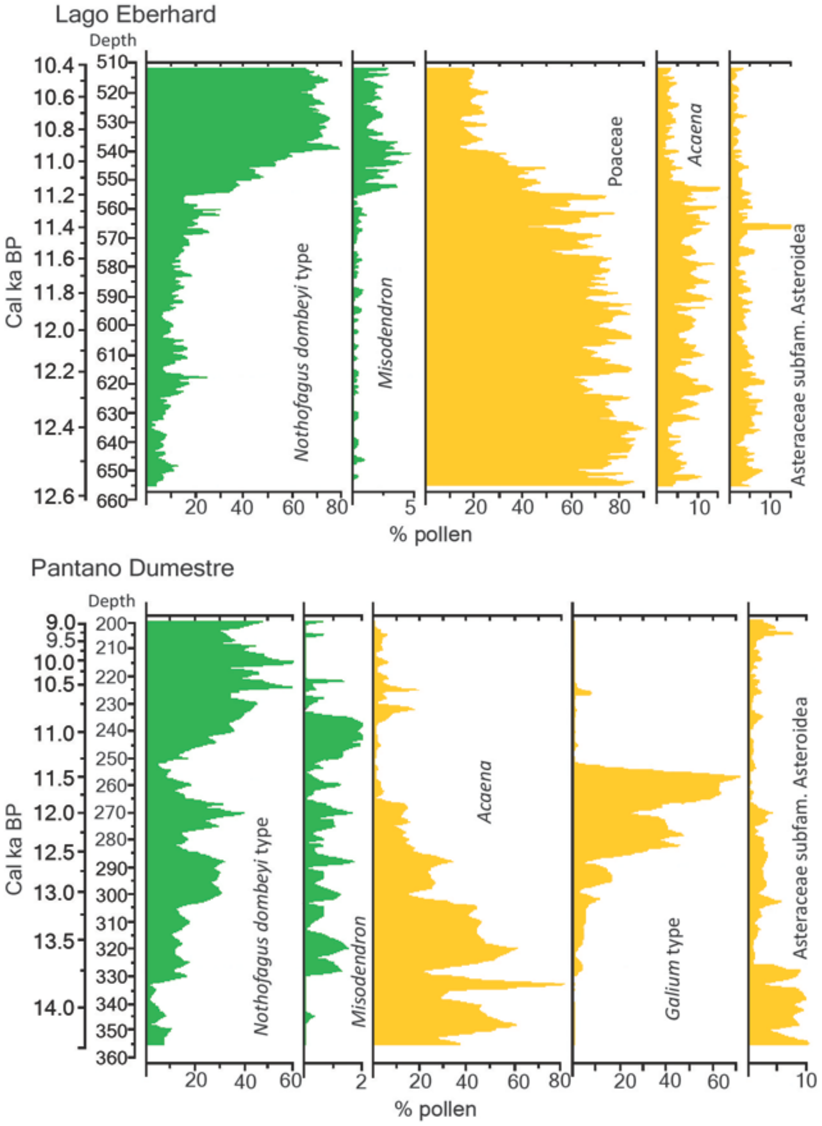

Figure 3. Percentage diagram of pollen from Lago Eberhard and Pantano Dumestre, modified from Moreno et al., 2012. Pollen percentages are showed as the proportion of terrestrial pollen total sum. Only taxa most informative for inferring vegetation changes relevant to megafauna extinction are shown. For a complete presentation and analysis of these records see Moreno et al., 2012.

7. Fire history (Figure 2C-2H)

Macroscopic charcoal analyses from the cores retrieved at Lago Eberhard and Pantano Dumestre sites show a decline in the percentage of grass charcoal as *Nothofagus* became more persistent in the landscape (Fig. 2C and 2D). Both sites present high frequency of fire events at

~12.5 cal ka BP and between 11.6 and 10 cal ka BP (Fig. 2E and 2F), but events recorded at Lago Ebehard appear to be of greater magnitude at ~12.5 cal ka BP compared to the ones seen at Pantano Dumestre, with the reverse situation evident between 11.6 and 10 cal ka BP (Fig. 2G and 2H). In summary, both records coincide in showing a decline in fire frequency between ~12.7-11.6 cal ka BP, followed by an increase between 11.6 -10.9 cal ka BP, which is coincident with a warm pulse, a decline in precipitation and a general increase in *Nothofagus* forest cover. Finally there is a decline in fire frequency between ~10.9-10.5 cal ka BP. (Moreno et al. 2012).

8. Late Pleistocene megafauna and humans (Figure 4)

The late Pleistocene megafauna in Última Esperanza included the giant ground sloth *Mylodon darwini* (Mylodontidae), the American horse *Hippidion saldiasi* (Equidae), two species of extinct camels: *Lama gracilis* (Camelidae) and *Lama* cf. *owenii* (Camelidae), the saber tooth cat *Smilodon* (Felidae), the large jaguar *Panthera onca mesembrina* (Felidae), the bear *Arctotherium* (Ursidae), a member of the extinct mammal order Litopterna *Macrauchenia patachonica* (Macraucheniidae), and the extinct fox *Dusicyon avus* (Canidae). Other taxa reported from Última Esperanza include the vicuña *Vicugna vicugna* (Camelidae), which is locally extinct and today survives only in the high central Andes, the extant guanaco *Lama guanicoe* (Camelidae), undetermined deer (Cervidae), and the Culpeo fox *Pseudalopex culpaeus* (Canidae) (Latorre et al. 1998, Carrasco 2009, Nami and Menegaz 1991, Martin 2010). The extant *Puma concolor* has not been described from Late Pleistocene deposits of Última Esperanza, but it has been documented at Cerro Sota (52°04' S/ 70° 03', east southern Patagonia) presumably from late Pleistocene deposits, (Miotti and Salemme, 1999), although its age is questionable.

Remains of most of these taxa have been dated with a total of 67 robust published radiocarbon dates (Table 2) from the caves in and around Cerro Benítez and Cerro Señoret (Fig. 1), all of which are on bone, dung or skin from taxonomically identifiable elements. From the same vicinity are 25 published dates that record early human occupation (Table 3), all of which rank 11 or higher on the vetting scale published by Barnosky and Lindsey (2010). Of the archaeological dates, only 5 are of rank 13 or higher, which Barnosky and Lindsey (2010) considered the cut off for the most robust archaeological human occupation. We include archaeological dates of ranks 11 and 12 to increase sample size, which seems justified in this case in that they are consistent with the rank 13 dates.

All radiocarbon dates were calibrated using the Calib 7.01 program (Stuiver and Reimer, 1986-2014) and the Southern Hemisphere calibration curve SH13 (Hogg et al. 2013). Most of the dates are for mylodont ground sloths, including 25 from specimens identified simply as *Mylodon* and three ascribed to *Mylodon darwini*. The extinct carnivores are represented by a total of 8 dates, of which 3 are on *Smilodon* (one of them cf. to *S. populator*) and 5 on *Panthera* (3 of them identified as *Panthera onca mesembrina*). *Hippidion saldiasi* and *Lama* cf. L. *owenii* are represented by 4 radiocarbon dates for each taxon. Finally, *Vicugna vicugna,* extirpated from the area but not extinct, is represented by 3 radiocarbon dates and *Lama gracilis* by a single date. For more details about the provenance of these dates see Table 1.

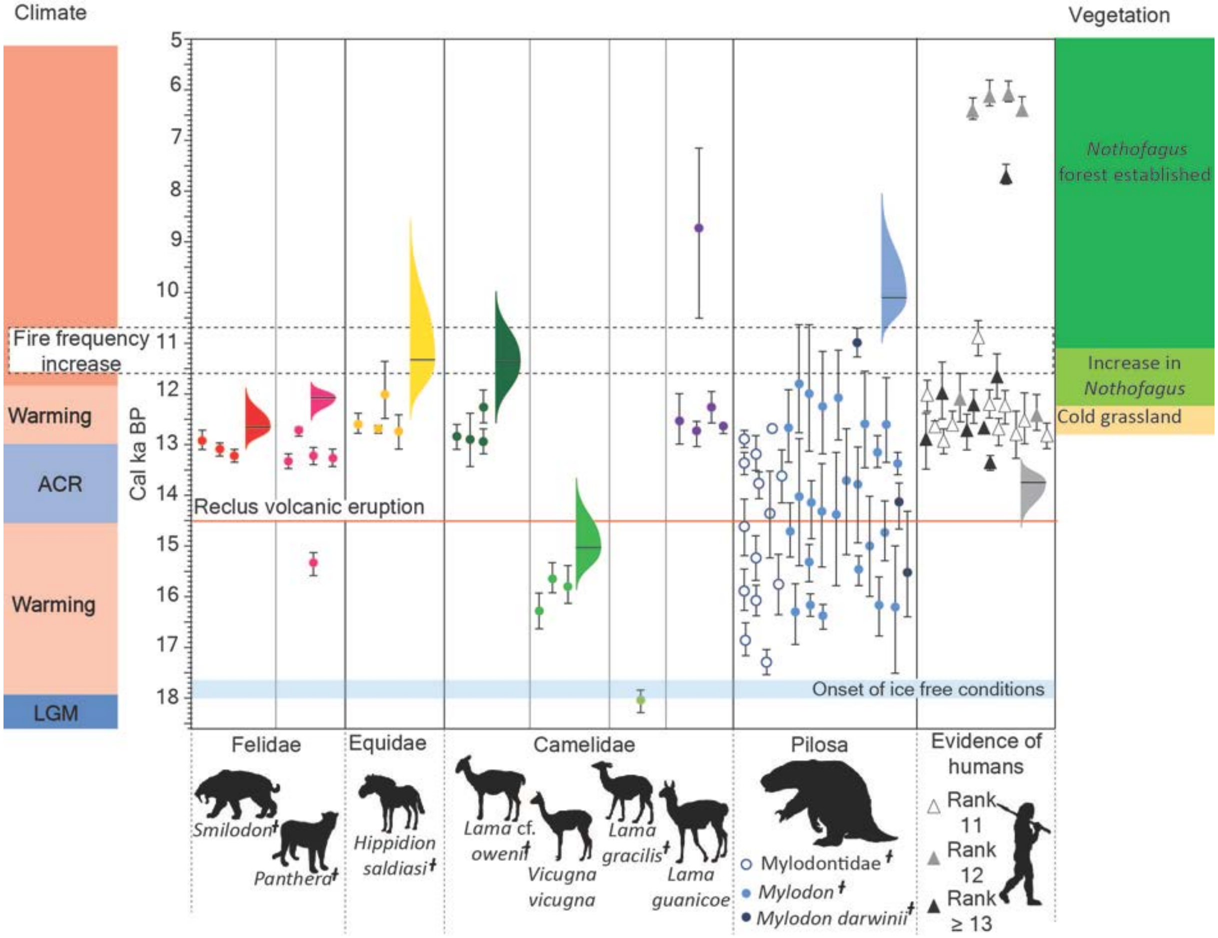

Figure 4. Chronology of megafaunal extinctions with estimated time of human arrival. Megafaunal extinction chronology is inferred from dates listed in Table 2 (colored dots) and the chronology of human arrival is based on dates from Table 3 (triangles, white, gray, and black indicate the different ranks calculated following Barnosky and Lindsey 2010). The GRIWM best-estimates of the time of extinction (or arrival in the case of the humans) is indicated by the colored normal distributions , with the 95% confidence band depicted by the colored areas around the mean (black line=most probable time of extinction). Warming and cooling events are inferred from the EDC Antarctic ice core (Jouzel et al., 2007, red and blue bands at left represent warming and cooling events respectively). Major vegetation changes (yellow, light green and dark green bands at right) and fire frequency information (black dashed rectangle) are extracted from Moreno et al., 2012. The timing of local ice free conditions estimated in Sagredo et al., 2011 (light blue dashed line rectangle) and the timing of the Reclús Volcano eruption (red line) is taken from Stern 2008 and Stern et al., 2011. The time axis is in calibrated years before present.

Table 2. Radiocarbon dates on megafauna (extinct and extant) from the Última Esperanza area of rank 11 or higher, which are considered robust according to the scale published in Barnosky and Lindsey 2010

Site Name	Taxa (Family, Genus or Species)	Lab number	14C Age (Uncalibrated) *AMS	Material Dated	Calib median	Calib old	Calib young	Rank	Reference
Cueva del Medio	*Hippidion saldiasi*	NUTA-1811	10710 ± 100*	bone	12605	12755	12403	12	Nami and Nakamura, 1995
Cueva del Medio	*Hippidion saldiasi*	NUTA-2331	10860 ± 160*	bone	12733	13076	12418	12	Nami and Nakamura, 1995
Cueva Lago Sofia 1	*Hippidion saldiasi*	OXA-9319	10780 ± 60*	bone	12684	12743	12627	12	Steele and Politis, 2009
Cueva Lago Sofia 1	*Hippidion saldiasi*	OXA-9504	10310 ± 160*	bone	12005	12457	11392	12	Steele and Politis, 2009
Cueva del Medio	*Lama* cf. *L. owenii*	NUTA-2197	11040 ± 250*	bone	12893	13430	12407	12	Nami and Nakamura, 1995
Cueva del Medio	*Lama* cf. *L. owenii*	NUTA-1734	10430 ± 100*	bone	12233	12558	11929	12	Nami and Nakamura, 1995
Cueva del Medio	*Lama* cf. *L. owenii*	NUTA-1737	11120 ± 130*	bone	12935	13155	12714	12	Nami and Nakamura, 1995
Cueva del Medio	*Lama* cf. *L. owenii*	NUTA-2330	10960 ± 150*	bone	12833	13094	12632	12	Nami and Nakamura, 1995
Cueva Chica	*Lama gracilis*	Beta-288231	14870 ± 70*	bone	18036	18263	17838	12	Martin et al. 2013
Cueva del Medio	*Lama guanicoe*	NUTA-1735	10450 ± 100*	bone	12257	12564	11947	12	Nami and Nakamura, 1995
Cueva del Medio	*Lama guanicoe*	NUTA-2332	10710 ± 190*	bone	12542	12979	12000	12	Nami and Nakamura, 1995
Cueva del Medio	*Lama guanicoe*	NUTA-1812	10850 ± 130 *	bone	12723	13013	12541	12	Nami and Nakamura, 1995
Cueva del Milodón	*Lama guanicoe*	BM-1207a	7785 ± 747	bone	8698	10512	7155	11	Saxon 1979
Cueva Lago Sofia 1	*Lama guanicoe*	OXA-8635	10710 ± 70*	bone	12629	12725	12542	12	Steele and Politis, 2009
Cueva del Medio	*Mylodon*	NUTA-2341	12720 ± 300*	bone	14968	15937	13996	12	Nami and Nakamura, 1995

Cueva del Milodón	*Mylodon*	A-1390	13560 ± 190	Sloth dung	16294	16900	15754	11	Long and Martin 1974
Cueva del Milodón	*Mylodon*	R-4299	13500 ± 410	Hair and Skin	16202	17476	15005	11	Long and Martin 1974
Cueva del Milodón	*Mylodon*	A-1391	10400 ± 330	Hide	12068	12863	11166	11	Long and Martin 1974
Cueva del Milodón	*Mylodon*	SA-49	10200 ± 400	Dung	11790	12743	10652	11	Long and Martin 1974
Cueva del Milodón	*Mylodon*	GX-6248	10575 ± 400	Dung	12242	13164	11189	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	GX-6243	10880 ± 300	Dung	12707	13319	11920	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	GX-6246	11775 ± 480	Dung	13699	15127	12705	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	GX-6247	11905 ± 335	Dung	13785	14912	13064	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	GX-6244	12020 ± 460	Dung	14020	15359	12912	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	A-2445	12270 ± 350	Dung	14329	15386	13388	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	A-2447	12240 ± 150	Dung	14142	14837	13730	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	GX-6245	12285 ± 480	Dung	14398	15780	13182	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	A-2448	12870 ± 100	Dung	15309	15701	14996	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	A-2446	13470 ± 180	Dung	16162	16747	15633	11	Markgraf 1985
Cueva del Milodón	*Mylodon*	BM-1375	12552 ± 128	Dung	14706	15170	14168	11	Saxon 1979
Cueva del Milodón	*Mylodon*	BM-728	12984 ± 76	Bone	15471	15748	15211	11	Burleigh et al., 1977
Cueva del Milodón	*Mylodon*	C-484	10832 ± 400	dung	12586	13420	11587	11	Arnold and Libby 1951, Bird 1988

Cueva del Milodón	*Mylodon*	W-2998	13040 ± 300	Hide	15517	16368	14330	11	Martinic 1996
Cueva del Milodón	*Mylodon*	LP-49	10377 ± 481	bone	11982	13095	10661	11	Tonni et al., 2003
Cueva del Milodón	*Mylodon*	LP-34	10812 ± 325	dung	12598	13302	11692	11	Tonni et al., 2003
Cueva del Milodón	*Mylodon*	LP-255	11330 ± 140	dung	13147	13417	12826	11	Borrero et al., 1991
Cueva del Milodón	*Mylodon*	LP-257	12570 ± 160	dung	14729	15264	14123	11	Borrero et al., 1991
Cueva del Milodón	*Mylodon*	Beta-164896	13480 ± 40	bone	16168	16342	15978	11	Martin 2010
Cueva del Milodón	*Mylodon*	Beta-164895	13630 ± 50	bone	16370	16608	16171	11	Martin 2010
Cueva Lago Sofía 4	*Mylodon*	PITT-0940	11590 ± 100	Bone	13379	13570	13167	11	Borerro et al., 1997
Cueva Lago Sofía 1	*Mylodon darwinii*	OXA-9506	12250 ± 110*	bone	14124	14647	13768	12	Steele and Politis, 2009
Cueva Lago Sofía 1	*Mylodon darwinii*	Gx-31641	9700 ± 100*	bone	10984	11236	10717	12	Borrero and Martin 2012 (P.Moreno, pers. Comm.)
Alero dos Herraduras	Mylodontidae	LP-421	11380 ± 150	Bone	13193	13466	12853	11	Borrero and Massone 1994
Alero dos Herraduras	Mylodontidae	AA-12574	12825 ± 110	bone	15237	15651	14798	11	Martinic 1996, Borrero and Martin 2013
Cueva Chica	Mylodontidae	Beta-284437	13970 ± 70*	bone	16885	17152	16579	12	Martin et al. 2013
Cueva Chica	Mylodontidae	Beta-288230	14240 ± 60*	bone	17286	17507	17070	12	Martin et al. 2013
Cueva Chica	Mylodontidae	Beta-288227	10780 ± 50*	bone	12687	12739	12641	12	Martin et al. 2013
Cueva del Medio	Mylodontidae	AA-12577	11990 ± 100	Bone	13791	14061	13555	11	Martinic 1996
Cueva del Medio	Mylodontidae	AA-12578	11570 ± 100	Bone	13362	13556	13155	11	Martinic 1996
Cueva del Milodón	Mylodontidae	Lu-794	13260 ± 115	Bone	15879	16236	15480	11	Håkansson 1976

Cueva del Milodón	Mylodontidae	BM-1208	13183 ± 202	bone	15749	16307	15159	11	Burleigh and Mathews 1982
Cueva del Milodón	Mylodontidae	BM-1209	12496 ± 148	Dung	14608	15152	14084	11	Burleigh and Mathews 1982
Cueva del Milodón	Mylodontidae	BM-1210	11810 ± 229	dung	13620	14140	13121	11	Burleigh and Mathews 1982
Cueva del Milodón	Mylodontidae	BM-1210b	12308 ± 288	Dung	14361	15255	13551	11	Burleigh and Mathews 1982
Cueva Lago Sofía 4	Mylodontidae	AA-11498	13400 ± 90	Bone	16068	16325	15774	11	Borrero et al., 1997
Cueva Lago Sofía 4	Mylodontidae	NSRL-3341	11050 ± 60	Bone	12874	13024	12730	11	Borerro 1999
Cueva Chica	*Panthera*	Beta-284439	12890 ± 60*	bone	15323	15590	15126	12	Martin et al. 2013
Cueva Chica	*Panthera*	Beta-319537	11470 ± 50*	bone	13266	13401	13137	12	Martin et al. 2013
Cueva Chica	*Panthera onca mesembrina*	Beta-288228	11520 ± 50*	bone	13328	13446	13200	12	Martin et al. 2013
Cueva del Medio	*Panthera onca mesembrina*	Ua-24687	11410 ± 80*	Bone	13213	13380	13071	12	Martin 2008; Prevosti and Martin 2013
Cueva Lago Sofia 4	*Panthera onca mesembrina*	Gx-31643	10840 ± 60	Bone	12711	12794	12652	11	Martin 2008; Prevosti and Martin 2013
Cueva del Milodón	*Smilodon*	OxA-14457	11420 ± 50*	Bone	13217	13320	13093	12	Barnett et al., 2005
Cueva del Milodón	*Smilodon*	OxA-13717	11265 ± 45*	Bone	13090	13192	12996	12	Barnett et al., 2005
Cueva del Medio	*Smilodon* cf. *S. populator*	Ua-37622	11100 ± 80*	Bone	12918	13072	12745	12	Prieto et al., 2010
Cueva Lago Sofía 4	*Vicugna vicugna*	Ua-36261	13545 ± 100*	bone	16260	16603	15945	12	Labarca y Prieto 2009
Cueva Lago Sofía 4	*Vicugna vicugna*	Ua-33262	13200 ± 100*	bone	15796	16107	15401	12	Labarca y Prieto 2009
Cueva Lago Sofía 4	*Vicugna vicugna*	Uncertain	13100 ± 70*	Bone	15642	15904	15329	12	Weinstock et al., 2009

Table 3. Radiocarbon dates on evidence of human presence in the Última Esperanza area; all are ranked 11 or higher according to the scale in Barnosky and Lindsey 2010.

