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INITIAL HUMAN DISPERSAL AND NATIVE FAUNA AT THE SOUTH AMERICAN SOUTHERN CONE, ARGENTINA. AN EXAMPLE CASE FROM THE REVISION OF THE FOSSIL COLLECTIONS

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Initial human dispersal and native fauna at the South American Southern cone, Argentina. An example case from the revision of the fossil collections

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I STATE that the present study, entitled "Initial human dispersal and native fauna at the South American Southern Cone, Argentina. An example case from the revision of the fossil collections", presented by Karina Vanesa Chichkoyan Kayayan for the award of the degree of Doctor, has been carried out under my supervision at the Department de Historia e Historia del Arte of this university.

Tarragona, 01 de Febrero de 2017

Doctoral Thesis Supervisors

Bienvenido Martínez Navarro

José Luis Lanata

Margarita Belinchón

I dedicate this dissertation to my beloved parents, who teach me
to fight for my convictions, the value of hard work
and the meaning of responsibility

Abstract

First dispersion in the Americas has particular characteristics: is the last of the bigger continental masses in being colonized by humans, dispersion is realized from higher to lower latitudes and higher latitudes again, and did not presented any hominids presence but *Homo sapiens*. The Americas also had a diverse and different fauna. Specially, South American had orders like the Xenarthra or Notoungulates that appeared during the Paleogene and survived several environmental fluctuations and invasion of Holartic species (known as GABI event). But at the end of the Late Pleistocene and the beginning of Early Holocene all the species of more than one tonne and most of the bigger mammals disappeared. This process, that extended several millennia, coincided with the environmental conditions produced after the Last Glacial Maximun (like changing climatic conditions and rise of the coast sea level) and *Homo sapiens* entrance. This coincidence between climate, extinctions and humans was (and still is) a much debated topic in the archaeology, palaeontology and human evolutionary ecology. Nevertheless, other aspects, such as the paleoecological relationships that humans developed with this fauna are less discussed. This topic, allows understanding how *Homo sapiens* intervened in an established native ecosystem that was never alter by hominid presence. The discussion of this aspect allows characterizing the existing trophic chain and describes the novel role that humans developed with different herbivore and carnivore species. Under this perspective, first human peopling in the Americas can be characterize as invasive, as *Homo sapiens* was a non-native species, with a fast dispersion that affected the established tropic chain, colonizing and/or modifying the existing niches.

Nevertheless, one of the causes of the lack of this type of debates, after decades of research, can be because of the scarcity of direct biological interventions (cut marks and carnivore marks) over megafauna bones. Even thought there is more evidence of association of humans and megaherbivores, there is almost an absence in the record related with carnivores. Thus just recently paleoecological relationship such as competition and predation between humans, megaherbivores and carnivores started to be considered. Given this lack of evidence, searching it in non-traditional sources in archaeological research, such as nineteenth collections of native fauna, is an alternative way to obtain new data.

These collections are the result of the commercialization of Pampean fossil native fauna developed between Argentina and different European museums from 18th to first decades of 20th century. The novelty of this fauna has caught the attention of the most important cientific researches of that time, such as Darwin, Cuvier, Owen or Ameghino, whose efforts were put in the taxonomic classification. But after the initial interest passed, they were kept in the shelves of the deposits of the museums. Even thought the exact place of encounter, associations or chronology can be absent or be general, this material can still give direct information of this type of interventions. When the material was extracted, the study of the marks was not done, or was done superficially, since the specific knowledge was not developed. More than one century latter of these transactions and with the technological advances of the related disciplines, these collections can give novel information and be interpreted at a coarse-grain scale

Taphonomy was used to differentiate biological marks from other surface modification, such as weathering, trampling, manganese precipitation, fluvial action or roots. Cut marks and carnivore marks were identified using, the information published in the different actualistic research and their position in the bones (morphological and configurational characteristics). Materials with anatomical and taxonomical identification, belonging to European and

Argentinean collections were selected. From two collections, indeterminated material was considered too, as they had more contextual information. The analyzed bones belong to different moments of the Pleistocene period. The fossil remains were examined with 3.5x and 12x magnifying glasses, the Dino-Lite Microscope AD4113T (at magnifications up to 120x) and the software Dino-Lite 2.0. Silicone casts were done over some bones (Provil Novo Light for the negative and Polyvinyl Siloxane for the positive) to be reviewed with the digital microscope Hirox KH-8700.

From the different reviewed collection a total of 6646 bones were examined. Human biological intervention was found over 46 bones (megafauna and smaller mammals), representing 0.69% of the material. Carnivore biological intervention was found in 29 bones (also of megafauna and smaller mammals) representing 0.43%. Megafaunal species with anthropical intervention was found in Mylodontidae, *Megatherium americanum* and Glyptodontidae, while Mylodontidae and Toxodontidae presented carnivore interventions. Over diaphyses and indeterminated bones of smaller species, both types of intervention where found. Considering the position of anthropic marks over megafauna bones, the main processing activities detected were: the separation of the cranial from the postcranial skeleton, disarticulation and filleting of apendiculars and, in Glyptodontidae, the processing of the muscles from the caudal vertebrae. These activities could have been realized by direct hunting and/or scavenging. Carnivore marks were registered in the epiphyses of long bones. The consumption of osseous tissue is indicating that megaherbivores should have been fully exploited, at least periodically, in hunting and/or scavenging events.

Considering the identified species with biological marks, humans should have depredate (or scavenge) over species that possessed defences to confront holartic carnivores (e.g. gigantism in *Megatherium americanum* case or armor in Glyptodontidae case). Smaller species of the megafauna, such as Mylodontidae, should have been exploited by carnivores and humans. In a hunting event, humans should have established new predation relationships over groups that were not hunted by native carnivores (*Megatherium americanum* o Glyptodontidae), while for Mylodontidae a new predator should have been added. In a scavenging event, humans should have been competing with carnivores for the carcasses. Nevertheless, as *Homo* genus was basically hunter since Early Paleolithic, the scavenging practice should have been marginal in the Americas.

It is concluded that after GABI event, carnivores should have consumed some taxa of the megafauna in different moments of the Pleistocene period. This situation was sustained thought time despite the environmental fluctuations should have influenced in the density and/or distribution of the populations. At the end of the Pleistocene, *Homo sapiens* entrance should have implied the addition of a new carnivore in the trophic chain. This new species not only could have scavenged, but also depredated in more effective ways (thanks to the technological innovations) over a major variety of fauna, even those ones not exploited by the native carnivores. Humans should have modified the existing ecological niches and colonized the empty ones, affecting the established competition and depredation relationships. *Homo sapiens*, as an invasive species, should have provoked direct and indirect impacts in the native trophic chain. In long term, this situation should have affected the sustainability of this ecosystem.

Resumen

La primera dispersión humana en las Américas tiene algunas características particulares: es la última de las grandes masas continentales en ser colonizada por los humanos, la dispersión se produce de latitudes altas, a bajas y nuevamente a altas y no presenció la entrada de homínidos más que de *Homo sapiens*. Las Américas también poseían una fauna diversa y diferente a otros continentes. En particular, la distintiva fauna de América del Sur, como los Xenarthra o Notoungulatas, que aparecieron durante el Paleógeno, sobrevivió a diversas fluctuaciones ambientales e invasiones de especies holárticas (lo que es conocido como el evento GABI). Sin embargo, hacia finales del Pleistoceno Tardío y principios del Holoceno Temprano todas las especies mayores a una tonelada y la mayoría de los grandes mamíferos (la megafauna) se extinguieron. Este proceso, que llevó varios miles de años, coincidió con los cambios ambientales sobrevenidos luego del Último Máximo Glaciar (como fluctuaciones climáticas, aumento del nivel de costas) y con la entrada de *Homo sapiens*. Esta coincidencia entre clima, extinciones y humanos fue (y sigue siendo) uno de los temas más controversiales dentro de la arqueología, la paleontología y la ecología evolutiva humana. Sin embargo otros aspectos de la entrada humana y la fauna nativa son menos discutidos. Entre ellos, las relaciones paleoecologicas que los humanos desarrollaron con esta fauna es una temática que permite entender cómo *Homo sapiens* intervino en un ecosistema nativo establecido y que nunca había sido alterado por la presencia homínida. Esto es sumamente provechoso, porque no solo permite caracterizar a gran escala la cadena trófica existente, sino que describe el rol inédito que los humanos desarrollaron con las distintas especies herbívoras y carnívoras. Bajo esta perspectiva, el primer poblamiento humano en las Américas puede ser caracterizado como de invasivo, ya que esta especie no nativa, tuvo una rápida dispersión afectando la cadena trófica conformada, colonizando y/o modificando nichos existentes.

Sin embargo, una de las causas de la falta de este tipo de debates, luego de décadas de investigación, pueda deberse a la escasez de marcas biológicas (huellas de corte y marcas de carnívoros) sobre restos de megafauna. Si bien hay mayor evidencia de asociación entre humanos y megaherbivoros, las tafocenosis que vinculan a carnívoros son prácticamente nulas. En consecuencia, sólo recientemente las relaciones paleoecológicas de competencia y depredación entre humanos, megaherbivoros y carnívoros empezaron a ser consideradas. Ante la falta de marcas biológicas, buscar este tipo de información en fuentes no tradicionales dentro de la investigación arqueológica, como las colecciones decimonónicas de fauna nativa, es una manera alternativa de obtener datos.

Estas colecciones son el resultado de la comercialización de fósiles pampeanos de fauna nativa, que se desarrolló entre Argentina y distintos museos europeos desde el siglo XVIII a las primeras décadas del siglo XX. La novedad de estas faunas, llamó la atención a los científicos más importantes de la época, como Darwin, Cuvier, Owen o Ameghino, entre otros, que se abocaron a su clasificación taxonómica. El cambio de intereses en la subsiguiente parte del siglo XX llevó a que estos materiales pasaran a formar parte de los fondos museísticos. A pesar de que el lugar de hallazgo, asociaciones, posición estratigráfica o cronología, pueden estar ausentes o ser generales, este material puede brindar información directa de este tipo de intervenciones. Cuando se excavó, el estudio de marcas biológicas no se hacía o se realizaba de forma somera ya que no se tenían los conocimientos suficientes al respecto. A más de un siglo de estas transacciones, y con los adelantos tecnológicos en la materia, estas colecciones pueden aportar datos inéditos, y ser interpretados a gran escala.

Se hizo uso de la tafonomía para diferenciar intervenciones biológicas, de otro tipo de modificaciones como las realizadas por los efectos de la meteorización, el pisoteo, la precipitación de manganeso, la acción fluvial y las raíces, entre otros. Se consideraron las huellas de corte y marcas de carnívoro según lo descripto en distintos trabajos actualísticos y según su posición en los restos óseos (características morfológicas y configuracionales). Se estudiaron huesos pertenecientes a colecciones europeas y argentinas de distintos momentos del Pleistoceno, que tuviesen identificación anatómica y determinación taxonómica (a excepción de dos colecciones donde, gracias a su mayor contextualización, se consideraron fragmentos indeterminados). Se utilizaron lupas de mano de 3,5X y 12X, el microscopio Dino-Lite AD4113T (y su software Dino-Lite 2.0) con aumentos de hasta 120X. Sobre algunos huesos se han realizado moldes de silicona (con Provil Novo Light para el negativo y Polyvinyl Siloxane para el positivo) para ser revisados con el microscopio digital Hirox KH-8700.

Se han revisado un total 6646 huesos en las distintas colecciones visitadas. Se han registrado 46 huesos con huellas antrópicas (megafauna y fauna menor), lo que representa un 0.69% del material con este tipo de intervención. En cuanto a las marcas carnívoras, se han encontrado 29 huesos de megafauna y grupos menores, representando un 0.43% del total. En la megafauna, se han registrado huellas antrópicas en Mylodontidae, *Megatherium americanum* y Glyptodontidae, mientras que las marcas carnívoras fueron registradas en Mylodontidae y Toxodontidae. Además, en diáfisis e indeterminados de especies menores se han registrado ambos tipos de marcas. A partir del análisis de la posición de las huellas de corte en la megafauna, las principales actividades identificadas fueron la separación del esqueleto craneal del postcraneal, la desarticulación y fileteado de apendiculares, como también, en Glyptodontidae, el procesamiento de músculos adheridos a las vértebras caudales. Este tipo de actividades se podrían haber llevado a cabo por caza directa o por carroñero. En cuanto a las marcas carnívoras, se registraron principalmente en epífisis de huesos largos. El consumo de hueso en los casos analizados, estaría indicando que los megaherbivoros habrían sido, al menos periódicamente, consumidos en forma completa, tanto en eventos de caza como de carroñeo.

A partir de las especies registradas, los humanos habrían depredado (y/o carroñado) sobre especies que poseían defensas desarrolladas para confrontar carnívoros holárticos (por ejemplo gigantismo en el caso de *Megatherium americanum* o coraza en Glyptodontidae) mientras que especies más pequeñas dentro de la megafauna (Mylodontidae) habrían sido explotada por carnívoros y humanos. En consecuencia, en un escenario de caza, los humanos habrían establecido nuevas relaciones de depredación sobre grupos no cazados por los carnívoros (*Megatherium americanum* o Glyptodontidae), mientras que, para el caso de Mylodontidae se habría agregado un nuevo depredador. En este caso, además, los humanos habrían competido con los carnívoros por este taxon. En un escenario de carroñeo, los humanos habrían sido competidores de los carnívoros por los cadáveres. Sin embargo el género *Homo* fue básicamente cazador desde el Paleolítico Inferior, por lo que una estrategia de carroñeo sería una práctica marginal en la entrada a las Américas.

Se concluye que luego del evento GABI, los carnívoros habrían explotado algunos taxones de esta megafauna en distintos momentos del Pleistoceno. Esta situación se mantuvo a pesar de las fluctuaciones ambientales, que habrían influido en la densidad y/o distribución de las poblaciones. Al final de este período, el ingreso de *Homo sapiens*, supuso añadir un nuevo carnívoro en la cadena trófica. Esta especie no solo habría carroñeado, sino que, gracias a su tecnología, habría cazado en forma más efectiva una mayor variedad de especies, muchas de ellas, no explotadas por los carnívoros presentes. Es así que la presencia de grupos humanos, habría modificado los nichos ecológicos existentes y habría colonizado nichos vacantes, afectando las relaciones de competencia y depredación establecidas dentro del ecosistema. *Homo sapiens*, como especie invasora, habría provocado impactos directos e indirectos en la cadena trófica nativa, lo que a largo plazo habría afectado la sustentabilidad de este ecosistema.

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The most dangerous predator of all.....
John Locke
(LOST, 01x13)

INSTUTIONS ABBREVIATIONS

Museo de Ciencias Naturales de Valencia: MCNV
Museo Geologico Giovanni Capellini di Bologna: MGGCB
Museo Civico di Storia Naturale di Milano: MCSNM
Museo Regionali di Scienze Naturali di Torino: MRSNT
Museo di Storia Naturale di Firenze: MSNF
Natural History Museum (London): NHM
Muséum d'Histoire Naturelle de la Ville de Genève: MHNVG
Paläontologisches Institut und Museum (Zürich): PIMUZ
Naturhistorisches Museum Wien (Vienna): NMW
Museum für Naturkunde (Berlin): MN
Statens Naturhistoriske Museum (Zoologisk Museum) (Copenhaguen): ZMK
Muséum National d' Histoire Naturelle (París): MNHN
Museo Argentino de Ciencias Naturales Bernardino Rivadavia: MACN
Museo Municipal de Ciencias Naturales Carlos Ameghino: MCA
Museo de La Plata: MLP

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1. INTRODUCTION

Different topics have been surveyed in this thesis in order to deepen our knowledge on one complex subject: human dispersal in the Americas and its relationship with the native megafauna. Historical fossil collections from the Pampean region of Argentina (Figure 1.1) have been analyzed to search for different types of biological marks/interventions[1]. Those collections are housed in different European museum (Figure 1.2). During the 19th century, scientific research was relying on those assemblages. However nowadays, they remain unsearched in drawers and shelves of the deposits, because they are considered as they can't provide new information besides paleontological research. In addition to the European collections, Argentinean institutions, such as Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Museo Municipal de Ciencias Naturales Carlos Ameghino and Museo de La Plata were visited, allowing to have a sample of the historical collections conserved in that part of the world. Questions from History to Ecological systems have been integrated: from fossil megafauna's commerce in the 19th century to how these animals could have interacted in the past among themselves and with the new recently arrived humans. Paleontological, archaeological, ecological and taphonomical tools will be used. Also, political, economic and, even, national identity issues will be incorporated. Current revision of fossil collections under the novel academic standards is necessary to revalorize this type of patrimony from new perspectives, and most of all because they provide a new perspective on today´s problematic with fresh data and ideas to this complex thematic that is still on the eve of its research (compared with other parts of the world as Europe or Africa).

Human development supposes a different relation with the rest of the ecosystem. The creation of sophisticate tools and implements for food intake implied an innovative resource in species evolution. Thus, *Homo* behavior is divergent in comparison with the rest of the species (Carbonell et al. 2010). On the contrary, dispersal into different paleoenvironments is a characteristic that our species and most of the vertebrate fauna shared (Martínez-Navarro and Palmqvist 1995, 1996; Arribas and Palmqvist 1999; Martínez-Navarro 2010; Martínez-Navarro and Rabinovich 2011). *Homo* records are extensively characterized by moving across different landscapes, especially *Homo sapiens* whom has occupied different latitudes through time (Erlandson 2001).

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[1] Biological marks/interventions will be the denomination used along this work to refer both to carnivores and humans marks

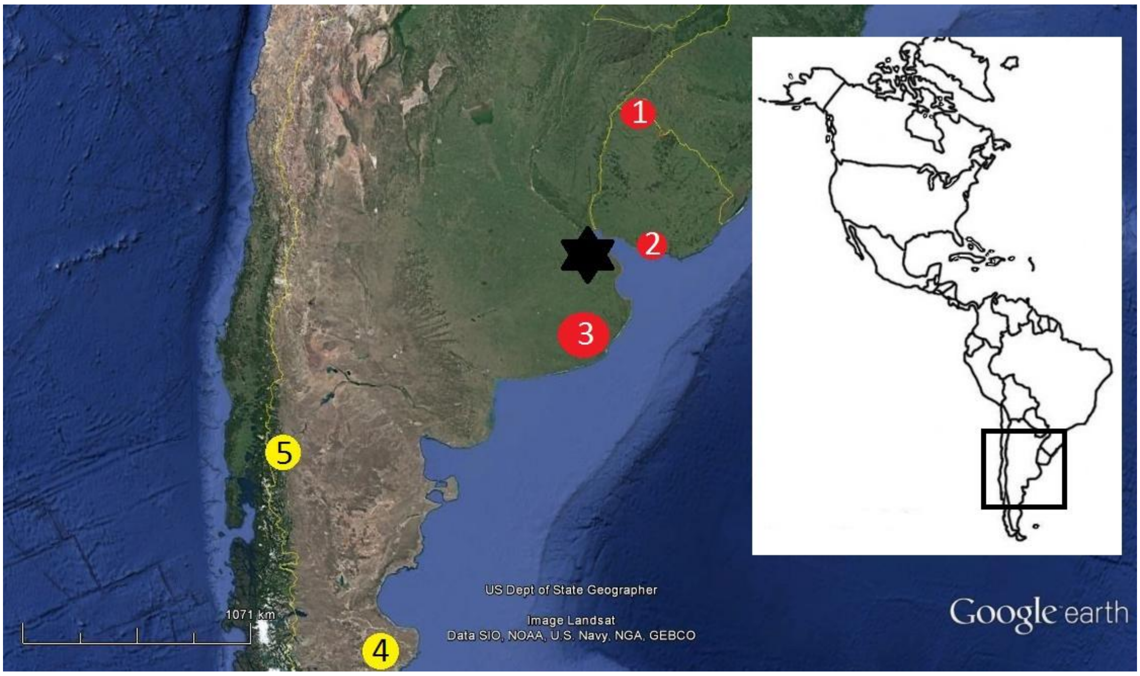

Figure 1.1. Sites with megafauna associations named in Table 1.1 (see below). Points in red Pampean sites: 1. Pay Paso; 2. Arroyo del Vizcaíno; 3. Arroyo Seco 2, Campo Laborde, La Moderna, Paso Otero 5 (general localization). Points in yellow Patagonian sites in Argentina: 4. Casa del Minero, Cueva Túnel, Piedra Museo AEP-1, Los Toldos (general localization); 5. El Trébol. The star indicates De la Plata Basin, the general provenance of the reviewed collections.

Human dispersal in the Americas is specific for several reasons. This big part of emerge land extend latitudinally and was not occupied by any other type of hominin species (Martin 1973; Goebel et al. 2008; Lanata 2011; Pitbaldo 2011). Compared with the worldwide human dispersion (except for Australia and some islands), this situation was new for *Homo*. Indeed, during the Pleistocene they moved to partially hominins occupied continents, as Africa with *Homo ergaster*, Europe with *Homo antecessor*/ *Homo neanderthalensis* and Asia with *Homo erectus*. In opposition, *Homo sapiens* have crossed from Asia to America during the Late Pleistocene, between 30ka and 15ka[2] (Surovell et al. 2005; Goldberg et al. 2016), arriving to South American Southern cone as early as 14.500 or even 19.000 cal BP (Dillehay 2009, Dillehay et al. 2016). In general terms, it coincides with the colder and arid paleoenvironmental conditions of the Last Glacial Maximum (18/20 ka) (Rabassa et al. 2005). Thus, American peopling is a peculiar case given late entrance of human in unprospected hominins lands. Besides, this continent also contained novel resources for humans. Not only as for the floristical, marine and medium mammals' variety, but also because American isolation implied the development of a different native fauna characterized by its big and diverse forms (Patterson and Pascual 1968; Cione et al. 2009; Vizcaíno et al. 2012; Fariña et al. 2013).

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[2] Dating will be quoted as published given the different procedures authors use to present the chronology (calibrated or not calibrated)

Large mammals of more than 44 kg, and megamammals of more than 1000 kg have dominated this continent during the Cenozoic. Through the Pampean region during the Pleistocene- Holocene times, at least 83 species distributed in 48 genera lived. But between 20.000 to 10.000 BP (probably 7.000 BP) 52 species distributed in 38 genera have gone extinct: 100% megamammals and 80% of large mammals. Consequently American faunal diversity is astonishingly different from the past one (Fariña 1996; Cione et al. 2009; Vizcaíno et al. 2012; Fariña et al. 2013). These communities were affected by the changing environmental conditions when humans appeared. Thus humans/climate factors, or combination of both causes, have been the most discussed events which have influenced this extinction episode (Martin 1973; Graham and Lundelius 1984; Coltorti et al. 1998; Anderson and Gillian 2000; Alroy 2001; Prado et al. 2001, 2015; Barnosky et al. 2004; Brook and Bowman 2004; De Vivo and Carmignotto 2004; Diniz-Filho 2004; Fiedel and Haynes 2004; Koch and Barnosky 2006; Burney and Flannery 2005; Surovell et al. 2005, 2016; Miotti 2006; Haynes 2007; Borrero 2008; Gutiérrez and Martínez 2008; Cione et al. 2009; Sodhi et al. 2009; Lanata 2011; Lorenzen et al. 2011, Pitblado 2011; Borrero and Martin 2012; Fariña et al. 2014a, Abramson et al. 2015; Grayson and Meltzer 2015; Bartlett et al. 2016; Monjeau 2016; Martínez et al. 2016, among others).

Nevertheless, paleoecological relationships between the different species composing this stock of native fauna with the recently arrived humans have been discussed in shallower way (Abramson et al. 2015). To a certain extent, this is because of the scarce and feeble association of early archaeological and paleontological sites found, that allow to infer how carnivores/herbivores and humans could have relate. Due to this lack of solid evidences, researchers have mainly focused their studies on the description of new species and the geographic distribution and phylogenetic relationships among those species (Patterson and Pascual 1968; de Paula Couto 1979; Hoffstetter 1981; Alberdi et al. 1995; Cione and Tonni 1995; Gaudin 1999; Bargo 2003; Miño-Boilini et al. 2006; Fernicola 2008; Gaudin et al. 2008; Soibelzon et al. 2008b; Delsuc and Douzery 2009; Krmpotic et al. 2009; Mcafee et al. 2009; Miño-Boilini and Carlini 2009; Elissamburu 2012; Hubbe et al. 2013b; Scanferla et al. 2013; Soibelzon et al. 2010; among others). The consequence is that little is known about the interactions of these groups of mammals with the first *Homo sapiens* dispersal in the Americas. Consequently, the core of subject treated here is to consider the interaction between human and its faunal environment, and predators with megafauna as it haven't been prospected in the 19th collections.

Then, the first issues we have raised and proposed to solve are the following: what were the relationships between carnivores and these large mammals and megamammals herbivores before humans' presence? Which types of relationships have been established between humans and this native fauna? How humans have influenced or modified the ecological niches? What have been the consequences of those interactions?

Fossil museums, if we had to focus on then only, will not have provided all the answers. But integrated into a wider framework, including other disciplines and taphonomic research will be essential to explore these interrogations at a coarse-grained level. Consequently this bias of information of this material has been taken into account and, as it will be developed further, they were minimize through a new approach or the combination of other field's methodology.