Site name	Lab number	14C Age (Uncalibrated) *AMS	Material Dated	Archaeological evidence	Calib median	Calib old	Calib young	Rank	Reference
Cueva del Medio	Beta 52522	10430 ± 80	Charcoal	lithics, hearth	12233	12447	11965	11	Nami 1987; Nami and Nakamura 1995
Cueva del Medio	PITT 0344	9595 ± 115	Charcoal	lithics, hearth	10893	11198	10574	11	Nami 1987; Nami and Nakamura 1995
Cueva del Medio	Gr-N 14913	10310 ± 70	Charcoal	lithics, hearth	12010	12312	11756	11	Nami 1987; Nami and Nakamura 1995
Cueva del Medio	Beta 39081	10930 ± 230	Charcoal	lithics, hearths	12795	13259	12370	11	Nami 1987; Nami and Nakamura 1995
Cueva del Medio	NUTA 1811	10710 ± 100*	Bone	lithics, hearths	12605	12755	12403	11	Nami and Nakamura 1995
Cueva del Medio	NUTA 1737	11120 ± 130*	bone	lithics, hearths, burnt bone	12935	13155	12714	11	Nami and Nakamura 1995
Cueva del Medio	NUTA 2330	10960 ± 150*	bone	lithics, hearths, burnt bone	12833	13094	12632	11	Nami and Nakamura 1995
Cueva del Medio	NUTA 1735	10450 ± 100*	bone	lithics	12257	12564	11947	11	Nami and Nakamura 1995
Cueva del Medio	NUTA 2332	10710 ± 190*	bone	lithics	12542	12979	12000	11	Nami and Nakamura 1995
Cueva del Medio	NUTA 1812	10850 ± 130*	bone	lithics	12723	13013	12541	11	Nami and Nakamura 1995
Lago Sofía 1	OxA 8635	10710 ± 70*	bone	hearth, lithics	12629	12725	12542	11	Prieto et al. 1991; Massone and Prieto 2004
Cueva del Medio	Beta 58105	10350 ± 130	burnt bone	fireplace, lithics	12100	12557	11602	12	Nami 1987; Nami and Nakamura 1995
Cueva del Medio	GR-N 14911	10550 ± 120	burnt bone	fireplace, lithics	12409	12687	12026	12	Nami 1987; Nami and Nakamura 1995
Cueva del Milodón	BM 1201a	5366 ± 55	Charcoal	Artifacts	6104	6219	5986	12	Saxon 1976
Cueva del Milodón	BM 1201b	5395 ± 58	Charcoal	Artifacts	6133	6283	5991	12	Saxon 1976

Cueva del Milodón	BM 1204b	5643 ± 60	Charcoal	Artifacts	6382	6506	6282	12	Saxon 1976
Cueva del Milodón	BM 1204a	5684 ± 52	Charcoal	Artifacts	6423	6551	6302	12	Saxon 1976
Cueva del Medio	NUTA 2331	10860 ± 160*	bone	fireplace, lithics	12733	13076	12418	13	Nami and Nakamura 1995
Cueva del Medio	NUTA 2197	11040 ± 250*	bone	fireplace, lithics	12893	13430	12407	13	Nami and Nakamura 1995
Cueva del Medio	NUTA 1734	10430 ± 100*	bone	fireplace, lithics	12233	12558	11929	13	Nami and Nakamura 1995
Lago Sofía 1	PITT 0684	11570 ± 60	charcoal	hearth	13367	13482	13238	13	Prieto et al. 1991
Lago Sofía 1	OxA 9319	10780 ± 60*	bone	hearth, lithics	12684	12743	12627	13	Prieto et al. 1991; Massone and Prieto 2004
Lago Sofía 1	OxA 9504	10310 ± 160*	bone	hearth, lithics	12005	12457	11392	13	Prieto et al. 1991; Massone and Prieto 2004
Lago Sofía 1	OxA 9505	10140 ± 120*	bone	hearth, lithics	11670	12058	11245	13	Prieto et al. 1991; Massone and Prieto 2004
Alero quemado	Ua 35652	6920 ± 50*	charcoal	lithics	7714	7834	7611	14	Sierpe et al., 2009

9. Estimating the Last Occurrences of the Megafaunal taxa (Figure 4)

With an incomplete fossil record the youngest fossil of a taxon typically predates the true time of its local extinction (Marshall 1990). A simple way of rectifying this bias is to extend the known temporal range a distance equivalent to the average temporal gap size between the fossils from within the known temporal range (Strauss and Sadler, 1989). However, this method assumes that the likelihood of finding a fossil is the same everywhere within its true range – but if a taxon is being driven to local extinction by changing climate/vegetation and/or human activity, then the probability of finding fossils is likely to decrease as the taxon is going extinct. Furthermore, the likelihood of finding fossils may also vary through time due to a variety of changing taphonomic conditions. Finally, the uncertainties associated with the radiometric dates (Fig. 4) are often relatively large making it hard to determine the temporal gap sizes between the fossils. To accommodate these complexities we used the Gaussian-resampled, inverse-weighted method (GRIWM) of McInerny et al. described in Bradshaw et al. (2012) to estimate true times of local extinction. This approach deals with non-random fossilization by progressively up-weighting the gap sizes the closer they are to the time of disappearance from the fossil record. It also takes into account the uncertainties associated with the radiometric dates, providing a 95% confidence band around the estimated time of extinction. We also applied the method to estimate the true time of arrival of humans into the area. Analyses were run in the R programing environment (R Core Team 2014) and the R code can be accessed in Saltré et al. 2015 , appendix A -supplementary data.

Turning to the fossil record (Fig. 4), *Lama gracilis* disappears earliest, but this taxon is represented by only one date, so it is impossible to ascribe any significance to its time of disappearance (with only one fossil occurrence there are no gaps within its range, and thus no scale-length to judge how far beyond the last fossil the species became extinct). *Vicugna vicugna* also appears to drop out of the record early, with its time of local disappearance estimated to be between 13.7 and 15.9 cal ka BP. It is difficult to attribute much confidence to this, however, as this taxon is represented by only three dates. With fewer dates the GRIWM method tends to overestimate the uncertainty associated with the final extinction time (Bradshaw et al. 2012). A bootstrap technique discussed by Barnosky and Lindsey (2010), which mimics analytic methods (Marshall 1990, 2010), suggests that at least 10 dates are desirable for estimating true times of extinction.

As a guild, carnivores seem to disappear slightly earlier than any of the well-dated herbivores; this is the reverse of the general expectation that the demise of carnivores results from the loss of their megafauna prey, sometimes invoked to explain their extinction in the LQE event (for example, see the keystone hypothesis of Owen-Smith 1989, Barnosky 1989, Haynes 2002, Cione et al. 2003). The last appearance for *Smilodon* has a youngest limit of ~11.9 cal ka BP, with a best estimate: 12.6 cal ka BP, and for *Panthera*, an upper limit of ~11.7 cal ka BP, with a best estimate of 12.0 cal ka BP. In contrast, the best estimate for the disappearance of *Hippidion saldiasi* and *Lama owenii* is several hundred years later, approximately 11.3 cal ka BP for both taxa, with upper limits at least 2,000 years later, but with oldest estimates (~12.6 cal ka BP) that might pre-date the time of disappearance of the large carnivores. Mylodont sloths drop out later yet, with the best estimate of their time of local extinction 10.1 cal ka BP, with an upper limit as young as 8 cal ka BP. There is no overlap between the probable extinction intervals of carnivores and mylodont sloths.

The GRIWM method estimates the earliest likely human arrival into the Última Esperanza area between 14.6 and 13.3 cal ka BP. Thus, it seems likely that humans began visiting the Última Esperanza region ~4,000 years after it became ice-free (Fig. 4), and well after *Panthera*, *Vicugna vicugna*, and *Mylodon* were well established in the region. Humans then locally co-existed with the extinct mylodonts, *Hippidion saldiasi* and *Lama*. cf. *owenii* for several thousand years. The GRIWM confidence intervals suggest that *H. saldiasi* coexisted with humans for at least ~700 years and could have coexisted for as long as ~5,800 years. *L*. cf. *owenii* appears to have coexisted with humans for at least ~700 years and perhaps as much as ~4,700 years. Mylodonts, probably co-occurred with humans for at least ~2,300 years and perhaps for as much as ~6,600 years.

10. Causes of Megafauna Extinction (Figure 4)

The pattern of extinction illustrated in Fig. 4 suggests that the timing of megafaunal extinction in the Última Esperanza region was controlled by a complex interaction between climate changes that precipitated vegetation change, combined with growing human impacts. Of particular note are: (1) the co-existence of megafauna with humans for at least hundreds and more likely thousands of years, although the archeological evidence suggests that human presence during this interval was probably ephemeral (Jackson and Prieto 2005, Martin 2010, Nami and Menegaz 1991; and further supported by the fact that Cueva del Milodón is less than 2 km away from Cueva del Medio – it seems unlikely that humans and mylodonts could have continuously occupied sites in such close proximity over thousands of years); (2) the apparently earlier loss of carnivores relative to horses (*Hippidion saldiasi*), *Lama* cf. *owenii*, and mylodonts; (3) the disappearance of horses and *L.* cf. *owenii* near the time dominant vegetation transforms from grasslands to increasingly dense *Nothofagus* forest; (4) and the loss of mylodonts only after dense *Nothofagus* forests established.

This pattern is most consistent with a model that sees: (1) megafauna thriving near the UEIL margins during the LGM and colonizing the newly deglaciated terrains following the ice front or proglacial lake margins of Lago Puerto Consuelo and colonizing our study area after Cerro Benítez and Cerro Señoret became broadly connected to the mainland; (2) humans arriving and ephemerally co-existing with the abundant megafauna in a cool late glacial climate dominated by grasslands; (3) loss of the carnivores through exclusion by humans; (4) loss of horses and *L.* cf. *owenii* as grasslands rapidly transformed into *Nothofagus* forest, reducing their preferred open-landscape habitats, and potentially as human population sizes, or frequency of visits to the area, increased and exerted more hunting pressure at the same time; and (5) loss of mylodonts due to grassland habitat loss once *Nothofagus* forests finally became dominant.

Consistent with this model are the apparent dietary preferences of Lama cf. *owenii*, *Hippidion saldiasi*, and mylodonts. All three of these taxa preferred grasses, as inferred from dental characteristics and, in the case of mylodonts, from abundant dung samples in Cueva del Milodón (Markgraf 1985, Moore 1978, Bargo et al. 2006, Fariña et al. 2013). Also, despite some assertions that carnivore extinctions during the LQE resulted from the disappearance of their prey base (Owen-Smith 1989; Barnosky 1989; Cione et al. 2003, Haynes 2002), other ecological models may be more consistent with our observation of earlier disappearance of carnivores. Humans too are meat-eating megafauna; thus, once they enter into a new ecosystem they utilize the same prey base as other mega-carnivores. Once human numbers/visits reach a critical threshold, it is not unlikely that people would command enough of the prey base to cause population crashes in other large carnivores. Moreover, in historic and modern ecosystems where humans interact with carnivores, they selectively kill large carnivores in an effort to protect both themselves and the large herbivores they depend upon (Musiani and Paquet 2004, Alagona 2013). The biggest carnivore that persists in the ÚItima Esperanza region today is *Puma concolor* which, compared with the two large extinct carnivores is much smaller (*Smilodon*: 350-405 kg [Anyonge 1993, Fariña et al. 1998]; *Panthera onca*: 120 kg [Prevosti and Vizcaino 2006]; *Puma*: 25-68 kg [Chester 2008]) and usually avoids direct conflict with humans.

This hypothesis rests in part on the assumption that humans and mega-carnivores consume the same prey items. In the Última Esperanza region, there is good evidence that ancient humans and ancient felids exploited at least some of the same extinct megafauna taxa. Evidence of human consumption of *Hippidion saldiasi* and *Mylodon* is found in Cueva Lago Sofía 1, as bones belonging to these two taxa, and others from extant faunas, were found in association with lithic material and hearths, and are reported to display cut marks (Prieto 1991, Alberdi and Prieto 2000, Jackson and Prieto 2005). At Cueva del Medio, burnt bones of *Hippidion saldiasi* and *Lama* cf. *owenii* are found along with remains of *Myolodon* and in association with hearths and lithics including Fishtail projectile points, and cut marks have been identified on the horse bones (Nami and Menegaz 1991, Alberdi and Prieto 2000, Martin 2010). On the other hand, sites identified as carnivore dens (Cueva Lago Sofía 4 and Cueva Chica) offer a good source of evidence for mega-carnivore consumption of some prey items such as *Lama gracilis*, *Mylodon*, *Vicugna* and *Hippidion saldiasi* as revealed by taphonomic studies and isotopic analyses (Borrero 1997, Martin 2008, 2013, Prevosti and Martin 2013).

The model we suggest above implies that the chief cause of the mega-carnivore extinction resulted primarily from human impacts, with the mega-carnivores able to co-exist with people only as long as human population sizes/visits remained below a critical threshold. In contrast, the available evidence indicates that the key driver of extinction of horses, Lama cf. *owenii*, and mylodonts was climate-driven vegetation change which reduced the availability of open environments. It may well be that growing human population sizes around the time of the vegetation change exacerbated the decline of the megafauna herbivores at that time, but so far the data are not available to robustly quantify human population growth through the critical time intervals in Última Esperanza. Human impacts combined with a reduction of open areas as a driver of the megafaunal extinction in South America has been discussed in earlier works (Cione et al. 2003).

The role of humans in changing vegetation structure through the use of fire has been proposed as a possible driver of megafauna extinction, especially in Australia (Miller et al., 1999). In the case of Última Esperanza, climate changes and the consequent changes in vegetation and wood fuels have been proposed as the main factor leading to the fire frequency increases recorded at Lago Eberhard and Pantano Dumestre (Moreno et al., 2012), a pattern that has been reported for other sites of southern South America (Whitlock et al.,2006). While the role of humans as providers of the ignition source and causing then an important impact on the vegetation is still an open possibility, our data analysis does not support that hypothesis, mainly because the observed changes in vegetation do not fit the expectations from widespread human-induced fires in the region (Vidal and Reif 2011). The extinction chronology summarized in Fig. 4 also highlights potential correspondence between the last appearance of *Vicugna vicugna* in the Última Esperanza region, the Antarctic Cold Reversal, and the eruption of the Reclús volcano. It may be that one or both of these factors decimated what may have been a small population of *V. vicugna* at that time, but given that there are only three dates on the taxon, it is impossible to draw any firm conclusions. Other specimens identified as *Vicugna* and radiocarbon dated to 12,564 cal yr BP have been found in the site Tres Arroyos 1 located in Tierra del Fuego, more than 300 km to the south east of Última Esperanza (Massone and Prieto 2004, Weinstock et al. 2009), suggesting that this taxon could have persisted longer, at least in that area of Patagonia. The Reclús eruption, though producing widespread ash, does not seem to correspond with the loss of any of the other megafauna.

Lama gracilis is known by only a single date. Therefore, at this point nothing definitive can be said about that taxon's disappearance, but the date does verify that megafauna occupied the Última Esperanza region very shortly, and/or very sparsely, after it became ice-free.

There is the possibility that the changes in vegetation observed in Última Esperazna could be the result of herbivore release due to the extinction of the megaherbivores, as has been proposed for other regions of the world (Gill 2014, Rule et al. 2012, among others). However, that is not supported by the data presented here. The herbivores that became extinct in the area were mainly grazers, specializing on grasses in open habitats, so were not likely to exert a control over forest growth by direct consumption. *Mylodon*, the biggest herbivore that could have had the capability to influence the growth of *Nothofagus* by trampling, felling trees or carving pathways, did not become extinct until long after the major expansion of *Nothofagus* was underway.

Conclusions

A detailed compilation of robust radiocarbon dates on megafauna from the Última Esperanza region, compared with archaeological dates and existing pollen and paleoclimate data, helps to elucidate the causes of the Late Quaternary Extinction event in Chile's southern Patagonia. Megafauna colonized the region fairly soon after glaciers retreated and ancient pro-glacial lake Lago Puerto Consuelo margin was low enough (~>120 m.a.s.l.) to leave habitable land open after ~18 thousand years ago. Humans arrived 4,000 years later and co-existed, at least ephemerally, for several millennia with most of the megafaunal taxa living in the area. The chronology of extinction of different genera compared to the timing of climate and vegetation change reveals that extinction of the mega-carnivores *Smilodon* and *Panthera* likely slightly preceded extinction of the most abundant megaherbivores (*Hippidion saldiasi* and *Lama* cf. *owenii*; and almost certainly the mylodont sloths). We suggest that humans caused the mega-carnivore extinctions, either by indirect interactions via commandeering more of the megaherbivore prey base once human population sizes/visits reached critical mass/frequency, or by targeting carnivores directly to make the region safer for humans, or a combination of both. *Hippidion saldiasi*, *Lama* cf. *L. owenii*, and mylodont sloths all drop out of the record coincident with major vegetation changes that were triggered by end-Pleistocene climate changes. The first two disappear as grasslands begin to rapidly transform to *Nothofagus* forest and mylodonts drop out once dense *Nothofagus* cover is fully established. This correspondence points to environmental change that resulted in the loss of their preferred grassland habitats as a key driver of these taxa's demise, although it may be that growing human population sizes exacerbated the pressures; adequate data on human-population growth/frequency of visits is not available for the crucial time period. *Vicugna vicugna* may have been extirpated from the region coincident with some combination of the eruption of the Reclús volcano and the Antarctic Cold Reversal, but with only three dates on the taxon it is not possible to come to definitive conclusions as to cause of its demise (and with the large confidence bands on the estimated times of extinction, by chance alone any volcanic eruption is likely to overlap with one or more times of plausible extinction).

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Incorporpation of Recently Published Radiocarbon Dates into the Analysis of Megafaunal Extinctions in Última Esperanza

After Villavicencio et al. (2016) was published, 42 new radiocarbon dates on extinct megafauna for UE were reported (Meltcalf et al. 2016, Martin et al. 2015, Table 1), making it possible to update the earlier analyses by adding the new dates to those reported in Villavicencio et al. (2016). This brought the total number of highly ranked radiocarbon dates to 104. In the combined dataset, best-estimates of local extinction times were obtained (as in Villavicencio 2016) using the Gaussian-resampled, inverse-weighted method (GRIWM) of McInerny et al. (described in Bradshaw et al. 2012). The resulting updated figure of the chronology of extinction is presented in Figure 5.

When the new dates are added, the general patterns of extinction as inferred from the GRIWM best-estimates appear almost the same as those calculated from the original 62 dates (Fig. 1). Slightly different estimates resulted for the extinction of *Panthera* and *Hippidion,* which appear somewhat older using the new, combined dataset. With the addition of the new dates, *Lama gracilis*, which was previously known by a single radiocarbon date, gained a more resolved record showing possible coexistence with humans for 900 to 1,200 years. This taxon disappears from the record between 12.6-12.2 cal ka BP, when the landscape was still dominated by cold grasslands. Four out of the eight taxa shown in Figure 1 become locally extinct after the Antarctic Cold Reversal (ACR) cooling period, during the second warming phase observed in the EDC core. *Mylodon*, and possibly *Hippidion*, disappear later from the record, between 12-10 ka.

Current archaeological evidence is scant and the number of dated occupation events implies that UE was visited on an ephemeral basis (Martin and Borrero 2015). However, the pattern of extinction remains evident, even after adding new radiocarbon dates to the analysis, and does not rule out the possibility of humans playing a role in driving some of these extinctions. As it was proposed in Villavicencio et al., 2016, competition with humans would be consistent with the disappearance of the large felids from the area between 700 and 2,000 years before some of the largest herbivores went extinct. On the other hand, slow attrition of megaherbivores by human hunting, coupled with vegetation change, could also explain the later disappearance of mylodontids, horses and some of the extinct camels. Interestingly, and not mentioned in the published article, human presence in the area fades at the same time of the last megafaunal extinction (*Mylodon*), reemerging more than 3000 years later. Whether this disappearance from the record is a true absence of humans or a gap in the sedimentation and deposition processes is currently unknown (L. Borrero and F. Martin, pers. comm.).

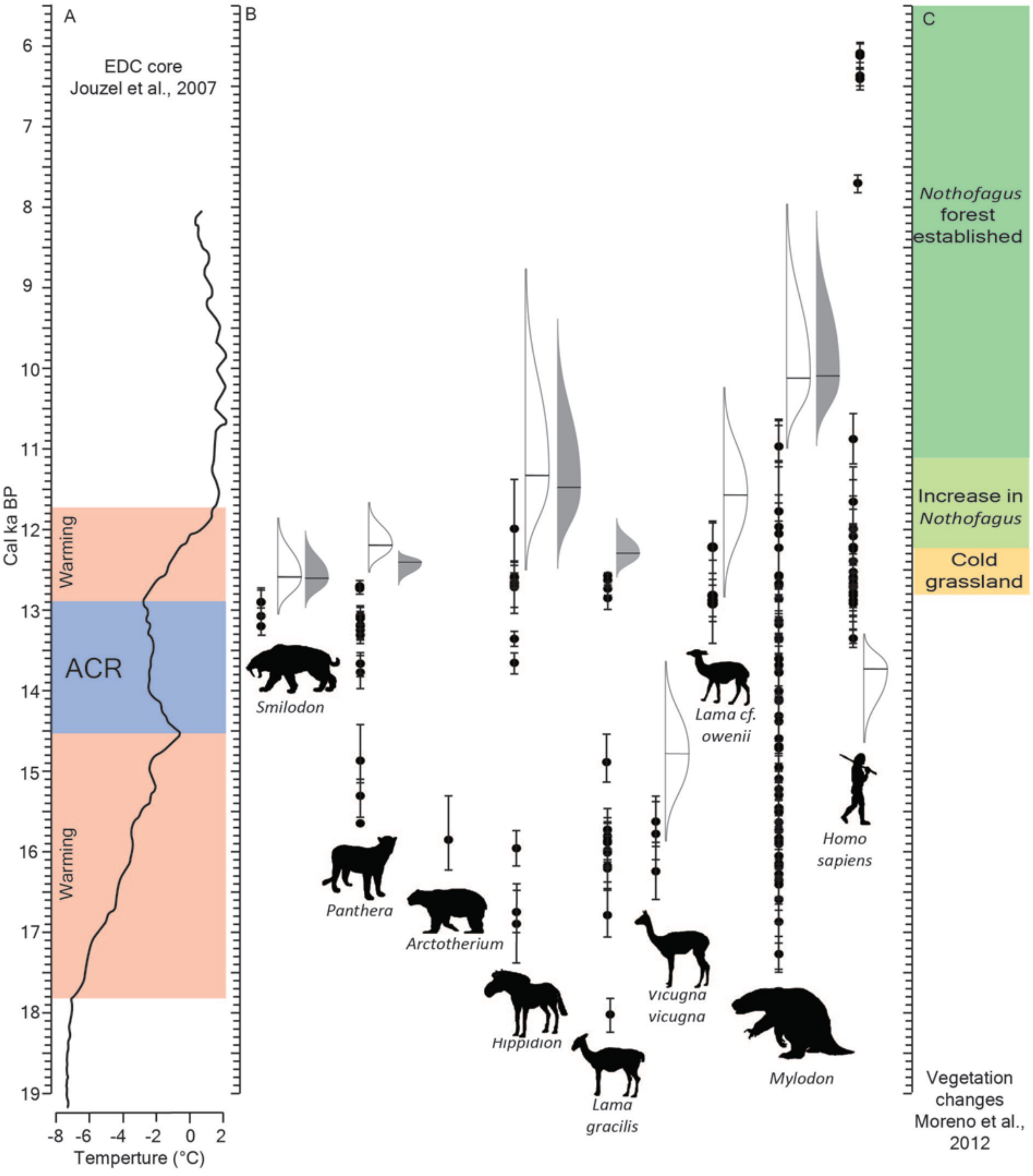

Figure 1: A) Temperature record from EDC ice core, Antarctica. Blue bar: Antarctic Cold Reversal, red bars: warming events (Jouzel et al. 2007); B) Chronology of megafaunal extinctions and human arrival in Última Esperanza, modified from Villavicencio et al. 2016; C) Vegetation change estimations from Moreno et al. 2012. Black circles: direct radiocarbon dates on extinct megafauna and radiocarbon dates on human evidence, all of them calibrated to calendar years using Calib 7.04 (Stuvier and Reimer 2014). The GRIWM best-estimates of extinction timing (or human arrival timing) are indicated by the unshaded (from Villavicencio et al., 2016) and shaded (this work) normal distributions, with the 95% confidence band depicted by the areas around the mean (black line: most probable time of extinction).

Conclusions

The extinction pattern observed in the record of Última Esperanza cannot be attributed to a single cause. It is likely that a combination of human impacts, climate and vegetation changes acted together to trigger the extinction of megafauna in Southern Patagonia.

The main conclusions reported in Villavicencio et al., 2016 are supported by the new dates.

1) Mega-carnivores (*Panthera* and *Smilodon*) disappear slightly before the extinction of most of the herbivores, contrary to what is expected in a situation of trophic collapse.

2) *Hippidion*, *Lama* cf. *owenii* and mylodontids apparently coexisted with humans for hundreds of years (*Hippidion* and *Lama* cf. *owenii*) to millennia (mylodontids), ruling out a scenario of blitzkrieg overkill of these taxa by humans.

3) *Hippidion* and *L.cf. owenii* disappeared when cold grasslands were replaced by *Nothofagus* forest followed by loss of mylodontids, which occurred when the forests finally dominated the landscape.

The critical information provided by the new dates is a more resolved extinction chronology for *Lama gracilis*. This species disappears before any vegetation changed occurred, during the middle of the second warming phase observed in the EDC core and, after coexisting with humans for about 900 years. Explanations for its disappearance could involve sensitivity to increasing temperatures at the time and/or more susceptibility to human impacts than seemed to be the case with the other herbivores.

Table 4: New radiocarbon dates on extinct megafauna from the Última Esperanza area published in Martin et al., 2015 and Metcalf et al., 2016. All of them are AMS dates and 12 which are considered robust according to the scale published in Barnosky and Lindsey 2010.