1.1. WHY TO REVIEW PALEONTOLOGICAL COLLECTIONS: THEIR IMPORTANCE FOR CURRENT RESEARCH

American environments have attracted European attention since the Spanish "discovery", in 1492. People, fauna and flora were part the mysteries that this "new land" cover for the European peopling (Galeano 2000 [1971]; Powells 2005; Salzano 2011; Mazières 2011). Especially, during the 18th century, discoveries of non-identified mammals' skeletons throughout the Pampean region (especially in the Southern East of de la Plata Basin, currently Buenos Aires Province) (Figure 1.1) started to be known. Consequently, a profuse fossil commercial trend between this country and Europe followed during the 19th century (Hoffstetter 1981; López Piñero and Glick 1993; Podgorny 2000, 2001a, 2011; Fucks et al. 2008; Ottone 2008; Fernicola et al. 2009; Pasquali and Tonni 2008; Toledo 2009; Cowie 2011). But, as the enthusiasm from the novelty petered out, this trade slowly faded away. Nowadays, the results of those uncontrollable picking remain housed in the deposits of different museums, as a testimony of that era (Figure 1.2). Some of the most bigger or complete specimens have been assembled and are now exposed. Therefore they continue to amaze the audience, but regarding the modern standard of scientific research, they are outdated. Even though they were used as primary material in different research, especially paleontological ones, they are practically not used in current archaeological debates (Christiansen and Fariña 2003; Christiansen and Harris 2005; Christiansen and Wroe 2007; Krmpotic et al. 2009; Miño-Boilini and Carlini 2009; Straehl et al. 2013; Welker et al. 2015, for some paleontological studies based on museum collections).

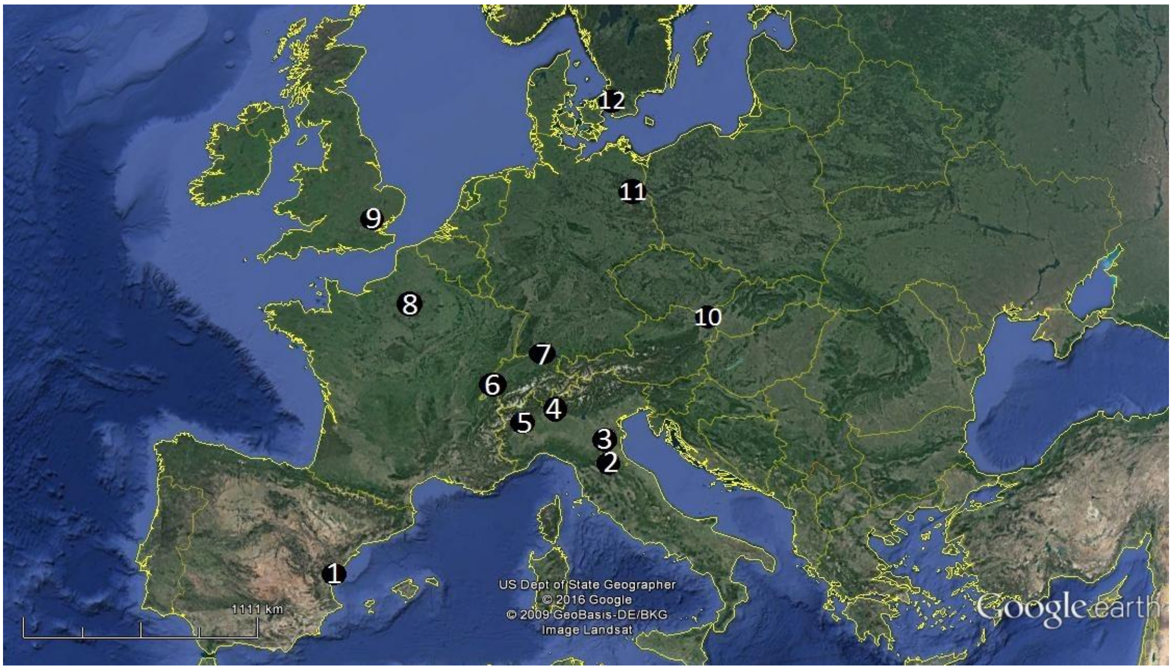

Figure 1.2. European museums with megafauna collections reviewed: 1. Museo de Ciencias Naturales de Valencia, 2. Museo di Storia Naturale di Firenze; 3. Museo Geologico Giovanni Capellini di Bologna; 4. Museo Civico di Storia Naturale di Milano; 5. Museo Regionali di Scienze Naturali di Torino; 6. Muséum d'Histoire Naturelle de la Ville de Genève; 7. Paläontologisches Institut und Museum, Zurich; 8. Muséum National d' Histoire Naturelle, Paris; 9. Natural History Museum, London; 10. Naturhistorisches Museum Wien, Vienna,; 11. Museum für Naturkunde, Berlin; 12. Statens Naturhistoriske Museum (Zoologisk Museum), Copenhagen.

The principal causes are to be found in their feeble proveniences and context associations (Figure 1.3). Unlike other archaeological and paleontological deposits (which convey post-depositional process) they also convey important anthropogenic bias. On the one hand, bone assemblages pass through different natural process that implies the transformation of the original deposition. These natural processes can destroy the evidence, but they also contribute with new information to fossil assemblages (Behrensmeyer and Kidwell 1985; Kidwell and Behrensmeyer 1988; Fernández-López 2000; Denys and Patou-Mathis 2014). Therefore bones surviving to biostratinomy and fossildiagenesis filters are information carriers. Not only do they inform about past conditions of burial, but this data is useful to make paleoecological assumptions at different scales (Behrensmeyer 1978; Behrensmeyer and Kidwell 1985; Fernández-López 2000; Fernández-López and Fernández-Jalvo 2002). Fossil collections were also subject to equal biostratinomy and fossildiagenesis filters that scattered, eroded and buried the bones. However they also added paleobiological information, as it happens with all past assemblages.

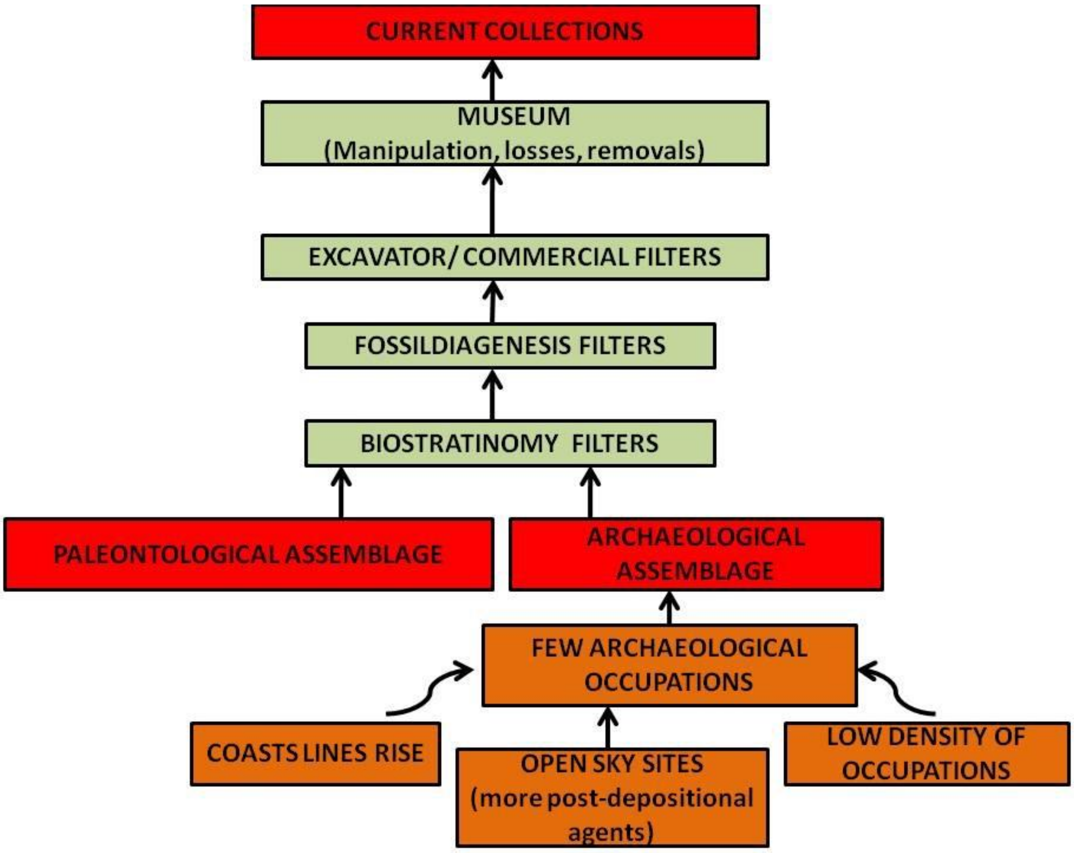

Figure 1.3. Conformation of current collections. Both paleontological and/or archaeological assemblages could have been excavated for commercialization. In this last case, the low amount of archaeological sites given the rise of the coast lines is to be considered, also the presence of open spaces that could have suffer for more post-depositional agents and the low density of occupation considering at a continental space (these factors will be explained in the next chapter). Paleontological/ archaeological assemblages suffer from biostratinomy and fossildiagenesis filters as with all the assemblages. To them, excavator and commercialization filters must be added. At last, when housed in the museums, the collection suffered of different historical aspects that also affected their compositions.

On the other hand, to these two filters must be added also anthropogenic ones, as excavation and merchandising. During the 19th century trafficking operations, importance was given to the monetary side of fossil extraction. When the material was extracted, the focus was put on the most complete specimens or elements given that museums paid more for them. Consequently fragments or possible associations were ignored. An alternative strategy was that collectors usually tried to complete specimens with bones from different individuals (Podgorny 2000, 2001a, 2011; de Renzi 2002). This situation implied that control of biological mark was not usually realized or, consideration of the information that these fossils could have render was generally ignored. In addition, excavation localities were sometimes informed, along with a general topographical reference, but not always. Competition and conflicts among different researchers and excavators, participation of scientific or natural voyagers but also amateurs, and the development of a big network of fossil traffic, were variables that influenced in the low specific localization of the fossils deposits (Podgorny 2000, 2005, 2011). In this network, personal interests, financial issues, scientific recognition and competition interweave. Exceptions to this situation can be found in some academic researchers that made their own excavations and had certain control, as Ameghino's case, an important Argentinean paleontologist. His research focused on the coexistence of humans and this native fauna. Consequently in some of his works, he used to publish along with the descriptions of the bones, references of the context, the stratigraphical position and association of the material (Ameghino 1915 [1880]).

Thus, these collections are the final product of what excavators rescued, what it was offered by the commercial sponsors and what museums wanted to buy (Wolff 1975; de Renzi 2002; Podgorny, 2001a and b, 2011; Turvey and Cooper 2009). Anthropogenic bias has deepened the disassociation with the primary context or provenience of these collections. Above all, over the last 150 years, losses of records, removal of the deposits and even wars have deteriorated this fragile contextual association. However, those weaknesses do not mean that the collections can't provide us new informations. Fossil collections in general are archives of past diversity (Allmon 1997; de Renzi 2002; Suarez and Tsutsui 2004). Their maintenance consumes space, staff and curation (Allmon 1997). Revision of this type of collections can save money and time and is a firsthand resource. Fossil collections have turned a good investigation realm for paleontology, but also to genetics, biology and even global climate change (Suarez and Tsutsui 2004). Consequently their study for archaeology cannot be ignored. In this sense, the last decades have increase investigation on lithics, ceramics and historical fossil collection from archaeological and paleontological sites in different parts of the world (Saunders 1977, 2007; Haynes 1980; Prous 1986, Saunders and Daeschler 1994; Pérez de Micou 1998; Balesta and Zagorodny 2000; Labarca 2003; Perez et al. 2005; Gordón 2008; Martin 2008; Bonomo et al. 2009; Fisher 2009; Toledo 2009; Dominato et al. 2011; Chichkoyan 2013, 2016; Huster 2013; Redmond et al. 2012, Dowd and Carden 2016).

Especially in relationship with fossil collections, reviewing material from old archaeological excavations has been a more extended practice:

(i) In North America, Saunders and Daeschler (1994) and Saunders (1977, 2007) had reviewed several old Clovis excavations with *Mammuthus columbis* associations. Saunders and Daeschler (1994) reviewed the collection of Blackwater Draw excavated in 1936 and 1937. Lehner discover in 1955-1956 and Dent in 1932-1933 were reviewed by Saunders (1977, 2007).

(ii) In Brazil, Prous (1986) reports 2 bones with cut marks discovered in paleontological collections.

(iii) Also Labarca (2003) has inspected old excavations from Quereo, Chile. He found some bones of *Cuvieronius hyodon* with human and carnivore marks.

(iv) In the South American Cone, Bonomo et al. (2009) have analyzed different collections excavated at the late 19th- early 20th centuries in Delta del Paraná, Argentina. The authors emphasized that material from these early campaigns cannot be ignored, although they are decontextualized, and they have to be integrated to current research (Bonomo et al. 2009:70).

(v) Borrero et al. (1989) and Martin (2008, 2013, 2016) reviewed collections of Cueva Mylodon in Chile. Carnivores marks were found that passed unnoticed to the original excavators.

(vi) Recently Dowd and Carden (2016) have described a cut-marked patella of a brown bear from Ireland. Although this intervention was noticed by the original excavators, the material was “forgot” in boxes since 1920 in the National Museum of Ireland.

Other authors have reviewed paleontological findings where they found both human and carnivore intervention.

(i) In relation with carnivore marks, pioneer work of Haynes (1980) had reviewed several museums’ collections with low contextual information where he found bones with carnivore intervention.

(ii) Perez et al. (2005), for example, found cut-marked bones of giant lemurs in Madagascar. The authors stated that given low record of direct evidence of butchery in that country, paleontological collections are susceptible in having human intervened bones. Focus must be put especially in collections coming from regions where other types of indicators reveal human presence (Perez et al. 2005:724).

(iii) Also, some of the collections that will be mention in this work have been previously analyzed and anthropic cut-marked bones were found (Toledo 2009). Nevertheless, detailed analysis of the evidence and integration with carnivore marks has to be deepened.

(iv) Revision of specimens housed in North American museums with low context information has revealed cut marks in a foot of a mastodon (Fisher 2009) and in a femur of *Megalonyx jeffersonii* (Redmond et al. 2012). The first one was previously reported without marks, but they appear when the exposed skeleton has being cleaned.

(v) Particularly, previous works realized over the Rodrigo Botet Collection housed in the Museo de Ciencias Naturales de Valencia (Chichkoyan 2011, 2013; Chichkoyan et al. 2013, 2015) have revealed cut-marked bones. Nevertheless focus was put only on human intervention, what resulted in having partial picture of past relationships among mammals. Also in that work indeterminate fragments and plates were taken into account. But if this evidence is considered then, the contribution of identify biologically intervened bones is diluted and the final numbers are unnecessarily inflate.

(iv) Dominato et al. (2011) have found *Protocyon troglodytes* marks in *Haplomastodon waringi* bones in an assemblage excavated in 1944.

Even thought the last decades have seen the publication of some works regarding the study of fossil collections assemblages, this type of evidence generally lacks of confidence in the research community, especially when referring to anthropic intervention (e.g. Hubbe et al. 2013b; Borrero 2015; Grayson and Meltzer 2015). Nevertheless cut marks are the most direct evidence of faunal exploitation (Yravedra et al 2012) (and this logic can also be assume for carnivore marks).

Consequently it is true that the information obtained from collections will not have the same resolution as systematic excavated materials. The low context information as associations, stratigraphy position or sedimentary matrix go against a fine-grained analyses and data interpretation are indeed be limited. However, last decades have advanced with new methodologies and techniques that can help to extract valuable data (Fariña et al. 2014b). Definition of different surface modification as weathering, trampling, chemical corrosion, fluvial erosion among others, helps to differentiate biological interventions (Behrensmeyer 1978; Binford 1981; Shipman 1981a and b; Shipman and Rose 1983a, 1988; Olsen and Shipman 1988, Lyman 1994; Fisher 1995; Stiner et al. 1995; Coard 1999; Denys 2002; Fernández-Jalvo and Andrews 2003, 2016; Alcántara 2006; Domínguez-Rodrigo and Barba 2006; Domínguez-Rodrigo et al. 2009; López-González et al. 2006; Denys and Patou-Mathis 2014, among others). Also different morphological and configurational features have been defined during the last decades in order to detect human interventions (Shipman and Rose 1983a; Binford 1981; Fiorillo 1989; White 1992; Lyman 1994; 2005; Fisher 1995; Domínguez-Rodrigo et al. 2009; 2010; Merrit 2015; Fernández-Jalvo and Andrews 2016; among others). Several actualistic works have identified the type of marks that carnivores can leave over bones when feeding (Haynes 1980, 1983a; Binford 1981; Lyman 1994; Borrero et al. 2005; Martin 2008, Muñoz et al. 2008; Saladié et al. 2013; Yravedra et al. 2011; Domínguez-Rodrigo et al. 2012; Burke 2013; Arilla et al. 2014; Sala et al. 2014; Kaufmann et al. 2016; Sala and Arsuaga 2016). Consequently current research posses the instruments and knowledge to detected and characterize biological interventions in these assemblages. Thus, albeit the diverse filters these collections have passed through, they are still useful for current axis of investigation.

In addition, fossils collections are highly useful for dissemination, institutional aspects and scientific research, as explained in the published article below. This work is the result of an oral communication in the XVII UISPP Congress in Burgos, 2014, in the session “International Relations in the History of Archaeology”.

1.1.1.FROM FAR AWAY: MUSEUMS, COLLECTIONS AND SCIENTIFIC RESEARCH

From far away: museums, collections and scientific research

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Abstract

The 19th-century South American fauna fossil collections currently held in Europe were part of the transactions carried out between these two continents at a time when the former looked forward to being included in the economic system and the latter needed new areas in which to expand. Today these collections are being used for different purposes including dissemination, institutional aspects and research. In this way, despite its decontextualisation, this material can provide archaeology with new data. The taphonomic analysis carried out on the Rodrigo Botet Collection in the Natural Science Museum in Valencia (Spain) is an example of this new focus. Thus, these old collections are being given new value in the today's scientific research.

Key-words: *19th century, Pampean Region, international transactions, Rodrigo Botet Collection*

Résumé

Les collections du XIX siècle de fossiles sud-américains de faune indigène déposés en Europe faisaient partie de transactions réalisées quand la première région cherchait de s'insérer dans le système économique et la deuxième avait besoin de nouveaux espaces pour développer. Actuellement, ces collections ont des utilisations différentes dans des domaines tels que la diffusion, institutionnel et de recherche. Ainsi, en dépit de sa contextualisation, ce matériau peut fournir de nouvelles données pour l'archéologie. L'analyse taphonomique dans la collection Rodrigo Botet déposé au Musée des Sciences Naturelles de Valencia est un exemple de cette nouvelle orientation. Par conséquent, ces anciennes collections sont réévalués pour la présente recherche.

Mots-clés: *Dix-neuvième siècle, Pampa, Transactions internationales, Collection Rodrigo Botet*

1. Introduction

The 19th century was characterised by several large migratory movements from Europe to South America, especially to Argentina (Devoto 2003). This also included the exchange and storage of fossil materials in different museums, as happened, for example, to the Pampean palaeontological collections, which were taken to Europe (Podgorny 2000, 2001). These collections are now to be found in several museums and institutions many miles away from their points of origin. They are witnesses of a crucial era in the formation of the modern world, as they were moved for political, economic and scientific reasons that developed at the time.

The aim of this paper is to analyse the international movement of museum collections in the nineteenth and early twentieth centuries and the context in which this took place. The use of these collections today will be examined, looking at dissemination, institutional and research aspects. With reference to this last point, in spite of their lack of context, modern techniques can allow new data to be obtained from them (Chichkoyan 2011; Chichkoyan *et al.* 2013, 2015). The research carried out at the Natural Science Museum of Valencia, Spain, where Rodrigo Botet's collection is kept, is an interesting example of this. The study of this material has contributed new data to the question of the first peopling of the Americas and its impact on the original palaeolandscape (Chichkoyan 2011, 2013; Chichkoyan *et al.* 2013, 2015).

2. The origin of South American collections in Europe

The South American mammal collections, especially those from the Pampas, Buenos Aires, were formed in the late 18th century and throughout the 19th century (Podgorny 2000, 2001; Cowie 2011).

These collections represent a special period in the formation of the different nations all over the world. In fact, the independence of the Spanish Empire in 1810 was very significant for the incorporation of Argentina (and the rest of the South American countries) into the global commercial/political terrain (Devoto 2003). Meanwhile, Europe was marked by colonial and internal wars, the industrial revolution and scientific developments (Hobsbawm 2009, 2010).

The 19th century was a period of transition for Argentina during which the independence movements of the 1810s, internal struggles for political power and the constitution of the modern state in 1880 took place (Devoto 2003). At the same time, knowledge of its land, its natural wealth and its past increased. The land was first explored by missionaries and then by foreign and local naturalists (Podgorny 2000, 2001; Cowie 2011). The finding of the *Megatherium americanum* in the Luján River in 1787 revealed the considerable potential of these lands for fossil hunting. The observations made by Darwin in the Pampean and Patagonic territories during the 1830s reinforced this idea (Podgorny 2000). At the end of the century, Florentino Ameghino, a local scientist and heir to Darwin's intellectual ideas, extended the classification of the Pampean fossils. He also postulated the tertiary origin of humanity in the Pampean region (Pérez Gollán 1995; Bonomo 2002). His controversial ideas were widely heard and many contemporary scientists came to check his findings. Ameghino also travelled to Europe, where he met the best European scientists of the day (Bonomo 2002).

Ameghino's work had some influence on the liberal political project of the last decades of the 19th century, which was designed to modernise the country using Europe as a model. To do this it was considered necessary to educate the workers and the political class invested not only in education but also in establishing good museums and expanding existing ones. In them evolutionist ideals justified the need to 'civilise' the country (Pérez Gollán 1995; Perazzi 2008). All these events led the Pampean region to become known in Europe, which led to the development of a trade network in native fauna (Podgorny 2000, 2001). The network had a very good exploration and extraction system, with instructions being given about deliveries and travellers and scientists who participated in selection of the material to be sent. This same network was supported and facilitated by the government.

Parallel to this, Natural Science Museums began to be opened in Europe and the exploration that was taking place in the New World provided information about the exploitable resources there (Podgorny 2000, 2001; Cowie 2011). For this continent, the development of knowledge of the past went hand-in-hand with the exploratory voyages of the 18th and 19th centuries, which implied the link with unknown ways of life (Hobsbawm 2009; Cowie 2011). Moreover, the discovery of human fossils and stone tools in different European locations was also important because it added to the discussion about human origins, which until then had always been explained from a religious point of view (Hobsbawm 2009). Darwin and his evolutionist ideas on species gave a vital boost to the consolidation of the natural sciences as the way of learning about the past and to justify the system of progress prevailing those days (Hobsbawm 2010). All this made the opening of museums necessary, not only to widen knowledge of faraway territories, but also to study their riches and classify them according to the schemes developed in the era (Podgorny 2000, 2001; Cowie 2011). This novelty involved, as in Argentina, the intervention of the governments which sought to obtain the best pieces for study to increase the collections with overseas materials (Podgorny 2000, 2001; Cowie 2011). As a result, in the evolutionary paradigm held at that time, the 'strange' species from the Pampean region represented the different paths that evolution had found in those faraway lands.

In this way, both sides of the Atlantic were interested in developing this Pampean fossil trade network. On the Argentine side, the network permitted the development and consolidation of the country in opposition to the prevailing European powers at that time and allowed the development of a local scientific system to be endorsed. European museums competed to acquire new species. They linked them to prestige and the domination of the explored regions (Podgorny 2000, 2001; Cowie 2011).

Spain was a pioneer in procuring Argentinean fossils, although the practice extended to other countries, including France, England, Switzerland, Germany, Denmark and Italy. These are some of the European countries that nowadays possess such collections whose origins are to be found in the aforementioned political and economic juncture between South America and Europe. As is customary, most of these museums have some items on display, while others are in storage (Lozano and Menéndez 2013). These finds not only have a historical value due to their origins, but are also useful for research purposes.

3. Fossils in context: the value of these collections

As it can be seen from the previous section, the material was mobilised with the consent of the governments of the nations involved, which encouraged such trade (Pérez Gollán 1995; Pérez de Micou 1998; Podgorny 2000; Phillips 2005). This situation, however, later came to a halt. The political and economic events of the countries involved, especially after the world wars, led to a break and a dramatic decrease in scientific curiosity in these finds (Pérez Gollán 1995; Pérez de Micou 1998; Phillips 2005; Huster 2013). Interest would re-emerge in the last decades of the 20th century, although initially from a heritage point of view. In Argentina and other countries of the world, the issue of heritage has become a matter of concern in various international organisations, with new norms and regulations governing the traffic of archaeological and palaeontological material. It is now maintained that this type of material should stay in the country of origin (especially human remains), although it is still being argued who should be the legal custodians of such materials: museums, associations, ethnic groups, etc. (Phillips 2005; Guráieb and Frère 2008; Cosmai *et al.* 2013). Without going into the legal controversy involved (which is beyond the scope of this paper; for details see Guráieb and Frère 2008), it should be noted that the fossil collections deposited in different museums are a good sample of the natural past of species (De Renzi 2002; Lozano and Menéndez 2013) and as such they are a resource capable of being used by those institutions (De Renzi 2002; Phillips 2005; Guráieb and Frère 2008). Fossil collections from the 19th century have dissemination, research and institutional values.

Starting with dissemination, it must be highlighted that the fossil collections of foreign materials allow the dissemination of the heritage of the country where the fossils originated, not only to local inhabitants and tourists, but also to schools (Lozano and Menéndez 2013). The institutional aspect corresponds to the participation of the institutions and universities of the country of origin and the deposit of the materials. Due to this participation, efforts can be joined to enable the mobilisation of the personnel involved, and the generated knowledge can strengthen ties between participants in national and international cooperation programmes. Finally, in research terms, the materials from these collections are suitable for study, even though they are now out of context, as will be explained below. In the case of the palaeontological material, it is not only useful for studies related to that discipline (De Renzi 2002), but also for answering questions related to archaeology, biology, ecology and other areas of study. In the case of the Argentinean collections that are the focus of this study, new techniques, methodologies and even novel theoretical frameworks are applied. These collections are an essential tool for new generations of investigators, conservators and educators.

4. The reason for studying decontextualised collections

Nineteenth-century excavations focused on finding the most attractive and complete pieces. This was linked to the need of museums to exhibit spectacular pieces and, in the context of the competition between institutions at that time, of museum scientists to define new species (Wolff 1975; Podgorny 2000, 2001; De Renzi 2002). As a result, most of the information related to these remains, their sedimentary context, their association with other remains, the presence of small species and the collection of fragments has been lost (Wolff 1975, Lozano and Menéndez 2013). In this sense, the loss of a related context and the partial nature of the selected finds can be compared to surface finds (Chichkoyan *et al.* 2013). Despite this, fossil remains in museum collections possess invaluable information that can be used in the present (De Renzi 2002; Lozano and Menéndez 2013).

The renewed interest in museum pieces from these 19th-century collections is also related to excavations procedures. On the one hand, archaeology and palaeontology are destructive disciplines, which makes their record a non-renewable resource (Pérez de Micou 1998; Guráieb and Frère 2008); on the other, the investment required for fieldwork is considerable and not always affordable. Thus, the study of fossil collections deposited in museums is an easier, more direct and accessible means of research for many of the current projects and it also means less impact on the environment (Pérez de Micou 1998). The study of museum collections can be carried out thanks to the scientific advances in recent decades and the development of new ideas for material research studies (Balesta and Zagorodny 2000). Progress in the molecular field and genetics allows DNA from the finds to be studied, dating them or analysing the chemical composition of the fossils (Cotterill 1997; De Renzi 2002; Poinar 2002). Moreover, the taphonomic study of the bones allows part of their deposition context to be deduced. This is due to the fact that they still include signs of the work of different natural agents, including erosion, weathering, trampling, manganese staining or even sediment concretion (Chichkoyan 2011). This allows the reconstruction of both the biostratinomy and the fossildiagenesis processes that affected the remains. These post-mortem processes may indirectly indicate certain environmental conditions and, therefore, allow the past landscape to be reconstructed (De Renzi 2002). Furthermore, if the study is directed towards the human-fauna relation, as in this case, biological agents such as carnivores and human cut marks can be recognised to determine the link to past communities (Martin 2008). The use of these new developments yields fresh data not covered so far by the classical way of looking at the finds (Wolff 1975; Cotterill 1997; Pérez de Micou 1998; Perez *et al.* 2005; Huster 2013) and which can be interpreted within an interdisciplinary theoretical framework.

In recent years, some tests are being performed on material from collections, both of animal and human bones, as well as on pottery and lithics (Pérez de Micou 1998; Balesta and Zagorodny 2000; Perez *et al.* 2005; Martin 2008, 2013; Gordón 2009; Bonomo *et al.* 2009; Toledo 2009; Huster 2013; among others). A step in this direction was the revision of the Rodrigo Botet Collection in the Natural Science Museum of Valencia (Spain), whose study was recently resumed. The following section will briefly discuss its history and the analyses currently being carried out.

5. The first peopling of the Americas and the Rodrigo Botet Collection

The study carried out at the Natural Science Museum of Valencia (Spain) is an example of what can be done with 19th-century museum collections. This is the most important collection of South American megafauna fossils in Europe. Its fossils come from the Pampean region of Argentina and were initially studied by Boscá Casanoves, the museum's first curator (Belinchón *et al.* 2009). My work was initially undertaken during my Erasmus Mundus Master in the Quaternary and Prehistory programme in 2009/2010 and is currently part of a PhD thesis in the same study programme. My research will include finds from Argentina kept in various museums in Europe with the aim of understanding human peopling of America.

The particularity of this collection is its private origin, since it was brought to Valencia in 1889 by the civil engineer Rodrigo Botet (1842-1915), a Valencian who worked in Argentina for several years. When he arrived in that country in 1876 he soon established relationships with the ruling class. Thanks to his contacts, he became involved in engineering projects that were being carried out at a time when the province of Buenos Aires was opening up to international trade and the most important cities were being planned. Thus he participated in the building of different ports around the coasts of the province: Buenos Aires, especially Dock Sud, Ensenada and Campana. He also worked on the construction of the city of La Plata and the Buenos Aires-Bahía Blanca railway (Antoni Zaragozà pers. comm., 2015). It is during this period that he met Enrique de Carles, a Catalan travelling naturalist who worked for the Museum of Buenos Aires and who carried out non-systematic excavations in the north-eastern sector of the Pampas Region. De Carles began working at the museum around 1884 under the leadership of Karl Hermann Konrad Burmeister (1807-1892).

He continued there with the Ameghino brothers until the 1920s (Bonomo 2002; Perazzi 2008) and was a loyal defender of their ideas about the presence of Tertiary Man in the region (Bonomo 2002). As a travelling naturalist he was responsible for collecting fossils for the museum, but he also traded with them (Pérez Gollán 1995; Perazzi 2008). By the time de Carles came into contact with Botet he was in possession of a large number of finds that he had originally planned to sell to the Museum of Copenhagen. However, it was Botet who finally acquired the collection and then returned to Valencia. It is the most important collection of Pampean fossils in Europe thanks to its abundance and diversity of species (De Renzi 2002). It also contains important human remains, such as the 'Samborombon skeleton', which unleashed a controversy in Spain regarding the antiquity of the first American peoples, as postulated by Ameghino at that time (Bonomo 2002).

Today this collection is being taphonomically and zooarchaeologically studied to be able to understand the impact of the first American human settlement on native fauna (some preliminary results can be seen in Chichkoyan 2011, 2013; Chichkoyan *et al.* 2013, 2015). Using magnifying glasses and microscopes the material is being observed to detect any marks of biological intervention. Species and skeletal parts are being analysed in order to see which resources were exploited. A comparison with other sites in the region is being made, allowing us a better understanding of the way dispersion developed in the different regions. Dating different bone elements together with human anthropic actions will most likely provide information about when this interaction occurred, when *Homo sapiens* was present in the region and until when these animals survived. Therefore, the study of this collection is providing previously unknown information about current research concerns, despite the lack of context and associations.

6. Conclusions

The 19th-century collections of native South American fauna held in Europe are the result of transactions carried out by different agents: governments and local scientists, travelling naturalists and entrepreneurs. The New World opened up as a natural space, but also as a place for new opportunities for immigration for those seeking to distance themselves from the political and economic changes Europe was going through. European museums were eager to expand their collections and thus encouraged many of the expeditions and acquired material at a time when the natural sciences were at their peak as a form of scientific knowledge. In addition, this happened in a context in which the continent was seeking economic expansion into new territories. Within this context, Rodrigo Botet's collection appears to be a paradigmatic case. Apart from benefiting from the economic and social success enjoyed by Spanish migrants in Argentina, Botet, who held the scientific ideas of his time, invested in one of the most precious materials within the established scientific and liberal environment. Few European collections of this type have such a private origin; in general they were either sponsored by institutions or received donations from local scientists.

The collections that are still housed in Europe continue to attract the interest of the different agents that used them, both in terms of institutional dissemination and research. This type of use does not only give renewed value to this material, but also allows it to be used in further work to provide new data on current research. In spite of its lack of context, advances in theoretical models, methodologies and dating procedures allow a contextualisation of the material and a novel understanding of the new data. The research carried out on Botet's collection is a good example of this.

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1.2. WHY TO REVIEW PALEONTOLOGICAL COLLECTIONS: CONTRIBUTION TO THE REGION

To consider these historical collections for current research is also necessary given that early sites or associations of biological intervention in the Americas is scarce (Roosevelt et al. 1996; Barnosky et al. 2004; Burney and Flannery 2005; Koch and Barnosky 2006; Surovell and Grund 2012; Hubbe et al. 2013b; Grayson and Meltzer 2015; Bartlett et al. 2016), especially in the Northern part of South America (Borrero 2009). This absence of early sites can be the result of different natural and anthropic influences that affected past record. Natural conservation bias can be related to the climatically changes this continent suffered during the Pleistocene- Holocene period. Late Pleistocene transgressive event has covered early coastal sites, which are now underwater (Pitbaldo 2011). Rain forest as the Amazonia has created low visibility patches for detecting sites (Roosevelt et al. 1996) or even lack of long term investigation projects had influence in this situation (Aceituno et al. 2013).

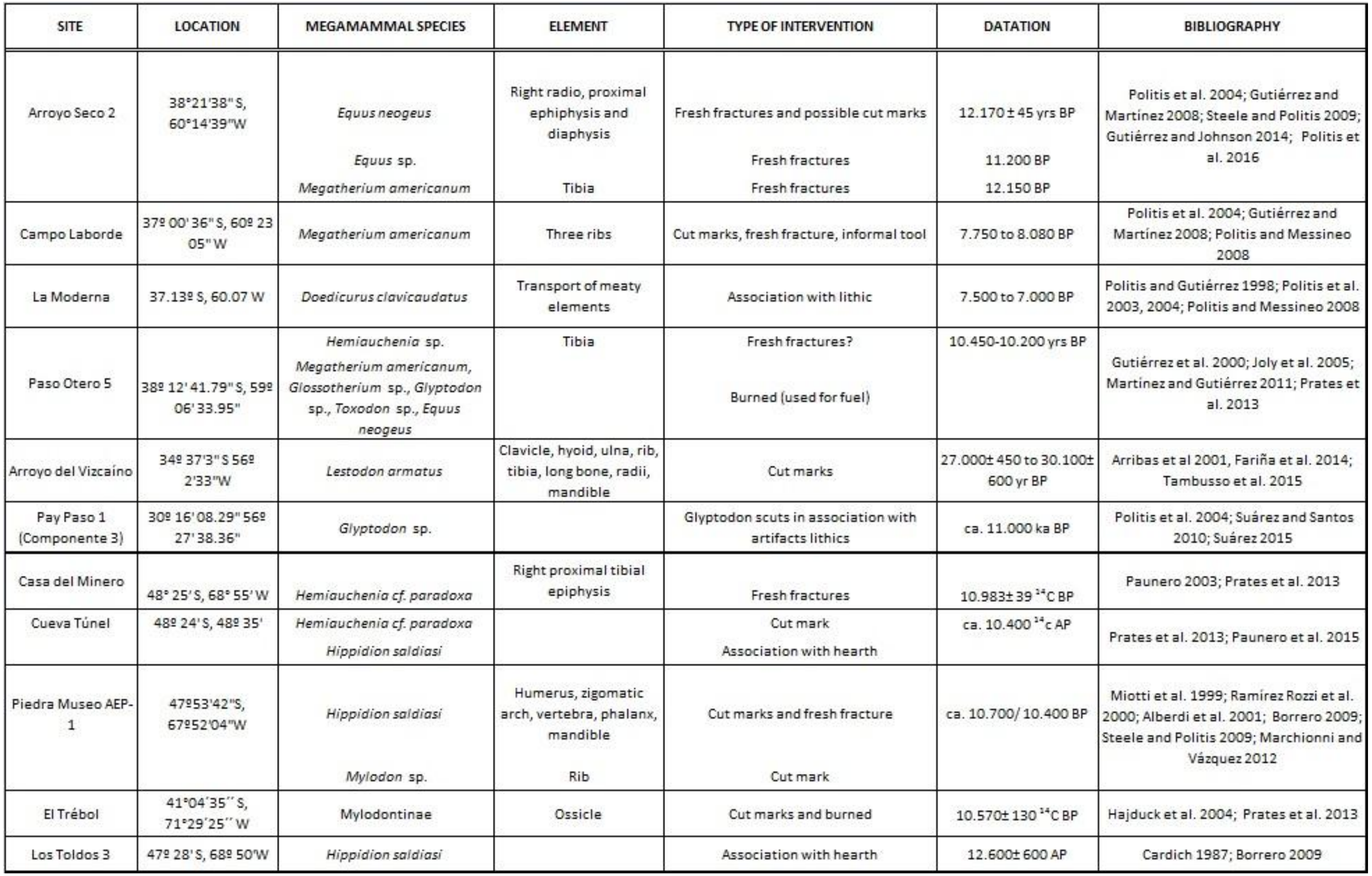
In comparison with the Northern part of the continent, South American Southern cone has a better presence of early sites, even though the record of biological intervention as cut marks, are hardly presence (Arribas et al. 2001; Haynes 2007; Borrero 2009). The Table 1.1 and Figure 1.1 summarize the main archaeological sites of the Pampean (Argentina and Uruguay) and Patagonia (Argentina) were megafauna was recorded. In De La Plata Basin, there are no current known sites with megafauna association. This situation contrast with what has been found more to the South, where sites as Arroyo Seco, Campo Laborde, La Moderna or Paso Otero 5 are present. Among them, only the first two sites have revealed humanly modified bones (Politis et al. 2004, 2016; Gutiérrez and Martínez 2008; Politis and Messineo 2008; Steele and Politis 2009; Gutiérrez et al. 2010; Gutiérrez and Johnson 2014). The third one present association of bones and lithic artefact and the absence of appendiculars would be indicating transport of meaty elements (Politis and Gutiérrez 1998; Politis et al. 2004; Politis and Messineo 2008; Gutiérrez et al. 2010). In Paso Otero 5, the dominance of burned bones from different taxa would indicate their use as fuel, and a *Hemiachuenia* sp. bone has cut marks (Gutiérrez et al. 2000; Joly et al. 2005; Martínez and Gutiérrez 2011; Prates et al. 2013). In Uruguay two important archaeological sites, Arroyo del Vizcaíno and Pay Paso, have presented megafauna, but only the first one has cut marks in different elements of *Lestodon armatus* (Arribas et al. 2001; Politis et al. 2004; Suárez and Santos 2010; Fariña et al. 2014a; Suárez 2015; Tambusso et al 2015). In Patagonia the evidence is even sparser given that few sites in this extended region have evidence of megafauna intervention, especially in Equids remains (Cardich 1987; Miotti et al. 1999; Ramirez Rozzi et al.

2000; Alberdi et al. 2001; Hajduck et al. 2004; Paunero 2003; Borrero 2009; Steele and Politis 2009; Marchionni and Vázquez 2012; Prates et al. 2013; Paunero et al. 2015).

The emptiness in De La Plata Basin is even more astonishing considering that a human skeleton excavated by Ameghino in the 19th century in Mercedes Town (located in de la Plata Basin) was recently dated in 10.300±60 and 9.520 ^{14}C AP (ca. 12.250 and 10.975 AC) (Politis 2014), making this one of the earliest dates for human remains in the continent (Lanzelloti and Acuña Suarez 2014). This evidence indicates that *Homo sapiens* would have had an early dispersal in this region. As pointed before by Perez et al. (2005), paleontological collections can be a good research tool in the light of other evidences that points to an early presence of humans.

Regarding carnivore interventions the almost absence of evidences in the region increase the difficulty to assess their role and interactions among other native fauna and with humans: One cf. *Eosclerocalyptus lineatus* (Hoplophorini) neural apophysis from the Pliocene (Olavarría) has a carnivore tooth imprint, attributed to Chapalmalania (Carnivora; Procyonidae) (de los Reyes et al. 2013). Recently, in the margins of the Salado River a taphocenosis comprising *Hippidion principale* and some indeterminate bones with carnivore marks were associated with *Smilodon* sp. (Scanferla et al. 2013). In the archaeological site Arroyo Seco 2 different bones, and among them, extinct species such as *Equus* sp., present carnivore marks (Gutiérrez and Johnson 2014; Politis 2016). Thus, reviewing non controlled collections of de la Plata Basin can palliate, at least partially, this situation.

The scarce evidence of archaeological sites or taphocenosis generated by carnivores can be related with current anthropic intervention in this region. The de la Plata Basin is highly altered by both the development of cities and agricultural activities (Fucks and Deschamps 2008; Fucks et al. 2012). Since the 19th century, the expansion of important urban concentrations implied the loss or modification of different classical paleontological and archaeological sites (Cione and Tonni 1995; Soibelzon et al. 2008a and b; Blasi et al. 2010; Cenizo et al. 2011; Toledo 2011; Tassara and Cenizo 2014; Lanzelotti and Acuña Suarez 2014; Ali and Camino 2013). Canalization of the stream and rivers started to be realized at that moment too, since the region has always been subject to periodic flows thanks to the low pendent (Violante and Parker 2004; Vázquez et al. 2009; Banzato 2014). These are the places where more possibility of finding association exists, because Late Pleistocene-Early Holocene sediments were deposit in the riverbanks (Quattrocchio et al. 2008). For example, archaeological and paleontological record discovered during the 19th century is near these flows. Thus, the destruction of original landscape would imply not only losing these classical sites, but also influence in current detection of early taphocenosis with low visibility (Burney and Flannery 2005). The same was notice by Haynes (2007:91) for North American record when he states that many of the Clovis sites can be under interstate highways. Similar observations point that mining and agriculture activities in the Andes can imply losing important early occupations (Fraser 2014). In more general terms the evidence to understand megafauna extinction could have been easily overlooked because of discovery, excavation and research procedures (Cannon and Meltzer 2004; Haynes 2007) and also academic standards of each epoch (for a recent discussion see Monjeau et al. 2016). Thus, given the scarcity of archaeological sites for de la Plata Basin, the general low recording of cut marks, or of carnivore-herbivore associations, the contribution of these collections is highly important, especially when considering the amount of modern intervention activities in the zone.



SITE	LOCATION	MEGAMAMMAL SPECIES	ELEMENT	TYPE OF INTERVENTION	DATATION	BIBLIOGRAPHY
Arroyo Seco 2	38°21'38" S, 60°14'39"W	*Equus neogeus*	Right radio, proximal ephiphysis and diaphysis	Fresh fractures and possible cut marks	12.170 ± 45 yrs BP	Politis et al. 2004; Gutiérrez and Martínez 2008; Steele and Politis 2009; Gutiérrez and Johnson 2014; Politis et al. 2016
		Equus sp.		Fresh fractures	11.200 BP	
		Megatherium americanum	Tibia	Fresh fractures	12.150 BP	
Campo Laborde	37º 00' 36" S, 60º 23 05" W	*Megatherium americanum*	Three ribs	Cut marks, fresh fracture, informal tool	7.750 to 8.080 BP	Politis et al. 2004; Gutiérrez and Martínez 2008; Politis and Messineo 2008
La Moderna	37.13º S, 60.07 W	*Doedicurus clavicaudatus*	Transport of meaty elements	Association with lithic	7.500 to 7.000 BP	Politis and Gutiérrez 1998; Politis et al. 2003, 2004; Politis and Messineo 2008
Paso Otero 5	38º 12' 41.79" S, 59º 06' 33.95"	*Hemiauchenia* sp.	Tibia	Fresh fractures?	10.450-10.200 yrs BP	Gutiérrez et al. 2000; Joly et al. 2005; Martínez and Gutiérrez 2011; Prates et al. 2013
		Megatherium americanum, Glossotherium sp., *Glyptodon* sp., *Toxodon* sp., *Equus neogeus*		Burned (used for fuel)		
Arroyo del Vizcaíno	34º 37'3" S 56º 2'33"W	*Lestodon armatus*	Clavicle, hyoid, ulna, rib, tibia, long bone, radii, mandible	Cut marks	27.000± 450 to 30.100± 600 yr BP	Arribas et al 2001, Fariña et al. 2014; Tambusso et al. 2015
Pay Paso 1 (Componente 3)	30º 16' 08.29" 56º 27' 38.36"	*Glyptodon* sp.		Glyptodon scuts in association with artifacts lithics	ca. 11.000 ka BP	Politis et al. 2004; Suárez and Santos 2010; Suárez 2015
Casa del Minero	48° 25' S, 68° 55' W	*Hemiauchenia cf. paradoxa*	Right proximal tibial epiphysis	Fresh fractures	10.983± 39 ^{14}C BP	Paunero 2003; Prates et al. 2013
Cueva Túnel	48º 24' S, 48º 35'	*Hemiauchenia cf. paradoxa*		Cut mark	ca. 10.400 ^{14}c AP	Prates et al. 2013; Paunero et al. 2015
		Hippidion saldiasi		Association with hearth		
Piedra Museo AEP-1	47º53'42"S, 67º52'04"W	*Hippidion saldiasi*	Humerus, zigomatic arch, vertebra, phalanx, mandible	Cut marks and fresh fracture	ca. 10.700/ 10.400 BP	Miotti et al. 1999; Ramírez Rozzi et al. 2000; Alberdi et al. 2001; Borrero 2009; Steele and Politis 2009; Marchionni and Vázquez 2012
		Mylodon sp.	Rib	Cut mark		
El Trébol	41°04´35´´ S, 71°29´25´´ W	Mylodontinae	Ossicle	Cut marks and burned	10.570± 130 ^{14}C BP	Hajduck et al. 2004; Prates et al. 2013
Los Toldos 3	47º 28' S, 68º 50'W	*Hippidion saldiasi*		Association with hearth	12.600± 600 AP	Cardich 1987; Borrero 2009

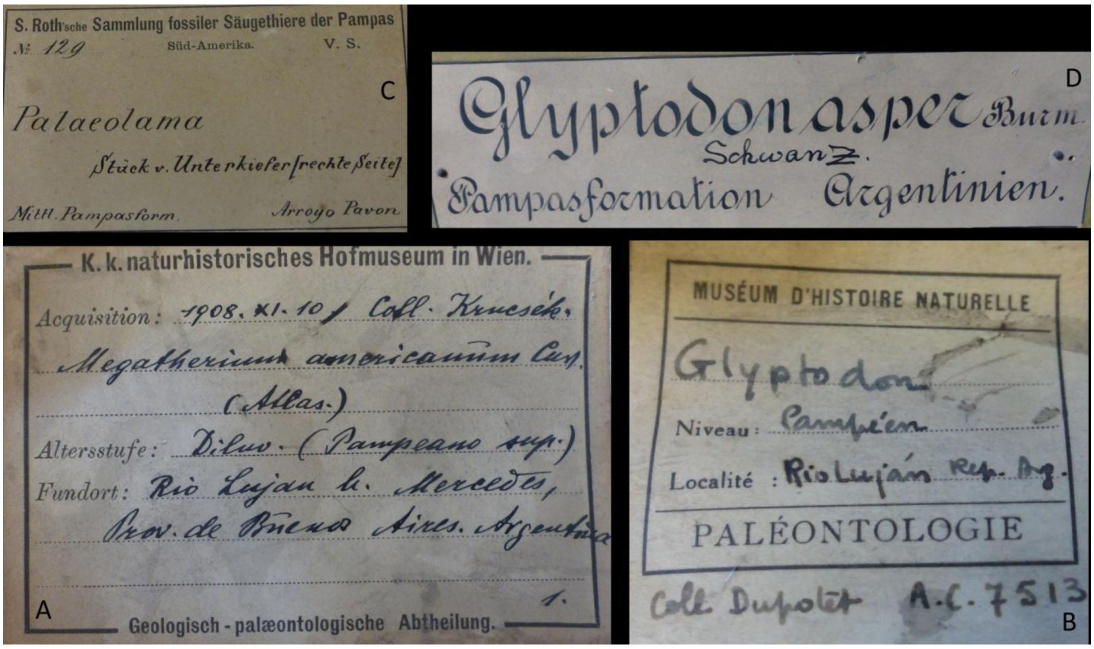
Table 1.1. Pampean and Patagonian sites with association or evidence of anthropic intervention in megamammals' species

1.3. DE LA PLATA BASIN: GEOLOGICAL CONTEXT

Most of the material reviewed proceeds from the Quaternary of De La Plata Basin (DLPB) located in the Pampean region (Figure 1.1). This is a flat, extended geomorphological unit that functions as an ecotone between the Brazilian and Patagonian subregions (Tonni et al. 1999b; Prado and Alberdi 2010; Baratas Díaz and Bueno 2014). Zoogeographically belongs to the Pampasic dominion of the Guayano-Brazilian subregion (Ringuelet 1961, Tonni et al. 1999b; Fucks et al. 2005) Currently, the different subunits composing this region are differentiated by the vegetation, the soils, the environmental conditions and the crystalline basement (Zárate and Folguera 2009; Fucks et al. 2012). The DLPB is part of the Pampa Ondulada subunit (Zárate 2003; Zárate et al. 2009; Blasi et al. 2016) that is located in the Northern rim of geologic Province named Salado basin (Cavallotto 2002).

This region is being studied since the beginning of 19th century by different researchers, including d'Orbigny, Darwin and Ameghino among others (Cione and Tonni 1995; Tonni et al. 1999a; Nabel et al. 2000; Zárate 2003; Toledo 2005, 2011; Tonni and Pasquali 2006; Blasi et al. 2009; Rabassa et al. 2009; Tonni 2009b, Zárate and Folguera 2009; Zárate et al. 2009). During these early times, the term Pampean/ Pampean Formation was used to identify the homogeneous deposition of loess beds this region (Tonni et al. 1999a; Zárate 2003; Tonni and Pasquali 2006; Zárate and Folguera 2009; Tonni 2011). It was first applied by d'Orbigny and afterwards used and/or redefined by the following researchers (Tonni and Pasquali 2006; Tonni 2011). Reference to "Pampean"/"Pampean Formation" was generally attached onto the bones of the reviewed collections (Figure 1.4).