Site Name	Taxa	Lab number	14C Age (Uncalibrated)	Material Dated	Calib median	Calib old	Calib young	Rank	Reference
Cueva del Milodón	*Arctotherium*	WK-20234	13257±147	Bone	15866	1626	15360	12	Metcalf et al., 2016
Cueva del Medio	*Hippidion*	Beta-344428	10680±40	Bone	12617	1269	12551	12	Martin et al., 2015
Cueva del Medio	*Hippidion saldiasi*	AA-100235	10860±110	Bone	12730	1299	12554	12	Martin et al., 2015
Cueva del Medio	*Hippidion saldiasi*	OXA-26125	10810±45	Bone	12700	1274	12658	12	Metcalf et al., 2016
Cueva del Medio	*Hippidion saldiasi*	OXA-26126	11570±50	Bone	13368	1346	13267	12	Metcalf et al., 2016
Cueva del Milodón	*Hippidion saldiasi*	OXA-26120	13325±60	Bone	15971	1618	15751	12	Metcalf et al., 2016
Cueva del Milodón	*Hippidion saldiasi*	Beta-371877	11900±60	Bone	13666	1379	13542	12	Martin et al., 2015
Cueva Lago Sofía	*Hippidion saldiasi*	OXA-26122	10750±45	Bone	12675	1272	12633	12	Metcalf et al., 2016
Cueva Nordenskiöld	*Hippidion saldiasi*	AA-100230	13990±150	Bone	16910	1739	16421	12	Martin et al., 2015
Cueva escondida	*Hippidion saldiasi*	Beta-310944	13890±60	Bone	16764	1701	16491	12	Martin et al., 2015
Cueva del Medio	*Lama gracilis*	OXA-21469	10925±45	Bone	12752	1283	12695	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-20708	13270±65	Bone	15899	1612	15673	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21459	13500±50	Bone	16193	1640	15983	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21460	13365±55	Bone	16025	1623	15811	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21375	10640±45	Bone	12590	1267	12537	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21461	12610±45	Bone	14902	1515	14554	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21462	13255±65	Bone	15880	1611	15652	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21378	13345±55	Bone	15998	1620	15783	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21464	13210±55	Bone	15822	1604	15604	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21465	11050±45	Bone	12869	1300	12734	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21466	10705±45	Bone	12644	1270	12555	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21967	13520±65	Bone	16221	1648	15993	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21467	13155±50	Bone	15739	1598	15482	12	Metcalf et al., 2016
Cueva Lago Sofía 4	*Lama gracilis*	OXA-21968	13915±65	Bone	16802	1705	16509	12	Metcalf et al., 2016
Cueva del Medio	*Mylodon*	AA-100228	11830±130	Bone	13621	1395	13353	12	Martin et al., 2015
Cueva del Medio	*Mylodon*	AA-100232	12760±140	Bone	15108	1563	14419	12	Martin et al., 2015
Cueva del Medio	*Mylodon*	Beta-344435	12990±50	Bone	15474	1571	15260	12	Martin et al., 2015
Cueva del Medio	*Mylodon*	Beta-319539	13100±50	Bone	15648	1586	15361	12	Martin et al., 2015

Cueva del Medio	*Mylodon*	Beta-344436	13670±50	bone	16422	1666	16213	12	Martin et al., 2015
Cueva del Medio	*Mylodon*	Beta-341902	13790±60	Bone	16607	1689	16342	12	Martin et al., 2015
Cueva del Medio	*Panthera*	Beta-344430	10860±40	Bone	12718	1276	12679	12	Martin et al., 2015
Cueva del Medio	*Panthera onca mesembrina*	Ua-24687	11410±80	Bone	13213	1338	13071	12	Martin et al., 2015
Cueva del Milodón	*Panthera onca mesembrina*	OXA-4450	12610±60	Bone	14887	1516	14452	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-14451	11405±55	Bone	13205	1331	13084	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-14453	11925±55	Bone	13684	1383	13548	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-14454	11285±55	Bone	13108	1324	12999	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-14455	11995±55	Bone	13792	1398	13591	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-22144	11305±50	Bone	13123	1325	13040	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-22145	10905±45	Bone	12740	1281	12691	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-22146	11260±50	Bone	13086	1320	12980	12	Metcalf et al., 2016
Cueva del Milodón	*Panthera onca mesembrina*	OXA-22147	11925±50	Bone	13683	1380	13556	12	Metcalf et al., 2016

Chapter 3: Radiocarbon dating of extinct South American Megafauna.

Introduction

Understanding the association between the Late Quaternary megafaunal extinctions (LQE) and environmental factors, such as climate changes and arrival of humans, requires detailed knowledge of the timing of extinction. Therefore it is crucial to build robust extinction chronologies for the different taxa that became extinct during the LQE in different regions of the world.

Almost all the analyses of megfaunal extinction published are based on datasets of radiocarbon dates from megafaunal remains (i.e. Guthrie 2006, Stuart 2005, Stuart and Lister 2011, 2012). An exception to this is the case of Australia where the megafaunal extinction and human arrival happened near 50,000 years BP,close to or exceeding the limit of radiocarbon dating, necessitating the use of other radiometric techniques usually on materials associated with the megafaunal remains (Roberts et al. 2001). Also useful has been analysis of spores of *Sporormiella*, a fungus associated with large-herbivore dung that can be found in lake sediment records (Gill 2013, Rozas-Davila et al., 2016, Rule et al., 2012). The use of *Sporormiella* offers the opportunity to estimate the timing of extinction in areas where the fossil record is scant (for instance, in the tropics) and can provide a continuous record of presence and decline of megafauna in time in a particular region, as the analyses typically involve counting spores along with pollen grains from lake cores. However, *Sporormiella* records sometimes indicate megafaunal decline long before the youngest radiocarbon dates (e.g., Barnosky et al. 2015).

Although compilations of radiocarbon dates on megafauna are one of the best tools to build taxon-specific chronologies of extinction, the approach is usually limited by the number of dates available, which is generally limited by the number of specimens that exist for each taxon in a determined region and by the preservation of those specimens.

State of the art in South America

A compilation of radiocarbon dates on extinct South American megafauna by Barnosky and Lindsey (2010), included 138 dates, from which about 94 were of desirable quality. Since then, additional radiocarbon dates have come to light (i.e. Hubbe et al., 2013, Prado et al., 2015; Metcalf et al., 2016), bringing the number of highly-ranked radiocarbon dates on megafauna to more than 175 dates (See Chapter 1, Table 10.1).

This chapter reports 27 new dates on a variety of taxa, and summarizes my attempts to date numerous bone samples of South American megafauna plus some from North America (Mexico), Central America and the Caribbean. This work was done in collaboration with researchers from Latin America and the United States as part of an NSF funded initiative (NSF 1148181), the main goal of which was to test for possible synergistic effects between climate changes and human arrival in driving Late Quaternary megafaunal extinctions. The work reported here was an effort to increase the robustness of the extinction chronology by radiocarbon dating dozens of megafauna bone samples.

The Samples

A total of 280 samples of megafauna bones from paleontological and archaeological deposits in South America, Central America and North America were analyzed, plus five more from medium (1 sample) and small-sized rodents (3 samples), and a turtle (1 sample). These samples were comprised of specimens provided to the project by other participating researchers, as well as samples I collected from various museums. The locations of samples from Mexico, Belize, Costa Rica and Dominican Republic are shown in Fig. 1, and those from Argentina, Brazil, Bolivia, Paragauay, Chile, Peru and Ecuador in Fig. 2.

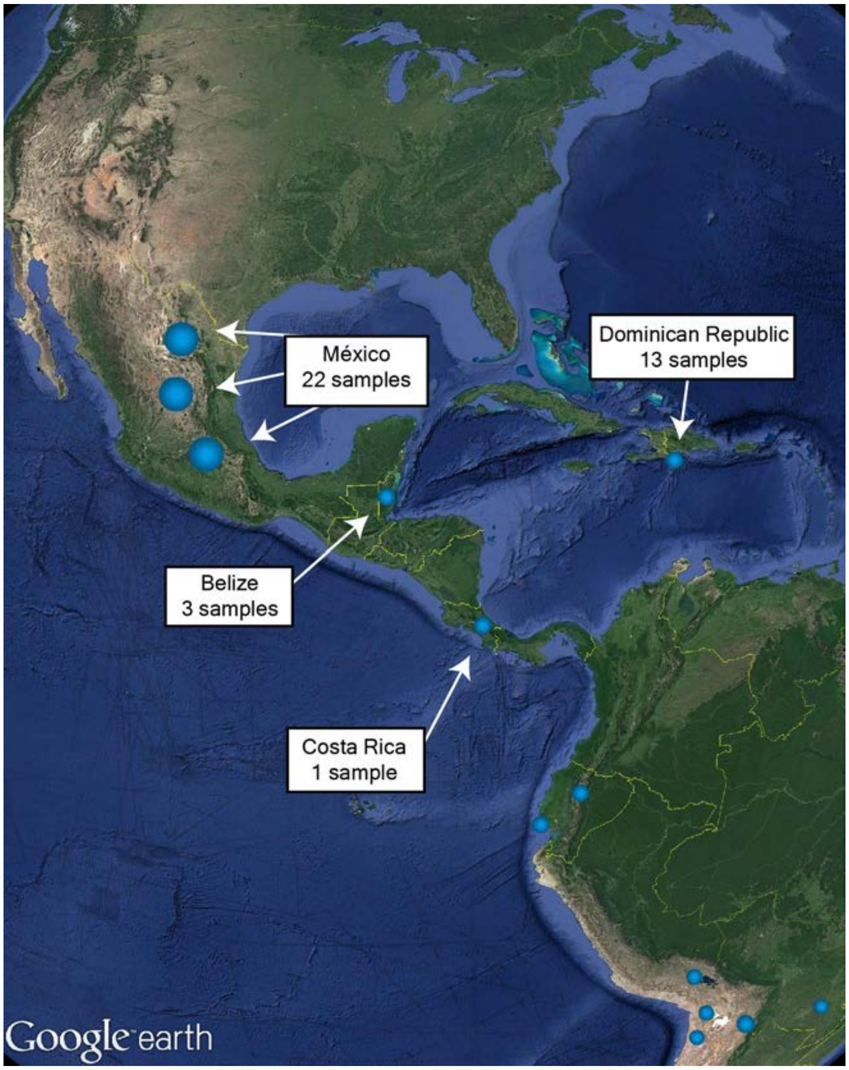

Fig. 1: Approximate location of the sites in North America, Central America and the Caribbean that yielded megafaunal samples used in this work. For site names per country see Appendix Chapter 3.

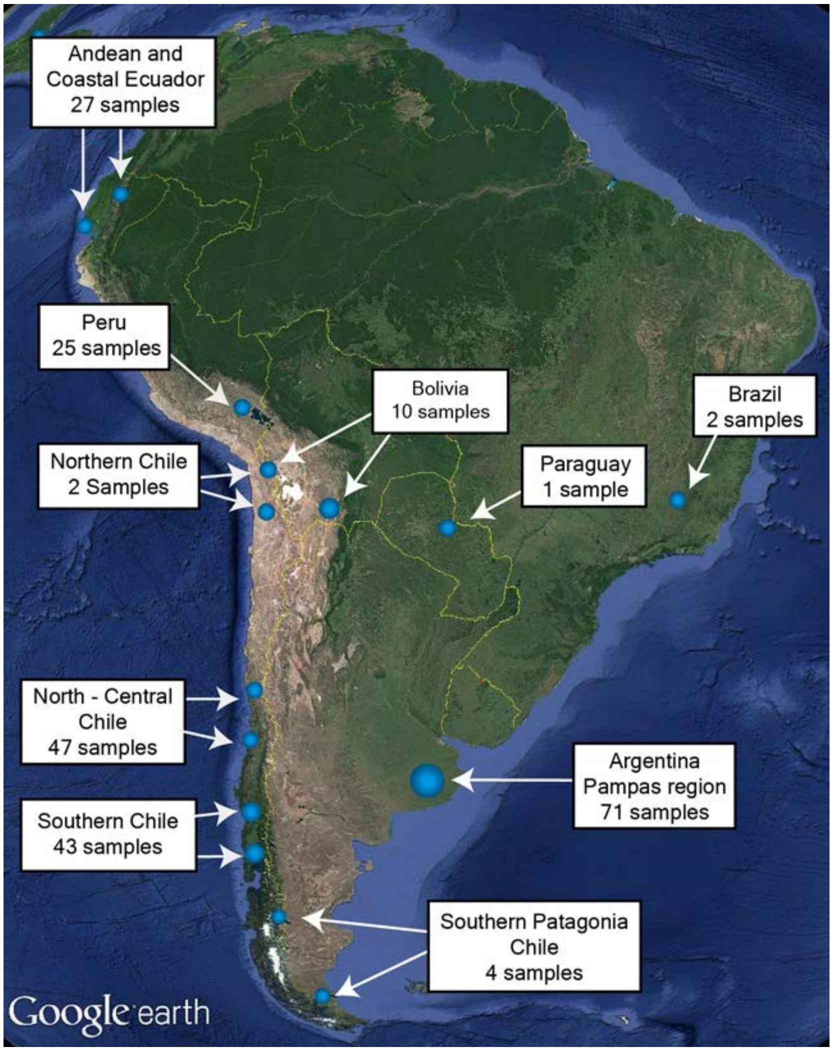

Figure 2: Map of South America showing the areas from which megafaunal samples used in this work were obtained. For site names per country see Appendix Chapter 3.

Non-mammalian and undetermined megafauna were excluded from the analysis (Testudinidae, undetermined cingulate, and an undetermined mammal), which left 282 samples on which I focused.

The samples represented several different mammalian families (Figure 3). Most specimens were from Gomphotheridae, Equidae and Mylodontidae, with a total of 76, 59 and 43 samples respectively. The higher representation of these families was intentional as these were focal taxa for the overall project because they have the most widespread geographic distribution in the Pleistocene of South America. The families Glyptodontidae, Megatheriidae, Megalochynidae, Camelidae, and Toxodontidae are represented by 10 to 15 samples each. Mammutidae and Elephantidae are represented by 7 and 5 samples, respectively, and are known only from North and Central America; they have not been found in South America. Felidae, Macrauchenidae, Mesotheriidae and Cervidae are represented by 6, 4, 3 and 2 two samples, respectively. The rodents, Cricetidae and Myocastoridae are represented by to samples each and Abrocomidae just by a single specimen. Likewise, for Bovidae, Tayassuidae, Pampatheriidae, Ursidae and Dasypodidae, only a single sample from each was available.

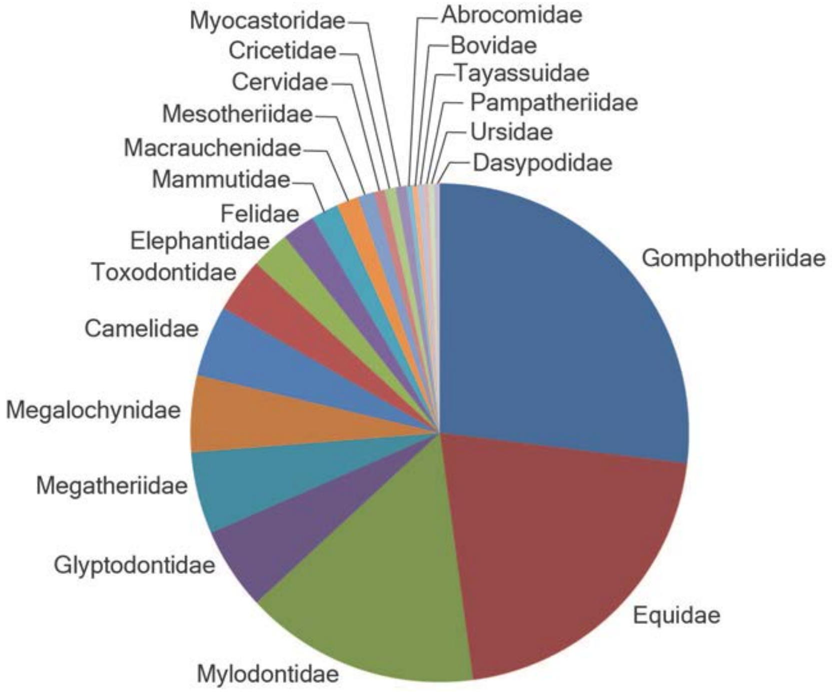

Figure 3: Representation of different mammalian faunas in the total set of 282 samples for radiocarbon dating.

Principles of Radiocarbon Dating (^{14}C) and Radiocarbon dating of Bone

Radiocarbon dating is a technique for determining the age of organic matter, based on the radioisotopic properties of the atom of Carbon ^{14}C.

When the radiocarbon dating method was developed and presented by Willard Libby (1955), it caused a revolution in many fields of Late Quaternary research, especially in archaeology. He won the Nobel Prize in chemistry in 1960 for this work. Today, improved through many advancements since Libby's time, radiocarbon dating is the most widely used method to build chronologies in late Quaternary archaeology, paleontology, paleoclimatology, geomorphology, glaciology, and many other fields which focus on studying recent prehistory.

Principles of ^{14}C dating

Radiocarbon ^{14}C is formed in the upper atmosphere by neutrons bombarding atoms of ^{14}N, and is an unstable and radioactive isotope of carbon. It decays to ^{14}N releasing a β particle. The half-life of radiocarbon is 5,730 years, which means that from a given starting amount of ^{14}C atoms in a sample (100% of ^{14}C) there will be just 50% remaining after 5,730 years, with the other half of the initial amount having decayed into ^{14}N. After another 5,730 years passes, the measured amount of ^{14}C in the sample would be 25% of the initial amount, and so on through time. This decay ratio (the 'radioactive clock') is the most basic principle behind not only radiocarbon dating but behind any radioisotopic dating.

In the atmosphere, radiocarbon atoms oxidize quickly into $^{14}CO_2$ and mix with the rest of the CO_2 present in the atmosphere ($^{12}CO_2$; $^{13}CO_2$), becoming available to enter into the different chemical pathways of the earth system. Living organisms can take ^{14}C atoms from the atmosphere through photosynthesis along with the other stable isotopes of carbon ^{12}C and ^{13}C and assimilate it in different living tissues, as Libby pointed out in 1955: "Since plants live off the carbon dioxide, all plants will be radioactive; since the animals on earth live off the plants, all animals will be radioactive. Thus . . . all living things will be rendered radioactive by the cosmic radiation" (Extracted from Bradley 2015). In short, ^{14}C becomes present in all organic matter, being incorporated into organisms by photosynthesis and trophic pathways. All living organisms are in equilibrium with the atmosphere, which means they incorporate new carbon atoms (including ^{14}C atoms) through photosynthesis and feeding at different trophic levels, and release it back into the atmosphere through respiration and as cells die in their bodies and are replace by new ones, thus there is constant replacement of ^{14}C in the tissues of living organisms. Once an organism dies, the replacement of ^{14}C ceases and the 'radioactive clock' starts running. Basically, by knowing the starting amount of ^{14}C in a sample and the amount at present, the age of that organic matter can be determined.

Conventional radiocarbon dating measures beta particles emitted during the decay of ^{14}C, the same technique used when the ^{14}C dating was first developed. Since the 1970s, advances in the radiocarbon dating saw the advent of Accelerator Mass Spectrometry (AMS), which today is the most frequently used technique to calculate ^{14}C ages. The AMS method counts the number of ^{14}C atoms in a sample, along with estimates for the numbers of atoms of ^{12}C and ^{13}C, which are stable isotopes of carbon that organic matter contains. From these values, the 'fraction modern' is calculated. The 'fraction modern' is defined as the ratio between $^{14}C/^{12}C$ in the sample and $^{14}C/^{12}C$ in modern carbon (the ratios $^{14}C/^{13}C$ in the sample and in modern carbon are also used). Modern carbon is defined based on measurements of ^{14}C made in 1950 AD. The values used to calculate the 'fraction modern' are corrected by ratios measured in the standards and in specific backgrounds (See McNichol et al., 2001 for more details).

At the same time, the 'fraction modern' is also corrected for natural isotopic fractionation (fractionation that is related to the different biochemical pathways that make organic matter), for lab isotopic fractionation (fractionation that may occur during the chemical processing of the sample), and for any intrusion of carbon that may occur when the carbon in sample is being counted in the AMS (McNichol et al., 2001). From the corrected 'fraction modern' the ^{14}C age is estimated.

Each age estimate comes with an error associated (plus/minus some amount of years) which is based in the size of the sample (the amount of carbon the samples contained) and on the time the sample is required to be analized. Most of AMS labs calculate the sample error based on an internal error, which is related to the number of ^{14}C counts, and an external error associated with the operation of the AMS (McNichol et al., 2001)

Another important source of error is the change in the concentration of ^{14}C in the atmosphere through time (de Vries 1958). ^{14}C has not remained constant through time and it continues to vary due to several factors such as changes in the rate of production of ^{14}C in the upper atmosphere, injection of old carbon into the atmosphere from reservoirs like the deep ocean or burning of fossil fuels, and alterations of the atmosphere's chemistry by nuclear tests made in the 1950s (de Vries 1958, Stuvier and Suess 1966, Reimer et al., 2004). To correct for this, a system of calibration to calendar years has been developed (Klein et al., 1982, Stuvier and Reimer 1986). The method consists of a curve that relates radiocarbon years to its equivalent in calendar years against which each ^{14}C age obtained from samples is compared. This curve has been developed by estimating ^{14}C ages from organic matter with a known age that has been calculated using other independent methods (i.e. tree rings, sediment layers, and wood from archaeological sites) (Stuvier and Reimer 1993, Stuvier et al., 1998, Reimer et al., 2009, Hogg et al., 2013). The calibration is made with the help of specialized software developed to convert ^{14}C ages to calendar years. In this work I use Calib 7.02 (Stuvier and Reimer 1986-2014) for all the calibrations.

Radiocarbon dating of bone

Historically, the advantages of radiocarbon dating bone have been neglected given the inaccuracy of the results (Stafford et al., 1991). These inaccuracies are related to the chemistry and to preservation differences which mainly depend upon the depositional environment of the samples. Obtaining an accurate versus inaccurate radiocarbon date on bone depends heavily on the pretreatment given to the sample before combustion, graphitization and analysis in the AMS.

Due to exchange reactions with modern carbon that is present in soils, sediments and in the atmosphere, dates obtained from bulk samples of fossil bone are unreliable (Olsson et al., 1974). It is necessary to analyze the different components of the bone in order to select the fraction that is most amenable to providing reliable dates.

Bone can be separated into two main phases: one made of carbonate hydroxyapatite which makes up the 80% of the total bone weight, and the organic protein phase which accounts for the remaining 20% of the weight of a bone. Both phases can be dated using ^{14}C, nevertheless the use of the apatite fraction for isotopic analyses is not recommended given the susceptibility of this phase to exchange carbon with the environment after deposition of the bone (Stafford et al., 1987). At the moment, the isolation of the organic fraction of the bone for radiocarbon dating seems to be the most reliable approach. Even if this phase can be contaminated with carbon from external sources as the apatite phase, there are several methods, which are discussed below, that can help to separate external contamination from bone organic phase elements.

The organic phase of a bone is made up of 88% collagen, 8-9% glycoproteins and 3-4% non-collagenous proteins (Ursist et al., 1983, Termine 1986). The amino acid composition of modern bone is the same as collagen (see Stafford et al., 1991 for details), and it remains very similar during bone diagenesis until the bone has as little as 5% of the original protein content remaining. Bellow this proportion the amino acid composition changes and is mainly characterized by the total loss of some conspicuous bone amino acids such as hydroxyproline and proline (Stafford et al., 1988, Stafford et al., 1991 and references there).

The methods used to isolate the organic phase of carbon start with the decalcification of bone with acid (usually HCL), which dissolves and eliminates the hydroxyapatite, followed by the posterior treatment of the remaining collagen phase. Three main methods currently are used to isolate the organic fraction from decalcified bone.

Isolation of bone collagen by ultrafiltration: The main characteristic of this method is the use of ultrafilters (i.e. Vivaspin™ 15 30kD MWCO) to separate the molecules over 30,000 Daltons (= 30 kD) of mass from smaller ones. The goal is to retain all large collagen chains and discard the small-molecular size fraction where most of the organic contaminants are. The main assumption is that the remaining fraction consists only of large molecules of collagen. This method is by far the most widely used in many radiocarbon dating laboratories. Nevertheless, several examples in the literature demonstrate that sometimes the results from ultrafiltered samples are inaccurate when compared with the results coming from samples subjected to more extensive pre-treatments methods of collagen isolation (Zazula et al., 2014).

Radiocarbon dating of a single amino acid: This method consists of breaking up the collagen into amino acids to isolate a single type, which is then combusted and radiocarbon dated. Hydroxyproline has been chosen by the community as the amino acid to date from bone as it is relatively abundant in collagen and rare in other organic compounds (Ho et al., 1969). While this is the gold standard for radiocarbon dating of bone, is not always the best answer due mainly to the fact that hydroxyproline is scant or absent in old and degraded samples (Stafford et al., 1991). New advances have been made in order to be able to use this method with highly degraded and old samples (Marom et al., 2013).

XAD purifications of hydrolizates: this method consists of the hydrolysis of purified collagen to break it into single amino acids. Individual amino acids are then passed through a column of XAD-2 resin. This resin has been shown to effectively separate the polar amino acid molecules from the slightly polar humate contaminants (Stafford et al., 1988). The result is a fraction of individual amino acids that are then radiocarbon dated. Compared to the other two techniques previously described, there are at least two main advantages that the XAD purification offers: a) removing humates and fulvic acids at the molecular level, and b) allowing dating of degraded bones that would not been datable by any of the other methods. For example, a very degraded bone would have mostly broken molecules of collagen that could pass through the filter during ultrafiltration and would be discharged along with the <30 kD molecular fraction, leaving insufficient material to radiocarbon date. In a similar manner, highly degraded bone would not have enough hydroxyproline to be dated by single amino acid methods.

In the present work I present the results of radiocarbon dating of bone for several samples of extinct megafauna. I used mainly the XAD-purification method to pre-treat the bone samples, but ultrafiltration was used in a few cases. Only the XAD dates are reported here.

Methods

All samples were pieces of bone, not powder. Sample preparation was done in the Barnosky lab in the Department of Integrative Biology, University of California (UC) Berkeley, and at the Center for Accelerator Mass Spectrometry (CAMS) in Lawrence Livermore National Laboratories, California.

Nitrogen content analyses in whole bone: When samples were large enough, a small portion was used to perform nitrogen content analyses of the sample. The bone was freeze dried for 3 or more days, then pulverized and submitted for %N analyses at the Silver lab (Environmental Science and Policy Management, UC Berkeley). This step helps to assess the preservation and quality of the bone. Samples were categorized as to their likelihood of providing usable radiocarbon dates by employing the %N criteria outlined by Stafford et al., 1988 (Table 1).

Table 1: Classification of bone quality according to %N present in whole bone. Extracted from Stafford et al., 1988

	Class 1 Modern bone quality	Class II Very well to well preserved bone	Class III Moderately well preserved bone	Class IV Poorly preserved bone	Class V Extremely poorly preserved bone
Whole bone % nitrogen	4.5-3.5	3.5-0.6	0.9-0.4	0.5-0.1	0.1 to < 0.01

The results of %N analyses are shown in Fig. 4. Of the 282 samples, 31% were not tested for %N primarily because of their small size mainly (i.e., not enough sample was available to run both nitrogen and radiocarbon analyses). Eighteen percent (51) of the samples had 0% of nitrogen content and where therefore not dated (51 samples).

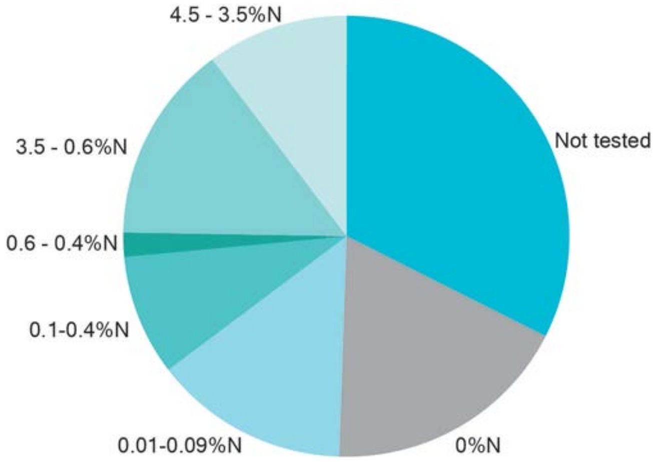

Figure 4: Results for %N in whole bone. Total of samples: 282.

Samples with %N > 0.08% were cleaned and decalcified, as were the samples that were too small to be analyzed for %N and were priorities for radiocarbon dating because of taxon, location, or other considerations.

Cleaning of samples prior to decalcification: All samples, unless very degraded, were externally cleaned using a dremel tool before decalcification. Some of the samples came from old museum collections where they were treated with hardeners, glues, or other preservatives. When a sample was reported or suspected as having been treated by preservatives, acetone and methanol washes were applied as necessary to totally remove external glues. After the solvent washes, samples were dried inside test tubes and under a fume hood for 2 days before starting the decalcification process.

Decalcification: This two-step process removes the apatite and inorganic carbonate fraction from the bone. Step 1 was to leave samples in a solution of HCL 2M for 30 seconds to 1 minute. This step cleans the sample by removing dirt, rootlets or any other external matter on the surface. For samples that potentially still contained preservatives (glues, hardeners, etc.) after the solvent washes, a HCL 6M (instead of HCL 2M) was applied. Then the samples were washed with deionized water (DI H_2O) 3 to 5 times. Step 2 entailed low decalcification with HCL 0.5M. Samples were left in a solution of 0.5M HCL for one to two weeks in refrigeration at 4° C. Acid was changed at least twice a day. Between every change of acid, the samples were washed with DI H_2O. The time required for decalcification depended on the size of the sample, the frequency of changing the acid, and the quality of the bone. The process can take just a few days, as is the case for small rodent samples, to more than 1 week in the case of very well preserved gomphothere molar fragments. After a sample was decalcified, it was washed with DI H_2O and left in a solution of 0.05M HCL until the next step, extraction of humic acids.

Basic extraction of humic acids: Decalcified samples were washed with DI H_2O and left in a solution of potassium hydroxide (KOH) 0.1M for 48 hrs; the KOH extraction removes humic acids but possibly not all of them, and the following steps described below will remove the remaining contaminants. Highly degraded decalcified samples were left in the solution for less than 2 hours or not subjected to this step at all. After 48 hours, samples were removed from the KOH solution and washed 3 to 5 times with DI H_2O before the next (gelatin) step.

Gelatin: Samples were placed in a solution of 0.05M of HCL and left on a hot plate at 90°C for approximately 1 hour or as long as necessary to obtain a solution of collagen gelatin. This step removes contaminants, such as chitin, that are insoluble in weak acid and precipitate out during this step. Using a disposable syringe, the gelatin solution was passed through a 0.4 micron syringe filter which removed the precipitated contaminants.

Hydrolization of collagen: Samples were left for 22 hrs at 110° C in a hot plate and in a solution of HCL 6M. This step breaks collagen down into amino acids and breaks covalent bonds between fulvic acids and the collagen chains.

XAD purification: The solution of hydrolizates was passed through a column of XAD-2 resin that was previously washed with acetone and bathed in a solution of HCL 0.5M for until used. XAD resins are non-polar to weakly-polar porous absorbents that help to isolate weakly or non-ionizrd aliphatic and aromatic molecules from aqueous solutions (Stafford et al., 1988). The XAD resin column was stabilized by pouring HCL 6M for 6 bed volumes. After this, the solution containing the sample was poured into the column. If resin was not white at bottom, a second purification with a new resin column was made.

Final steps: Hydrolizates were dried with a high speed centrifuge at 65° C. A good dried XAD fraction is golden and viscous like honey. Five to 8 mg of dried XAD hydrolizates were placed in combustion tubes to be graphitized.

Standards and background: Standards and background routinely used at CAMS were processed along with the samples. The standards are Tiri whale bone, which is late Pleistocene in age, and ACT III, which is whale bone of early to middle Holocene age. The background is EL 10-145, ‘bison paw', which is old bone beyond the limit of ^{14}C dating.

After this step, the samples were submitted to combustion and graphitization, which was done by the staff at the CAMS lab.

Results

The procedures described above resulted in the production of 54 radioacarbon dates distributed among different mammalian families as shown in Fig. 5, which amounted to dates on 20% of all the samples that were available to date. From North America, Central America and the Caribbean region, only the samples from Mexico and Costa Rica (Fig. 1) were radiocarbon dated; none of the analyzed samples from Dominican Republic and Belize had enough organic matter. For South America, radiocarbon dates were obtained for samples from all the regions depicted in Figure 2 except for Paraguay and coastal Ecuador.

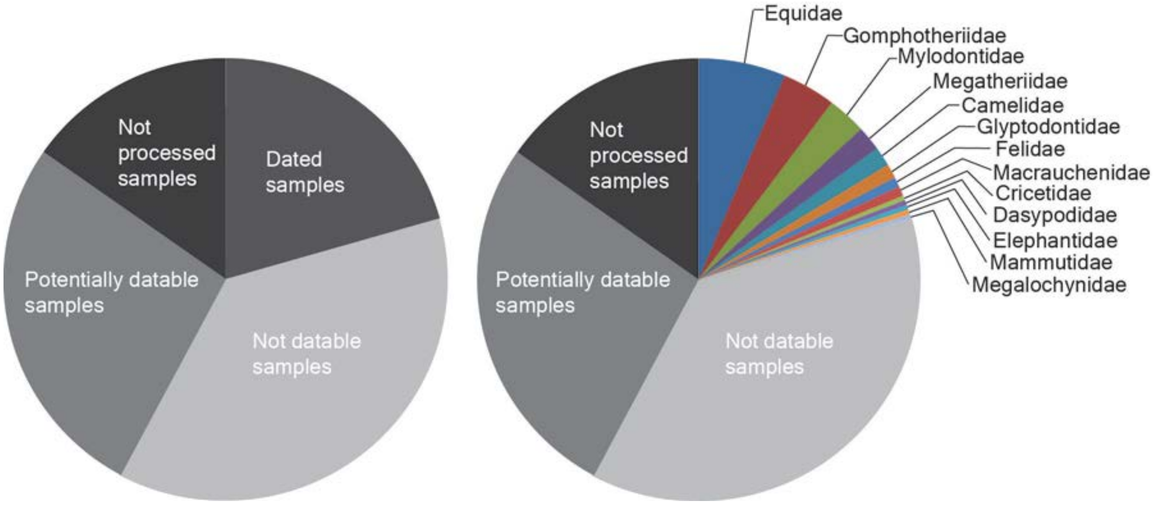

Figure 5: Right: Results of sample processing; the "not processed" samples are those which were deemed lower priority in the context of available funds. Left: proportion of dated samples per mammalian family.

Figure 5 shows the proportion of samples at different stages of processing (left) and the proportion of dated samples per mammalian family (right). "Not datable" samples include those that were determined to have 0% nitrogen content as well as samples that were decalcified and processed but did not have enough collagen or carbon to be radiocarbon dated; this group of samples accounts for about a 37% of the original 282 samples. "Potentially datable" samples include those that contain at least some nitrogen according to the whole-bone nitrogen content analyses, and/or were decalcified and appear to have sufficient collagen but were not radiocarbon dated due to insufficient funds in hand; this group corresponds to about a 26% of the total samples. Finally, "Not processed" samples are those on which no analyses have been performed so far, about 15% of the original 282 samples; these were deemed least critical to date given available funding, but are expected to be valuable in future analyses. More details about the taxonomic distribution of samples are listed in the Appendix for chapter 3 (Figures A3.1 and A3.2).

Of 54 dated samples, here I describe details for the 27 (Table 2) for which I contributed substantially to performing the pretreatment and dating. The remaining 27 radiocarbon dates will be described in detail in other publications coming out of collaborative efforts with participants of the NSF grant that funded this research

Table 2: New radiocarbon dates published in this work. Co.: Country; Submitt.: Submitter of the samples. **Repository**: [a]NRS: Naturhistoriska Riksmuseet, Stockholm; [b]MRA: Museo Regional de Azapa, Chile; [c]ZMK: Zoologisk Museum Copenhagen; [d]MNHN-CH: Museo Nacional de Historia Natural-Chile; [e]UACh: Universidad Austral de Chile; [f]NR: Not reported. **Co.** : Country. **Sample Submitters (Sub.)**: N.V: Natalia Villavicencio, E.G: Erwin Gonzales, M.P: Prof. Mario Pino; R.L: Dr. Rafael Labarca; P.L: Dr. Patricio Lopez; F.M: Dr. Francisco Mena. All radiocarbon dates were calibrated using Calib 7.01 (Stuvier and Reimer 1986).

CAMS#	**Specimen no.**	**Taxon**	**Element**	**Site**	**Co.**	**^{14}C age**	**Calib median**	**Calib old**	**Calib young**	**µg C**	**Sub.**
175033	M4290 [a]	Megatheriidae indet.	astragalus	Casa del Diablo	Peru	19180±260	23061	23660	22465	810	N.V.
175034	M4286 [a]	*Diabolotherium nordenskioldi*	humerus	Casa del Diablo	Peru	16300±180	19624	20075	19145	920	N.V.
175035	M1917c [a]	*Hippidion*	mandible	Casa del Diablo	Peru	11740±100	13528	13744	13326	1090	N.V.
175036	M4098 [a]	*Hippidion*	mandible	Casa del Diablo	Peru	12480±110	14576	15067	14135	950	N.V.
175037	M1910 [a]	*Hippidion*	mandible	Casa del Diablo	Peru	10980±90	12825	13017	12699	1090	N.V.
175038	M4093 [a]	*Hippidion*	mandible	Casa del Diablo	Peru	11980±100	13776	14058	13549	830	N.V.
175039	M4103 [a]	*Hippidion*	III metacarpal	Casa del Diablo	Peru	11980±100	13776	14058	13549	840	N.V.
175734	M4099 [a]	*Hippidion*	Mandible	Casa del Diablo	Peru	12400±80	14412	14862	14072	830	N.V.
175745	M4445 [a]	*Scelidotherium*	mandible	Casa del Diablo	Peru	13690±100	16462	16839	16462	1230	N.V.
175751	M1937a [a]	*Lama guanicoe*	carpal	Casa del Diablo	Peru	13260±90	15884	16184	15582	970	N.V.
175750	M4200 [a]	*Vicugna*	carpal	Casa del Diablo	Peru	12780±90	15168	15513	14768	960	N.V.
175752	M5202 [a]	*Punomys*	mandible	Casa del Diablo	Peru	16870±150	20299	20677	19918	840	N.V.
175739	43219 [b]	*Hippidion*	ulna	Salar de Surire	Chile	11360±70	13173	13303	13057	810	C.S.
175736	M1848q [a]	*Equus insulatus*	phalanx	Tarija	Bolivia	11950±80	13726	13991	13550	1220	N.V.
175737	M1848H [a]	*Equus insulatus*	phalanx	Tarija	Bolivia	125±35	---	---	---	1170	N.V.
175735	ZMK 1/1845 [c]	*Equus neogeus*	Tibia	Lapa da Escrivania 5	Brazil	16900±150	20332	20712	19951	420	N.V.

175732	SGO.PV.267A [d]	Gomphotheriidae indet.	molar root	Quereo, Los Vilos	Chile	10970±70	12799	12980	12703	940	E.G.
175817	SGO.PV.267 [d]	Gomphotheriidae indet.	rib	Quereo, Los Vilos	Chile	10940±80	12748	12981	12688	940	R. L.
175743	SGO.PV.47K [d]	Gomphotheriidae indet.	molar root	Tagua Tagua	Chile	12260±80	14123	14524	13802	1030	E.G.
175740	[d]SGO.PV.2 [d]	*Glossotherium lettsomi*	vertebra	Lonquimay	Chile	10960±70	12791	12975	12700	790	N.V.
175048	[e]GEOUACH 126	Gomphotheriidae indet.	rib	Monte Verde	Chile	13420±120	16092	16460	15734	1210	M.P.
175049	GEOUACH 96 [e]	*Hemiauchenia*	tibia	Pilauco	Chile	11320±90	13143	13325	12940	920	M.P.
175749	GEOUACH 108 [e]	Gomphotheriidae indet.	molar	Los Lagos	Chile	11790±80	13575	13751	13434	980	M.P.
175744	SGO.PV.43 [d]	Gomphotheriidae indet.	molar	San Pablo, Tramalhue	Chile	11380±70	13188	13317	13064	980	E.G.
175733	SGO.PV.44 [d]	Gomphotheriidae indet.	molar	Rio Bueno	Chile	11090±70	12910	13062	12979	980	E.G.
175746	#11 [f]	Mylodontidae indet.	dermal ossicle	Baño nuevo	Chile	11290±60	13114	13258	13001	1230	P.L.; F.M.
175047	#12 [f]	Mylodontidae indet.	dermal ossicle	Baño nuevo	Chile	12040±100	13857	14093	13581	1110	P.L.; F.M.

The new radiocarbon dates presented in Table 2 are discussed below by region.

Central Andes (Fig 6)

Casa del Diablo, Peru: Twelve radiocarbon dates come from Casa del Diablo in the Puno District of Peru. This site is a cave located in the high Andes near the locality of Tirapata, at about 3800 masl. It was explored by the Swedish ethnographer Erland Nordenskiöld in 1904-1905, shortly after he excavated the cave and collected an important set of faunal remains including Late Pleistocene extinct mammals and extant mammals. Today, all of these collections are housed at the Swedish Museum of Natural History, in Stockholm. Nordenskiöld published in 1908 what it is until today the only detailed information about the site. According to this publication, the bone deposits in Casa del Diablo derive from the action of carnivores, as evidenced by many of the bones showing marks attributable to carnivore action and an over-representation of limb bones. Humans were not likely to have contributed to the bone accumulation given the lack of cut marks on the bones and paucity of archaeological evidence (Nordenskiöld, 1908). The cultural evidence at the site is scant, consisting of a single artifact from the cave but no other evidence of humans. Nordenskiöld (1908) also highlighted the excellent preservation of the bones.

Among the 12 radiocarbon dated samples, 9 are for extinct megafauna, 2 for extant megafauna and 1 for a small extant rodent species. Dating animals besides the extinct megafauna was undertaken to gain a better understanding of the overall nature of the deposit.

Salar de Surire, Chile: This is a salt flat located in northernmost Chile, in the Arica y Parinacota region. I radiocarbon dated one sample coming from this area which corresponds to an ulna fragment from a complete skeleton of *Hippidion* found in the salt flat itself (Prof. C. Santoro pers. comm.).

Prior to this work just a handful of good quality radiocarbon dates on extinct megafauna were known for fossil materials coming from the Central Andes area. Schockey et al., 2009 reported a radiocarbon date of the megalochynidae ground sloth *Diabolotherium nordenskioldi* from the site of Trigo Jirka and one radiocarbon date for *Hippidion devillei* from the site Cueva Roselló (*Onohippidion devillei* in Shockey et al., 2009). Both sites correspond to high Andean caves located at about 900 and 600 km north of Casa del Diablo respectively (Fig. 6). In the same publication a radiocarbon date for a specimen of the extant *Vicugna vicugna* from Cueva Roselló site was reported. All previously published radiocarbon dates are specified in Table A3.1 (Appendix, Chapter 3).

Fig. 6: Central Andes of Peru and Chile. For details about the archaeological sites see Table A3.2 in the Appendix.

Two other radiocarbon dates, both for *Hippidion saldiasi*, are reported from the site of Betecsa, in the Calama Basin in Chile, south of Casa del Diablo and Salar de Surire. (Fig. 6 and Alberdi et al., 2007).

The previously published dates from Betecsa, Cueva Rosselló and Trigo Jirka, along with the new radiocarbon dates reported here, are older than the radiocarbon dates for Casa del Diablo and Salar de Surire by at least 2000 years and as much as 10,000 years (Fig. 7).

The radiocarbon dating record from Casa del Diablo spans from 23.1 to 12.7 cal ka BP, the oldest date being for Megatheriidae indet., followed by *Punomys* (Rodentia, extant; 20.3 cal ka BP (CAMS 175752) and then *Diabolotherium nordenskioldi* (Megalochynidae), which falls around 19.7 cal ka BP (CAMS 175034). This last radiocarbon date is more than 13,000 years younger than the occurrence for *D. nordesnkioldi* at Trigo Jirka. *Scelidotherium* (Mylodontidae) and the extant camels *Lama guanicoe* and *Vicugna vicugna* are represented in the Casa del Diablo record by one date each as well, that is, 16.3, 15.9 and 15.1 cal ka BP respectively (CAMS 175745, CAMS 175751 and CAMS 175750). Finally, *Hippidion* (Equidae) is represented by 6 radiocarbon dates, all of them ranging between 14.5 and 12.8 cal ka BP (CAMS 175035, CAMS 175036, CAMS 175037, CAMS 175038, CAMS 175039, CAMS 175734). It is very possible that two of the dates (Specimen numbers M4093 and M4103) come from the same individual. The date on *Hippidion* from Salar de Surire is around 13.2 cal ka BP (CAMS 175739) and falls in the same temporal range as the dates from Casa del Diablo.

I compared the chronology of the presence of megafauna from Casa del Diablo and that reported from other localities in the Central Andes with the radiocarbon record for human presence in the area, which consists of data from archaeological sites located within 500 km of Casa del Diablo, and over 3,000 masl (Figure 7, Table A3.2). Also included in Figure 7 are the estimated changes in vegetation as they are recorded in Lake Titicaca (Fig. 6 and Paduano et al., 2003), the *Sporormiella* record from Lake Pacucha (Rozas-Davila et al., 2016 and Fig. 6) and the record of major pluvial events recorded in the Central Andes (Placzek et al., 2009 and Fig. 6). For the record of *Hippidion* from Casa del Diablo and for human presence in the area, data were sufficient to enable me to estimate confidence intervals for the timing of extinction (and of human arrival) using the GRWIM method (Bradshaw et al., 2012) used in Villavicencio et al., 2016 (Chapter 2).

Comparing the chronology of megafauna presence from Casa del Diablo to the changes in vegetation it reveals that large megafuana, such as a members of the Megatheriidae, were present in the area even when it was just sparsely vegetated as it is shown by the pollen record from Titicaca. The rest of radiocarbon dates document the presence of megafauna during a time of vegetation changes from *Puna brava* vegetation to *Puna* vegetation. The *Puna* vegetation is characterized by grasses (Poaceae) and herbs and shrubs of the families Asteraceae, Brassicaceae, Gentianaceae and Valerianaceae, among others; this vegetation belt is today found at 4500 to 3700 masl (Paduano et al., 2003). On the other hand, *Puna brava* vegetation has basically the same taxonomic composition as the *Puna* but with much less vegetation cover and is common at altitudes higher than 4500 masl (Paduano et al., 2003). Given that megafauna was present in the area ~23 cal ka BP until 12.8 cal ka BP, it seems that both vegetation types offered conditions to support some megafauna species in the area during the transition from the Last Glacial Maximum to the Holocene. Today this vegetation-type still supports vicuñas and llamas in the Andes Mountains. The last appearances of megafauna in the area were just before and during (taking into account the GRIWM estimates for *Hippidion*) a relatively short dry event that was characterized by a drop in the water level of Lake Titicaca and the presence of more open vegetation (Paduano et al., 2003).

More interesting is the fact that *Hippidion* disappears from the record shortly after the arrival of humans to the high Andean region. Taking into account the best estimates for the timing of extinction of *Hippidion* and for the arrival of humans, these two mammal species coexisted in the area for 900 years, whereas if only the last radiocarbon date on megafauna and first radiocarbon date on evidence of humans are considered, the time of coexistence is a bit less, about 600 years. Humans arrived in the area during the Coipasa pluvial event (Placzek et al., 2009). This period of wetter conditions has been associated with higher water tables and higher plant productivity in various places along the Central Andes, which may have facilitated human migration in the area (Placzek et al., 2009). Making a firm connection between the pluvial events and megafauna abundance, diversity and extinction is not possible with the data available so far.