Subsequent studies have demonstrated that sediments deposition sequence was complex (Cavallotto 2002; Zárate 2003; Toledo 2005, 2011; Zárate and Folguera 2009; Zárate el al. 2009) as the region functioned as a basin tramp for the sediments of the surrounding regions (Nabel et al. 2000; Zárate 2003; Fucks and Deschamps 2008; Zárate and Folguera 2009) like the Andean, the North Patagonian, the Sierras Pampeanas and Paraná Basin (Nabel et al. 2000; Zárate 2003; Tonni and Pasquali 2006). Deposition timing during 19th century was chronologically related to what is currently recognized as Pleistocene to Early Holocene (Tonni and Pasquali 2006; Zárate and Folguera 2009; Tonni 2011). Summing to this, current geological conformation, the usage of similar names to identify both lithological and paleontological features, extension of the different layers and the use of different classification scheme are still a much discussed topics and contrasts with the simple classification schemes of 19th century (Tonni et al. 1999a; Tonni and Pasquali 2006; Tonni 2009b; Blasi et al. 2009, 2016; Zárate and Folguera 2009; Prado and Alberdi 2010; Toledo 2011).



S. Roth'sche Sammlung fossiler Säugethiere der Pampas
№ 129 Süd-Amerika. V. S.
Palaeolama
Stück v. Unterkiefer [rechte Seite]
Mittl. Pampasform. Arroyo Pavon

Glyptodon asper Burm.
Schwanz.
Pampasformation Argentinien.

K. k. naturhistorisches Hofmuseum in Wien.
Acquisition: 1908. XI. 10 / Coll. Kruesek.
Megatherium americanum Cuv.
(Atlas.)
Altersstufe: Diluv. (Pampeano sup.)
Fundort: Rio Lujan b. Mercedes,
Prov. de Buenos Aires. Argentina
1.
Geologisch-palæontologische Abtheilung.

MUSÉUM D'HISTOIRE NATURELLE
Glyptodon
Niveau: Pampéen
Localité: Rio Luján Rep. Arg.
PALÉONTOLOGIE
Coll. Dupotet A.C. 7513

Figure 1.4. Labels from different museums with the reference to "Pampean"/"Pampean Formation". A. Naturhistorisches Museum Wien (Vienna), B. Muséum National d' Histoire Naturelle, (Paris) C. Paläontologisches Institut und Museum (Zürich), D. Museum für Naturkunde (Berlin).

In general terms, as a worldwide trend, Pleistocene glacial and interglacial periods have affected the configuration of the region. Pleistocene and Holocene periods were important in terms of sedimentation and formation of the current soils, with deposition of eolic, fluvial and lacustrine beds (Fucks and Deschamps 2008, Tonni 2009a; Zárate et al. 2009; Prado and Alberdi 2010; Toledo 2011; Fucks et al. 2012).

Early and Middle Pleistocene periods are characterized by cold, dry climate, intensive aeolian activity and loess deposition, but also aluvial process and warm trends (specially at the beginning of Middle Pleistocene) (Prado and Alberdi 2010). These factors have imprinted the current morphology of flat relief, depressions, isolated elevations, dune field, and formation of the drainage system (Tonni et al. 1999a; Nabel et al. 2000; Zárate 2003, 2009; Rabassa et al. 2005, 2009; Fucks and Deschamps 2008; Zárate et al. 2009; Toledo 2011; Fucks et al. 2012). Currently Ensenada and Buenos Aires formations are recognized for this period (Figure 1.5) (Nabel et al. 2000; Tonni 2009b; Zárate and Folguera 2009; Prado and Alberdi 2010). Loess and loess-like deposition predominated during glacial periods through eolic and fluvial action. Sediments are characterized by sandy silts or silty sands with concretions of calcium carbonate. Warmed pulses of these periods are represented by the interglacial and are characterized by paleosols formation (Tonni et al. 1999a; Nabel et al. 2000; Cavallotto 2002; Zárate

2003, 2009; Rabassa et al. 2005; Fucks and Deschamps 2008; Tonni 2009a; Zárate and Folguera 2009; Toledo 2011, Fucks et al. 2012). Although its apparent homogeneity, different paleosols, fluvial sequences and faunistic turnover compose this period (Tonni et al. 1999a; Fucks and Deschamps 2008; Fucks et al. 2007, 2012; Zárate and Folguera 2009) implying a complex sedimentary dynamic (Quattrocchio et al. 2008; Zárate et al. 2009). Transgresive and regressive event had produced change in the cost lines, which consequences in the climatic continentality such as diminution of the precipitation and extreme temperatures (Rabassa et al. 2005).

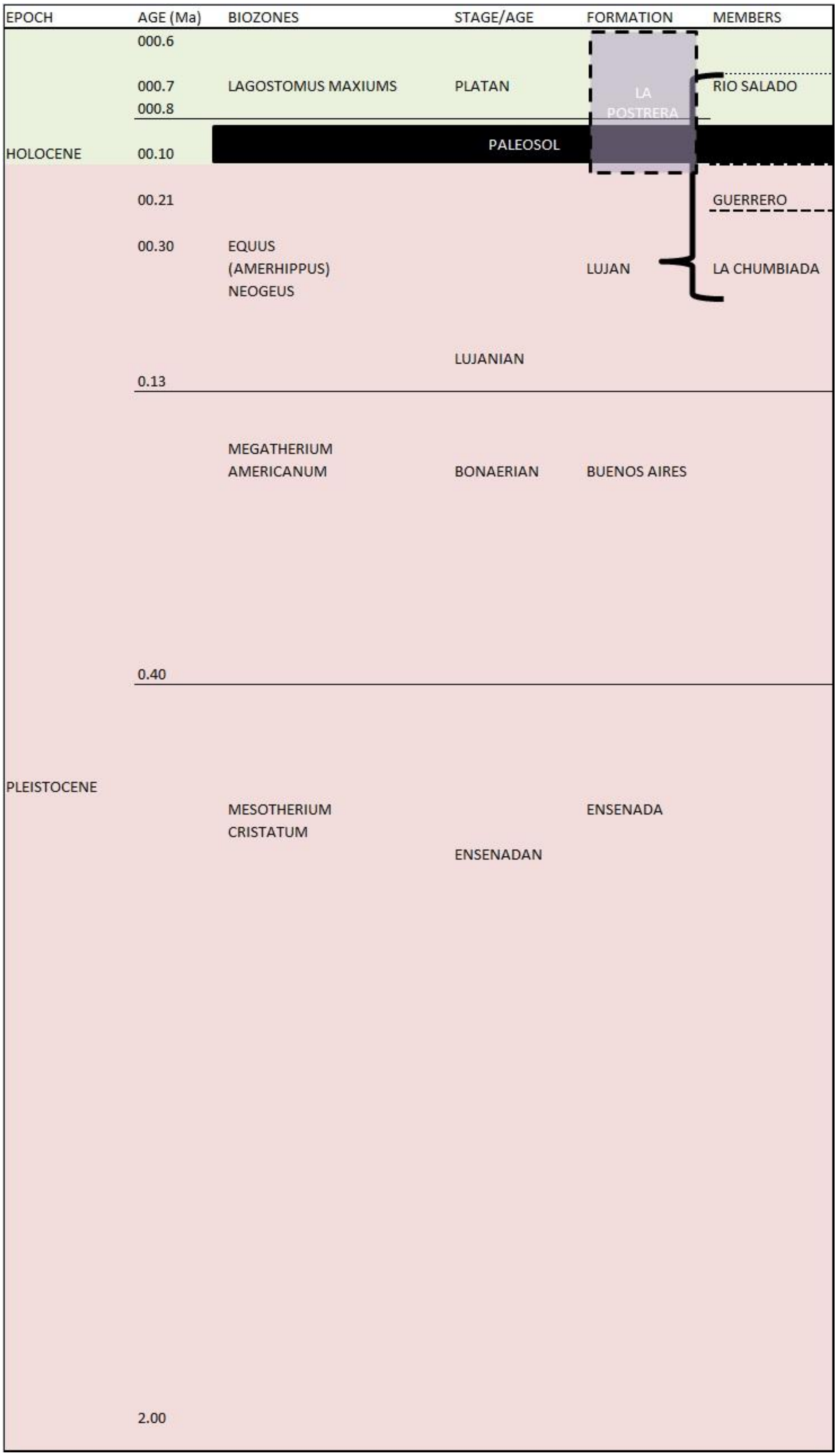
Late Pleistocene was important in terms of fluvial process and loess deposition that influenced the conformation of current landscape (Cavallotto 2002; Zárate 2003; Cavallotto et al. 2005; Fucks and Deschamps 2008; Zárate et al. 2009). The beginning of this period coincides with the MIS 5e and with a marine transgression known as Belgranense (Fucks et al. 2005; Toledo 2011). Warm, estuarine conditions and shallow marginal environments with moderate energetic conditions predominated (Fucks et al. 2005). From 60 ka BP to 25 ka BP the interstadial related with MIS 3 was developed (Gasparini et al. 2016), with temperate colder to subhumid and drier conditions in the region (Blasi et al. 2016). The Atlantic coast was further east, with its maximum extension in the Province of Buenos Aires, a characteristic that continued at least until MIS 2 (Rabassa and Ponce 2016).

Afterwards, this period is most related with the Luján formation that represents fluvial sequences deposited until Early Holocene especially along the main river systems (Prado and Albedi 1999). It is composed of three members: La Chumbiada, Guerrero and Rio Salado (Figure 1.5) (Fidalgo et al. 1973; Tonni et al. 1999b, 2003; Fucks and Deschamps 2008; Prado and Alberdi 2010). La Chumbiada and Guerrero Member were formed during glacial events (Tonni et al. 1999b; Zárate 2003; Rabassa et al. 2005). La Chumbiada is older than 30ka BP and accumulated in the valleys as clayed silts produced by reworked sediments of the Buenos Aires formation (Tonni et al. 1999b; Tonni 2009a). Clayed silts of Guerrero Member were in the fluvial valleys and in depression left by old lagoons especially between 21 to 10 ka BP, during Last Glacial Maximum and subsequent climatic events (Tonni et al. 1999b, 2003; Tonni 2009a). It represents open, arid, cold and steppe landscapes with low temperature that current period and associated with continental conditions (Tonni et al. 1999b; Fucks and Deschamps 2008; Quattrocchio et al. 2008; Tonni 2009a; Prado and Alberdi 1999, 2010; Toledo 2011). The transgressive event, after Last Glacial Maximum, fulfilled the Rio de La Plata paleovalley and cover the exposed coasts (Cavallotto 2002; Cavallotto et al. 2005; Fucks et al. 2005; Violante and Parker 2004). In addition to the Luján formation, La Postrera Formation was described for that moment. It represent eolic pulses of loess deposition accumulated, in basin divides, and partly in the valleys since Late Pleistocene, around 13.000 BP, and during all the Holocene (Tonni et al. 1999b; Fucks and Deschamps 2008; Tonni 2009a; Zárate and Folguera 2009; Zárate et al. 2009).

The Salado member locates over Guerrero member (Figure 1.5) and represents a low energy-lagunar paleoenvironment with an amelioration of the climate and different dry and cold/humid and wet pulses. Different authors located this member around Early to Middle Holocene (Tonni et al. 1999b; Walther et al. 2004; Fucks and Deschamps 2008; Tonni 2009a; Prado and Alberdi 1999, 2010; Toledo 2011). The base of this unit and of the La Postrera Formation has the last records of megafauna (Tonni et al. 1999b; Tonni 2009a). During the top of Late Pleistocene and Early Holocene, humid conditions and important fluvial sediment deposition predominates (Walther et al. 2004; Quattrocchio et al. 2008; Toledo 2011; Fucks et al. 2012). Pedogenetics events at the end of the Pleistocene produced a paleosol over Guerrero Member in coincidence with the beginning of the Holocene (Tonni et al. 2001; Walther et al. 2004; Fucks et al. 2007; Tonni 2009a; Quattrocchio et al. 2008; Prado and Alberdi 2010; Toledo 2011). It was originally named by Fidalgo et al. (1973) as Puesto Callejón Viejo and latter proposed to be the limit between the Pleistocene-Holocene (Figure 1.5) (Fidalgo 1992; Tonni et al. 1999b; Walther et al. 2004; Fucks et al. 2007; Fucks and Deschamps 2008; Tonni 2009a). Although currently the name is discussed or its dating varies from locality to locality, it is related with humid conditions, extension of lacustrine and palustrine environments of Early Holocene and it is composed of fluvial sediments and organic matter (Tonni et al. 1999b; Tonni et al. 2001; Walther et al. 2004; Fucks et al. 2007; Quattrocchio et al. 2008; Toledo 2011).

The Pleistocene-Holocene sequence is the current parental material for agriculture activities of the region and is where the largest cities in the region have developed (Zárate 2003; Fucks and Deschamps 2008; Zárate and Folguera 2009; Toledo 2011; Fucks et al. 2012). It occupies around 3 to 5m of the depositional sequence (Zárate 2003). Currently the region suffers of cyclical flood thanks to the low pendent and low runoff capacity (Fucks et al. 2012).

The amplitude and frequency of environmental changes during the Quaternary and the entrance of Holartic fauna have affected the native community of species (Ortiz-Jaureguizar and Cladera 2006; Prado and Alberdi 2010). In drier and cold climate Patagonian faunas had advance over the region, while during warmer and wetter period, the Brazilian ones (Tonni et al. 1999b; Nabel et al. 2000; Cione et al. 2003, 2009; Rabassa et al. 2005; Ortiz-Jaureguizar and Cladera 2006; Prado and Alberdi 2010). As a result the region is characterized by an excellent fossil assemblage (Prado and Alberdi 2010) that was used to defined the biostratigraphy from this region, and was subsequently used to establish the chronology of late Cenozoic of South America (Patterson and Pascual 1968; Pascual and Ortiz-Jaureguizar 1990; Cione and Tonni 1995, 2005; Nabel et al. 2000; Cione et al. 2009; Tonni 2011).



EPOCH	AGE (Ma)	BIOZONES	STAGE/AGE	FORMATION	MEMBERS
	000.6				
	000.7	LAGOSTOMUS MAXIUMS	PLATAN	LA POSTRERA	RIO SALADO
	000.8				
HOLOCENE	00.10		PALEOSOL		
	00.21				GUERRERO
	00.30	EQUUS (AMERHIPPUS) NEOGEUS		LUJAN	LA CHUMBIADA
			LUJANIAN		
	0.13				
		MEGATHERIUM AMERICANUM	BONAERIAN	BUENOS AIRES	
	0.40				
PLEISTOCENE					
		MESOTHERIUM CRISTATUM		ENSENADA	
			ENSENADAN		
	2.00				

Figure 1.5. Correlation of the different Biozones, Stages/Ages, Formations and Members named in the text for the Pampean region (not scaled).

Early and Middle Pleistocene correspond to corresponds to *Mesotherium cristatum* and *Megatherium americanum* biozones and provide the biostratigraphic basis for Ensenadan and Bonaerian Stages/Ages that correlate with the Ensenada and Buenos Aires formations (Figure 1.5) (Nabel et al. 2000; Fucks and Deschamps 2008; Soibelzon et al 2008a; Tonni 2009a and b; Rabassa et al. 2009). Ensenadan Stage/Age probably started at 2MA or around the Matuyama-Brunhes limit (Nabel et al. 2000; Rabassa et al. 2009; Toledo 2011), although its beginning is unknown (Soibelzon et al 2008a; Tonni 2009a). Bonaerian Stage/Ages is younger than 0.78 Ma and probably started at 0.5/0.4Ma (Nabel et al. 2000; Soibelzon et al 2008a; Cione et al. 2009; Tonni 2009b). An important mammal turnover differentiates both. During Ensenadan Stage/Age several extinctions occur and different Holartic species make its first appearance, then new species were added in the Middle Pleistocene (Pascual and Ortiz-Jaureguizar 1990; Tonni et al. 1999a; Cione and Tonni 1995, 2005; Nabel et al. 2000; Tonni 2009b). This implied an increase in the faunistic richness during these times (Nabel et al. 2000).

Another turnover was registered at 130.000 BP (Nabel et al. 2000; Cione and Tonni 2005), defined as the *Equus (Amerhippus) neogeus* biozone that is the basis of the Lujanian Stage/Age (Nabel et al. 2000; Tonni 2009b) that extends until 7.000 BP (Figure 1.5). The base of this biozone is the La Chumbiada Member and extends until the Guerrero Member from the Luján Formation (Figure 1.5) (Cione and Tonni 1995). In the top of this biozone disappear most of the native megamammals and some of the Holartic ones (Cione and Tonni 1995, 2005).

The next biozone is *Lagostomus maximus* that is the biostratigraphic base of the Platense Stage/Age. The base of this one coincides with the Rio Salado Member from the Luján Formation (Figure 1.5) (Tonni et al. 1999b; Nabel et al. 2000; Cione and Tonni 1995, 2005).

1.4. OBJECTIVES AND WORKING HYPOTHESIS

The general objectives of this work are:

- To identify biological interventions in historical fossil collections of native fauna from argentine Pampean region;
- To characterize humans/ carnivore primary and secondary access to the carcass;
- To propose different types of paleoecological relationships among species;
- To interpret this information at coarse-grain level with ecological concepts;
- To understand human impact in the region;

- To revalorize historical fossil collections in the light of new research.

The specific objectives of this work are:

- To apply different techniques to review fossil collections;
- To identify different non-biological surface modification;
- To differentiate cut marks from carnivore marks;
- To categorize different types of biological interventions;
- To compare biological interventions per taxon and element;
- To compare this information with what it is know on the findings of other regions of this continent.

The general hypothesis takes into account the novelty presence of *Homo sapiens* and the changes that could have been produced over the native biota: *"Homo sapiens entry had provoked qualitative variations in the relationship among native species and consequently it had diversified existing ecological niche"*

This ecological niche can be characterized as a hunter-gatherer-scavenger one. Anatomically modern humans would have access to megafauna's resources both by primary and secondary access. Thus 2 derivate hypotheses are proposed: 1. *"Humans have modified the existing hunter/scavenger niche, establishing relationships of competition with carnivores"* and 2. *"Humans have colonized hunter niche, establishing novel relationships of predation with megafauna"*

1.5. ARCHAEOLOGICAL EXPECTATIONS

In order to analyze the evidence, different expectations were proposed:

1. To find few biological interventions over the bones. This is related with several issues: (i) As pointed before, usually, small amount of biological interventions are registered in control excavated sites, consequently the same situation is expected for the fossil collections. (ii) Biased representation of the collections. As explained previously these assemblages have been through several natural and cultural filters. The last one had determined current representation of species and/or elements. For example, fragmented bones (e.g. residues of past processing action), if ever existed, were not usually included in the recollections and mix of elements of different species was usually realized. In addition museum manipulation and/or restoration activities could have blur marks. (iii) In general terms megamammal species tend to have few such marks because their size, skin and the periosteum mean that their bones are not easily modified (Crader 1983; Haynes and Krasinski 2010; Haynes and Klimowicz 2015).

2. To find different types of human intervention: cut marks and/or modified bones. As was documented in some American sites (Johnson 1976, 1989; Hannus 1989; Dillehay 1997; Hemmings

2007; Politis and Messineo 2008; Jackson et al. 2011) these native fauna have been used not only for feeding purpose, but also their bones were raw material for tool confection.

3. To find cut marks in epiphysis on long bones ends and also in axial bones indicating the different butchering activities as proposed by Binford (1981).
4. To find carnivore marks in long bone ends or fractured diaphyses for marrow extraction. These are the clearer marks to detect carnivore's activity.
5. To find different species bearing biological intervention

1.6. ABOUT THE ANALYSIS OF THE COLLECTIONS

As already stated, European and some Argentinean fossil collections have been reviewed. The first ones are composed by the fossil traffic of 19th century and early 20th century, as was explained before. Argentinean collections, not only have some important historical collection, but also are composed of isolated donated findings. In the Museo de La Plata case two Ameghino`s collection with more contextual information were included.

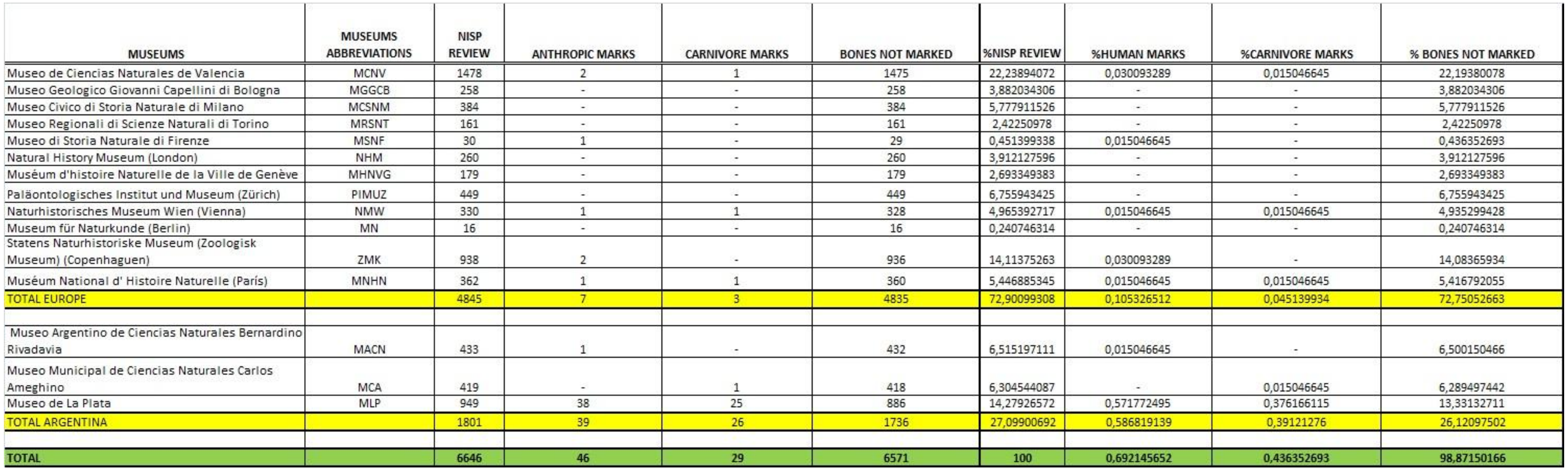
Taphonomic information and actualistic studies regarding non-biological activity and biological interventions have been used to confront the different collections. Cast for some of the elements, the use of hand glasses and different microscopes was applied for the identification of biological interventions. Dating was realized in the University of Berkeley (California) for most of the bones (even though until now not results were obtained) (Appendix Table 1) and also in Centre for Isotope Research' (Groningen) but also no positive results were obtained.

Table 1.2 summarizes the total quantity of the reviewed material in each museum, the quantity of anthropic and carnivore intervention. It can be observed few biological intervened marks in relation with the amount of material reviewed. However the results obtained are highly valuable in the light of the mentioned past excavations bias and the low quantity of biological marks in the region. In addition, it supports the premise that these collections still have important data to be used in current research.

Based on the biased nature of this material and scarce information of this type for the region, coarse-grained scale was used to explore past human-megafauna interaction. The evidence was interpreted at different levels

1. Human's marks can be related with the different butchering stages, as defined by Binford (1981). This step is important because of the general lack of this kind of information for native South American fauna (Jackson et al. 2011). It is also necessary, in order to detect which parts of the

herbivores' bodies humans were accessing and to compare them with carnivore's exploitation of the different body parts.



MUSEUMS	MUSEUMS ABBREVIATIONS	NISP REVIEW	ANTHROPIC MARKS	CARNIVORE MARKS	BONES NOT MARKED	%NISP REVIEW	%HUMAN MARKS	%CARNIVORE MARKS	% BONES NOT MARKED
Museo de Ciencias Naturales de Valencia	MCNV	1478	2	1	1475	22,23894072	0,030093289	0,015046645	22,19380078
Museo Geologico Giovanni Capellini di Bologna	MGGCB	258	-	-	258	3,882034306	-	-	3,882034306
Museo Civico di Storia Naturale di Milano	MCSNM	384	-	-	384	5,777911526	-	-	5,777911526
Museo Regionali di Scienze Naturali di Torino	MRSNT	161	-	-	161	2,42250978	-	-	2,42250978
Museo di Storia Naturale di Firenze	MSNF	30	1	-	29	0,451399338	0,015046645	-	0,436352693
Natural History Museum (London)	NHM	260	-	-	260	3,912127596	-	-	3,912127596
Muséum d'histoire Naturelle de la Ville de Genève	MHNVG	179	-	-	179	2,693349383	-	-	2,693349383
Paläontologisches Institut und Museum (Zürich)	PIMUZ	449	-	-	449	6,755943425	-	-	6,755943425
Naturhistorisches Museum Wien (Vienna)	NMW	330	1	1	328	4,965392717	0,015046645	0,015046645	4,935299428
Museum für Naturkunde (Berlin)	MN	16	-	-	16	0,240746314	-	-	0,240746314
Statens Naturhistoriske Museum (Zoologisk Museum) (Copenhaguen)	ZMK	938	2	-	936	14,11375263	0,030093289	-	14,08365934
Muséum National d' Histoire Naturelle (París)	MNHN	362	1	1	360	5,446885345	0,015046645	0,015046645	5,416792055
TOTAL EUROPE		4845	7	3	4835	72,90099308	0,105326512	0,045139934	72,75052663
Museo Argentino de Ciencias Naturales Bernardino Rivadavia	MACN	433	1	-	432	6,515197111	0,015046645	-	6,500150466
Museo Municipal de Ciencias Naturales Carlos Ameghino	MCA	419	-	1	418	6,304544087	-	0,015046645	6,289497442
Museo de La Plata	MLP	949	38	25	886	14,27926572	0,571772495	0,376166115	13,33132711
TOTAL ARGENTINA		1801	39	26	1736	27,09900692	0,586819139	0,39121276	26,12097502
TOTAL		6646	46	29	6571	100	0,692145652	0,436352693	98,87150166

Table 1.2. Detail of the material reviewed per museum and quantity of biological marks found.