Besides the few radiocarbon dates on extinct megafauna from the central Andes of Peru, records of the dung-fungus spore *Sporormiella* have been reported and purportedly document the presence of megaherbivores around Lake Pacucha in central Peru (Rozas-Davila 2016). *Sporormiella* spores are associated with the presence of large herbivores and the relative abundance of these spores in lake records has been used as a proxy to estimate the presence and decline of ecologically functional megafaunal populations around lakes (Davis and Shafer 2006, Raper and Bush 2009, Gil et al., 2013). In the case of the Lake Pacucha, the *Sporormiella* record suggests a two-step decline in megaherbivores, with the initial drop in *Sporormiella* at 21 cal ka BP and later drop between 16.8-15.8 cal ka BP, with megaherbivores functionally extinct in the area after 15.8 cal ka BP (Rozas-Davila et al., 2016). The new data presented here that records the presence of megafauna after 15.8 cal ka BP does not necessarily contradict the conclusions of Rozas-Davila et al., 2016, since it may simply document the presence of a small group of megafauna in the area which does not necessarily represent an ecologically functional megafaunal population. Moreover, this new record documents only the presence of *Hippidion* along with extant herbivores in the area, and no other extinct megaherbivores are reported here after 15.8 ka BP. Nevertheless, it appears that extinct megafauna persisted in the area for ~ 3000 years after the decline of functional population of megafauna documented by Rozas-Davila. A similar pattern of substantially younger megafauna occupation based on megafauna bone dates relative to purported disappearance based on *Sporormiella* counts has also been observed in the northeastern United States (Barnosky et al. 2015).

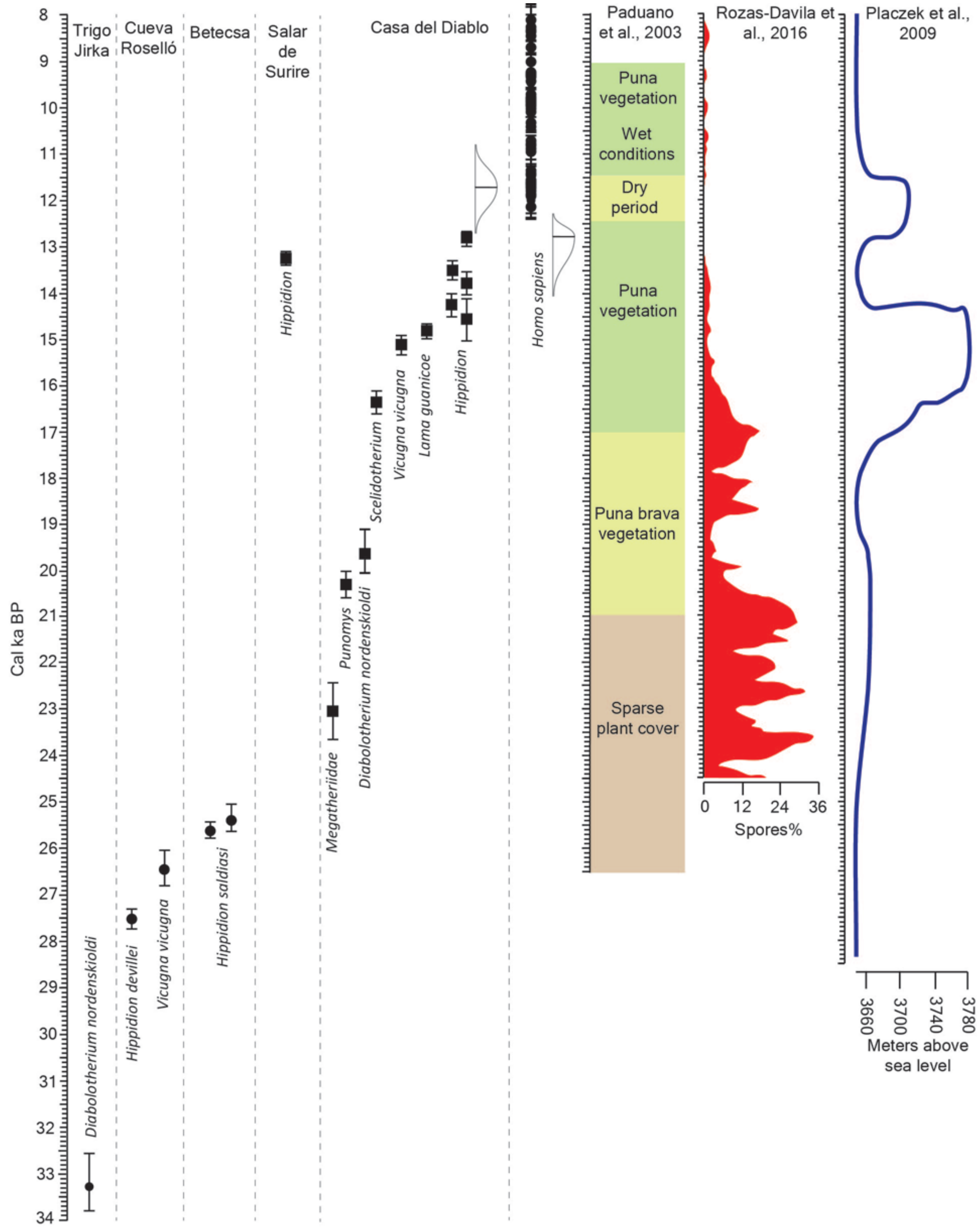

Figure 7: Chronology of presence and extinction of megafauna and of human arrival in the Central Andes of Peru and Chile. Black dots: calibrated radiocarbon dates from the literature (see Tables A3.1 and A3.2). Black squares: calibrated new radiocarbon dates published in this dissertation. Record of changes in vegetation from Lake Titicaca (Paduano et al., 2003). Record of *Sporormiella* from Lake Pacucha (Rozas-Davila et al., 2016). Major Pluvial events in the Central Andes (Placzek et al., 2009).

Tarija-Bolivia (Figure 8)

The fossiliferous area of Tarija in southern Bolivia is offers one of the most abundant records of Late Quaternary faunas on the continent. This geographic area has yielded thousands of Late Quaternary fossil specimens that are now part of collections of many museums around the world. Today, one of the main controversies about the deposits is their age. On one hand there are those that believe in a middle Pleistocene age for the deposits based on magnetostratigraphic analyses (MacFadden et al. 1983), while on the other hand are proponents of a late Pleistocene age for the deposits based on radiocarbon dating of the alluvial stratigraphic sequences of the fossil-bearing subunit (Coltorti et al., 2007). No radiocarbon dates on specimens coming from this area have been published before.

Here I present 2 radiocarbon dates for specimens coming from Tarija (Specimen numbers M1848q and M1848h). The specimens were part of the collections of the Swedish Museum of Natural History and were collected by an expedition led by E. Nordenskiöld in 1901-1902. The elements dated correspond to two phalanges attributable to *Equus insulatus*, but further analyses to corroborate this species assignment are needed (Wederlin 1991, Figure 5) (although the specimens clearly are from an *Equus* species).

Surprising is the fact that one of the dates (specimen number M1848h) gave modern values, while the other is clearly late Pleistocene with a calibrated age of 14,726 cal yr BP (CAMS 175736). Two hypotheses may explain the modern age for one of the specimens: 1) Contamination with modern carbon; and 2) intrusion of modern horse bones into the fossil deposits. Modern horses arrived in South America with European colonization after 1492.

Figure 8: Elements of *Equus insulatus* from Tarija radiocarbon dated in this work. Right: 14,683 cal yr BP, left: modern in age.

Given the fact that high-standard pre-treatment procedures were used in dating these samples, it seems unlikely that contaminants remained after the XAD filtering. Contamination during the treatment of the sample in the lab cannot be definitively discounted, but nothing unusual was noticed during the sample treatment that would indicate anything other than bone amino acids were radiocarbon dated, and both elements exhibited similarly good overall quality (Figure 8). Moreover both samples showed over 500 mg of C (Table 2) content after graphitization, which indicates a high quality of the sample. With respect to the second hypothesis, that specimen M1848h is a modern intrusive into the deposit, it has been suggested that more than one species could be present in the elements assigned to *Equus insulatus* (=*E. curvidens*) (Hoffstetter 1952). However, overall this collection has been described as quite homogenous (Wederlin 1991). Specimens attributable to *E. insulatus* are abundant in Nordenskiöld's collections from Tarija (Wederlin 1991) and have been considered in taxonomic revisions (Sefve 1912), but no reported information would shed light on the possibility of modern horses being included among the elements of this collection. Further research analyzing the morphology of the elements could perhaps help in reaching an answer.

Despite the complication of the modern date, the date on specimen M1848q supports the proposal of a late Pleistocene age for the deposits (Coltorti et al., 2007).

Figure 9: Map of South America showing the location of the site of Tarija, Quereo-Los Vilos, El Membrillo, Lapa da Escrivana 5, Tagua Tagua, Lonquimay and Baño Nuevo.

Lapa da Escrivâna 5-Lagoa Santa, Brazil (Fig. 10).

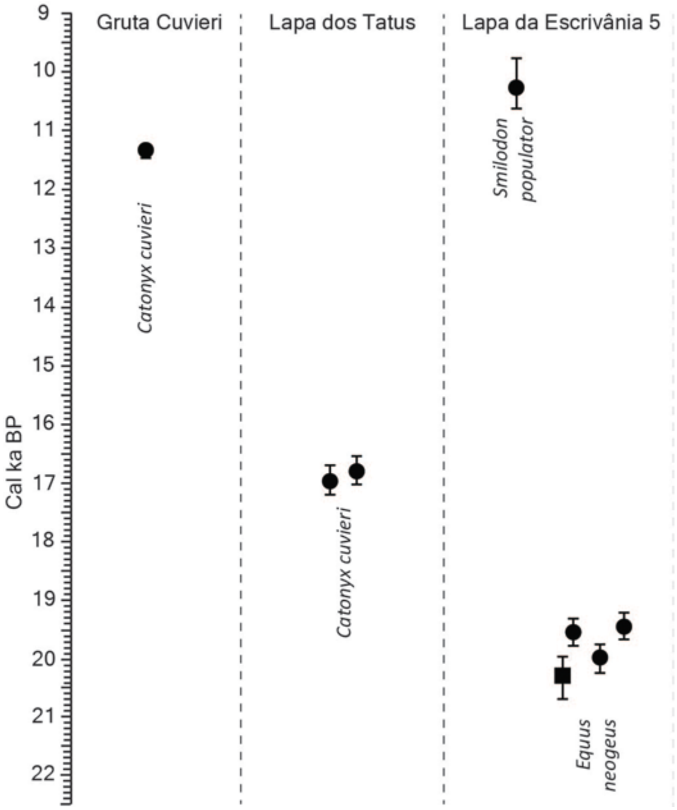

Figure 10: Radiocarbon chronology of megafauna presence in Lagoa Santa, Brazil. Black dots: Calibrated radiocarbon dates previously published (See table A3.1), black squares: calibrated new radiocarbon date published in this work.

I obtained one radiocarbon date for a specimen of *Equus neogeus* from the Lund collection in the Natural History Museum of Denmark. The Lund collection contains thousands of specimens from Minas Gerais state, Brazil collected by P.W. Lund, one of the first paleontologists in South America and the so-called "father of Brazilian paleontology." Among the most famous specimens of this collection is the holotype of the saber-tooth cat *Smilodon populator* and other megafauna found in potential association with human remains in a cave. This work by Lund is acknowledged to be among the earliest reporting stratigraphic association of humans with extinct mammals (Cartelle 2002).

At least seven radiocarbon dates on extinct megafauna from the area of Lagoa Santa have been published previously (Neves & Pilo 2003). From these, all of those on *Equus neogeous* come from the same locality (Lapa da Escrivâna 5) as the sample that is reported here. The new radiocarbon date presented here is falls around the same time of previously reported radiocarbon dates being somewhat older with an age of 20,332 cal yr BP (CAMS 175735) (Fig. 10).

Quereo-Los Vilos, Northern Chile (Figure 9)

Quereo is a site located in northern Central Chile, close to the town of Los Vilos. The site is a late Pleistocene-early Holocene archaeological site with evidence of interaction of humans with extinct megafauana (Nuñez et al., 1994a). The late Pleistocene-Holocene human settlement is constrained by 12 radiocarbon dates on wood and charcoal, but up to now had only one date on extinct megafauna (Paskoff, 1971). This date, on a specimen of *Notiomastodon platensis* is around 10.1 cal ka BP (9,100 ± 300 ^{14}C, extracted from Labarca et al., 2015); however, the quality of the date cannot be assessed with the information available in the publications where it is mentioned.

The new radiocarbon dates reported here come from a rib fragment and a molar root, possibly both from the same individual, a gomphothere of indeterminate species. Dates on the two specimens are statistically indistinguishable: 12,799 cal yr BP for the molar and 12,748 cal yr BP for the rib (CAMS 175732 and CAMS 175817).

Besides these two new dates and the one published by Paskoff (1971), one other radiocarbon date on extinct megafauna is known for the area, from the archaeological site of El Membrillo. It documents the presence of a Xenarthran of indeterminate species at 16.1 cal ka BP (Jackson et al., 2003).

The new dates published here fall into the temporal range of the radiocarbon dates documenting human presence in the site of Quereo, the record of which starts at 13.3 cal ka BP and ends during the late Holocene (Nuñez et al., 1994a). The new dates are consistent with the hypothesis that the accumulation of extinct megafauna (at least of gomphotheres) in the site was mostly due to human activities (Nuñez et al., 1994a).

Tagua Tagua- Central Chile (Figure 9)

Tagua Tagua is known for being one of the first hunter-gatherer kill sites containing megafauna reported for South America (Montané 1968). The site is rich in megafaunal remains of gomphotheres associated with evidence of Paleoindian hunter-gatherers. The Paleoindian site is radiocarbon dated between 11.7 and 11.9 cal ka BP, but only one date on extinct megafauna has been previously published, documenting a gomphothere's presence ~11.7 cal ka BP (10,190 ± 130 ^{14}C, Nuñez et al., 1994b).

Here I present a new radiocarbon date—14.1 cal ka BP (CAMS 175743)—for the site, which was obtained from a molar root of a gomphothere; the material was not adequate to permit species identification. This new date is some 3000 years older than the previously-known radiocarbon date on a gomphothere from the site and is also older than the Paleoindian occupation documented in Tagua Tagua (Nuñez et al., 1994b), raising questions about the relationship between this particular specimen with the Paleo-indian occupation of the site.

Lonquimay, Chile (Figures 8 and 9)

The Araucania Region is located in the Araucania district of Southern Chile. Extinct megafauna findings are scant in the area but include extinct Camelidae and Gomphotheriidae, neither of which can be identified to species, from Los Sauces locality, indeterminate Gomphotheriidae and Equidae from near the town of Carahue, and the only specimen of *Glossotherium* known from the Chile. The *Glossotherium* specimen, a complete skeleton of *G. letssomi* (Casamiquela 1968), was found at the locality of Lonquimay, in the Andean region of southern Chile. I report here a radiocarbon date from a piece of a vertebrae of taken from this specimen, which yielded a date of 12,791 cal yr BP (CAMS 175740) (Fig. 11).

Los Lagos and Los Rios districts, Chile (Figure 11)

The Los Lagos region in southern Chile is world famous because of the archaeological site of Monte Verde, which is known as one of the oldest sites with evidence of humans in South America (Dillehay 2000). At this site, coexistence and interaction of humans with extinct megafauna such as *Palaeolama* and gomphotheres has been documented (Dillehay 1989, 1997). Another well studied site, this one in the Los Rios district, is Pilauco in the city of Osorno (Pino et al., 2008, Pino et al., 2013). Pilauco was discovered when a residential complex constructed in 1986. Years later, systematic research activities at the site started and still continue (Pino et al., 2013). Along with several dates on charcoal, sediments and plant material documenting the presence of humans in Monte Verde and the age of the deposits in Pilauco, several dates on extinct megafauna have also been published for these sites (Table A3.1). The previous work yielded 10 highly ranked radiocarbon dates that document the presence of Gomphotheridae (Gomphteriidae indet. and *Notiomastodon platensis*), *Equus*, and Mylodontidae indet. Other two dates on gomphotheres are known from the localities of Nochaco and Mulpulmo in Los Lagos region (Labarca 2015, Veischet 1958, 1964 in Casamiquela 1969) but given the time at which these analyses were performed (1958 and 1964) and the lack of information about the dating process to evaluate the radiocarbon dates, their quality is uncertain.

Here I present 5 new dates on extinct megafauna for the region. Besides adding two new dates on gomphotheres for Monte Verde and one new date for Pilauco (on the camelid *Hemiauchenia*), I also dated gomphotheres from 3 additional localities (Figs. 11, 12).

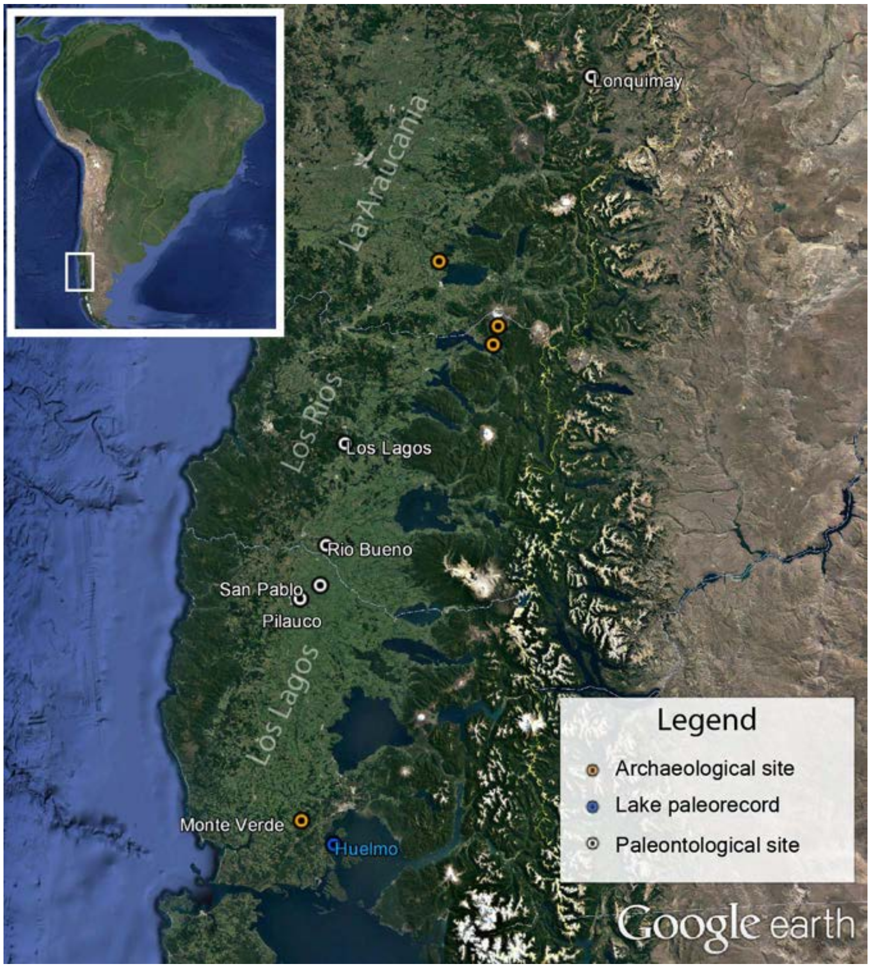

Figure 11: Location of the sites discussed for the Los Lagos and Los Rios regions. For details about the archaeological sites see table A3.2.

The chronology of megafauna presence and extinction in the Los Lagos / Los Rios region is shown in Figure 12, along with radiocarbon dates documenting the presence of humans in the area, alongside vegetation changes and fire frequency as recorded in lake sediments of the Huelmo site (Moreno and Leon 2013). I calculated confidence intervals showing the probable timing of extinction of gomphotheres and human arrival using the GRWM method (Bradshaw et al., 2012) as used in Villavicencio et al., 2016 (Chapter 2). Also included in Figure 12 is the radiocarbon date for *Glossotherium lettsomi* from Lonquimay, which is only 300 km north of the sites clustered in Los Lagos and Los Rios regions.

The radiocarbon record of extinct megafauna shown in Figure 12 spans from 16.5 to 13.1 cal ka BP. Humans arrived into the area at 16.3 cal ka BP and could have been present as early as 17.7 cal ka BP according to the confidence bands ascribed to estimates of human arrival by applying the GRWIM method. Gomphotheres, the taxon with the most robust radiocarbon record in the area, seems to have coexisted with humans for at least 2,900 years and perhaps as long as 5,400 years if the GRWIM confidence intervals are taken into account for extinction of gomphotheres and the arrival of humans calculated. This long time of coexistence rules out the possibility of a blitzkrieg overkill of gomphotheres by humans. *Equus* and *Hemiauchenia* from Pilauco, and also *G. lettseomi* from Lonquimay, are represented by only one radiocarbon date each, all of which fall between 13.1-13.3 cal ka BP. This documents the presence of these three extinct taxa after more than 3,000 yr of human presence in the area.

The record of changes in vegetation from the Huelmo site documents a forested landscape through the entire record, with arboreal pollen representing around an 80% of the total pollen counts (Moreno and Leon 2003, data not presented in figure 12). Some of the main changes in vegetation recorded at this site are shown in Figure 12. An initial drop in *Nothofagus dombeyi* –type was followed by an increase in abundance of thermophilous species of the Myrtaceae family. These changes are attributable to warming as deglaciation proceeded and apparently correspond to the time when humans arrived into the area. A drop in Poaceae is also observed during this time. Between 13.4-12.2 cal ka BP a cold reversal is inferred from an increase in *Nothofagus dobeyi*-type along with an increase in *Podocarpus nubigena* and a drop in Myrtaceae. This cooling event has also been recorded in the eastern side of the Andes and it is known as the Hulemo/Mascardi Cold Reversal (Hadjas et al., 2002). Following the Huelmo/Mascardi Cold Reversal a second warming trend towards Holocene conditions is represented in Figure 12 by the increase in the thermophilous taxa *Eucryphia*/*Caldicluvia*. Two pulses of increase in fire frequency are recorded between 12.9-12.3 and 11.7-10.7 cal ka BP, along with an increase in *Weinmania trichosperma* pollen, which is an opportunistic taxon and a proxy for detecting perturbed environments. During the Huelmo/Mascardi Cold Reversal, grasses show a slight increase and remained at a relatively constant level during the rest of the record.

Comparing the record of extinction for gomphotheres with the changes observed in vegetation and climate, it appears that gomphotheres drop out of the record around the time of the Huelmo/Mascardi Cold Reversal and during a period of increased fire frequency together with evidence of disturbed plant communities. At the same time, the time period between 12.2-11.1 cal ka BP marks the transition between a landscape dominated by a closed-canopy and cold North Patagonian forest to a more open Valdivian temperate forest (Moreno and Leon 2003). According to stable isotope studies, gomphotheres from south-central Chile were exclusively feeding on C3-plants, eating parts of trees, bushes, shrubs and forbs (Sanchez et al., 2004). This isotopic study used individuals from San Pablo and Rio Bueno, two of the sites from which samples were radiocarbon dated in this work. Whether these gomphotheres preferred C3 plants of the North Patagonian forest vs. plants from Valdivian forest is unknown, which makes it difficult to infer how the changes from one type of forest to the other affected them. Nevertheless, it is conceivable that the observed changes in vegetation, plus the increase in fire frequency and the greater disturbance in the plant communities, along with consumption by humans, contributed to the extinction of these megaherbivores in the region.

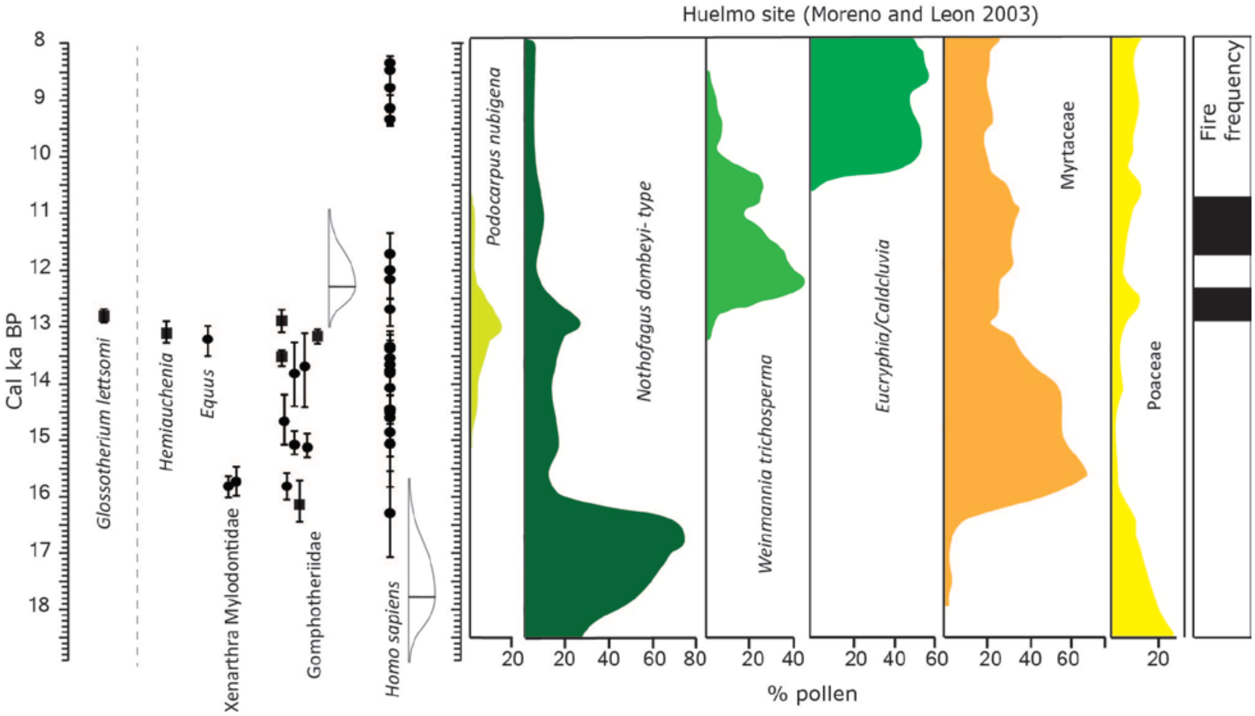

Figure 12: Radiocarbon chronology of megafauna presence and extinction and chronology of human arrival for the area of Los Lagos and Los Rios regions. Black dots: calibrated radiocarbon dates previously published (Table A3.1 for more information). Black squares: calibrated new radiocarbon dates presented in this work. The pollen record and the estimated pulses of increased fire frequency are from the Huelmo site (Moreno and Leon 2003).

Baño Nuevo, Chile (Figure 9)

The site of Baño Nuevo is located in Chilean Patagonia (Fig. 9). The site is mainly known for human remains belonging to early Holocene individuals (Mena et al., 2002). The cave contains several layers with cultural evidence above deposits that contain Late Pleistocene megafauna (Velasquez and Mena 2006). So far, there is no evidence of direct association of extinct megafauna with humans in the site.

Prior to this work, six radiocarbon dates on extinct megafauna were known (Velasquez and Mena 2006), five on them on dermal ossicles belonging to an extinct mylodontid xenarthran and one documenting the presence of *Macrauchenia*. I was able to radiocarbon-date two new samples from this site, both on dermal ossicles from a mylodontid. Both dates fall in the temporal range previously known for the presence of megafauna at Baño Nuevo (Fig. 13).

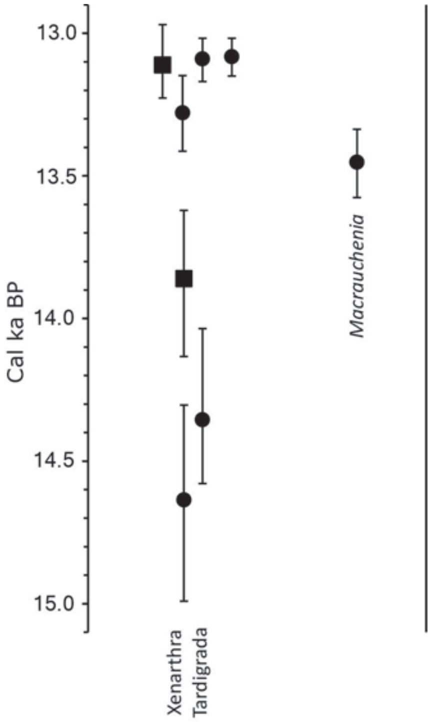

Figure 13: Radiocarbon chronology of extinct megafauna presence in Baño Nuevo. Black dots: calibrated radiocarbon dates previously published (Table A3.1 for more information). Black squares: calibrated new radiocarbon dates presented in this work

Conclusions

This large radiocarbon dating initiative highlights the magnitude of effort required to obtain 54 new radiocarbon dates on megafaunal bone samples. Thirty-seven percent of them were not datable, reflecting that many bone samples do not have enough organic matter to be radiocarbon dated, even though they may appear to be datable upon cursory inspection. Subjecting samples to initial %N analyses is helpful in identifying such specimens before considerably more funds are expended on further processing. Other researchers that have been involved in efforts to improve the chronology of extinction of megafauna for different regions in the world have also noted that dozens of samples are needed in order to get a handful of dates (J.L. Prado pers. comm., A. Lister pers. comm.). Nevertheless, directly radiocarbon dating bone remains the most accurate and robust approach to developing extinction chronologies for the Late Quaternary extinction event.

The 27 new radiocarbon dates presented here improve the chronology of extinction for several areas of Latin America, especially for the Central Andes of Peru and Chile, where only 4 radiocarbon dates on extinct megafauna were previously known. Comparing the two regional analyses developed in this chapter (Central Andes and Los Lagos-Los Rios regions) two different histories of extinction are evident. First, for the Central Andes, the coexistence of humans and extinct megafuana was apparently not long; *Hippidion*, which is the extinct taxon with the latest radiocarbon record, seems to disappear from the area very close in time to the arrival of humans. On the other hand, in the Los Lagos and Los Rios districts, reveal that extinct megafauna and humans coexisted for several thousands of years. There, gomphotheres disappeared at a time when a combination of changes in vegetation, climate and landscape disturbance were occurring, which opens the possibility of a synergistic scenario for their extinction. This difference in patterning between the two regions emphasizes the need to analyze extinction chronologies on a region-by-region basis in order to fully understand the causes of extinction, rather than attempting to do so with only continental-scale data.

Finally, it is striking that several of the dates reported here were either the first or second radiocarbon dates ever produced for extinct megafauna from the respective localities. This fact highlights the urgent need to obtain more radiocarbon dates in order to fully understand the pattern of extinction in the different regions of the South American continent, a fruitful avenue for future research.

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Appendix-Chapter 1

Table A1: Tropical Northern South America. †= extinct.

	Pleistocene				Holocene	Recent
Taxon	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Palaeolama weddelli †				X		
Palaeolama major †				X		
CERVIDAE						
Agalmaceros blicki †	X					
Odocoileus salinae †	X			X		
Odocoileus virginatus					X	X
Odocoileus				X		X
Order CARNIVORA						
CANIDAE						
Canis dirus †				X		
Protocyon troglodytes †				X		
Protocyon †				X		
FELIDAE						
Homotherium †		X	X			
Smilodon populator †	X			X		
Smilodon fatalis †				X		
Smilodon gracilis †		X	X			
Smilodon †	X		X	X		
Puma concolor						X
Panthera onca	X		X	X		X
URSIDAE						
Arctotherium wingei †				X		
Arctotherium †				X		
Tremarctos ornatus						X
Order PROBOSCIDEA †						
GOMPHOTHERIIDAE †						
Notiomastodon platensis † (1)	X			X		
Cuvieronius hyodon †	X			X		
Order LITOPTERNA						
MACRAUCHENIIDAE						
Macrauchenia †	X			X		
Order NOTOUNGULATA †						
TOXODONTIDAE †						
Mixotoxodon larensis †	X			X		
Order PERISSODACTYLA						
EQUIDAE						
Equus andium †				X		
Equus santaelenae †				X		

Equus lasallei †				X		
Equus	X			X		
Hippidion †				X		
TAPIRIDAE						
Tapirus terrestris	X			X		X
Tapirus bairdii						X
Tapirus kabomani						X
Tapirus pinchaque						X
Tapirus	X			X		
Order RODENTIA						
CAVIIDAE						
Hydrochoerus				X		X
Hydrochoerus hydrochaeris					X	X
Neochoerus †	X			X		
Neochoerus aesopi †	X					
Order CINGULATA (XENARTHRA)						
DASYPODIDAE						
Pachyarmatherium tenebris †				X		
Propraopus sulcatus †	X			X		
Priodontes maximus						X
PAMPATHERIIDAE †						
Holmesina occidentalis † *(3)*	X		X	X		
Holmesina majus †				X		
Pampatherium humbolditi †				X		
GLYPTODONTIDAE †						
Glyptodon clavipes † *(2)*				X		
Glyptodon †				X		
Glyptotherium cylindricum †				X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Catonyx chiliense †				X		
Scelidotherium †			X	X		
Glossotherium tropicurum †	X					
Glossotherium wegneri † *(1)*	X					
Megatherium (P.) elenense †				X		
Eremotherium laurillardi †	X		X	X		
Eremotherium †	X			X		

Table A2: Amazon basin. †= extinct.

	Pleistocene				Holocene	Recent
Taxon	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Hemiauchenia †	X					
Palaeolama major †				X		
Lama	X					
CERVIDAE						
Odocoileus virginatus						X
Blastocerus dichotomus						X
Order CARNIVORA						
CANIDAE						
Protocyon troglodytes †				X		
Protocyon †	X					
FELIDAE						
Smilodon †	X					
Panthera onca				X		X
Puma concolor				X		X
Order PROBOSCIDEA						
GOMPHOTHERIIDAE						
Notiomastodon platensis † (1)	X			X		
Order LITOPTERNA						
MACRAUCHENIIDAE						
Macrauchenia †	X					
Order NOTOUNGULATA						
TOXODONTIDAE						
Trigodonops lopesi †	X					
Mixotoxodon †	X					
Order PERISSODACTYLA						
EQUIDAE						
Equus	X					
TAPIRIDAE						
Tapirus rondonensis †				X		
Tapirus terrestris						X
Tapirus kabomani						X
Order RODENTIA						
CAVIIDAE						
Hydrochoerus hydrochaeris					X	X
Order CINGULATA (XENARTHRA)						
Priodontes maximus						X
PAMPATHERIIDAE						
Holmesina rondonensis †				X		

Suborder GLYPTODONTIA						
Hoplophorus euphractus †	X					
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE						
Eremotherium † (1)	X			X		

Table A3: North eastern Brazil. †= extinct.

	Pleistocene				Holocene	Recent
Taxon	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Hemiauchenia †	X					
Lama guanicoe				X		
Lama	X					
Palaeolama major †				X		
CERVIDAE						
Morenoelaphus brachyceros †				X	X	
Morenoelaphus †				X		
Blastocerus dichotomus						X
Order CARNIVORA						
CANIDAE						
Protocyon troglodytes †	X			X		
Protocyon †	X					
Chrysocyon brachyrus						X
FELIDAE						
Smilodon populator †				X		
Smilodon †	X					
Panthera onca				X		X
Puma concolor						X
URSIDAE						
Arctotherium wingei †	X			X		
Arctotherium †				X		
Order PROBOSCIDEA †						
GOMPHOTHERIIDAE †						
Notiomastodon platensis †	X			X		
Order LITOPTERNA †						
MACRAUCHENIIDAE †						
Macrauchenia patachonica †	X			X		
Macrauchenia †	X					
Xenorhinotherium bahiense †				X		
Order NOTOUNGULATA †						
TOXODONTIDAE †						
Trigodonops lopesi †	X					
Order PERISSODACTYLA						
EQUIDAE						
Hippidion †	X		X	X		
Equus neogeus †				X		
Equus	X					
TAPIRIDAE						
Tapirus critatellus †				X		
Tapirus terrestris				X		X
Order RODENTIA						

CAVIIDAE						
Hydrochoerus hydrochaeris						X
Order CINGULATA (XENARTHRA)						
DASYPODIDAE						
Pachyarmatherium brasiliense †				X		
Propraopus sulcatus †			X			
Priodontes maximus						X
PAMPATHERIIDAE †						
Holmesina paulacouti †				X		
Holmesina majus †				X		
Pampatherium humboldti †			X	X		
Suborder GLYPTODONTIA †						
Hoplophorus euphractus †	X					
PANOCHTIDAE †						
Panochthus greslebini †	X					
Panochthus jaguaribensis †				X		
GLYPTPDONTIDAE †						
Glyptodon clavipes †	X			X		
Glyptodon †				X		
Glyptotherium cylindricum †				X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Ocnotherium giganteum †	X			X		
Catonyx cuvieri †				X		
Scelidotherium †			X			
Valgipes bucklandi †				X		
Mylodonopsis ibsensi †				X		
MEGATHERIIDAE †						
Eremotherium laurillardi † *(3)*	X		X	X		
Eremotherium †	X					
Nothrotherium maquinense † *(1)*				X		
MEGALOCHYNIDAE						
Aytherium aureum †				X		
Australonyx aquae †				X		

Table A4: Coastal and Andean arid to semi-arid regions and High Andean Altiplano. †= extinct.

	Pleistocene				Holocene	Recent
Taxon	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Hemiauchenia paradoxa †	X					
Lama castelnaudi †	X			X		
Lama guanicoe			X	X	X	X
Lama	X			X		X
Palaeolama weddelli †	X			X		
Palaeolama major †				X		
Palaeolama hoffstetteri †	X					
Vicugna provicugna †				X		
Vicugna vicugna (1)				X		X
CERVIDAE						
Hippocamelus		X		X		
Hippocamelus antisensis						X
Charitoceros tarijensis †	X	X		X		
Agalmaceros blicki †	X			X		
Odocoileus virginatus						X
TAYASSUIDAE						
Platygonus †			X			
Catagonus stenocephalus †	X					
Order CARNIVORA						
CANIDAE						
Canis dirus †	X					
Protocyon troglodytes †	X					
Protocyon tarijensis †	X					
Protocyon †		X				
FELIDAE						
Panthera onca	X					
Smilodon populator †		X				
Smilodon †				X		
Puma concolor						X
URSIDAE						
Arctotherium wingei †		X				
Arctotherium tarijente †		X	X			
Arctotherium angustidens †		X	X			
Tremarctos ornatus						X
Order PROBOSCIDEA †						
GOMPHOTHERIIDAE †						
Notiomastodon platensis†	X					
Cuvieronius hyodon †	X		X			
Order LITOPTERNA †						
MACRAUCHENIIDAE †						

Macrauchenia patachonica †		X		X		
Macrauchenia †	X					
Order NOTOUNGULATA †						
TOXODONTIDAE †						
Toxodon platensis †		X				
Order PERISSODACTYLA						
EQUIDAE						
Hippidion saldiasi † (2)				X		
Hippidion principale †			X			
Hippidion devillei † (1)		X	X	X		
Hippidion †		X		X		
Equus santaelenae †	X					
Equus neogeus †		X				
Equus	X			X		
TAPIRIDAE						
Tapirus tarijensis †				X		
Tapirus terrestris	X					
Order RODENTIA						
CAVIIDAE						
Hydrochoerus hydrochaeris		X				
Neochoerus tarijensis †	X					
Order CINGULATA (XENARTHRA)						
DASYPODIDAE						
Propraopus sulcatus †			X			
PAMPATHERIIDAE †						
Holmesina occidentalis †				X		
Pampatherium humboldti †		X				
Pampatherium typum †				X		
Suborder GLYPTODONTIA †						
Hoplophorus euchazui †	X					
Neuryurur †			X			
PANOCHTIDAE †						
Panochthus tuberculatus †			X			
Panochthus intermedius †		X	X			
Panochthus †	X					
GLYPTPDONTIDAE †						
Glyptodon clavipes †	X	X				
Glyptodon reticulatus †		X		X		
Glyptodon †	X		X			
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Lestodon armatys †		X		X		
Catonyx tarijensis †		X				
Catonyx chiliense † (1)	X					
Scelidotherium †	X	X		X		
Glossotherium robustum †		X				

Mylodon †				X		
MEGATHERIIDAE †						
Megatherium (M.) americanum †	X	X		X		
Megatherium (P.) celendinense †				X		
Megatherium (P.) medinae †	X					
Megatherium (P.) sundti †	X					
Megatherium (P.) tarijensis †				X		
Megatherium (P.) urbinai †				X		
Megatherium (P.) elenense †				X		
Megatherium †	X			X		
Eremotherium sefvei †	X					
Nothorpus tarijensis †		X				
MEGALOCHYNIDAE †						
Diabolotherium nordenskioldi † (1)				X		

Table A5: Central and Southern Brazil. † = extinct.

	Pleistocene				Holocene	Recent
Taxon	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Palaeolama major †				X		
CERVIDAE						
Ozotoceros	X					X
Ozotoceros bezoarticus						X
Blastocerus dichotomus						X
TAYASSUIDAE						
Catagonus stenocephalus †				X		
Order CARNIVORA						
CANIDAE						
Protocyon troglodytes †				X		
Chrysocyon brachyrus						X
FELIDAE						
Panthera onca	X					X
Smilodon populator † *(3)*	X			X	X	
Puma conolor						X
URSIDAE						
Arctotherium wingei †				X		
Arctotherium vetustum †	X					
Order PROBOSCIDEA †						
GOMPHOTHERIIDAE †						
Notiomastodon platensis †	X			X		
Order LITOPTERNA †						
MACRAUCHENIIDAE †						
Xenorhinotherium †	X					
Xenorhinotherium bahiense †				X		
Order NOTOUNGULATA †						
TOXODONTIDAE †						
Toxodon platensis † *(3)*	X			X		
Toxodon †	X					
Order PERISSODACTYLA						
EQUIDAE						
Hippidion †	X					
Equus neogeus † *(3)*	X			X		
TAPIRIDAE						
Tapirus critatellus †				X		
Tapirus terrestris	X					X
Tapirus	X					X
Order RODENTIA						
CAVIIDAE						
Hydrochoerus hydrochaeris					X	X
Neochoerus sulcidens †				X		

Order CINGULATA (XENARTHRA)						
DASYPODIDAE						
Priodontes maximus						X
PAMPATHERIIDAE †						
Pampatherium humboldti †				X		
Suborder GLYPTODONTIA †						
Hoplophorus euphractus †	X					
GLYPTPDONTIDAE †						
Glyptodon clavipes † (1)	X			X		
Glyptodon reticulatus †	X					
Glyptodon †	X					
Glyptotherium cylindricum †				X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Lestodon armatus †	X					
Ocnotherium giganteum †				X		
Catonyx cuvieri † (4)	X					
Valgipes bucklandi †				X		
Mylodonopsis ibsensi †				X		
MEGATHERIIDAE †						
Eremotherium laurillardi † (1)	X			X		
Eremotherium †	X					
Nothrotherium maquinense †				X		
Nothrotherium escrivanense †				X		
MEGALOCHYNIDAE						
Aytherium aureum †				X		

Table A6: North-central Chile. †= extinct.

	Pleistocene				Holocene	Recent
Taxon	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Lama guanicoe						X
Lama				X		
Palaeolama †				X		
CERVIDAE						
Hippocamelus				X		
Antifer ultra †				X		
Order CARNIVORA						
FELIDAE						
Puma concolor						X
Order PROBOSCIDEA †						
GOMPHOTHERIIDAE †						
Notiomastodon platensis (1) †	X			X		
Order PERISSODACTYLA						
EQUIDAE						
Hippidion principale †			X			
Hippidion †				X		
Equus andium †				X		
Equus				X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Catonyx chiliense †	X					
Mylodon (1) †				X		

Table A7: El Gran Chaco and North-western Patagonia. †= extinct.

	Pleistocene				Holocene	Recent
Taxon	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Hemiauchenia paradoxa †	X			X		
Lama castelnaudi †				X		
Lama guanicoe						X
Palaeolama weddelli †	X					
CERVIDAE						
Hippocamelus				X		
Blastocerus dichotomus	X					X
Blastocerus				X		
Epieurycerus proximus	X					
Ozotoceros bezoarticus						X
Antifer †				X		
Morenoelaphus brachyceros †	X			X		
Morenoelaphus †				X		
TAYASSUIDAE						
Catagonus carlesi †			X			
Catagonus wagneri						
Order CARNIVORA						
CANIDAE						
Protocyon troglodytes †			X	X		
Protocyon †		X	X			
Chrysocyon brachyrus						X
FELIDAE						
Panthera onca	X					
Smilodon populator †	X			X		
Simlodon †			X			
Puma concolor						
URSIDAE						
Arctotherium †			X			
Order PROBOSCIDEA †						
GOMPHOTHERIIDAE †						
Notiomastodon platensis †	X			X		
Order LITOPTERNA †						
MACRAUCHENIIDAE †						
Macrauchenia patachonica †	X		X			
Macrauchenia †	X					
Order NOTOUNGULATA †						
TOXODONTIDAE †						
Toxodon gracilis †			X			
Toxodon ensenadensis †			X			
Toxodon platensis †				X		
Toxodon †	X			X		

Mixotoxodon †				X		
Order PERISSODACTYLA						
EQUIDAE						
Equus neogeus †			X	X		
Equus				X		
Order RODENTIA						
CAVIIDAE						
Hydrochoerus hydrochaeris				X		X
Order CINGULATA (XENARTHRA)						
DASYPODIDAE						
Propraopus sulcatus †				X		
Priodontes maximus						X
PAMPATHERIIDAE †						
Holmesina paulacouti †				X		
Pampatherium typum †				X		
PANOCHTHIDAE †						
Neosclerocalyptus paskoensis †				X		
Neosclerocalyptus ornatus †		X	X			
Nesoclerocalyptus †			X	X		
Panochthus tuberculatus †	X		X			
Panochthus †				X		
GLYPTPDONTIDAE †						
Glyptodon clavipes †	X					
Glyptodon reticulatus †			X			
Glyptodon elongatus †				X		
Glyptodon †	X			X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Lestodon armatus †	X			X		
Catonyx tarijensis †	X					
Catonyx chiliense †	X			X		
Scelidotherium leptocephalum † (1)				X		
Scelidotherium bravardi †	X					
Scelidotherium †	X					
Glossotherium robustum †	X			X		
Mylodon †	X			X		
Mylodon darwini †			X	X		
MEGATHERIIDAE †						
Megatherium (M.) americanum †	X	X		X		
Megatherium †				X		

Table A8: Pampas. †= extinct.