2. This information can be useful in a second level of interpretation. Butchering stages and bony intervened elements can be analyzed to understand types of access by both humans and carnivores. Marks left by both agents are in relationship not only with the size of the herbivore, but also with the presence/absence of muscles, viscera or marrow. Thus, identification of the processing stages (in humans' case) and of the marked bony elements are useful to evaluated different esceneries of primary and secondary access (hunting and scavenging) in general terms.

3. At last, this general data can give some insights about the relationships among the species. Ultimately marks are signs of food intake, thus, they can be interpreted in terms of predation/competition relationships among species (Brugal and Fosse 2004) in possible hunting/ scavenging situations.

As human-megafauna interaction is beyond archaeological sphere itself (Burney and Flannery 2005; Surovell et al 2016), its study needs an interdisciplinary approach. Ecological information of present and past biodiversity is useful to characterize both humans and the native fauna. This, at the same time, allows integrating the evidence found in more general terms with the lifestyle of the species. In this sense, the presence of a unique *Homo* species in the Americas can be seen as an invasive species (Lanata et al. 2008a and b; Lanata 2011; Goldberg et al. 2016). These are organisms that disperse through exotic environments, overcoming both biotic and abiotic barriers, setting up in new environments and with a high reproduction rate. These novel organism establish new types of predation/competition/mutualism interactions with native fauna (Shea and Chesson 2002; Cadotte et al. 2006; Lockwood et al. 2007; Davis 2009; Sodhi et al. 2009), and this can imply modification, diversification and colonization of existing niches (Mooney and Cleland 2001; Odling-Smee 2003) as could have been the case of *Homo sapiens* in the Americas. By the way the megamammal species are a group that share especial ecological characteristics. They have a slow reproductive rate which means they have a delay sexual maturity and few offspring per individual (Johnson 2002; Sodhi et al. 2009). Their populations are less abundant than smaller species and their size can be a natural defense to carnivore predation (Johnson 2002; Surovell et al. 2005; Owen-Smith and Mills 2008; Cione et al. 2009; Sodhi et al. 2009; Vizcaíno et al. 2012). In this way, *Homo sapiens* as new and invasive species in these ecosystems found, coexisted and exploited this fauna that was adapted for a certain type of ecological situation. Humans would have taken advantage over this community. This is materialized in the archaeological record by the presence of different sites, but also by the cut-marked bones that will be presented here. Carnivores also were part of this past tropic web, and its relation with the megafauna and, indirectly with *Homo sapiens* will be explored with the carnivores marks found.

Thus, taphonomical revision of this material can provide with "raw data" as cut marks that can helps to understand humans-megafauna relation or carnivores' marks to know how the relation among the different mammal species was. Through this way, these collections can be revalued and integrate at a coarse-grain level and impulse new ideas and studies axis (Bonomo et al. 2009).

Next sections will complete the ideas developed here. In the next chapter, the antecedents of American peopling and megafauna extinction will be presented. Afterward, in Chapter 3, Materials and Methods will be described. For the former, the different collections will be presented and the general locations of fossil's extraction, according to archive information, will be mention. For the latter the used methodology will be described. Taphonomical concepts used, along with the different non-biological and biological surface modification identified will be explain. Also, the different techniques utilized will be presented. In Chapter 4 the theoretical framework will be expanded. In this section, the concepts of invasive species, niches, paleoecological relationships of competition and predation will be explained. In Chapter 5 published and not published information results will be described. Chapter 6 will discuss the obtained results in relationship with the expectations. At last, this information will be used to give some insights about relationship of *Homo sapiens* with the native fauna. Also, some comparison with the Old World will be mentioned. At last, in Chapter 7, the Conclusions will be developed.

2. ANTECEDENTS RELATED WITH AMERICAN PEOPLING AND MEGAFAUNA EXTINCTION

Information about first human dispersal across the Americas and extinction of the megafauna will be presented. This was (and is) a much debated issue since 19th century (see a recent discussion in Monjeau et al. 2016). Different researches from diverse disciplines worldwide have discussed this subject. Mention all the works, evidences, American sites and positions would take more space than can be commit here. Consequently the principal authors, theories and some lines of evidences that have been discussed along the years will be presented.

Particular characteristics differentiate America from the rest of the continents. It is the only one that extends latitudinally across both North and South Hemisphere and contains a big array of different climates, biomes and geographical accidents (Borrero 1999; Lanata 2011). This continent was practically isolated from the rest of the emerge lands. The development of the flora, fauna, and even humans, had their own rhythm of evolution. North America occasionally joined to Eurasia when Beringia, the land between Siberia and Alaska, emerged. This land was useful for the interchange of fauna between both continents (Webb 1977; Hoffstetter 1981) including *Homo sapiens* who cross it during Late Pleistocene times (Tamm et al. 2007; Goebel et al. 2008; Pitblado 2011; Cione et al. 2015; Bourgeon et al. 2017; among others). North and South America had a similar relation pattern (Patterson and Pascual 1968; Webb 1978; Cione et al. 2015). The last one was almost in complete isolation until 3Ma ago, when Isthmus of Panama emerged (Patterson and Pascual 1968; Webb 1978; Hoffstetter 1981; Lessa et al. 1997; Baskin and Thomas 2007; Fariña et al. 2013; Cione et al. 2015). Its isolation allowed the development of a different native fauna, as the Xenarthra and Notoungulata orders (Patterson and Pascual 1968; McDonald 2005; Baskin and Thomas 2007; Carlini and Zurita 2010; Cione et al. 2015). As in Beringia's case, this bridge was used by different faunal communities from both sides that adapted to various niches and habitats. This biogeographic event was called GABI (Great American Biotic Interchange) and had important biological consequences. Although South American marsupials' lineages extinguished, most of the Placental groups have survived and Holartic mammals added to this stock. In fact Pleistocene period was characterized by the enrichment of the fauna, including humans (Patterson and Pascual 1968; Webb 1978; Lessa and Fariña 1996; Baskin and Thomas 2007; Prado and Alberdi 2010; Woodburne 2010; Cione et al. 2015).

Late Pleistocene times registered not only the entrance of *Homo sapiens*, but also the megamammals' extinction (Martin 1967; Patterson and Pascual 1968; Hoffstetter 1981; Borrero 2008; Koch and Barnosky 2006; Fiedel 2009; Barnosky and Lindsey 2010; Cione et al. 2009, 2015; Prado et al. 2015;

Fernandez 2016; among others). This supposed losing between 70 to 80% of the diversity this continent had during the Cenozoic (Alroy 2001; Barnosky et al. 2016). At least 66 species were lost in North America between 13.000 and 11.000 years ago (Barnosky et al. 2016). South America is the continent that most suffered diversity lost worldwide (Patterson and Pascual 1968; Barnosky et al. 2004; Borrero 2008; Barnosky and Lindsey 2010) with the extinction of around 52 genera and 66 species (83% of the fauna) (Koch and Barnosky 2006; Barnosky and Lindsey 2010; Villavicencio et al. 2016). As notice in the introduction, current American environments sharply contrast with past fauna diversification this continent had in the past (Borrero 2009; Cione et al. 2009; Fariña et al. 2013).

The loss of this diversified and strange fauna along the American continent has caught the attention since 19th century, but it is not until middle of 20th century that this thematic has started to be profusely discussed. Martin (1967, 1973, 1984) was the author that fuelled this debate with his theory of humans' fast dispersal and rapid extinction of all the megafauna across the continent (see below for detail). This theory has abstracted not only much of the ecological concepts still discussed, but also divided the academic agenda between "climate hypothesis defenders" and "human hypothesis defenders" opponents. Despite its weakness, this theory is one of the most popular and it is still defended or attacked by different researchers (Grayson 1984a, 2001; Coltorti et al. 1998; Grayson and Meltzer 2002, 2003; Fiedel and Haynes 2004; Lyons et al. 2004 a and b; Wroe et al. 2004; 2006; Burney and Flannery 2005; Steadman et al. 2005; Koch and Barnosky 2006; Haynes 2007, 2009a; Hubbe et al. 2007; Surovell and Waguespack 2009; Lorenzen et al. 2011; Grund et al. 2012; Surovell and Grund 2012; Lima-Ribeiro and Diniz-Filho 2013; Abramson et al. 2015; Araujo et al. 2015; Cooper et al. 2015; Fernandez 2016; Monjeau et al. 2016; Meltzer 2015; Metcalf et al. 2016, Surovell et al. 2016; among others).

Thus, megafaunal extinction in this continent is intimately related with human dispersion. In the next section brief overview is realized about the different models and evidences that support the principal positions.

2.1. AMERICAN PEOPLING MODELS

American human dispersion always implied two interrelated discussion topics: the "tempo" (when) and the "modo" (how) (Lanata 2011). Humans' presence has caught the attention and imagination of the first European explorers, erudites, naturalists, priests, historians, force members or even common people. They all wandered how these people were, where they came from, who were their ancestors, and even some of them thought they were not humans (Kozlowski and Bandi 1992; Galeano 2000 [1971]; Powells 2005; Meltzer 2009; Salzano 2011; Mazières 2011). Biblical references, mythological questions and judgment of the "humanity" interbreed to explain their existence (Pelayo 1999; Galeano

2000 [1971]). Nevertheless José de Acosta, a Jesuit priest, enlightened the most current accepted proposition. In the 17th century he affirmed that humans entered through the North of the continent, from Asia, as a consequence of a natural expansion (Kozlowski and Bandi 1992; Politis et al. 2009; Lanata 2011; Powells 2005).

Nevertheless other probable entries routes were discussed along the 19th, 20th and 21th centuries: Australia/ Polynesia, and Europe. It was even proposed that *Homo sapiens* has evolved in South America. Rivet (1925) sustained that linguistic, anthropological and ethnographical evidence proved that groups from pacific island (including Australia) have populate the Americas. A recent mtDNA study (Faria Gonçalves et al. 2013) has found Polynesian haplogroups in ancient skulls of Botocudo Indians of Brazil. One of the hypotheses given by the authors is that this can reflect prehistoric migrations to South America (even though more work is needed to confirm this theory). Bradley and Stanford (2004, 2006) have proposed that the American populations could have come from Europe. A Solutrean wave could have cross trough the ice that covered most part of the Northern Atlantic Ocean and disperse through the Atlantic side of North America. Similarities between North American Clovis points and Solutrean points would be the evidence of this migration. Nevertheless, the critics remark that this was a convergent case. Also the difference of almost 6.000 years between Solutrean industry and Clovis point deny this possibility (Powells 2005; Straus 2005; Goebel et al. 2008; Fiedel 2009). The discoveries of several older sites in the Atlantic side of North America and the variability registered in Solutrean technologies (and in this North American sites) are arguments proposed by Bradley and Stanford (2006) to maintain their proposition of European colonization.

Unlike these exogenous entrance routes, Ameghino proposed that mammals, and, as a consequence, humans' ancestors, have evolved in Patagonia, in the Southern part of the South American cone (Ameghino 1915 [1880]; Kozlowski and Bandi 1992; Podgorny and Politis 2000; Podgorny 2005, 2015; Politis et al. 2009; Català Gorgues 2011). Human would have developed in Tertiary times and expanded to the rest of the world. This theory produced one of the most important polemics at the end of the 19th century about human origin (Català Gorgues 2011; Podgorny 2015). Although rapidly dismissed, especially by Hrdlička, a Czech anthropologist, the polemic continued during 20th century. Hrdlička et al. (1912) probed that the material presented by Ameghino was modern, not corresponding to human ancestral. Defender of late peopling of the America, this would have been realized through a series of now-sunken islands located between Siberia and Alaska (Powells 2005). One of Ameghino proposals, that these first population groups coexisted and exploited megamammals proved to be true with the next century discoveries.

As the rest of faunal communities, humans' most probable way of entering must have been through Beringia. Nevertheless discussion continued regarding the entry routes and when this happened. Two different propositions were developed: on one side, humans would have cross, between ca. 13.000-12.000 years ago, the ice-free corridor located between the Laurentide and Cordilleran ice sheets covering most of current Canada and North part of United States during the Pleistocene (Figure 2.1). A second choice proposed was that humans have entered through the Pacific Coast around Last Glacial Maximum and move along this margin. Both will be briefly explain next.

2.1.1.Who were Clovis? First models

The first route proposed was related with series of sites discovered during the first decades of 20th century in Central North America. They were composed of association of mammoths and bifacial fluted points used to kill these animals. The points and the people who produced them started to be known as Clovis given that the first discovery was realized near that city. Clovis sites were characterized by being small and mobile in the sense that they seem short-term camps or caches (Grayson 2001; Mandryk et al. 2001; Waguespack and Surovell 2003; Powells 2005; Goebel et al. 2008; Meltzer 2009; Politis et al. 2009; Barnosky and Lindsey 2010; O' Rourke and Raff 2010). The sites also range in the determinate period of time: between 13/13.5 kyrbp to 11.5 kyrbp (11.4 and 10.8 rcbp) (Grayson 2001; Barnosky et al 2004; Burney and Flannery 2005; Goebel et al. 2008; Barnosky and Lindsey 2010; Pedersen et al. 2016). Recent revaluation of Clovis sites put them between 11.050 and 10.800 ^{14}C yr BP (Watters and Stafford 2007), a time shorter and younger and in coincidence with Allerød interstadial (14.700 cal BP) and the start of the Younger Dryas stadial (12.900 cal BP) (Goebel et al. 2008). During most of the 20th century it was supposed that Clovis represented the first spread of anatomically modern humans into the Americas or what was known as “Clovis First” model (Pucciarelli 2004; Watters and Stafford 2007; Dillehay 2009). The regular association with proboscideans implied that they were specialized megamammals hunters. Martin (1967, 1973, 1984) synthesized these ideas: Humans would had entered in North America by the ice-free corridor and rapidly expanded through the entire continent. Their high hunting specialization made them moving fast in the new territory. Homogeneous expansion and high demographic grow would have allow to explore all the continent in 1.000 or 500 years and at the same time produce the extinction of the megafauna (see below for more details) (Martin 1973; Kelly 1999; Meltzer 2002; Goebel et al. 2008; O' Rourke and Raff 2010; Surovell et al. 2016; Pedersen et al. 2016).

Conditions of the ice-free corridor are the key to analyze when humans could have used this route. Beringia Land Bridge connected Asia and Americas prior to 18.000 cal BP (15.000 ^{14}C BP) and until 10.000 cal BP. Nevertheless around 24 ky Eastern Beringia was blocked by Glaciers that difficult the expansion further South (Figure 2.1) (Goebel et al. 2008). Thus the ice-free corridor would have been closed for Last Glacial Maximum times. Its deglaciation would have occurred between 15.000 and 14.000 cal BP (12.500-12.000 ^{14}C BP) (Goebel et al. 2008; Dixon 2013; Pedersen et al. 2016). At deglaciation times, this corridor was a narrow passage crossed by melting current water, glacier deposits and patches of ices. This would have supposed scarce resources and limitations for human occupation (Dixon 2013; Pedersen et al. 2016). At 13.500/13.000 cal BP (11.500/11.000 ^{14}C BP) deglaciation have progress enough to sustain some vegetation coverage and bison population that moved both from the South and the North into the corridor (Goebel et al. 2008; Dixon 2013; Pedersen et al. 2016).

At first sight, this model explained both the archaeological evidence and at the same times the Pleistocene extinctions of the megamammals and coincides with the opening of ice-free corridor. However a recent study based on lake sediments core from the corridor bottleneck (55ºN to 60ºN) has established that before 12.6 cal. kyrbp was unlikely its usage. Evidence of steep vegetation, bison and mammoth emerged at this time. Moose and elk were date at about 11.5 cal kyrbp and boreal forest established at 10 cal kyrbp (Pedersen 2016). This finding complicates Clovis migrations in the central plains circa 13.5 cal kyrbp (Pedersen et al. 2016). However since 1970 this model is being challenged too.

2.1.2. Monte Verde and other sites challenge Clovis

During 1970 a South American site, early than Clovis, challenged this model. The site was Monte Verde (Figure 2.1), and its date of 14.600 cal BP, implied that people enter before Clovis times (Dillehay 1999; Meltzer 2002; Koch and Barnosky 2006; Goebel et al. 2008; Pitblado 2011). This site is located by the Chinchihuapi Stream, near Puerto Montt in the South of Chile. Its coastal position implied that a Pacific route was possible in earlier times. Last decades have presence an emergence of other early North American sites (Figure 2.1) that also have defy the view of “Clovis First”: Cactus Hill, Meadowcroft Rock Shelter, Chesrow complex, Miles Point; Schaefer, Hebior, Topper or Paisley Cave (this last with human coprolites) among some of them (Overstreet 1993, 1998; Dillehay 2009; Lowery et al. 2010; Halligan et al. 2016). Thus, Clovis would not have been the first American settler nor would the ice-free corridor have been the first choice route to enter to the continent (Mandryk et al. 2001; Meltzer 2002, 2009; Goebel et al. 2008; Dixon 2013; Pedersen et al. 2016).

In this sense, in the latest 1970’s a coastal migration route started to be proposed (Fladmark 1979, but see Heusser 1960). Northwest coast from the Pacific Ocean would have been suitable for early entrance, after Last Glacial Maximum. In contrast to the Atlantic coast, this region would have been ice free circa 16.000 cal BP (13.500 ^{14}C BP). It was a refugee for maritime, mammals and vegetation resources and could have supported human groups. An “aquatic adaptation” would have been possible given their high availability. Using watercraft technology, this route would have allowed moving to the South and expanding subsequently into the Americas (Fladmark 1979; Erlandson 2001; Mandryk et al. 2001; Goebel et al. 2008; Dixon 2013; Bourgeon 2017). Early human entrance through this part of the continent is implied in this model. Clovis can be explained as an archaeological visibility of previous invisible populations, not a sudden immigration (Meltzer 2002; Bettinger and Young 2004). It can even been a Northern migration from the South (Anderson and Gilliam 2000).

But when there were people in the region that could have done this voyage? Southern Siberia was colonized by modern humans between 45-40/35 kya (Goebel 1999; Goebel et al. 2008) and expanded across the Northward around 32 cal BP (Goebel et al. 2008). The region was covered by the "mammoth-steppe", an environment compound of tundra like that supported a diverse fauna, as mammoth, bison and horse, although plants and waters would have been scarce (Guthrie 2001; Goebel 1999). Sites located here, as the Yana Rhinoceros Horn implied that Siberian population were well adapted to handle with extreme environments (Pitulko et al. 2004; Goebel et al. 2008). Other sites in the region, as Mal'ta site dated at 23±5 kya shown that populations were exploiting both megamammals and medium size fauna and were characterized by Upper Palaeolithic assemblages (Goebel 1999; Richards et al. 2001; Goebel et al. 2008) (Figure 2.1).

Figure 2.1. General localization of quoted sites and principal features of Clovis First Model. 1. Mal'ta, 2. Yana Rhinoceros Horn/ Berelekh, 3. Ushki, 4. Swan Point / Little John / Bluefish Cave/ Nenana, 5. On Your Knees Cave, 6. Paisley Cave, 7. Lovewell/ La Sena, 8. Schaefer/ Hebior/ Chesrow complex, 9. Miles Point, 10. Meadowcroft Rock Shelter, 11. Cactus Hill, 12. Topper, 13. Pedra Furada, 14. Santa Elina Rockshelter, 15. Quebrada de Jaguay, 16. Monteverde, 17. Arroyo del Vizcaíno. A. Cordilleran Ice Sheet, B. Laurentide Ice Sheet, C. Ice-free corridor. In white: Maximun extend of ice sheets at 24 kyrbp. Modified from Goebel et al. (2008).

According to “Out of Beringia” or “Beringia Standstill” hypothesis, humans probably get “stuck” in this region at least for 10.000 years until deglaciation would allow moving ahead (Tamm et al. 2007; Rourke and Raff 2010; Hoffecker et al. 2014; O’ Bourgeon 2017). Although lack or archaeological evidence, paleoecological information indicates shrub tundra, thus making possible human existence in this high latitudes (Tamm et al. 2007). Archaeological sites in both sides of Beringia indicate humans’ simultaneous occupation ca. 14 kyrbp. In Western Beringia, Ushki and Berelekh sites were dated between 14 to 12 kyrbp (Goebel 1999; Goebel et al. 2003, 2008) and in Eastern Beringia, Swan Point in central Alaska was dated at 14.600 cal BP (Goebel et al. 2008; Pitblado 2011; Holmes 2011) and Little John site circa 14.000 cal BP (Easton et al. 2011; Dixon 2013). On Your Knees Cave located in the Alexander Archipelago in Southeast Alaska indicates humans had a maritime-based diet circa 12.000 cal years BP (Dixon 2013). Moreover, there was a certain degree of connection between both sites of Beringia given the similarities of the blade and bifacial technologies (Hoffecker 2001) between Nenana archaeological complex of Central Alaska dated between 13.800 to 13.000 (11.7 and 11 kyrbp) and Ushki site (Goebel et al. 2008). In addition it is not discarded the existence of submerge sites after Post-Glacial deglaciation that would be indicating the Beringia standstill and Post Glacial maximum occupations of Eastern Beringia (Erlandson 2001; Mandryk et al. 2001; Dixon 2013; Pitblado 2011; Pedersen et al. 2016) (Figure 2.1). In this sense, a recent date of 24.000 cal BP (19.650 ± 130 ^{14}CBP) in Bluefish cave push back the peopling of this region and confirms the duration of the standstill (Bourgeon et al. 2017).

But until now, current evidence supports an American colonization, after 15 or maybe 17 kyrbp, when conditions of Last Glacial Maximum would have temperate and allow the transition through the “mammoth steppe” to this continent (Goebel 1999; Goebel et al. 2008). Already in Americas, these groups would have followed the coastal route, as evidence by On Your Knees Cave or Monte Verde (Dillehay 1999). Other coastal sites as Quebrada de Jaguay in Peru (Figure 2.1), dated circa 13 cal BP could be related with this dispersion event too (Sandweiss et al. 1998; Pitblado 2011).

2.1.3. Integration of the models

Pitblado (2011) has integrated both models in two independent pulses. One circa 16.000-15.000 years, entering in the Americas by the Pacific rim of Alaskan coast. These populations would have a wide diet-base, exploiting plants, animals and maritime resources and used watercraft. A second pulse associated with Clovis sites would have cross the ice-free corridor when it was ecological viable, around 1.000 year later. They would have exploited Central North America resources, as the megafauna.

Nevertheless the timing of these pulses does not explain the existence of some North America sites. Among them: Topper and Cactus Hill dated at 20.000-16.000, with a generalist diet and without Clovis industry (McAvoy and McAvoy 1997; Goodyear and Steffy 2003; Goodyear 2006; Macphail and McAvoy 2008; Sain 2016). Meadowcroft Rockshelter is dated between 18.500 cal BP and 15.200/13.400 cal BP, Clovis technology is also absence and it has exploitation of medium-size mammals and vegetables (Adovasio et al. 1990). Schaefer and Hebior are dated at 14.800-14.200 cal BP and Lovewell and La Sena are dated at 22-19 k cal BP. These have mammoth exploitation without clear Clovis associations (Joyce and Blazina-Joyce 2002; Overstreet and Kolb 2003; Joyce 2006; Holen 2006, 2014; Holen and Holen 2011, 2014) (Figure 2.1). Older dating of the sites than proposed routes, location in the Atlantic coast, or not correspondence with diet and/or technology associated with Clovis are anomalous features in the scenario proposed by Pitblado (2011). Their existence must have implied early exit of the Ice Free corridor before Last Glacial Maximum, probably between 30.000 and 24.000 years ago. Since last decades now, discovery of different earlier South American sites as Arroyo del Vizcaíno in Uruguay (Fariña et al. 2014a and b) or several sites in the region of Sao Raimundo Nonato, as Boqueirao da Pedra Furada and Vale da Pedra Furada (Guidon and Delibrias 1986; Guidon 1989, Parenti et al. 1996; Boëda et al. 2014) or Santa Elina Rockshelter (Vilhena Vialou 2003, 2011) (all in Brazil) with dates over 20.000 years would imply earlier American peopling than currently supposed nowadays (Figure 2.1). Nevertheless acceptance of these sites is still debated in the scientific community (see Borrero 2015 and papers in that volume for discussion).

2.1.4. Genetic, craniofacial and linguistic evidence

Greenberg et al. (1986) were one of the first researchers that integrated linguistic, dental and genetic evidences to understand American peopling. According to them three waves would have populated the continent. The first one near to end of the Late Pleistocene epoch and was Amerind in linguistic terms. The other two were modern ones, represented by the Na-Dene and the Aleut-Eskimo. The three types of evidences the authors presented suggested that Amerinds would have entered around 12.000 years ago and spread into the continent. Previous entrance was difficult since neither their evidence, nor the archaeological presented solid information to a Pre-Clovis peopling.

Nevertheless new lines of research developed in last decades provide novel evidences, although consensus among the researches is far away. The most investigated ones are genetic and cranial information. They have presented different types of results in relation of the timing and how many waves had entered to Americas, even though still they all point to a Northeast Asiatic origin.