	Pleistocene				Holocene	Recent
	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Hemiauchenia paradoxa †	X			X		
Lama guanicoe			X	X	X	X
Lama	X			X		X
Palaeolama major † *(1)*				X	X	
Vicugna vicugna				X		
CERVIDAE						
Eulamaops paralellus †				X		
Paraceros fragilis†	X			X		
Ozotoceros				X	X	
Ozotoceros bezoarticus				X		X
Epieurycerus truncus †			X			
Epieurycerus proximus †			X	X		
Blastocerus	X					
Blastocerus dichotomus						X
Antifer ultra †				X		
Antifer ensenadensis †			X	X		
Antifer †				X		
Morenoelaphus brachyceros †	X			X		
Morenoelaphus †				X		
TAYASSUIDAE						
Platygonus cinctus †	X					
Platygonus †		X	X			
Catagonus bonaerensis †			X	X		
Catagonus metropolitanus †		X	X			
Catagonus stenocephalus †			X	X		
Catagonus wegnery	X			X		
Catagonus		X	X	X		
Order CARNIVORA						
CANIDAE						
Protocyon troglodytes †		X	X	X		
Protocyon scagliaruen †	X					
Theriodictis platensis †		X	X			
Theriodictis †				X		
Chrysocyon brachyrus						X
FELIDAE						
Panthera onca				X		
Smilodon populator † *(1)*				X		
Smilodon †	X		X	X		
Puma concolor						X
URSIDAE						
Actotherium vetustum †			X			

Arcotherium tarijense †		X	X	X		
Arctotherium angustidens †		X	X			
Arctotherium bonariense †			X	X		
Arctotherium †				X		
Order PROBOSCIDEA †						
GOMPHOTHERIIDAE †						
Notiomastodon platensis † (3)	X			X		
Order LITOPTERNA †						
MACRAUCHENIIDAE †						
Macrauchenia patachonica † (2)	X		X	X	X	
Macrauchenia †				X		
Macrauchenopsis †			X			
Windhausenia †	X					
Neolicaprhium recens †		X	X	X		
Order NOTOUNGULATA †						
TOXODONTIDAE †						
Toxodon platensis † (1)			X	X		
Toxodon †	X		X	X		
Mesotherium cristatum †			X			
Order PERISSODACTYLA						
EQUIDAE						
Hippidion principale † (3)			X	X		
Hippidion † (1)	X			X		
Equus neogeus †(6)	X			X		
Equus insulatus †	X					
Equus	X			X		
TAPIRIDAE						
Tapirus mesopotamicus †				X		
Tapirus greslebini †	X					
Tapirus oliversai †		X				
Tapirus				X		
Order RODENTIA						
CAVIIDAE						
Hydrochoerus hydrochaeris				X		x
Hydrochoerus ballesterensis†		X				
Hydrochoerus				X		
Neochoerus †				X		
Neochoerus sulcidens †				X		
Neochoerus tarijensis †	X					
Order CINGULATA (XENARTHRA)						
DASYPODIDAE						
Eutatus seguni †			X	X		
Eutatus pascuali †	X					
Propraopus sulcatus †	X			X		
PAMPATHERIIDAE †						
Holmesina paulacouti †	X			X		

Holmesina majus †				X		
Pampatherium humboldti †	X			X		
Pampatherium typum †				X		
GLYPTODONTIA †						
Neuryururs trabeculatus †	X					
Neuryururs rudis †	X					
Neuryururs † *(1)*	X					
PANOCHTHIDAE †						
Neosclerocalyptus paskoensis †				X		
Neosclerocalyptus ornatus † *(1)*		X	X			
Neosclerocalyptus gouldi †			X			
Nesoclerocalyptus †			X	X	X	
Nesoclerocalyptus pseudornatus †		X	X			
Panochthus tuberculatus †			X	X		
Panochthus frenzelianus †			X			
Panochthus intermedius †		X	X			
Panochthus subintermedius †		X	X			
Panochthus †			X	X		
GLYPTPDONTIDAE †						
Doedicurus clavicaudatus † *(3)*			X	X	X	
Palxhaplous †	X					
Doedicuroides eguiai †	X					
Glyptodon clavipes †				X		
Glyptodon reticulatus †	X			X		
Glyptodon munizi †		X				
Glyptodon †	X		X	X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Lestodon armatus †	X		X	X		
Catonyx tarijensis †	X		X	X		
Catonyx cuvieri †	X					
Scelidotherium leptocephalum † *(2)*	X		X	X	X	
Scelidotherium bravardi †		X		X		
Scelidotherium †				X		
Glossotherium robustum † *(3)*				X		
Glossotherium lettsomi †	X					
Mylodon †	X			X		
Mylodon darwini †				X		
MEGATHERIIDAE †						
Megatherium (M.) americanum † *(6)*			X	X	X	
Megatherium (M.) gallardoi †		X	X			
Megatherium †	X			X		
Eremotherium laurillardi †				X		
Nothropus priscus †				X		
Nothropus carcaranensis †				X		

Table A9: Western Northern Patagonia. †= extinct.

	Pleistocene				Holocene	Recent
	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Hemiauchenia cf. paradoxa †				X		
Lama gunaicoe						X
CERVIDAE						
Hippocamelus bisulcus						X
CARNIVORA						
FELIDAE						
Puma concolor						X
PROBOSCIDEA						
GOMPHOTHERIIDAE						
Notiomastodon platensis † (3)	X			X		
PERISSODACTYLA						
EQUIDAE						
Equus andium †				X		
Equus (1)				X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Glossotherium lettsomi †				X		

Table A10: Southern Patagonia. *†*= extinct.

	Pleistocene				Holocene	Recent
	P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA						
CAMELIDAE						
Lama guanicoe (33)				X	X	X
Vicugna vicugna (4)				X		
CERVIDAE						
Hippocamelus					X	
Hippocamelus bisulcus						X
CARNIVORA						
FELIDAE						
Panthera onca mesembrina † (16)				X		
Smilodon † (5)				X		
Puma concolor (2)				X	X	X
URSIDAE						
Arctotherium tarijense † (1)				X		
Arctotherium † (2)				X		
Order LITOPTERNA †						
MACRAUCHENIIDAE †						
Macrauchenia patachonica † (1)				X		
Macrauchenia †				X		
PERISSODACTYLA						
EQUIDAE						
Hippidion saldiasi † (20)				X		
Hippidion † (1)				X		
Order TARDIGRADA (XENARTHRA)						
MYLODONTIDAE †						
Mylodon † (33)				X		
Mylodon darwini † (10)				X	X	
MEGALOCHYNIDAE						
Diabolotherium				X		

Table A11: All Pleistocene to present taxa in South America. Body mass is included. See the body of the chapter for references. †= extinct.

Taxon	Body mass (kg)	Pleistocene				Holocene	Recent
		P. indet	Early	Middle	Late	Early	
Order ARTYODACTYLA							
CAMELIDAE							
Eulamaops paralellus†	*150*				X		
Lama castelnaudi †	*>100*	X			X		
Lama guanicoe	*120*			X	X	X	X
Vicugna provicugna †	*50*				X		
Vicugna vicugna	*50*				X		X
Hemiauchenia paradoxa †	*300*	X			X		
Palaeolama †	*250*				X		
Palaeolama hoffstetteri †	*250*	X					
Palaeolama major †	*250*				X	X	
Palaeolama weddelli †	*250*	X			X		
CERVIDAE							
Agalmaceros blicki †	*60*	X			X		
Antifer ensenadensis †	*86*			X	X		
Antifer ultra †	*86*				X		
Blastocerus	*83*	X			X		
Blastocerus dichotomus	*83*	X					X
Charitoceros tarijensis †	*70*	X	X		X		
Epieuryceros proximus †	*86*			X	X		
Epieuryceros truncus †	*86*			X			
Hippocamelus	*69*		X		X		
Hippocamelus antisensis	*68*						X
Hippocamelus bisulcus	*70*						X
Morenoelaphus †	*50*				X		
Morenoelaphus brachyceros †	*50*	X			X	X	
Odocoileus	*55*				X		X
Odocoileus salinae †	*indet.*	X			X		
Odocoileus virginatus	*55*	X				X	X
Ozotoceros	*30*	X			X	X	
Ozotoceros bezoarticus	*35*				X		X
Paraceros fragilis †	*30*	X			X		
TAYASSUIDAE							
Catagonus bonaerensis †	*90*			X	X		
Catagonus carlesi †	*indet.*			X			
Catagonus metropolitanus †	*90*		X	X			
Catagonus stenocephalus †	*45*	X		X	X		
Catagonus wagneri	*35*	X			X		X
Platygonus †	*52*		X	X			
Platygonus cinctus †	*indet.*	X					
Order CARNIVORA							

CANIDAE							
Canis dirus †	*66*	X			X		
Protocyon †	*16*	X	X	X	X		
Protocyon scagliaruen †	*11*	X					
Protocyon tarijensis †	*indet.*	X					
Protocyon troglodytes †	*20*	X	X	X	X		
Theriodictis †	*37*				X		
Theriodictis platensis †	*37*		X	X			
Chrysocyon brachyrus	*23*		X		X	X	X
FELIDAE							
Homotherium †	*189*		X	X			
Smilodon †	*196*	X		X	X		
Smilodon fatalis †	*220*				X		
Smilodon gracilis †	*77*		X	X			
Smilodon populator †	*290*	X	X		X	X	
Panthera onca	*89*	X		X	X		X
Panthera onca mesembrina †	*190*				X		
Puma concolor	*51*				X	X	X
URSIDAE							
Arctotherium †	*352*			X	X		
Arctotherium angustidens †	*806*		X	X			
Arctotherium tarijense †	*267*		X	X	X		
Arctotherium vetustum †	*201*	X		X			
Arctotherium bonariense †	*335*			X	X		
Arctotherium wingei †	*150*	X	X		X		
Tremarctos ornatus	*200*						X
Order PROBOSCIDEA †							
GOMPHOTHERIIDAE †							
Notiomastodon platensis†	*7500*	X			X		
Cuvieronius hyodon †	*5000*	X		X	X		
Order LITOPTERNA †							
Macrauchenia patachonica †	*1100*	X	X	X	X	X	
Macrauchenopsis	*>1100*			X			
Windhausenia	*700*	X					
Xenorhinotherium †	*1100*	X					
Xenorhinotherium bahiense †	*1100*				X		
Neolicaprhium recens	*35*		X	X	X		
Order NOTOUNGULATA †							
Toxodon ensenadensis †	*indet.*			X			
Toxodon gracilis †	*235*			X			
Toxodon platensis †	*1700*	X	X	X	X		
Mixotoxodon †	*3700*	X			X		
Mixotoxodon larensis †	*3700*	X			X		
Mesotherium cristatum †	*138*			X			
Trigodonops lopesi †	*1600*	X					
Order PERISSODACTYLA							

EQUIDAE							
Equus	*328*	X			X		
Equus andium †	*220*				X		
Equus insulatus †	*350*	X					
Equus lasallei †	*350*				X		
Equus neogeus †	*370*	X			X		
Equus santaelenae †	*350*	X			X		
Hippidion †	*325*	X	X	X	X		
Hippidion devillei †	*250*		X	X	X		
Hippidion principale †	*460*			X	X		
Hippidion saldiasi †	*265*				X		
Tapirus bairdii	*300*						X
Tapirus critatellus †	*616*				X		
Tapirus greslebini †	*indet.*	X					
Tapirus kabomani	*110*						X
Tapirus mesopotamicus †	*525*				X		
Tapirus oliversai †	*indet.*		X				
Tapirus pinchaque	*193*						X
Tapirus rondonensis	*359*				X		
Tapirus tarijensis †	*363*				X		
Tapirus terrestris	*225*	X			X		X
Order RODENTIA							
CAVIIDAE							
Hydrochoerus ballesterensis†	*indet*		X				
Hydrochoerus hydrochaeris	*63*		X		X	X	X
Neochoerus sulcidens †	*90*				X		
Neochoerus tarijensis †	*90*	X					
Neochoerus †					X		
Neochoerus aesopi †	*200*	X					
Order CINGULATA (XENARTHRA)							
DASYPODIDAE							
Eutatus pascuali †	*32*	X					
Eutatus seguni †	*32*			X	X		
Pachyarmatherium brasiliense †	*106*				X		
Pachyarmatherium tenebris †	*indet.*				X		
Priodontes maximus	*32*						X
Propraopus sulcatus †	*50*	X		X	X		
PAMPATHERIIDAE †							
Holmesina majus †	*216*				X		
Holmesina occidentalis †	*200*	X		X	X		
Holmesina paulacouti †	*125*	X			X		
Holmesina rondonensis †	*<200*				X		
Pampatherium humboldti †	*94*	X	X	X	X		
Pampatherium typum †	*95*				X		
Suborder GLYPTODONTIA †							
Hoplophorus euchazui †	*280*	X					

Hoplophorus euphractus †	*280*	X					
Neuryururs †	*311*	X		X	X		
Neuryururs rudis †	*311*	X					
Neuryururs trabeculatus †	*311*	X					
PANOCHTIDAE †							
Neosclerocalyptus gouldi †	*>570*			X			
Neosclerocalyptus ornatus †	*598*		X	X	X		
Neosclerocalyptus paskoensis †	*574*				X		
Nesoclerocalyptus pseudornatus †	*indet.*		X	X			
Panochthus frenzelianus †	*1150*			X			
Panochthus greslebini †	*1150*	X					
Panochthus intermedius †	*>1150*		X	X			
Panochthus jaguaribensis †	*indet.*				X		
Panochthus subintermedius †	*>1150*		X	X			
Panochthus tuberculatus †	*1150*	X		X	X		
GLYPTODONTIDAE †							
Doedicuroides eguiai †	*indet.*	X					
Palxhaplous †	*indet.*	X					
Doedicurus clavicaudatus †	*2150*			X	X	X	
Glyptodon †	*1866*	X		X	X		
Glyptodon clavipes †	*2000*	X	X		X		
Glyptodon elongatus †	*2000*				X		
Glyptodon munizi †	*2600*		X				
Glyptodon reticulatus †	*862*	X	X	X	X		
Glyptotherium cylindricum †	*562*				X		
Order TARDIGRADA (XENARTHRA)							
MYLODONTIDAE †							
Lestodon armatus †	*3000*	X	X	X	X		
Ocnotherium giganteum †	*indet*	X			X		
Catonyx chiliense †	*1120*	X			X		
Catonyx cuvieri †	*1600*	X			X		
Catonyx tarijensis †	*1600*	X	X	X	X		
Scelidotherium †	*800*	X	X	X	X		
Scelidotherium bravardi †	*indet.*	X	X		X		
Scelidotherium leptocephalum †	*800*	X		X	X	X	
Valgipes bucklandi †	*1600*				X		
Glossotherium lettsomi †	*indet.*	X			X		
Glossotherium robustum †	*1200*	X	X		X		
Glossotherium tropicurum †	*1700*	X					
Glossotherium wegneri †	*indet.*	X			X		
Mylodon †	*1600*	X			X		
Mylodon darwini †	*1600*			X	X	X	
Mylodonopsis ibsensi †	*1600*				X		
MEGATHERIIDAE							
Eremotherium †	*3150*	X			X		
Eremotherium laurillardi †	*3900*	X		X	X		

Eremotherium sefvei †	*2400*	X					
Megatherium (M.) americanum †	*4000*	X	X	X	X	X	
Megatherium (M.) gallardoi †	*4000*		X	X			
Megatherium (P.) celendinense †	*4000*				X		
Megatherium (P.) elenense †	*indet.*				X		
Megatherium (P.) medinae †	*indet.*	X			X		
Megatherium (P.) sundti †	*indet.*	X					
Megatherium (P.) tarijensis †	*indet.*				X		
Megatherium (P.) urbinai †	*2600*				X		
Megatherium †	*3650*	X		X	X		
Nothorpus tarijensis †	*indet*		X				
Nothropus carcaranensis †	*indet*				X		
Nothropus priscus †	*indet*				X		
Nothrotherium escrivanense †	*indet*				X		
Nothrotherium maquinense †	*150*				X		
MEGALONYCHYDAE							
Ahytherium aureum	*1198*				X		
Australonyx aquae	*1149*				X		
Diabolotherium nordenskioldi †	*93*				X		

Table A12: Jaccard similarity index results at species level for Late Pleistocene taxa. Jaccard index: 0.0= 0% dissimilarity; 1.0 =100% dissimilarity.

Region	1	2	3	4	5	6	7	8	9	10
1	0.00									
2	0.89	0.00								
3	0.76	0.90	0.00							
4	0.90	0.96	0.93	0.00						
5	0.82	0.92	0.47	0.98	0.00					
6	0.93	0.89	0.97	1.00	0.96	0.00				
7	0.90	0.96	0.90	0.89	0.89	0.96	0.00			
8	0.86	0.94	0.80	0.87	0.82	0.94	0.66	0.00		
9	0.93	0.89	0.97	1.00	0.96	0.67	0.91	0.96	0.00	
10	1.00	0.93	0.94	0.80	1.00	1.00	0.96	0.90	1.00	0.00

Table A13: Jaccard similarity index results at genus level for Late Pleistocene taxa. . Jaccard index: 0.0= 0% dissimilarity; 1.0 =100% dissimilarity.

Region	1	2	3	4	5	6	7	8	9	10
1	0.00									
2	0.79	0.00								
3	0.57	0.78	0.00							
4	0.69	0.88	0.72	0.00						
5	0.69	0.82	0.45	0.82	0.00					
6	0.87	0.85	0.83	0.73	0.88	0.00				
7	0.69	0.93	0.70	0.67	0.84	0.77	0.00			
8	0.53	0.84	0.62	0.63	0.72	0.81	0.46	0.00		
9	0.89	0.90	0.93	0.96	0.90	0.80	0.83	0.89	0.00	
10	0.84	0.87	0.80	0.70	0.93	0.80	0.90	0.79	1.00	0.00

Table A14: Jaccard similarity index results at species level for present day taxa. Jaccard index: 0.0= 0% dissimilarity; 1.0 =100% dissimilarity.

Region	1	2	3	4	5	6	7	8	9	10
1	0.00									
2	0.40	0.00								
3	0.64	0.38	0.00							
4	0.58	0.64	0.73	0.00						
5	0.55	0.25	0.14	0.63	0.00					
6	0.80	0.75	0.71	0.63	0.75	0.00				
7	0.75	0.56	0.29	0.73	0.38	0.50	0.00			
8	0.83	0.66	0.43	0.70	0.50	0.40	0.17	0.00		
9	0.82	0.78	0.75	0.67	0.78	0.25	0.57	0.50	0.00	
10	0.82	0.78	0.75	0.66	0.78	0.25	0.57	0.50	0.00	0.00

Table A15: Jaccard similarity index results at genus level for present day taxa. Jaccard index: 0.0= 0% dissimilarity; 1.0 =100% dissimilarity.

Region	1	2	3	4	5	6	7	8	9	10
1	0.00									
2	0.29	0.00								
3	0.50	0.29	0.00							
4	0.44	0.60	0.73	0.00						
5	0.38	0.14	0.14	0.64	0.00					
6	0.71	0.71	0.71	0.63	0.75	0.00				
7	0.67	0.50	0.29	0.73	0.38	0.50	0.00			
8	0.78	0.63	0.43	0.70	0.50	0.40	0.17	0.00		
9	0.75	0.75	0.75	0.50	0.77	0.25	0.57	0.50	0.00	
10	0.75	0.75	0.75	0.75	0.50	0.77	0.25	0.57	0.50	0.00

Appendix—Chapter 3

Localities Figure 1:
Mexico: Lago Cuitzeo (Michoacan), Jicotlan (Nuevo León), Monterrey (Nuevo León), Laguna de las Cruces (San Luis de Potosí), Cd. Acuña (Coahuila), Huhuitlán (Miochacán), Mixteca Alta (Oaxaca), Rancho La Amapola - Cedral (San Luis de Potosí), Xico, Salinas (San Luis de Potosí), Culhuacán (Distrito Federal);.
Belize: Actun Halal.
Costa Rica: Bajo de Los Barrantes de San Ramón (Alajuela).
Dominican Republic: Cueva #2 (Tres Charcoals, Provincia de Pedernales), Cueva del Muerto (Tres Charcoals, Provincia de Pedernales), Cueva de Mono- Paraje de los Tres Charcos (Municipio de Oviedo, Provincia de Pedernales).

Localities Figure 2:
Ecuador: Tanque Loma, Barranco Arenas, Atahualpa Isla, La Merced, Quebrada Colorada, La Ronda (Pichincha, Quito), La Armenia (Quito), Guamote, El Colegio, Chalan, Manatul, Punin, Pena col. 24 de Mayo, La Carolina, Rio Chiche.
Peru: Casa del Diablo
Brazil: Lapa da Escrivana 5, Lapa da Escrivana II.
Bolivia: Tarija, Achiri.
Paraguay: Risso cavern (Vallemi).
Argentina: Arroyo Seco 2, Pescado Castigador River, Las Toscas 5, Laguna Cabeza de Buey 2, Arroyo Tapalque, Campo Laborde, Hara las Ortigas, Estancia Santa Rosa de los Cerrillos, Campo Gaete, Estancia el Trebol, La Chumbiada, Canal Aliviador, Estancia Los Tobianos, Camping El Danubio, Fontezuelas, La Moderna, Negro Muerto 3, Segundo Angostura, Puesto Mancilla, Arroyo Balta, Luján, Rio Areco, Arroyo del Medio, Rio Medio, La Plata countries.
Chile: Southern Patagonia (Tres Arroyos, Cueva de los Chingues, Baño Nuevo, Pali Aike, Fells Cave), Southern Chile (Pilauco, Choroico, Fresia, Los Lagos, La Plata, Nochaco, Caracol, Huilma, Mupulno, Monte Verde, Lonquimay, San Pablo de Tramalhue, Rio Bueno, Chillán, Alto Boroa), Central Chile (Quintero, Tagua Tagua, Quereo-Los Vilos). Northern Chile (Pampa del Tamarugal, Salar de Surire).

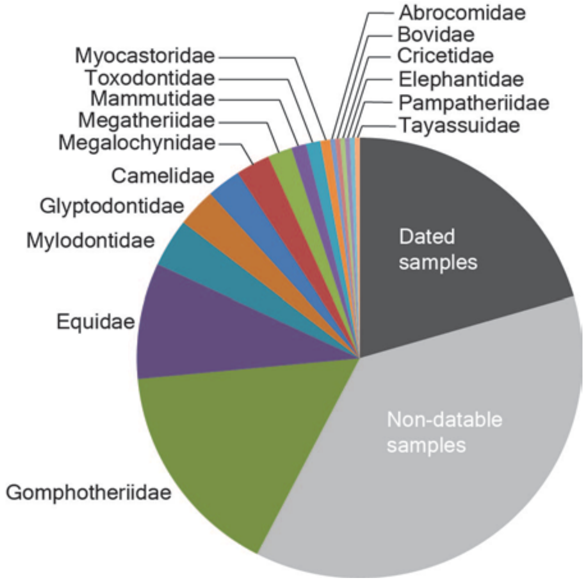

Figure A3.1: Proportion of not datable samples per mammalian family.

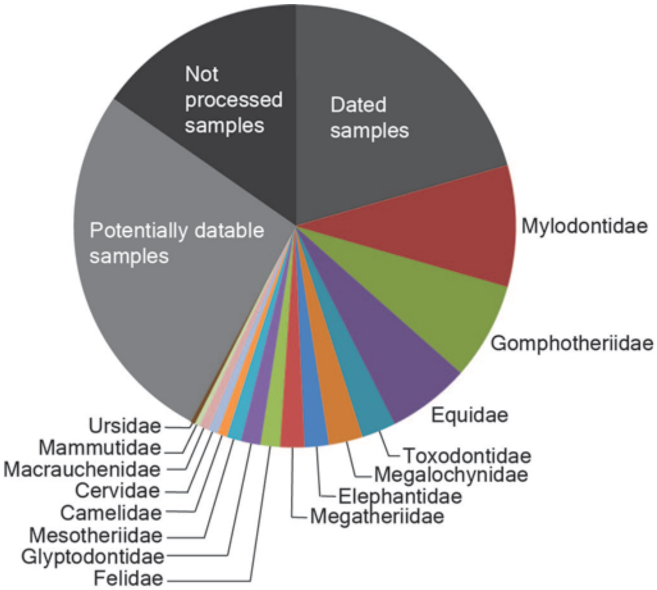

Figure A3.1: Proportion of potentially datable samples per mammalian family. In this graph, potentially datable samples are considered as 'Potentially datable + Not processed' samples from figure 2.

Table A3.1: Highly-ranked radiocarbon dates previously reported for megafauna that were used in this chapter. All dates have been calibrated to calendar years using Calib 7.02 (Stuiver and Reimer 1986-2014). Rankings follow methods in Barnosky and Lindsey (2010).

Taxon name	**Site**	**Country**	**14C lab code**	**14C**	**±**	**Material dated**	**Cal mean**	**Cal young**	**Cal old**	**Rank**	**References**
Hippidion devillei	Cueva Rosello	Peru	Beta-227440	23340	120	bone	27538	27327	27743	12	Shockey et al., 2009
Vicugna	Cueva Rosello	Peru	Beta-237786	22220	130	bone	26390	26042	26814	12	Shockey et al., 2009
Diabolotherium	Trigo Jirka	Peru	Beta-227438	29140	260	bone	33287	32612	33842	12	Shockey et al., 2009
Hippidion saldiasi	Betecsa	Chile	GrA-29389	21070	100	bone	25382	25110	25637	12	Alberdi et al. (2007)
Hippidion saldiasi	Betecsa	Chile	GrA-29388	21380	100	bone	25679	25431	25895	12	Alberdi et al. (2007)
Catonyx cuvieri	Gruta Cuvieri	Brazil	BETA 165398	9960	40	bone	11315	11223	11411	12	Neves & Pilo (2003)
Catonyx cuvieri	Lapa dos Tatus	Brazil	BETA 174688	14030	50	bone	16984	16708	17209	12	Neves & Pilo (2003)
Catonyx cuvieri	Lapa dos Tatus	Brazil	BETA 174689	13920	50	bone	16811	16552	17037	12	Neves & Pilo (2003)
Equus neogeus	Lapa da Escrivânia 5	Brazil	BETA 174711	16620	70	bone	20001	19741	20230	12	Neves & Pilo (2003)
Equus neogeus	Lapa da Escrivânia 5	Brazil	BETA 174712	16250	60	bone	19565	19340	19804	12	Neves & Pilo (2003)
Equus neogeus	Lapa da Escrivânia 5	Brazil	BETA 174713	16180	70	bone	19474	19230	19686	12	Neves & Pilo (2003)
Smilodon populator	Lapa da Escrivânia 5	Brazil	BETA-174722	9130	150	bone	10247	9739	10601	12	Neves & Pilo (2003)
Notiomastodon	Pilauco	Chile	UCIAMS101670	12725	40	bone	15108	14865	15278	12	Pino et al., 2008
Notiomastodon	Pilauco	Chile	UCIAMS101830	12760	50	bone	15153	14911	15330	12	Pino et al., 2008
Notiomastodon	Pilauco	Chile	UCIAMS101831	13220	60	bone	15835	15608	16065	12	Pino et al., 2008
Notiomastodon	Pilauco	Chile	TO11477	12540	90	bone	14697	14232	15107	12	Pino et al., 2008
Gomphotheriidae	Moteverde	Chile	OXA 105	12000	250	bone	13860	13274	14744	12	Dillehay (1997)
Gomphotheriidae	Moteverde	Chile	TX 3760	11990	200	bone	13817	13316	14433	12	Dillehay (1997)
Equus	Pilauco	Chile	GEOUACH55	11457	140	teeth	13260	13026	13547	12	Pino et al., 2013
Mylodontidae	Pilauco	Chile	UCIAMS101832	13165	55	dermal ossicle	15754	15490	16001	12	Pino et al., 2008
Mylodontidae	Pilauco	Chile	UCIAMS102087	13220	40	dermal ossicle	15836	15659	16029	12	Pino et al., 2008

Mylodontidae	Baño Nuevo	Chile	UCIAMS10107	12510	30	dermal ossicle	14636	14281	14969	12	Velasquez and Mena 2006
Mylodontidae	Baño Nuevo	Chile	UCIAMS10111	12400	30	dermal ossicle	14355	14131	14675	12	Velasquez and Mena 2007
Macrauchenia	Baño Nuevo	Chile	UCIAMS19491	11665	50	dermal ossicle	13452	13328	13567	12	Velasquez and Mena 2008
Tardigrada	Baño Nuevo	Chile	CAMS32685	11480	50	maxillary bone	13279	13145	13410	12	Velasquez and Mena 2009
Tardigrada	Baño Nuevo	Chile	UCIAMS10106	11265	35	dermal ossicle	13090	13011	13163	12	Velasquez and Mena 2010
Tardigrada	Baño Nuevo	Chile	UCIAMS10105	11255	30	dermal ossicle	13082	13014	13147	12	Velasquez and Mena 2011

Table A3.2: Radiocarbon dates on evidence of humans used in this chapter. All dates have been calibrated to calendar years using Calib 7.02 (Stuiver and Reimer 1986-2014). Dates were extracted from a compilation made by Goldberg et al., 2016. Dates on shells were excluded.

Site	**Country**	**Materia dated**	**^{14}C lab code**	**^{14}C**	**±**	**Cal median**	**Cal young**	**Cal old**	**Reference**
Ayamachay (Ac-102)	Peru	Charcoal	I-5694	7560	125	8318	8042	8548	Ziolkowski et al 1994
Cuncaicha	Peru	Collagen	AA-96336	8361	82	9317	9087	9491	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96337	8363	82	9320	9087	9492	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96331	8404	82	9360	9134	9523	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101132	8454	84	9416	9236	9543	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101131	8461	85	9422	9237	9545	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96329	8483	83	9446	9246	9553	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94255	10050	50	11492	11269	11718	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96321	10034	97	11502	11222	11828	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94257	10055	67	11510	11250	11772	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101137	10060	100	11539	11238	11838	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96318	10084	99	11572	11250	11845	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96330	10086	97	11573	11253	11845	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96319	10100	99	11597	11266	11962	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96322	10127	98	11643	11282	11991	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96306	10132	71	11653	11338	11969	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96312	10163	71	11721	11393	12009	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96309	10189	77	11772	11399	12035	Rademaker et al 2014
Cuncaicha	Peru	Collagen	PRI-12-029-06b	10180	40	11783	11601	12008	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94256	10200	69	11800	11592	12039	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94255	10211	69	11820	11594	12051	Rademaker et al 2014
Cuncaicha	Peru	Collagen	PRI-12-029-04b	10205	35	11836	11697	12008	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96308	10260	72	11899	11605	12156	Rademaker et al 2014
Cuncaicha	Peru	Collagen	PRI-12-029-05b	10265	35	11911	11770	12040	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96307	10306	72	12001	11750	12316	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101138	10310	100	12018	11611	12428	Rademaker et al 2014
Cuncaicha	Peru	Collagen	Beta-297423	10321	73	12039	11765	12317	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101130	10380	100	12170	11796	12439	Rademaker et al 2014
Hakenasa	Chile	Charcoal	I-13287	8340	300	9234	8509	9939	Moreno 2009
Hakenasa	Chile	Charcoal	B-187531	8789	60	9743	9545	9935	Moreno 2009

Hakenasa	Chile	Charcoal	B-187532	9170	70	10309	10187	10496	Moreno 2009
Hakenasa	Chile	Charcoal	B-187533	9260	60	10384	10243	10524	Moreno 2009
Hakenasa	Chile	Charcoal	B-187534	9520	70	10756	10559	10910	Moreno 2009
Hakenasa	Chile	Bone	B-187535	9580	40	10890	10698	10907	Moreno 2009
Hakenasa	Chile	Charcoal	UGAMS2953	9980	40	11343	11238	11415	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UGAMS-4588	8510	30	9492	9441	9531	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77765	8600	40	9530	9472	9564	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77764	8635	40	9549	9492	9662	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77767	8690	40	9601	9532	9701	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77766	8695	40	9605	9533	9704	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77768	8730	35	9630	9542	9749	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	QLH-S4-1	8785	30	9715	9582	9889	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	QLH-S4-2	8840	30	9821	9665	9946	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	QLH-S4-3A	8845	30	9829	9676	9948	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	AA-34477	9090	75	10210	10112	10411	Gayo et al., 2015
Iroco	Bolivia	Collagen	AA91569	8105	92	8945	8640	9154	Capriles 2011
Iroco	Bolivia	Collagen	AA91568	8273	82	9208	9014	9426	Capriles 2011
Jaywamachay (Ac-335)	Peru	Charcoal	I-4500	8250	135	9174	8765	9491	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-4501	8360	125	9295	9021	9526	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5686	8500	125	9440	9088	9700	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5276	8645	140	9633	9302	9958	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5277	8980	140	10009	9560	10299	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5275	9460	145	10685	10277	11127	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5695	9560	170	10835	10374	11235	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5683	9890	310	11345	10489	12412	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5699	10280	170	11942	11321	12439	Ziolkowski et al 1994
Las Cuevas	Chile	Charcoal	I-13128	8270	250	9155	8510	9698	Santoro & Chacama 1984
Las Cuevas	Chile	Charcoal	I-12835	9540	160	10810	10377	11214	Santoro & Chacama 1984
Puente (Ac-158)	Peru	Charcoal	I-5056	7420	125	8195	7965	8404	Ziolkowski et al 1994
Puente (Ac-158)	Peru	Charcoal	I-5057	8860	125	9882	9556	10187	Ziolkowski et al 1994
Quelcatani	Peru	Charcoal	Beta-18927	7250	170	8036	7701	8355	Rademaker et al 2013
Tojotojone	Chile	Charcoal	unknown	9609	30	10934	10738	11093	Gayo et al., 2015
Monte Verde	Chile	unknown	Beta-52012	6530	110	7392	7234	7578	Dillehay 1997
Monte Verde	Chile	wood	TX-4436	8030	130	8849	8538	9260	Dillehay 1997

Monte Verde	Chile	wood	BETA-6753	8270	110	9204	8976	9489	Dillehay 1997
Monte Verde	Chile	wood	BETA-59081	10330	160	12045	11400	12555	Dillehay 1997
Monte Verde	Chile	charcoal	TX-3207	10860	130	12733	12544	13029	Dillehay 1997
Monte Verde	Chile	wood	TX-3472	11600	120	13388	13121	13610	Dillehay 1997
Monte Verde	Chile	wood	BETA-52015	11640	90	13424	13224	13599	Dillehay 1997
Monte Verde	Chile	charcoal	BETA-68997	11800	80	13586	13441	13754	Dillehay 1997
Monte Verde	Chile	wood	TX-5374	11790	200	13592	13178	14053	Dillehay 1997
Monte Verde	Chile	wood	TX-5376	11920	120	13703	13459	14013	Dillehay 1997
Monte Verde	Chile	bone	BETA-68996	12000	110	13807	13552	14090	Dillehay 1997
Monte Verde	Chile	wood	TX-3760	11990	200	13817	13316	14433	Dillehay 1997
Monte Verde	Chile	collagen	OXA-105	12000	250	13860	13274	14744	Dillehay 1997
Monte Verde	Chile	wood	BETA-6755	12230	140	14113	13734	14763	Dillehay 1997
Monte Verde	Chile	charcoal	UCIAMS 10737	12450	40	14483	14169	14817	George et al 2005
Monte Verde	Chile	wood	BETA-65842	12420	130	14484	14034	15058	Dillehay 1997
Monte Verde	Chile	charcoal	UCR 4015	12450	60	14494	14149	14893	George et al., 2005
Monte Verde	Chile	charcoal	UCIAMS 10738	12455	40	14494	14175	14833	George et al., 2005
Monte Verde	Chile	wood	OXA-381	12450	150	14538	14031	15121	Dillehay 1997
Monte Verde	Chile	wood	UCR 4014	12510	60	14630	14240	15026	Dillehay 1997
Monte Verde	Chile	wood	TX-4437	12650	130	14888	14246	15315	Dillehay 1997
Monte Verde	Chile	charcoal	BETA-59082	12780	240	15096	14166	15845	Dillehay 1997
Monte Verde	Chile	charcoal	TX-3208	13565	250	16306	15574	17078	Dillehay 1997
Marfilo 1	Chile	charcoal	Beta-164476	7000	40	7787	7685	7868	Mera and Garcia 2004
Pucon VI	Chile	charcoal	Beta 36776	7650	80	8414	8295	8581	Navarro et al., 2010
Loconaco 2	Chile	unknown	Beta-195761	7810	50	8542	8422	8637	Garcia 2005
Marfilo 1	Chile	charcoal	Beta-138919	8420	50	9403	9269	9517	Mera and Garcia 2004
Marfilo 1	Chile	charcoal	Beta-164475	10190	120	11762	11268	12123	Mera and Garcia 2004
Pucon VI	Chile	charcoal	Beta 36998	10390	40	12208	12003	12318	Navarro et al., 2010

Table A3.1: Highly-ranked radiocarbon dates previously reported for megafauna that were used in this chapter. All dates have been calibrated to calendar years using Calib 7.02 (Stuiver and Reimer 1986-2014). Rankings follow methods in Barnosky and Lindsey (2010).

Taxon name	Site	Country	14C lab code	14C	±	Material dated	Cal mean	Cal young	Cal old	Rank	References
Hippidion devillei	Cueva Rosello	Peru	Beta-227440	23340	120	bone	27538	27327	27743	12	Shockey et al., 2009
Vicugna	Cueva Rosello	Peru	Beta-237786	22220	130	bone	26390	26042	26814	12	Shockey et al., 2009
Diabolotherium	Trigo Jirka	Peru	Beta-227438	29140	260	bone	33287	32612	33842	12	Shockey et al., 2009
Hippidion saldiasi	Betecsa	Chile	GrA-29389	21070	100	bone	25382	25110	25637	12	Alberdi et al. (2007)
Hippidion saldiasi	Betecsa	Chile	GrA-29388	21380	100	bone	25679	25431	25895	12	Alberdi et al. (2007)
Catonyx cuvieri	Gruta Cuvieri	Brazil	BETA 165398	9960	40	bone	11315	11223	11411	12	Neves & Pilo (2003)
Catonyx cuvieri	Lapa dos Tatus	Brazil	BETA 174688	14030	50	bone	16984	16708	17209	12	Neves & Pilo (2003)
Catonyx cuvieri	Lapa dos Tatus	Brazil	BETA 174689	13920	50	bone	16811	16552	17037	12	Neves & Pilo (2003)
Equus neogeus	Lapa da Escrivânia 5	Brazil	BETA 174711	16620	70	bone	20001	19741	20230	12	Neves & Pilo (2003)
Equus neogeus	Lapa da Escrivânia 5	Brazil	BETA 174712	16250	60	bone	19565	19340	19804	12	Neves & Pilo (2003)
Equus neogeus	Lapa da Escrivânia 5	Brazil	BETA 174713	16180	70	bone	19474	19230	19686	12	Neves & Pilo (2003)
Smilodon populator	Lapa da Escrivânia 5	Brazil	BETA-174722	9130	150	bone	10247	9739	10601	12	Neves & Pilo (2003)
Notiomastodon	Pilauco	Chile	UCIAMS101670	12725	40	bone	15108	14865	15278	12	Pino et al., 2008
Notiomastodon	Pilauco	Chile	UCIAMS101830	12760	50	bone	15153	14911	15330	12	Pino et al., 2008
Notiomastodon	Pilauco	Chile	UCIAMS101831	13220	60	bone	15835	15608	16065	12	Pino et al., 2008
Notiomastodon	Pilauco	Chile	TO11477	12540	90	bone	14697	14232	15107	12	Pino et al., 2008
Gomphotheriidae	Moteverde	Chile	OXA 105	12000	250	bone	13860	13274	14744	12	Dillehay (1997)
Gomphotheriidae	Moteverde	Chile	TX 3760	11990	200	bone	13817	13316	14433	12	Dillehay (1997)
Equus	Pilauco	Chile	GEOUACH55	11457	140	teeth	13260	13026	13547	12	Pino et al., 2013
Mylodontidae	Pilauco	Chile	UCIAMS101832	13165	55	dermal ossicle	15754	15490	16001	12	Pino et al., 2008
Mylodontidae	Pilauco	Chile	UCIAMS102087	13220	40	dermal ossicle	15836	15659	16029	12	Pino et al., 2008

Mylodontidae	Baño Nuevo	Chile	UCIAMS10107	12510	30	dermal ossicle	14636	14281	14969	12	Velasquez and Mena 2006
Mylodontidae	Baño Nuevo	Chile	UCIAMS10111	12400	30	dermal ossicle	14355	14131	14675	12	Velasquez and Mena 2007
Macrauchenia	Baño Nuevo	Chile	UCIAMS19491	11665	50	dermal ossicle	13452	13328	13567	12	Velasquez and Mena 2008
Tardigrada	Baño Nuevo	Chile	CAMS32685	11480	50	maxillary bone	13279	13145	13410	12	Velasquez and Mena 2009
Tardigrada	Baño Nuevo	Chile	UCIAMS10106	11265	35	dermal ossicle	13090	13011	13163	12	Velasquez and Mena 2010
Tardigrada	Baño Nuevo	Chile	UCIAMS10105	11255	30	dermal ossicle	13082	13014	13147	12	Velasquez and Mena 2011

Table A3.2: Radiocarbon dates on evidence of humans used in this chapter. All dates have been calibrated to calendar years using Calib 7.02 (Stuiver and Reimer 1986-2014). Dates were extracted from a compilation made by Goldberg et al., 2016. Dates on shells were excluded.

Site	Country	Materia dated	^{14}C lab code	^{14}C	±	Cal median	Cal young	Cal old	Reference
Ayamachay (Ac-102)	Peru	Charcoal	I-5694	7560	125	8318	8042	8548	Ziolkowski et al 1994
Cuncaicha	Peru	Collagen	AA-96336	8361	82	9317	9087	9491	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96337	8363	82	9320	9087	9492	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96331	8404	82	9360	9134	9523	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101132	8454	84	9416	9236	9543	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101131	8461	85	9422	9237	9545	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96329	8483	83	9446	9246	9553	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94255	10050	50	11492	11269	11718	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96321	10034	97	11502	11222	11828	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94257	10055	67	11510	11250	11772	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101137	10060	100	11539	11238	11838	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96318	10084	99	11572	11250	11845	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96330	10086	97	11573	11253	11845	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96319	10100	99	11597	11266	11962	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96322	10127	98	11643	11282	11991	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96306	10132	71	11653	11338	11969	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96312	10163	71	11721	11393	12009	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96309	10189	77	11772	11399	12035	Rademaker et al 2014
Cuncaicha	Peru	Collagen	PRI-12-029-06b	10180	40	11783	11601	12008	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94256	10200	69	11800	11592	12039	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-94255	10211	69	11820	11594	12051	Rademaker et al 2014
Cuncaicha	Peru	Collagen	PRI-12-029-04b	10205	35	11836	11697	12008	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96308	10260	72	11899	11605	12156	Rademaker et al 2014
Cuncaicha	Peru	Collagen	PRI-12-029-05b	10265	35	11911	11770	12040	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-96307	10306	72	12001	11750	12316	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101138	10310	100	12018	11611	12428	Rademaker et al 2014
Cuncaicha	Peru	Collagen	Beta-297423	10321	73	12039	11765	12317	Rademaker et al 2014
Cuncaicha	Peru	Collagen	AA-101130	10380	100	12170	11796	12439	Rademaker et al 2014
Hakenasa	Chile	Charcoal	I-13287	8340	300	9234	8509	9939	Moreno 2009
Hakenasa	Chile	Charcoal	B-187531	8789	60	9743	9545	9935	Moreno 2009

Hakenasa	Chile	Charcoal	B-187532	9170	70	10309	10187	10496	Moreno 2009
Hakenasa	Chile	Charcoal	B-187533	9260	60	10384	10243	10524	Moreno 2009
Hakenasa	Chile	Charcoal	B-187534	9520	70	10756	10559	10910	Moreno 2009
Hakenasa	Chile	Bone	B-187535	9580	40	10890	10698	10907	Moreno 2009
Hakenasa	Chile	Charcoal	UGAMS2953	9980	40	11343	11238	11415	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UGAMS-4588	8510	30	9492	9441	9531	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77765	8600	40	9530	9472	9564	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77764	8635	40	9549	9492	9662	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77767	8690	40	9601	9532	9701	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77766	8695	40	9605	9533	9704	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	UCIAMS-77768	8730	35	9630	9542	9749	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	QLH-S4-1	8785	30	9715	9582	9889	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	QLH-S4-2	8840	30	9821	9665	9946	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	QLH-S4-3A	8845	30	9829	9676	9948	Gayo et al., 2015
Ipilla 2	Chile	Charcoal	AA-34477	9090	75	10210	10112	10411	Gayo et al., 2015
Iroco	Bolivia	Collagen	AA91569	8105	92	8945	8640	9154	Capriles 2011
Iroco	Bolivia	Collagen	AA91568	8273	82	9208	9014	9426	Capriles 2011
Jaywamachay (Ac-335)	Peru	Charcoal	I-4500	8250	135	9174	8765	9491	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-4501	8360	125	9295	9021	9526	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5686	8500	125	9440	9088	9700	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5276	8645	140	9633	9302	9958	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5277	8980	140	10009	9560	10299	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5275	9460	145	10685	10277	11127	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5695	9560	170	10835	10374	11235	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5683	9890	310	11345	10489	12412	Ziolkowski et al 1994
Jaywamachay (Ac-335)	Peru	Charcoal	I-5699	10280	170	11942	11321	12439	Ziolkowski et al 1994
Las Cuevas	Chile	Charcoal	I-13128	8270	250	9155	8510	9698	Santoro & Chacama 1984
Las Cuevas	Chile	Charcoal	I-12835	9540	160	10810	10377	11214	Santoro & Chacama 1984
Puente (Ac-158)	Peru	Charcoal	I-5056	7420	125	8195	7965	8404	Ziolkowski et al 1994
Puente (Ac-158)	Peru	Charcoal	I-5057	8860	125	9882	9556	10187	Ziolkowski et al 1994
Quelcatani	Peru	Charcoal	Beta-18927	7250	170	8036	7701	8355	Rademaker et al 2013
Tojotojone	Chile	Charcoal	unknown	9609	30	10934	10738	11093	Gayo et al., 2015
Monte Verde	Chile	unknown	Beta-52012	6530	110	7392	7234	7578	Dillehay 1997
Monte Verde	Chile	wood	TX-4436	8030	130	8849	8538	9260	Dillehay 1997

Monte Verde	Chile	wood	BETA-6753	8270	110	9204	8976	9489	Dillehay 1997
Monte Verde	Chile	wood	BETA-59081	10330	160	12045	11400	12555	Dillehay 1997
Monte Verde	Chile	charcoal	TX-3207	10860	130	12733	12544	13029	Dillehay 1997
Monte Verde	Chile	wood	TX-3472	11600	120	13388	13121	13610	Dillehay 1997
Monte Verde	Chile	wood	BETA-52015	11640	90	13424	13224	13599	Dillehay 1997
Monte Verde	Chile	charcoal	BETA-68997	11800	80	13586	13441	13754	Dillehay 1997
Monte Verde	Chile	wood	TX-5374	11790	200	13592	13178	14053	Dillehay 1997
Monte Verde	Chile	wood	TX-5376	11920	120	13703	13459	14013	Dillehay 1997
Monte Verde	Chile	bone	BETA-68996	12000	110	13807	13552	14090	Dillehay 1997
Monte Verde	Chile	wood	TX-3760	11990	200	13817	13316	14433	Dillehay 1997
Monte Verde	Chile	collagen	OXA-105	12000	250	13860	13274	14744	Dillehay 1997
Monte Verde	Chile	wood	BETA-6755	12230	140	14113	13734	14763	Dillehay 1997
Monte Verde	Chile	charcoal	UCIAMS 10737	12450	40	14483	14169	14817	George et al 2005
Monte Verde	Chile	wood	BETA-65842	12420	130	14484	14034	15058	Dillehay 1997
Monte Verde	Chile	charcoal	UCR 4015	12450	60	14494	14149	14893	George et al., 2005
Monte Verde	Chile	charcoal	UCIAMS 10738	12455	40	14494	14175	14833	George et al., 2005
Monte Verde	Chile	wood	OXA-381	12450	150	14538	14031	15121	Dillehay 1997
Monte Verde	Chile	wood	UCR 4014	12510	60	14630	14240	15026	Dillehay 1997
Monte Verde	Chile	wood	TX-4437	12650	130	14888	14246	15315	Dillehay 1997
Monte Verde	Chile	charcoal	BETA-59082	12780	240	15096	14166	15845	Dillehay 1997
Monte Verde	Chile	charcoal	TX-3208	13565	250	16306	15574	17078	Dillehay 1997
Marfilo 1	Chile	charcoal	Beta-164476	7000	40	7787	7685	7868	Mera and Garcia 2004
Pucon VI	Chile	charcoal	Beta 36776	7650	80	8414	8295	8581	Navarro et al., 2010
Loconaco 2	Chile	unknown	Beta-195761	7810	50	8542	8422	8637	Garcia 2005
Marfilo 1	Chile	charcoal	Beta-138919	8420	50	9403	9269	9517	Mera and Garcia 2004
Marfilo 1	Chile	charcoal	Beta-164475	10190	120	11762	11268	12123	Mera and Garcia 2004
Pucon VI	Chile	charcoal	Beta 36998	10390	40	12208	12003	12318	Navarro et al., 2010