Genetic studies indicate low genetic diversity correlated with small founding populations. Sixteen major phylogenetic groups along the Americas have been detected (Achilli et al. 2013). Divergence with Asiatic population must have been before or around Last Glacial Maximum (Tamm et al. 2007; Goebel et al. 2008; O'Rourke and Raff 2010; González-José and Bortolini 2011; Mazières 2011; Salzano 2011). Beringia would have been a bottleneck, given the expansion to an extreme environment and the isolation of the population, implying the loss of the Asian lineages (Tamm et al. 2007; O'Rourke and Raff 2010; González-José and Bortolini 2011). After the Beringia standstill groups would have follow a rapid expansion and also more recent bi-directionality genetic contacts between Siberia and North American artic (Tamm et al. 2007). Investigations point to one or perhaps two waves of peopling with same genetic variation pool (Pitblado 2011). Recent analyses of ancient and modern genome-data (Raghavan et al. 2015; Llamas et al. 2016) support this scenario. Initial divergence with East-Asiatic braches would have been circa 23/24.9 kyrbp. The isolation in the Eastern Beringia refugium could have isolate the population for around 2.4 kyrbp and no longer than 9 kyrbp (Llamas et al. 2016) or no more than 8.000 years (Raghavan et al. 2015). At approximately 16 kyrbp this population entered in the Americas, dispersing fast into the continent throught a Pacific route (Llamas et al. 2016). At 13 ka this single wave diversified into two branches, one dispersed into North America and the other into South America (Raghavan et al. 2015).

Traditionally craniofacial traits were divided in two groups: the dolicocephaly, showing certain degree of "primitive" traits shared with Asiatic, African and Australian groups and some native ethnographic groups in the Americas, as the Yámana in Tierra del Fuego, Bocotudos in Brazil or Pericú in Lower California. This group, identified as "Paleoamericans" would represent a Late Pleistocene entrance in the Americas, before the evolution of more specialized traits in Asia (Neves and Pucciarelli 1991; Neves et al. 1996, 2005; Mazières 2011). A second group of skull, the braquicephaly identified as Mongoloid type are more slender and "evolved". They would represent a second group of peopling around 10.000 BP. This group called Amerinds would have expanded in the continent, leaving the Paleoamericans in some regions of the continent (Pucciarelli 2004; Neves et al. 2005, 2007). This evidence would contradict the similar genetic background of all the populations of the Americas given by the genetic information. Thus, another possible model is the Recurrent Gene Flow of four-periods explained by González-José et al. (2008). In the first of these four-periods, before 26.000 YBP undifferentiated and generalized cranial morphology characterized Northeast Asia. Between 26.000 and 18.000 YBP humans expand through Beringia to the Americas. Genetic information and undifferentiated cranial morphology would indicate this would be a bottleneck period. Afterwards between 18.000 and 12.000 BP some coastal migrations towards Americas started to be realized thanks to the melting of the ice masses. Diversification of craniofacial traits due to the adaptation and stochastic effects started to be produced. In Late Pleistocene-Early Holocene times more specialized morphology emerges. Similar traits in different areas expanded given gene flow between circumartic populations, Asian and American groups. This high variability trend of generalized-derivate trait, with some populations showing more extreme types is represented in the American skull morphology.

Nevertheless craniometric information can be influenced by climate, local environmental conditions or diet. Consequently this type of evidence is not always related with genetic divergence but reflect specifics adaptations to ecological situations (Perez and Monteiro 2009; Perez et al. 2011; Perez 2011).

Complexity around American peopling is seen in this short review. Current works not only deals with archaeological evidence per se, but also paleoenvironmental proxies and biology. To get deep into how human dispersal could have been new techniques and research evidences is being used. There is a general agreement on the Asiatic origin of Native American populations. Beringia would have been a refugee that expulsed one population through the pacific and the other through the ice-free corridor. Recent early sites from North and South American complicate this consensus. Genetic and cranial information also points to a certain degree of diversification. However the polemic around American peopling does not stop here, given the discussion surrounding humans' impacts in the megafauna.

2.2. MEGAFAUNAL EXTINCTION THEORIES

Exploitation of big animals around the world is a much debated topic (Speth 2010; Domínguez-Rodrigo et al. 2014). Nevertheless an important point in the discussion is how much megamammals species have contribute to hunter-gatherers diets. In the diet breadth model, high caloric return rate is expected from the prey. Megamammals are usually seen as a costly prey, given the associated difficulty in hunting and processing them. They are hard to find and not easy to catch, processing actions, manipulation and transport can be complex. In addition different individuals and groups can/have to participate in the hunting party reducing the return rate per individual. However once they are catched, they render benefits that include from important caloric return to social, prestige and reproductive benefits (Lyons et al. 2004a; Surovell and Waguespack 2009; Speth 2010). In this sense, no doubt that human have exploited in the past different types of megamammals, given that through scavenging or hunting actions different sites around the world have this type of association (Bunn and Kroll 1986; Gaudzinski et al. 2005; Yeshurun et al. 2007; Villa and Lenoir 2009; Agam and Barkai 2016; Mosquera et al. 2015; amog others). Ethnographical cases have also revealed current exploitation of them (Crader 1983; O'Connell et al. 1990, 1992; Kent 1993; Wroe et al. 2004; Surovell and Waguespack 2009; Haynes and Klimowicz 2015).

In this long term relationship of *Homo* with megafauna, extinction causes is a much discussed topic. Quaternary fossil assemblage shows an astonish variability of these communities. Unlike the past, there is a current declining trend in megamammals around the world (Lyons et al. 2004a; Morrison et al. 2007; Fernandez 2016). Thus American megafauna's extinction is included in this bigger scale topic. Nevertheless in the Americas the controversy has been intense given their disappearance in short time after human presence.

Several lines of research have been developed during these decades to explain it. Given the volume of information, the principal concepts of each hypothesis will be displayed separately. Most of them were formulated with North American record due to the extended information obtained there. Nevertheless models or information from South America (or from other parts of the world that were discussed along with North American evidence) will be taken into account. The theories can be resumed in “exogenous” and “endogenous” or biotic events (Table 2.1). In the first ones accent is put in external causes disequilibrating the environment, as disease, natural impacts or climate change. The second one is related with human action (Haynes 2009a). The most debated are climatic and anthropic causes (Haynes 2007). Consequently for them, information will be divided among the proposals, the evidence or study cases proposed and the critics that have received.

2.2.1.Diseases

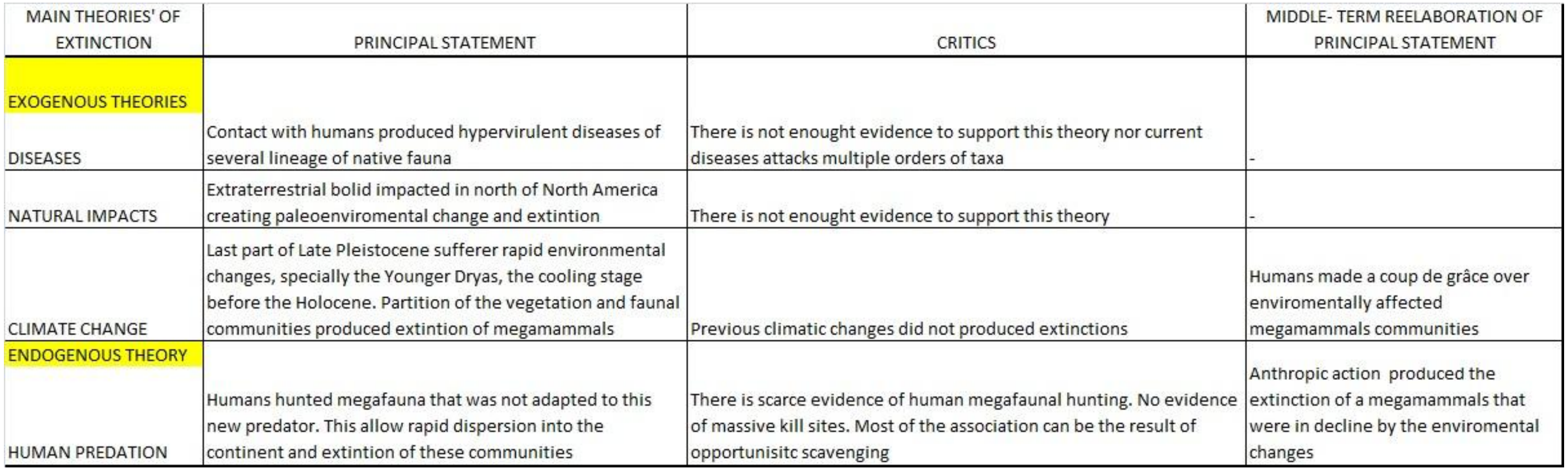
According to this cause, hypervirulent diseases produced by human contact (MacPhee and Marx 1997) or by pathogens (Ferigolo 1999) affected the megafauna. Given the isolation and lack of adequately defenses different lineage of animals would have rapidly succumb. Nevertheless the lack of evidence (Haynes 2007) and ignorance of current diseases behaving like this (Koch and Barnosky 2006) does not support this hypothesis. In addition Americas and Eurasia were not completely isolated given that during the Cenozoic land bridge sporadically connected them, and different species have interchange. By the way, current diseases only attack a single order, in multiple-order attack, low transmission rates is expected. At last, diseases do not explain the size-selection extinctions (Lyons et al. 2004b).

2.2.2.Natural impacts

This theory is related with “Black Mats” position over bone beds of megamammals and human sites. These layers of dark sediment with high organic matter content were lay down before Younger Dryas (12,9 kyrbp). They have been interpreted as a consequence of reduce evaporation and increase precipitation, resulting in wet and cold conditions (Firestone and Topping 2001; Firestone et al 2007; Johnson 2009).

Firestone et al. (2007) proposed that this was the results of the catastrophic impact of an extraterrestrial objet that felt in some part of Northeastern of North America. Important environmental changes that finally implied megafaunal collapse and anthropic behavioural shift was the consequence. Some animal could have survived in protected refugees, but inevitably became extinct.

Given that these Black Mats were registered in more than 50 sites in North America, the impact object (e.g. a comet) would have had continental effects.



MAIN THEORIES' OF EXTINCTION	PRINCIPAL STATEMENT	CRITICS	MIDDLE- TERM REELABORATION OF PRINCIPAL STATEMENT
EXOGENOUS THEORIES			
DISEASES	Contact with humans produced hypervirulent diseases of several lineage of native fauna	There is not enought evidence to support this theory nor current diseases attacks multiple orders of taxa	-
NATURAL IMPACTS	Extraterrestrial bolid impacted in north of North America creating paleoenviromental change and extintion	There is not enought evidence to support this theory	-
CLIMATE CHANGE	Last part of Late Pleistocene sufferer rapid environmental changes, specially the Younger Dryas, the cooling stage before the Holocene. Partition of the vegetation and faunal communities produced extintion of megamammals	Previous climatic changes did not produced extinctions	Humans made a coup de grâce over enviromentally affected megamammals communities
ENDOGENOUS THEORY			
HUMAN PREDATION	Humans hunted megafauna that was not adapted to this new predator. This allow rapid dispersion into the continent and extintion of these communities	There is scarce evidence of human megafaunal hunting. No evidence of massive kill sites. Most of the association can be the result of opportunisitc scavenging	Anthropic action produced the extinction of a megamammals that were in decline by the enviromental changes

Table 2.1. Main hypothesis to explain megafaunal extinctions.

Regrettably, geological and geochemical evidence cannot prove the existence of this object. Haynes (2009a) also pointed that several lineages of megafauna, even humans, have survived in different parts of the Americas and some groups as elk and moose have entered in North America at that time. Given the scarce evidence to support this type of theory, Johnson's (2009) alternative view is that Black Mats were the consequence of the extinctions.

2.2.3.Climate hypothesis

2.2.3.1. PROPOSALS

This is one of the most debated causes, since the coincidence of extinctions with a series of unusually faster and larger cycles of changing paleoclimatic conditions characterizing Late Pleistocene-Early Holocene transition, in contrast of earlier glacial-interglacial periods. In North America an important variability trend appeared. Bølling-Allerød warming/drying at 14.700 cal BP (12.500 rcbp) was followed by the Younger Dryas suddenly cooling at 12.900 cal BP (10.900/10.600 BP). This one extended for 1.100/1.300 years and finish with a sudden warning at 11.570 cal BP (10.000 rcbp) (Grayson 2001; Fiedel and Haynes 2004; Fiedel 2009). In South America Pleistocene-Holocene transition was characterized by a rapid cooling (Cold Reversal) between 13.3 and 11.5 kyrbp, then at 11.5 kyrbp a warming period raised in 5º the temperature. The timing was probable similar as North America although with regional variants (Barnosky and Lindsey 2010).

According to this position, Pleistocene extinctions were part of a worldwide trend that started 10 million years ago. In this trend extinctions episodes where always registered at the end of the Glacial cycle (Cooper et al. 2015). *Homo* species evolved in the last part of the Late Cenozoic and its arrival to the Americas coincides with the last of a series of extinctions episodes that began long before its evolution. As follows, only climatic deterioration was the cause of this last extinction (Webb 1984). In the Americas, given the sudden changes, both flora and fauna collapsed and finally extinguished. The ecological relationships established between the different components of the trophic web could not support the variable climate change at the end of the Pleistocene.

Different ecological models have been proposed: habitat loss hypotheses, mosaic-nutrient hypothesis, coevolutionary disequilibrum and self-organized instability (Lyons et al. 2004a; Koch and Barnosky 2006; Grund et al. 2012). In them climate change, habitat fragmentation, reduced vegetation diversity, changes in resources partitioning or perturbation of multicomponent ecosystems are analyzed as the processes producing megafaunal extinctions. Reorganization of the ecosystems was not possible given the very rapid cycle change that Late Pleistocene-Early Holocene had (Koch and Barnosky 2006). Guthrie (1984) and Graham and Lundelius (1984) proposed the most classical models. In them climate and vegetation patterns changes have impacted in the megafauna's survival. The succession of very cold Pleistocene and warm Holocene shrinked the environments, changed and decreased the vegetation, and disrupted the co-evolutionary relationship with the faunas. Ecological impacts were reflected in different evidences: alteration of the ungulates growing season, decreasing of the quality and quantity of resources for larger mammals, body size reduction of some species, reorganization ranges of many small mammals and plants, differential migration rates. The final result was the American environments collapse and extinction of several lineages of megamammals and small mammal communities. This was compatible with a worldwide climatic change and subsequent extinctions.

Related with this paleoecological imbalance scenery, Owen-Smith (1987) proposed that suppression of keystone species, as mammoths, was an important ecological gap that influenced extinctions. Adults individual of this group are invulnerable to predation, and their abundance make them engineer transformers of the vegetation's structure. Elimination of these groups can produce negative cascading effects in the trophic web, producing extinction of other species. Nevertheless the author considers also the interplaying of anthropic action.

By the way, extinctions were not synchronous with humans' appearance. Some mammal lineage have extinct or were almost extinguished before human's arrival. While in other regions different megafauna's species have survived until Middle Holocene approximately (Hubbe et al. 2007, 2013a; Lima-Ribeiro and Diniz-Filho 2013). Consequently humans would have not been implicated in this extinction event. In any case, according these authors, they could have been just opportunistic predators, probably scavengers.

According to this last position *Homo* could have produced a "*cup de grâce*" to fragmented, reduced and climatically affected communities (Boulanger and Lyman 2014). At a global scale, some places/regions would have been affected more than others by humans (like in New Zealand or some remote islands) (Brook and Browman 2002; Wroe et al. 2004; Lorenzen et al. 2011). Consequently humans would not have been responsible of the extinction of all the communities, especially considering also that groups would not have been enough dense (Wroe et al. 2004).

2.2.3.2. EVIDENCES

Works that have been done in order to analyze climatic influence in megamammals' extinction can be differentiated in studies related with the ecological relationship between the different components of the trophic web, the ones that study the chronology of extinction and others that analyzed DNA. Brief mention is realized to some of them.

2.2.3.2.1. Studies related with ecological relationship

(i) Different works have related large body size with higher probability of extinction in paleoenvironmental changing conditions. This factor would explain why process was size-selective (Lessa and Fariña, 1996; Lessa et al. 1997, Prado et al. 2001).

(ii) Guthrie (2003, 2006) presented a series of works to support his model of changing ecological relationship between vegetation and faunal communities. In Alaska vegetation change in the mammoth steppe, would have influenced in changes in mammal's size such as *Equus*. This one reduced its size, one millennia before its extinction. In Alaska and Yukon, some species as bison, wapiti and moose have increased their numbers, albeit human presence. This evidence disadvantages human influence over extinction

(iii) De Vivo and Carmignotto (2004) have compared Holocene biomes of South America and Africa. Conditions have produced increase vegetation cover in the first continent. Consequently, development of denser vegetational spaces could not support megamammals' species. In contrast, in Africa megamammals have survived given the maintenance of bigger regions of savanna/grassland in different parts of that continent.

(iv) The work of Gill et al. (2009) studies the *Sporormiella* and fossil pollen from Indiana and New York states. This fungus, developed in the dung of herbivores, can be used as a proxy of megafauna' biomass, given its abundance in late-glacial sediments. They found that a decline of this fungus coincides with the megafauna collapse, between 14.800 to 13.700 years ago, during the Bølling/Allerød warm period. In contrast to most of climate change hypothesis, their work highlights that this factor would have influenced megafaunal collapse. The removal of keystone species, subsequently influenced vegetation changes and enhanced fires. Even though human action could have influence also, collapse of megamammals long before Younger Dryas, goes against a rapid extinction produced by humans.

(v) According to Faith (2011) megafaunal population collapse in Late Pleistocene was due climate change. Increases in the atmospheric CO^2, temperature and precipitation, misbalance the interrelation between herbivores and plant nitrogen. Especially atmospheric CO^2 would have diminished plant nitrogen, affected food web, and, as a consequence increased competition among animals depending on rich nitrogen-plant. This produced megamammals' population collapse, making them vulnerable to final extinction by environmental or anthropogenic causes.

2.2.3.2.2. Studies related with the chronology of extinction

(i) Coltorti et al. (1998) proposed extinction waves for different species in the Late Pleistocene of Ecuador. Paleoenvironmental conditions would have affected first to mastodon, followed by mylodonts and latter equids. This differential extinction rates were related with climate changes that affected in the lineages. Absence of humans during that period excludes them as a cause of extinction.

(ii) In El Cautivo Site, Santa Elena Peninsula, Ecuador, megafauna have survived until Middle Holocene in refugees (Ficarelli et al. 2003). In this site authors had found an assemblage composed mastodons, megatherids, deers, camelids and equids. The assemblage was dated 8.680+-80 yrBP (7.914-7.541 yrBP non calibrated). The region functioned as a refugee for species of different habitats given the mix of forest and open habitats found. Also several migration events from the cordillera to the coast were registered. They were produced due to increased aridity and cooling to humid conditions registered during Pleistocene-Holocene transition. The refugee finally collapsed, due to the increased vegetation cover and the high faunal concentration that transformed the place into a trap. Survival species as deer, camelids and tapir can be explained by protective habitat preferences. Humans would have played a minor role.

(iii) Lima-Ribeiro and Diniz-Filho (2013) analyzed First-Appearance of Humans dates and Last-Appearance of Megafauna dates. According to these authors, non-sloths were extinct in Northern South America and, proboscideans and non- proboscideans in Alaska/Canada when humans arrived. Thus, at a continental scale, humans would not have influence in the extinction event.

(iv) Other place where megafauna has survived until Early Holocene was in São Paulo State, Brazil. Six samples of *Toxodon platensis*, *Eremotherium laurillardi*, Scelidotheriinae, *Smilodon populator* and *Catonyx* have been dated from two caves (Hubbe et al. 2013a). They range from circa 19.3 to 12.5 cal kyrbp. Taking into account Signor-Lipps effects, early dates suggest that these taxa survived until Early Holocene in the region. The analyzed material was not related with humans, although in the region was registered an occupation dated in 11.720-10.770 cal yr BP (9.810 ± 150 ^{14}C yrBP) without megamammals association, and characterized as Umbu tradition. It was described as mobile generalistics groups exploiting different environments but without megafauna's predation. A *Toxodon* tooth with cut marks in the roots was found in another site in that state, and dated circa 13.000 cal yrBP. However, according to the authors, it is not enough evidence to support human predation given that it could have been used from fossilized assemblage. In the same work, they explained that the region registered abrupt climatic transitions from glacial times to Holocene. They vary from humid, to dryer to a very large wet phase between 13 and 11.5 kyrbp. This trend was faster than past cycles registered since 120 kyrbp. Thus given climate changes and low human density, the authors supports that the extinction was due to the first factor more than by anthropic causes.

(v) In Patagonia it was recently proposed that megafauna extinction between ca. 12.5/12.2 kyrbp survived the Antartic Cold Reversal (between ca. 14.4 to 12.7 kyrbp) and humans presence in the region (ca. 14.6 in Monteverde and around ca. 13.2 to 12.9 in other regions of Patagonia) (Metcalf et al. 2016). These authors, following Cooper et al. (2015) highlight the negative impact that interstadial had for the survival of megamammals communities. Humans would had disrupted the metapopulation processes, used by these groups to survived previous interstadial events. Consequently humans would have been an additional extinction force in a complex process of ecosystem alteration.

2.2.3.2.3. DNA studies

DNA studies have revealed that genetic variability has diminished in Late Pleistocene (Shapiro et al. 2004; Drummond et al. 2005; Lorenzen et al. 2011). Lorenzen et al. (2011) have studied DNA diversity in woolly rhinoceros, woolly mammoth, wild horses, reindeer, bison and musk ox from Europe and North America. They link population size to amount of habitat availability. They found a general pattern of genetic diversity loss in most of the lineages. This process started between 50.000 to 30.000 years ago, although bison and horses must had certain human influence in their extinction. Shapiro et al. (2004) and Drummond et al. (2005) arrived to the same conclusion for the Beringian Bison, given its genetic diversity starts to fall, after a growing period, around 37.000 years ago. Although human presence was recorded in the region at that time, associations are scarce and demographic grow is registered after 15.000 years ago. Decreasing population would have been related with the shrinking of the steppe-tundra due to environmental shift.

2.2.3.3. CRITICS

Climatic hypothesis cannot explain the asynchrony at a global way. Extinctions occurred along different moments of the Pleistocene, in the different continents, while in islands they were registered in recent time (Holocene). Size-selectiveness of the extinctions, or survival of the most arboreal or nocturnal mammals, cannot be explained by climatic change too. This cause would have affected homogeneously the different species around the world (Koch and Barnosky 2006; Fernandez 2016). In past extinction events, when climate was an important extinction factor, not only megamammals, but also other groups disappeared (Burney and Flannery 2005). In this sense, megafauna still persist in the oceans, although it also suffered the glaciations events (Martin 1984; Lyons et al. 2004a; Flores 2014). Thus climate hypothesis can be only useful to explain some regional extinctions (Koch and Barnosky 2006) but in large-scale, extinctions did not follow a “climate rule”.

In the American case, previous glacial and interglacial periods from the Quaternary have succeeded without producing the megamammals losses registered at the end of the Pleistocene (Lyons et al. 2004a; Wroe et al. 2004; Cione et al. 2009; Fiedel 2009; Fernandez 2016) nor they produced complex vegetation transformation (Lyons et al. 2004a; Johnson 2009). It is also not clear the link of the vegetation transformation and the extinction. The ample latitudinal grade in the Americas, would have allowed migrations among favourable zones, instead of extinctions (Molina 2008). In addition, changes in the vegetation structures must not imply extinctions, given the flexible diet to different plants that the Late Pleistocene fauna had. Different browsers, grazers and mixed feeders have extinguished simultaneously (Koch and Barnosky 2006; Haynes 2009a). Guthrie's work in Beringia, for example, cannot be extended to other parts of the continent, given the isolation of that region, blocked by the ice sheet (Fiedel 2009). By the way, megamammals' communities extinct on regions where the climate went colder, and also in regions where it went wetter, at the same time (Haynes 2007). It is also assumed that Pleistocene plant diversity was higher than in the Holocene. Nevertheless there is no evidence to sustain this (Koch and Barnosky 2006).

Lack of evidence was also pointed to sustain that the last glacial-interglacial transition was larger, and oscillations were faster than past ones (Koch and Barnosky 2006). Nevertheless climate hypothesis defenders reply similarly: there is not enough evidence to sustain that last glacial-interglacial period was equally the same that past ones (Wroe et al. 2004). Also climate variability cannot explain why most of the extinctions occurred especially at the beginning of Younger Dryas, given that these animals were supposedly adapted to this cold moment (Cione et al. 2009; Fiedel 2009). Also, some species were not affected by the climate change, as shown by Fisher (1996) for the proboscideans in the Great Lakes region, or not all the species had genetic declination. Especially in this last case, Haynes (2009a) argued that genetic variability losses do not necessarily produces extinction. Several species have suffer genetic constrictions (*Homo sapiens* itself) and this didn´t implied its extinction

At last, Owen-Smith (1987) proposal has been criticized given that mammoths were not the first ones to extinguish, but the last ones (Grayson 2001). In any case, the disappearance of these species did not led to a vegetation transformation (Guthrie 2006).

2.2.4. Humans hypothesis

2.2.4.1. PROPOSALS

As mentioned in the introduction of this section, Quaternary megafaunal extinctions are a global phenomenon (Koch and Barnosky 2006; Araujo et al. 2015; Fernandez 2016) given the losses of large body mammals in different continents (Barnosky et al. 2004; Koch and Barnosky 2006; Sodhi et al. 2009; Araujo et al. 2015). Thus, this event is generally related it with the "Sixth Mass Extinction" that unlike previous five ones, it coincides with the development of anatomically modern humans and started around 100.000 according to some authors (Molina 2008; Surovell and Grund 2012) or around 50.000 years ago for others (Burney and Flannery 2005; Sodhi et al. 2009; Flores 2014; Fernandez 2016). It intensified at around 10.000 with agriculture (Molina 2008) and after industrial revolution it became increasingly faster. This last stage would have implied losing a big amount of biodiversity (Molina 2008; Sodhi et al. 2009; Ceballos et al. 2015), not only big mammals, but also medium and smaller ones (Lyons et al. 2004a). Nowadays megamammals are threatened by humans' activities, more than by hunting itself (Lyons et al. 2004a; Morrison et al. 2007). Among them, deforestation, introduction of new species, land use, artificial fragmentation or global warming produce several impacts in current biodiversity (Lyons et al. 2004a; Morrison et al. 2007; Molina 2008; Sodhi et al. 2009; Abramson et al. 2015).

The strongest argument to see humans as intimately related with this extinction process is that, it was stepped, size-selective and coincided, in general terms, with the expansion and colonization of *Homo sapiens* in continents and islands (Wroe et al. 2004, 2006; Robinson et al. 2005; Koch and Barnosky 2006; Barnosky and Lindsey 2010; Grund et al. 2012; Surovell and Grund 2012; Bartlett et al. 2016; Fernandez 2016; Surovell et al. 2016). Unlike pass extinction events, the current one is taxa-specific and directly related with regions were humans most expanded into (Surovell et al. 2005; Sodhi et al. 2009). It is not being follow by speciation events that would replace the loss lineage, leaving several ecological niches empty (Coltorti et al. 1998; Barnosky et al. 2011; Bartlett et al. 2016). Fernandez (2016) observed three associated behaviours in relation with megafauna's exploitation in the past. Humans did not have agriculture, livestock or storage systems. Probably these would have emerged as a consequence of disappearance of this resource. First hunter-gatherers would have extensively used megamammals as an abundant resource. Given that these groups where "exploring the word", they lack of the sense of awareness that resources are short-end if they are not properly exploited.

Although it is recognized that humans had diversified resources system exploitation in the past, megamammals were the most affected by them (Johnson 2002; Lyons et al. 2004a; Wroe et al. 2004; Burney and Flannery 2005; Molina 2008; Sodhi et al. 2009; Surovell and Grund 2012; Bartlett et al. 2016). This group has certain ecological traits that make them sensible to extinction, unlike other smaller groups. Naivety is also mention as a key characteristic, especially when discussing American extinctions. After presenting briefly both in the next section, models related with megamammals extinction, in relationship with humans, or models where integration of ecological traits, naivety, humans and clime, will be mention

2.2.4.1.1. Specific ecological traits

Megamammals *K strategy* was one of the key characteristic that most affected extinctions worldwide (Fernandez 2016). This type of strategy means they have a slow a reproductive cycle (Johnson 2002; Cione et al. 2003, 2009, 2015; Surovell et al. 2005; Surovell and Grund 2012; Fernandez 2016) given that sexual maturity can be delay for more than 10 years, and have few offspring per individual (Cione et al. 2009; Hortolá and Martínez-Navarro 2013; Fernandez 2016). Consequently, low population growth rates and scarcity in the landscape, will be two associated characteristics (Surovell et al. 2005; Haynes 2009b; Surovell and Waguespack 2009). Thus targeting some of these slow reproductive species should had impacted in entire population (Johnson 2002; Surovell et al. 2005).

Unlike smaller, slow reproductive cycle mammals, that live in arboreal places or are nocturnal (Johnson 2002; Cione et al. 2009), megamammals occupy open spaces, feeding over a range array of resources (Haynes 2009a). The occupation of this type of biome makes them more easily exposed than arboreal or nocturnal ones that reduce contact with people, making less prone to hunting activities (Johnson 2002).

2.2.4.1.2. Naivety

The "naivety" factor is also an important component of this theory, especially when explaining American extinctions. Megamammal communities in this continent were not used nor to *Homo sapiens* nor either any other type of hominins species (Martin 1973; Kelly 1999; Wroe et al. 2004, 2006; Koch and Barnosky 2006; Fiedel 2009; Surovell et al. 2016). Hominins from Eurasia or Africa had a long-term history of co-evolution with these communities. This allowed developing the necessary anti-predators system to coexist with them, for thousands or millions of years, disadvantaging extinctions (Stuart 1999; Brook and Browman 2002; Johnson 2002; Barnosky et al. 2004; Lyons et al. 2004a; Wroe et al. 2004; Burney and Flannery 2005; Surovell et al. 2005; Koch and Barnosky 2006; Haynes 2009a; Araujo et al. 2015). However in Europe entrance of *Homo sapiens* implied some megamammal's extinction at 45 kyrbp and then, in a second turn at 14 kyrbp, associate with the rise of humans' populations (Stuart 1999; Koch and Barnosky 2006). Still they were minor looses, when compared with America or Australia, where humans entered latter (Wroe et al. 2004).

GABI event in South America can be an example of how megamammals adapted to new predators. This process was a slow type one, with different taxa entering in different stages (Woodburne 2010). Given that Carnivores' diversity increased after the GABI event, the coevolution with novel taxa such as Ursids, Canids and Felids implied the development of different defense strategies in native herbivores: development of accessories structures in Glyptodontidae or increased body size in most of the linkages (Zurita 2010; Vizcaíno et al. 2012). Nevertheless *Homo sapiens* would have been a faster super-predator, with weapons that were unusual to native fauna. In this sense the adaptive defenses developed during thousands of years to confront Holartic carnivores, were not useful against this new species (Patterson and Pascual 1968; Kay 2002; Cione et al. 2003, 2009; Surovell et al. 2005; Molina 2008).

2.2.4.1.3. Blitzkrieg model/ Sitzkrieg model

One of the presumptions in human dispersion across the Americas is that, it must have been fast and homogeneous in all the spaces (Martin 1973; Grayson and Meltzer 2003; Surovell et al. 2016) (Figure 2.2).

Humans entered in an empty-hominid land, where they found large megafauna stocks. Given their naivety, they were an easy target that fuelled fast expansion and high demographic grow through the continent (Martin, 1967, 1973, 1984; Kelly 1999; Wroe et al. 2004; Haynes 2009a; Surovell et al. 2005, 2016). This was called the *Blitzkrieg* model (Martin 1967, 1973, 1984; Haynes 2009a). From the 35 genera extinguished in North America, at least 15 were chronological dated in coincidence with Clovis times (Barnosky and Lindsey 2010). The loss was even bigger in South America, with the extinction of 50 genera. This included three orders of mammals: Notoungulata, Proboscidea and Litopterna, all the megafaunal xenarthrans and species over 320 kg (Koch and Barnosky 2006).

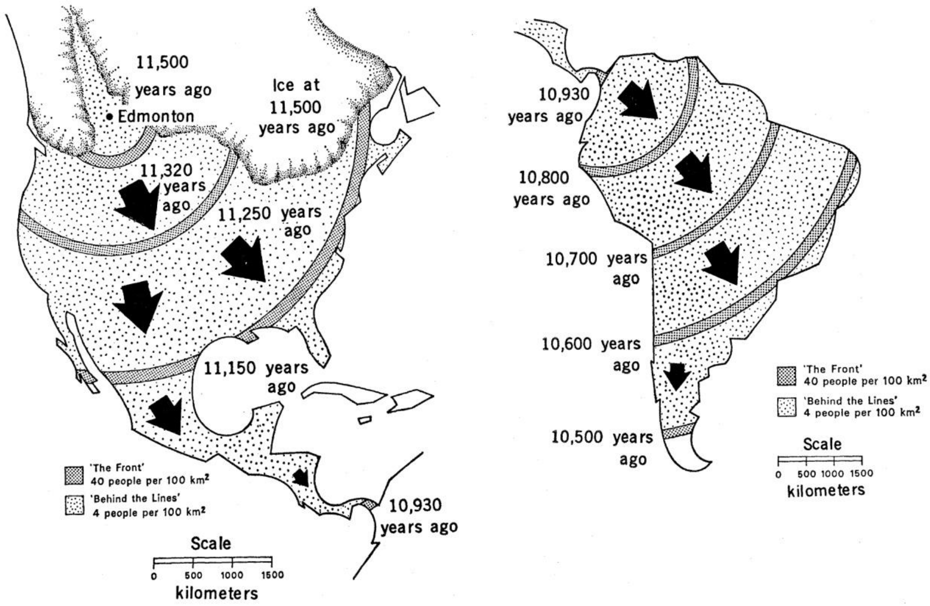


Figure 2.2. Human expansion timing and megafaunal extinction according to Martin´s model. Extracted from Martin (1973).

Direct hunting would not have been alone in the demise of the megafauna. Fire alteration of landscape, biological invasions and habitat transformation would have also influenced this type of intervention (Kay 2002; Lyons et al. 2004a; Burney and Flannery 2005; Koch and Barnosky 2006; Haynes 2007, 2009a). This was proposed as the "*Sitzkrieg*" model, and would have been a slower process (Barnosky et al 2004; Haynes 2009a) with cascading ecological effects, such as the loss of carnivores/scavengers that fed over these megafauna, or intensification of predation over other species (Patterson and Pascual 1968; Martin 1984; Lyons et al. 2004a; Koch and Barnosky 2006; Fernandez 2016). In addition, as these herbivores would have been already under pressure because of the carnivore predation, humans were added to this predator thropic chain (Janzen 1983; Kay 2002; Van Valkenburgh et al. 2016).

2.2.4.1.4. Combine climate/human causes: models for Americas

Other positions have integrated human factor in a climatically changing environment that was already affecting this *K-strategy* megafaunal population (Cione et al. 2003, 2009, 2015; Barnosky et al. 2004, Surovell et al. 2005; Nogués-Bravo 2008; Haynes 2009 a and b; Lima-Ribeiro et al. 2013; Fernandez 2016; Bartlett et al. 2016). In this sense, both in North and South America, different models that combine climatic shift, ecological traits, naivety of the species, and human action, have been proposed.

In North America Haynes (2009a) has exposed the “Opportunistic Model of First-Contact Extinction” of three-phase process. First, a foreshock occurred, where megamammals’ communities became fragmented with the changing conditions. Allerød phase that coincides with Clovis beginning was dryer than Younger Dryas, and would have influenced in decreasing within populations in the continent (although at continentinally, the range level maintained). Survival mammals communities rearranged in specific refugee during Late Pleistocene times. Current abundance of fossil quarries in specific regions of the continent would reflect these spots. Nevertheless increasing empty spaces and habitat fragmentation would have dominated. Stress conditions in these refuges, such as interfight for partners, more carnivore predation of young, delay maturation time, and few offspring per individual, would have reduced even more the presence of megamammals in the landscape. In this first stage, the communities would have experienced a bottleneck situation. In a second shock stage, humans found these weakened populations. Slight anthropic intervention would have been critical for species extinction in this destabilize situation. Nevertheless, encounters rates, would have depend with the distribution of the refuges in the landscapes. Therefore, in some points hunting rate would have been high, while in other places exploitation of smaller mammals is expected. Dispersals would have been non-homogeneous, complex and stimulated by the information of resources, not by population pressure. In the third phase, the aftershock, survival taxa would have extinguished, influenced by climate changes, human hunting and manipulation of the environment.

This type of model expects low archaeological evidence of early low-density sites. These one will reflect one time-use, without reoccupation, diversity of species in each site and low finding of kill-sites (except for larger taxa that could have preserved better).

Cione et al. (2003, 2009, 2015) have proposed the “Broke Zig Zag Model” for South America (Figure 2.3). The Zig Zag refers to the alternation of distribution of mammals’ biomass during the Pleistocene glacial and interglacial periods. The authors explained that since 400 kyrbp, fluctuations had characterized the environments, and the Holocene interglacial had the same characteristics of past ones. In this sense, megamammals and large mammals were adapted to dry and cold climate that dominated most of the Middle and Late Pleistocene. South America native fauna community contained the highest number of megamammal species in the world in those times. During Last Glacial Maximum open and middle areas predominate, while closed areas were only of 15%. In the interglacial, temperature and humidity increased and forested areas and their faunal communities expand. Open areas reduced and the biomass decreased, although species richness was stable. During these times, megamammals would have been under the minimum number and under ecological stress. In glacial periods both open-areas and fauna recovered. This trend maintained during the Pleistocene and the record does not show massive extinctions. Even though, some lineages became extinct, diversity was high due to the entrance of Holartic fauna of the GABI. In the Pampean region, Middle Pleistocene until Early Holocene mammal diversity was high than latter stages, since both extinct and extant mammals were present. During glacial times, cold environments species, such as the ones from Patagonia, predominate. In the interglacial, species of warmer climate, such as tapir, were registered. This migration pattern changed at the end of the Pleistocene. Last interglacial affected the same way to mammals' communities, but they did not relocated as in previous stages. Late Pleistocene and Early Holocene times register the extinction of all the megafauna and most of the large mammals: 90% of the species (large mammals and megamammals) extinct between 20.000 to 10.000 BP, both South American and Holartic ones.

The authors notice that these groups have low offspring per individual. Especially, females, need to survive at least 10 years to arrive to sexual maturity, and young individuals need the mother at least for the first years. Given that defenses system were developed against non-human carnivores, they could not be effective for *Homo sapiens* that was the only new biological and geological event registered in South America between 13.000 to 10.000 BP. At that moment, the climate was dry, there was a peak of temperature followed by a cold period between 12.700 and 10.300 BP (Antarctic Cold reversal and Younger Dryas chronozones). Near Pleistocene-Holocene boundary, temperatures start to rise and warmer and wetter conditions were registered. Last Pleistocene survival lineages were extinct during Early Holocene. Some large mammals that survived were living in difficult-accessing areas for humans, as forest and closed, mountains or wetlands, or they have nocturnal habits.

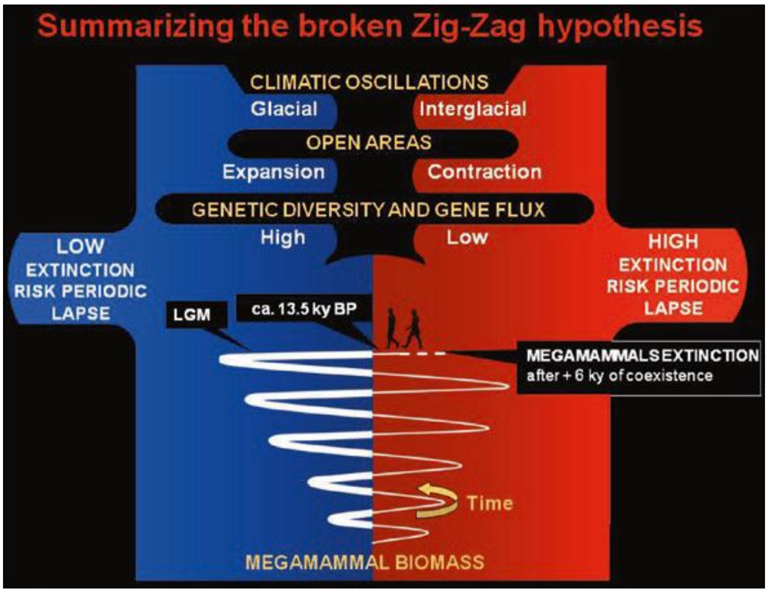


Figure 2.3. Zig Zag hypothesis (from Cione et al. 2015).

Thus, when humans arrived, they found weakened megamammals communities, with low reproduction rates, affected by the climate changes, and fragmented in shrinking open spaces. An occasional depredation over females, or offsprings, could have influenced in the entire group. On the other side, humans would not directly hunt all the species, but they provoked enough changes to influence in the entire trophic web, as extinction of the carnivores that exploited this fauna. In this sense, they propose that both human and carnivores could have been predating over the same herbivores. Smaller species exploited by humans, as the guanaco, had survived since they have fastest reproduction rate. The authors also affirm that scarce archaeological record can be reflecting reduced populations or preservation problems. They remark that, without human intervention, megamammals would have survived as other times in the Pleistocene.

2.2.4.2. EVIDENCES

In these cases evidences were related with global studies of distribution of humans and extinct species, proxies or simulation models.

2.2.4.2.1. Distribution of humans and fauna

(i) Surovell et al. (2005) had studied the distribution of proboscideans. According to these authors, this group only survived in regions were humans population did not advance, are less dense or are difficult to access, as sub-Saharan Africa and South Asia. Tropical forested biomes, where food for humans is difficult to digest, would have been good refugee for the proboscideans. While in the past they were abundant in Europe, Asia and Americas. Extinction timing in different continents succeeds after human appearance.

(ii) Similar work was realized by Steadman et al (2005). These authors proposed that the asynchronous extinctions of sloths in different parts of the American continent did not correspond with climate change. Late extinction of these species in islands, would have been produced by late human entrance.

(iii) Barnosky and Lindsey (2009) have compiled dates of megafauna and humans in South America. At least for Patagonia, Pampas (Argentina and Uruguay) and Brazil, extinctions were registered after humans' arrival and the intensification of climatic changes. Majority of last dates of megafauna were in the Cold Reversal, but also in coincidence of humans in some regions. Apparently in the North of the continent extinctions started first and before human arrival, while in the South they started later in coincidence with both causes. They also noted that it was a long process, taking 1000 years after humans' arrival, and in coincidence with climatic fluctuations. Even though both causes would have influenced megafauna's extinction, human ecological pressures would have been a determinant factor in a climatic changing environment. Lineages that survived Early Holocene times, such as *Megatherium*, *Doedicurus* and *Smilodon*, would have been less affected than the ones that extinct before, although history strategy and habitats life must be contrasted. Differences with extinction timing with North America can be related with the abundance of megafauna occupying this continent, although more information is need.

(iv) Lima-Ribeiro et al. (2013) have demonstrated that space fragmentation due to climate change after Last Glacial Maximun had affected survival rates of *Eremotherium laurillardi* and *Megatherium americanum* ranges. This coincided with the entrance of *Homo sapiens* that influenced in the extinction of these weakened communities.

(v) Surovell et al. (2016) examine radiocarbon dates to timing the extinction in the Americas. Although both in North America and South America there is a 6.000 years overlap of humans and megafauna, they found that process of extinction began in Beringia around 13.300-15.000 BP, in United States around 12.900-13.200 BP and in South America at ca. 12.600-13.900, following human expansion. Coincidentally in South America there are more Holocene sites than in North America given the late arrival of humans.

(vi) Villavicencio et al. (2016) compile information from dating, climate, vegetation changes, fire frequency and volcanic activity for the Última Esperanza region (Patagonia). They found a complex scenario, were human-carnivore interaction would have influenced extinction of these ones, while megaherbivores would have been influenced by climate and vegetation changes.

2.2.4.2.2. Proxies

(i) Waguespack and Surovell (2003) and Surovell and Waguespack (2009) have realized a database where they included different North American sites with Clovis-fauna interaction. Even though they considered taphonomic preservation bias, and sampled material from different regions, they found an overrepresentation of mammoths and mastodon in the different assemblages. In some sites, smaller mammals, turtles, fishes or other orders predominates, but the dominance of megamammals is absolute. In consequence, paleoindians would be using a specialized large-game predation strategy.

(ii) Robinson et al. (2005) have registered the amount of the *Sporormiella* fungus in four mammoth Quaternary deposits at the Southeaster New York State. High counts of this fungus mean abundant animals. *Sporormiella* decreases at different rates in each of them, and it is followed in each case by an increase of charcoal concentrations. This would have implied that animals were affected by humans' activities in the region, as intentional fire. The date of 11.000 ±80 ^{14}Cyr BP implies that the final collapse was a millennium after human entrance in the region.

(iii) Grund et al. (2012) have analyzed geographic ranges of 194 Pleistocene species from North America. They suppose that species with smaller geographic ranges will be more affected by climatic changes, and will have less survival chance. Migration from one patch to another, or the usage of a wide range of biomes, will be an effective way to confront environmental changes. Nevertheless they show that there was no correlation between range size, extinction risk and body size. Although climate affected both large and small mammals, large range taxa were the most affected ones. According to the authors, this patron cannot be explaining solely by climatic causes but anthropic intervention can alter the prediction of extinction risk based in climate changes.

2.2.4.2.3. Simulation models

Different simulation models taking into account variables such as quantity of extinct species, First and Last Apearance/Extinction of Humans/Megafauna Dates, prey-predation relationship, have demonstrated that extinctions occurred after humans arrival in different parts of the world and that they were size-selective (Alroy 2001; Brook and Bowman 2004; Diniz-Filho 2004; Lyons et al. 2004a; Flores 2014; Bartlett et al. 2016). Some simulations give equal importance to both humans and climate in this process (Prescott et al. 2012; Araujo et al 2015; Abramson et al. 2015).

2.2.4.3. CRITICS

In this case critics point to the proposals or the evidences presented.

2.2.4.3.1. Critics to the proposals

This is the most discussed hypothesis to explain megafaunal extinction given the low archaeological evidence, specially of extended kill sites that demonstrates that human have massively attacked all megafauna communities (Grayson 2001; Grayson and Meltzer 2003; Haynes 2007; Hubbe et al. 2007; Borrero 2009; Koch and Barnosky 2006; Surovell and Grund 2012). This is the “association critique” (*sensu* Grayson 1984b; Meltzer 1986): if there is not enough archaeological evidence of kill sites, subsequently it cannot be proclaim that extinction was human-based (even though indirect information indicates that humans would have prey on these species) (Wroe et al. 2004; Surovell and Waguespack 2009; Meltzer 2015). In North America more evidence can be found in comparison to the rest of the continents (Wroe et al. 2004), even though only two of the 35 extinct genera have been found in them (Grayson 2001; Surovell and Grund 2012). Critics in this case questions why in North America evidence, only mammoth/mastodon sites were discovered, while there were 35 genera extincted (Grayson 2001). Following this line of reasoning, it cannot be assumed Martin proposal that all the fauna has gone around 11.000 years ago because of human hunting (Grayson 2001). Taphonomical bias would have influenced in finding megamammals’ sites, with more visibility than smaller species sites. Consequently humans’ diets would have been over-represented onto this type of species. Research has also been oriented towards this type of evidence, or towards certain regions over others (Cannon and Meltzer 2004; Koch and Barnosky 2006; Surovell and Waguespack 2009). Consequently the statement that humans were “somewhere there”, and posing that no other mechanism could have produced the extinctions, is not enough to explain that humans were the casualty behind extinctions (Wroe et al. 2006; Meltzer 2015).

The answer to this critic is that, as the process was so fast, little evidence of sites will be preserved in the fossil record (Martin 1973, 1984; Grayson 2001). Scarcity of sites will be related to other questions too. Low human population density and the fact that megafauna was already affected by the climatic conditions would have influenced in low recording of human association (Surovell et al. 2005; Haynes 2009b). On the other side, although coexistence was long, as indicated by different dates, the probability that an individual person encounters an animal is small. Encounter rate is influenced by the extended landscape and low human and megafauna population density. Consequently short coexistence of humans and megamammals in each locality is expected. Thus, most of the megamammals’ evidence will not have anthropic association (Fernandez 2016).

In addition, taphonomical bias can influenced in low preservation probabilities (Fiedel and Haynes 2004; Koch and Barnosky 2006). Older deposits will tend to be more affected by postdepositional process, given the long term of exposition to them (Surovell and Grund 2012). Especially in American record, low density of the first human groups and small groups of megamammals near to extinction, decreases the chances to encounter human-megafaunal association (Surovell and Grund 2012). According to these authors also particular, contexts of the discipline in each region can also influence in finding evidence.

Even though taking in consideration these issues, North American record is not as scarce as proposed, given that at least the most accepted 14 Clovis sites were formed during 300/400 years (Grayson and Meltzer 2002, 2015; Haynes 2007; Surovell and Waguespack 2008, 2009; Fiedel 2009). Especially compared with other continents, as Europe, where there is a record of 50.000 years of occupation and the quantity and time formation is longer (Haynes 2007; Haynes 2009b). But this point also reflects another problem of the evidence: as Surovell and Waguespack (2008) question, how many sites are needed to demonstrate human influence? More kill sites in order to probe human causes does not resolve the question. In this sense, according to Koch and Barnosky (2006) even lack of archaeological sites does not mean that humans would not have hunted these megamammals.

American process of human dispersal must be seen neither as homogeneous, nor fast, nor of a growing population. In consequence extinctions were not equal in the different regions where humans entered, not chronologically the same, and not all the regions were occupied at the same time (Grayson 2001; Grayson and Meltzer 2003; Wroe et al. 2004; Haynes 2007; Lanata 2011; Lima-Ribeiro and Diniz-Filho 2013; Barnosky et al. 2016; Villavicencio et al. 2016). Human pressure would not have been enough in order to drive all the species to extinction (Lyons et al. 2004a). Monte Verde and pre-Clovis North American sites suggest that there was not a fast dispersion of human populations from North to South (Grayson 2001; Wroe et al. 2004; Koch and Barnosky 2006). Megafauna and humans have coexisted for at least 4.000/6.000 years (Politis and Messineo 2008; Cione 2009; Surovell et al. 2016). Both are different lines of evidences indicating that megamammals communities were not killed in a single event, as the *Blitzkrieg* model proposed (Koch and Barnosky 2006; Haynes 2007) and that not all the spaces were occupied at the same time by megamammals populations and humans (Haynes 2007).

Thus, it is neither expected one uniform way moving in the space, nor that the extinctions would have been produced all at the same time. This first population could have exploited these animals in relationship with their abundance or cost of pursuit. Nevertheless some authors still support the possibility of an overkill (Alroy 2001; Diniz-Filho 2004; Surovell and Waguespack 2009), while others see extinctions as a long process, given the absence of evidence of a fast megamammal diminution (Cione 2003, 2009; Haynes 2007, 2009a and b; Fernandez 2016).

Supposed naivety of the fauna has been questioned too, given that some studies affirmed that animals can learn very fast how to defend from the predator (Berger et al. 2001; Brook and Browman 2002; Wroe et al. 2004). Nevertheless, first human's entrance and its consequences cannot be compared with controlled current experiments (Burney and Flannery 2005). Besides, human-specific antipredator systems have to be still identified (Wroe et al. 2006). Africa, for example, is always cited as the continent where animals have developed this kind of defenses, but until now they were not documented (Wroe et al. 2004). Megamammals' survival here must have been related with other questions, more than with anti-predator systems. Area availability, greater climate stability, better equatorial exposure and mammalian diversity would have influenced in this sense (Wroe et al. 2004). These authors also question the fact that Africa and Europe have been inhabit almost the same time with *Homo* species and only Europe registered more extinctions. Did not the European fauna developed antipredator systems in all that time? (Wroe et al. 2004). Given that in the Americas coexistence of humans and fauna seems to be longer than originally supposed, it cannot be sustained that American megafauna did not had enough time to developed antipredator defense system. Nevertheless long coexistence time would be related with a certain stabilization of ecological relationship (Brook and Browman 2002), and pre-Clovis populations would not have been large and permanent to impacted in this way in the megamammals (Surovell et al. 2016). In this sense, if encounter with humans were sporadic, developing of the necessary defense strategies would be difficult (Koch and Barnosky 2006).

Critics also points that megamammals would not have been first choice for feeding (Haynes 2009a), given the high cost of finding and processing them (Byers and Ugan 2005). Human must have used a big arrange of resources, and not be characterized as a megamammals specialist (Goebel et al. 2008; Lima-Ribeiro and Diniz-Filho 2013). In the Americas there is evidence that smaller animals would have been exploited besides megamammals (Cannon and Meltzer 2004). In this sense, Wroe et al. (2004) suggested that the use of small and medium mammal alloweded population increases that, at the same time, have impact over megafauna. Thus predation would have varied in relation of the environment and prey availability (Cannon and Meltzer 2004; Byers and Ugan 2005). Nevertheless humans’ cause defenders do not deny that hunter-gatherer population had a diverse array of resource exploitation. Clovis groups were omnivorous, exploiting different types of resources (although proboscidean would have been an important one also) (Haynes 2007). According to him, megafaunal exploitation does not mean “specialization in” certain kind of resource. Humans groups not only select their prey in terms of “maximization”, but also other social questions influence their decision.

Other critic realized to this theory is that there is not ethnographic evidence that hunter-gatherers specialized in megamammals hunting. Nevertheless current groups cannot be 100% compare to past behaviour. Doing that would imply losing the great variability that human behaviour can have. American populations would have access to an especial ecological context that cannot be compared to current ethnographical cases, living in marginal environments (Kelly 1999; Koch and Barnosky 2006; Haynes 2007; Hubbe et al. 2007; Surovell and Waguespack 2009; Pitblado 2011).

It was also questioned that weapons used were not adequate for killing these types of animals (Wroe et al. 2004; Haynes 2007). Nevertheless not only lithic, but other organic sources, as wooden spears, could have been used for killing (Koch and Barnosky 2006; Haynes 2009b). Nevertheless according to Wroe et al. (2004) although hunting with more general tools can be possible, this reduces predation efficiency. But if it is considered that not all the megamammals would have been killed, just a small portion of it, efficiency downplays.

Some other critics are posed by Wroe et al. (2004). He questions the idea that introduced species by humans would have influence in the extinction process. Continental contacts and migration of fauna among them were done before humans and did not implied extinctions. On the other hand they also points that, knowledge of a first colonization of a landscape takes time. In this way, it cannot be sustained a fast overkill of all the species in a few generations.

2.2.4.3.2. Critics to the evidence

Steadman et al (2005) work was criticized by Hubbe et al. (2007). According to them, decline in the islands could have been product of either climate or human action. Hubbe et al. (2007) and Borrero (2008) also criticized the partial selection of South American sites made in this work. Besides, islands extinction cannot be extrapolated to continents. Effects of climate in island and in continents are not well studied. Consequently, it cannot be presupposed that effects was equal on both (Wroe et al. 2004, 2006). Fauna communities of islands cannot be compared with the continent, as their isolation gave them lack of any antipredator systems (Wroe et al. 2004).

Waguespack and Surovell (2003) work was criticized by Cannon and Meltzer (2004). According to them, artiodactyls seem to be the most used prey, and regional variability must be taken into account before pointing to a “large mammal specialization”. Taphonomical, research and geographical bias had favor the discovery of megamammals’ sites, and disregarding smaller mammals’ site. Nevertheless Surovell and Waguespack (2009) remark that record is naturally biased, and not knowing what happened in certain regions is not a useful approach to get deep into the specialization that Clovis could had had. Given the wide range of sites they considered (both with megamammals or other orders) and the narrow geographical and timing frame of them, the information is not skew.

Meltzer (2015) have questioned the methodology used by Grund et al. (2012) to affirm that animals’ ranges did not change. According to him, coarse-grained scale and delimiting the information to fossil quarries, is not useful to evaluate change of ranges. In fact some studies have shown that ranges of certain groups have changed.

Also simulation models had been criticized, since researchers can choose the variables and presumptions to realize the test. In this sense, simulations are skew by the interest of the researchers. Generally in them, humans are characterized as super predators, while other social facts are dismissed. Nevertheless choosing other variables can gives different results (Bulte et al. 2006).

2.2.5. Observation about the theories

It can be observed from the previous paragraph that megafaunal extinction has been long debated along these years and each side has contributed with both theoretical ground and evidences.

Nevertheless the debate continues (Lorenzen et al. 2011; Bartlett et al. 2016; Grund et al. 2012) adding complexities to this thematic. This has to do with several associated problems.

1. Most of the climate hypothesis defenders tried to analyze this problem only in archaeological grounds. No evidence or scarce evidence means that humans were not involved. Nevertheless hunting or scavenging megafaunal sites exists. However, for climate hypothesis defenders, this information is not enough to really probe human involvement with megafauna' species. As Haynes (2007) argued, the solution is not claiming for more sites, given that human "intentionality" cannot be really proven in them. Megamammals could have been scavenged, used from fossil context or just can be coincidentally associated. Thus having more human-megafauna sites will not finish the discussion. On the other side record is always biased, partial and its discovery depends not only in program research, but also in "luck" in detecting early sites, given the different problems that can affect them, as pointed by Surovell and Grund (2012). Record of smaller mammal predation exists, as there is megamammal record, probing that first American population had a wide range diet. Nevertheless, megafauna's extinction cannot be analyzed just in archaeological grounds. As Surovell et al. (2016) have indicated, this problem goes beyond archaeological record itself. In a broader way, different lines of evidence and ecological information must be taken into account in order to confront this problem. For example, chronology of First and Last dates of megamammals and human appearance is a tool used by different researchers, not only for the Americas, but worldwide. In general terms, they point to the astonishing coincidence between human arrival and extinction event. Also, ecological traits are important features that researchers have highlighted. Low reproduction rate, exposed communities, or naivety are shared characteristic of animals that extinguished. This fact differentiates Quaternary extinction in comparison with other extinction events, where wider taxa of orders were affected by climate change. Thus, climate hypothesis defenders, adjust their analysis to only one kind of evidence, not allowing to have a broad panoramic of the situation.

2. There is a problem of interpretation between both sides. Human hypothesis defenders argues that certainly first American peopling must have used a wide range of resources. Nevertheless they also consider that human impact in megamammals' communities was the most probable cause of extinction, given that climate change weakened these low-reproductive and naive groups. However climate hypothesis defenders continue pointing that "the other side" only consider specialization over megafauna to explain extinctions over human-based ground (Wroe et al. 2004; Boulanger and Lyman 2014; Meltzer 2015). Thus they deny the more general view of who consider human intentionality into a general climatically and ecologically background. In this sense the debate is blocked (Monjeau et al. 2016) and accusations crosses between both sides. At the same time climate hypothesis defender leaved humans almost out of play in the extinction process.

3. At last, the debates will continue since researchers have their own filters, on what to accept and not accept as good and bad evidence. Most of the sites, associations or marks are deny for different

questions. This happens with defenders of both sides. Fiedel (2009:26) for example have question one well excavated and analyzed site as Monte Verde. He affirms that one site is just an "anomalous" case in the record. In this sense, he uses the same logic that climatic defender pose to accuse: low evidence is no evidence. By the way, different authors question the validity of North American and South American sites with megafauna association depending on the position they defend. Different causes are claimed to reject the evidences, among them: material can be associated just by coincidence, sites are not well excavated, the information is not properly published, the pictures have low quality or there is lack or poverty of information. There is a sense of "authority" (Fiedel and Haynes 2004) in what good evidence is, or what bad evidence is, what can be "scientifically" accepted or not. If several sites are rejected or criticized, does not mean that the problem is the filter and not in the evidence itself? It this is the sense, not all the evidence can be evaluated under the same type of rules. Paleontological and archaeological record is very variable, thus it is not easy to apply the same taphonomical reasoning to all the sites (Surovell and Waguespack 2009).

In this complex panorama, this work will not resolve this non stopping debate. An incredible amount of work is published year after year, from different researchers in order to understand the causes of extinctions. Innumerable reviews of published evidence can defend or not the different positions, according to the theoretical ground of the researcher. At a broad way level, after human entered in the Americas, both direct and indirect types of impact would have been produced in the environment. Consequently, as pointed in the first part of the chapter this work, focus will be put in understanding paleoecological relationship between humans and megamammals native communities. Although very much debated, the evidence is still scarce, and was used generally to evaluate causes behind extinctions. Museum's collection can contribute with new information. Integration of it, with other sites, and with ecological information can be useful to get deep into how human scavenging/hunting activities could have incorporated in this new environment.

3. MATERIALS AND METHODS

This chapter is divided in two sections. On the first one, the historical context of the science during 19th century, in which the trafficking operations were developed, will be introduced, along with the description of each of the visited collection. The second part of this chapter will be devoted for the Methods, where the taphonomical variables considered for analyzing the collections, will be explained. In the last part of this section, the technical aspects will be presented.

3.1. DE LA PLATA BASIN AND ITS PALEONTOLOGICAL COLLECTIONS: HISTORICAL CONTEXT

As already was introduced in the Introduction, since the discovery of this continent South American faunas have attracted European attention. This led to the development of a highly sophisticated commercial system, especially between Argentina and Europe, along the next centuries (Podgorny 2000, 2001). The “official” departure point of this trend was the sending of *Megatherium americanum* complete skeleton to the *Real Gabinete de Historia Natural* of Madrid in 1787 (López Piñero and Glick 1993) (Figure 3.1). This was the first South American skeleton to be taxonomically classified by Cuvier (López Piñero and Glick 1993; Fernicola et al. 2009; Cowie 2011). Afterwards, a complete description of its anatomy was done by Owen in 1861. During 18th century, the Cabinets were the first attempts to make science, proliferating mostly among the courts and the high class society. An assembly of strange or new things were brought to these places after the worldwide exploratory voyages (Podgorny 2001; Perazzi 2008; Cowie 2011; Baratas Díaz and Bueno 2013).

One milestone point in the exploration of the Pampean region was Darwin’s visit (Fernicola et al. 2009; Vizcaíno et al. 2009). From 1832 to 1834 he travelled across the Patagonian and Pampean regions, making valuable observations about the fauna, the geological setting and even the traditions of the people (Fernicola et al. 2009; Zárate and Folguera 2009). Last decades of 19th century saw the professional institutionalization of Natural Science museums in Europe and in Argentina. The colonization of the world, the florescence of new ideas, like Darwin proposals, and, the necessity to frame the new discoveries explain the proliferation of the Cabinets and latter the museums. In addition, at that time also, science was a way to educate the new emergent social classes (Pérez Gollán 1995; Perazzi 2008; Baratas Díaz and Bueno 2013). In Argentina, Ameghino’s studies at the end of the 19th century have impulsed Natural Sciences. His vast paleontological and geological work provided the hallmark for disciplines, such as archaeology, geology or paleontology during the next century (Daino 1979; Vizcaíno et al. 2009; Lanzelotti and Acuña Suarez 2014; Podgorny 2001b, 2015). The currently European collections analyzed were formed in this historical context.

In the Figure 3.2 the provenance of the material per museum can be seen. Next, a brief review of the history of each of them (and the Argentinean ones) will be done.

Figure 3.1. Megatherium americanum skeleton exposed in Museo de Ciencias Naturales de Madrid.

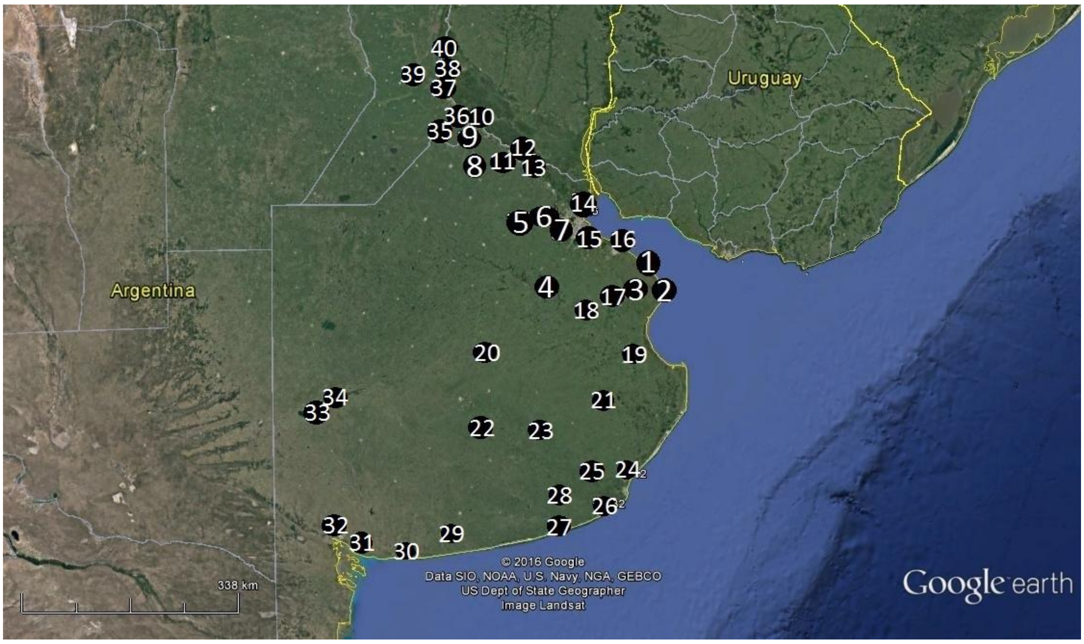
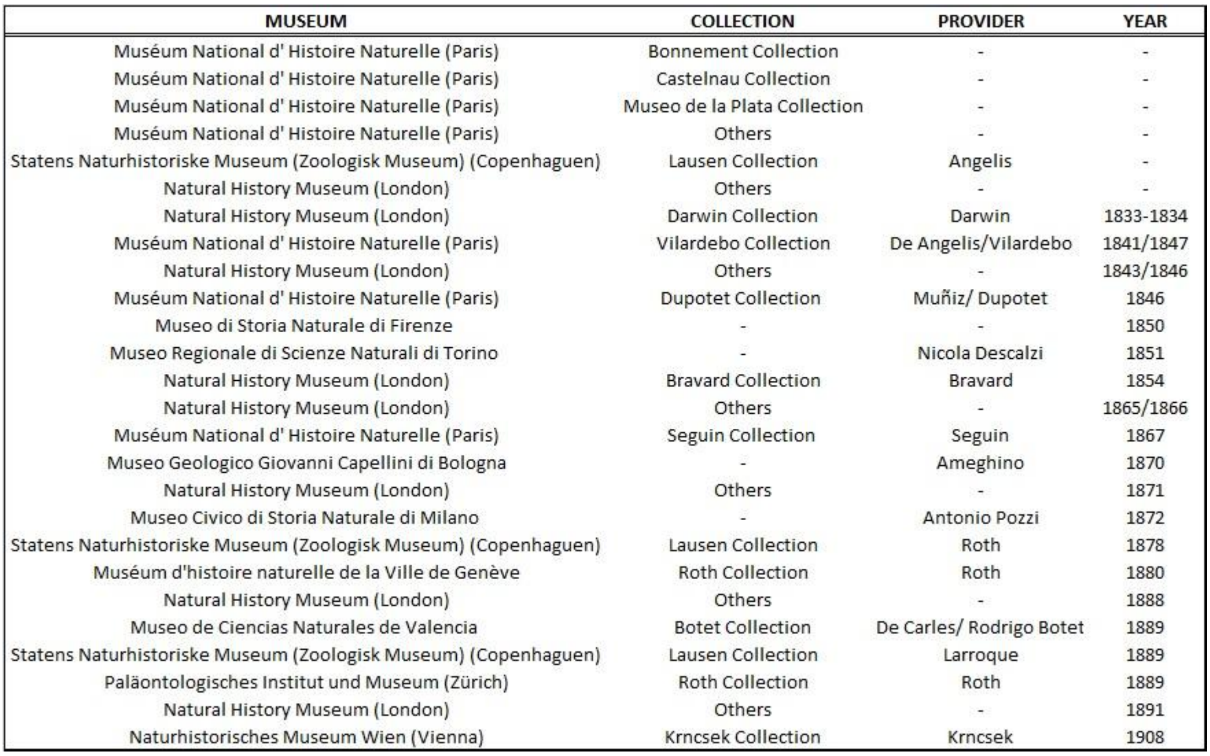


Figure 3.2. Localization of the reviewed material (considering the information availablity in the visited museums). 1. Rio de La Plata (MCNV, MSNF, NHM, MNHN, MACN), 2. Bahía de Samborombón (MCNV, MACN), 3. Río Samborombón (MCNV, PIMUZ, MACN), 4. Río Salado (MCNV, MCSNM, MNHN, MACN), 5. Mercedes

(MCSNM, NMW, ZMK, MACN, MLP, MCA), 6. Luján (NHM, MACN, MCA), 7. Cuenca Río Matanzas (MRSNT), 8. Arroyo Pergamino (PIMUZ, ZMK), 9. Arroyo Ramallo (PIMUZ, ZMK), 10. San Nicolás (PIMUZ, MNHN), 11. Río Arrecifes (ZMK, MACN), 12. Baradero (PIMUZ), 13. Cañada Honda (MLP), 14. Olivos (MACN), 15. Florencio Valera (MLP), 16. La Plata (NHM, MNHN, MLP) and Canal de Conjunción (La Plata) (MLP), 17. Chascomús (MACN), 18. Arroyo Poronguito, General Belgrano (MLP), 19. Dolores (MACN), 20. Talapaqué (MACN), 21. Arroyo Chelforo (MLP), 22. Laguna Barrancosa (PIMUZ), 23. Tandil (MLP), 24. Camet/Santa Elena (MHNVG, MLP), 25. Balcarce (Arroyo Grande) (MACN), 26. Mar del Sur/Miramar (MACN), 27. Necochea (MACN), 28. Rio Quequen Grande (MLP), 29. Quequen Salado (MLP), 30. Monte Hermoso (MACN, MLP), 31. Punta Alta (NHM, PIMUZ), 32. Tornsquist (MLP), 33. Carhué (MACN), 34. Laguna del Monte (MACN), 35. Arroyo del Medio/ Barranca Arroyo del Medio (PIMUZ, ZMK), 36. Pavón (PIMUZ), 37. Alverde pres Rosario (PIMUZ), 38. Barranca San Lorenzo Tonelero (PIMUZ), 39. Rio Carcaraña (NHM, PIMUZ), 40. Barraca del Paraná (PIMUZ, ZMK, MACN).

3.1.1.EUROPEAN COLLECTIONS

In Table 3.1 it is presented the general characteristics of European collection ordered by acquisition or entrance year.



MUSEUM	COLLECTION	PROVIDER	YEAR
Muséum National d' Histoire Naturelle (Paris)	Bonnement Collection	-	-
Muséum National d' Histoire Naturelle (Paris)	Castelnau Collection	-	-
Muséum National d' Histoire Naturelle (Paris)	Museo de la Plata Collection	-	-
Muséum National d' Histoire Naturelle (Paris)	Others	-	-
Statens Naturhistoriske Museum (Zoologisk Museum) (Copenhaguen)	Lausen Collection	Angelis	-
Natural History Museum (London)	Others	-	-
Natural History Museum (London)	Darwin Collection	Darwin	1833-1834
Muséum National d' Histoire Naturelle (Paris)	Vilardebo Collection	De Angelis/Vilardebo	1841/1847
Natural History Museum (London)	Others	-	1843/1846
Muséum National d' Histoire Naturelle (Paris)	Dupotet Collection	Muñiz/ Dupotet	1846
Museo di Storia Naturale di Firenze	-	-	1850
Museo Regionale di Scienze Naturali di Torino	-	Nicola Descalzi	1851
Natural History Museum (London)	Bravard Collection	Bravard	1854
Natural History Museum (London)	Others	-	1865/1866
Muséum National d' Histoire Naturelle (Paris)	Seguin Collection	Seguin	1867
Museo Geologico Giovanni Capellini di Bologna	-	Ameghino	1870
Natural History Museum (London)	Others	-	1871
Museo Civico di Storia Naturale di Milano	-	Antonio Pozzi	1872
Statens Naturhistoriske Museum (Zoologisk Museum) (Copenhaguen)	Lausen Collection	Roth	1878
Muséum d'histoire naturelle de la Ville de Genève	Roth Collection	Roth	1880
Natural History Museum (London)	Others	-	1888
Museo de Ciencias Naturales de Valencia	Botet Collection	De Carles/ Rodrigo Botet	1889
Statens Naturhistoriske Museum (Zoologisk Museum) (Copenhaguen)	Lausen Collection	Larroque	1889
Paläontologisches Institut und Museum (Zürich)	Roth Collection	Roth	1889
Natural History Museum (London)	Others	-	1891
Naturhistorisches Museum Wien (Vienna)	Krncsek Collection	Krncsek	1908

Table 3.1. European collections with information of collection name, provider, year of selling or entrance to the museum.

3.1.1.1. Italy

The lack of a general National Museum in this country resulted in several small collections dispersed in different cities.

The former Natural History Museum of Bologna (currently *Museo Geologico Giovanni Capellini di Bologna*, MGGCB) was organized by Giovanni Capellini (Fanti 2010). This pioneer Italian researcher had international ties with colleges such as Ameghino. The current Pampean collection was probably donated by him (Fanti 2010). It is composed of different Xenarthra species, among them, a complete skeleton of *Scelidotherium capellinii* named by Ameghino as a tribute to his friend (Figure 3.3). The material is identified as “Pampas” without more specifications.

Figure 3.3. Skeketon of Scelidotherium capellinii from MGGCB, Bologna.

The collection housed in the *Museo Civico di Storia Naturale di Milano* (MCSNM) was sold by Antonio Pozzi, an independent collector that used to collaborate with Ameghino, and was acquired by professor Cornalia (Farro 2008). The collection is composed of different Pampean specimens, as *Smilodon, Megatherium* or *Mylodon* (Cornalia 1872). Humans remains were supposedly part of this assemblage, even though this material was never found (Politis and Bonomo 2011) In 1943, during the Second World War, the museum was bombed and the collections were partially destroyed (Beneditti 2005) (Figure 3.4). Some locations identified in the labels were Rio Salado, Río Luján or Mercedes.

Figure 3.4. Ribs of different species from MCSNM, Milano.

The collection from *Museo Regionale di Scienze Naturali di Torino* (MRSNT) suffered a similar tragedy. The bombing of 1943 produced several looses (Gallo 2008), among them, the Pampean collection. A *Megatherium americanum* and *Glyptodon* skeleton donated by Nicola Descalzi in 1851 (Cimino et al. 2014) were partially destroyed (Figure 3.5). Descalzi was another collector that used to sell collections to different European museums during the first half of the 19th century (Podgorny 2011). He collected these specimens from the Basin of Río Matanzas.

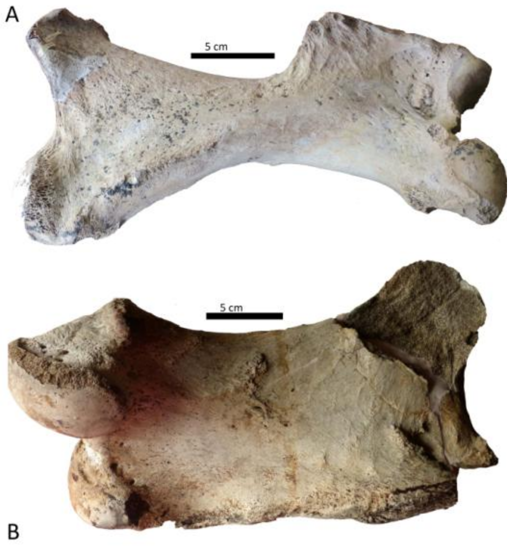


Figure 3.5. Femur of: A. Glyptodon and B. Megatherium americanum from MRSNT, Torino.

At last, the collection of the *Museo di Storia Naturale di Firenze* (MSNF) is composed mostly of *Megatherium americanum* bones coming from Río de La Plata, Buenos Aires province. According to the historical catalogue, currently housed in the *Museo di Storia Naturale La Specola*, the Megatheriidae collection was bought in 1850. Nevertheless in 1871 some Glyptodontidae remains (labeled "near Buenos Aires") were added (Figure 3.6).

Figure 3.6. Casts of Megatherium americanum and Glyptodon heads exposed in the MSNF, Firenze.

3.1.1.2. Spain

In the *Museo de Ciencias Naturales de Valencia* (MCNV) is housed one of the most important South American megamammals' collections from Europe. The material was gifted to Valencia City in 1889 by the engineer José Rodrigo Botet, who had obtained it from the collector, Enrique de Carles (Belinchón et al. 2009). He was a naturalist from the *Museo Público de Buenos Aires* and made excavations in different sites from where the collection comes from: De La Plata, Salado and Samborombon rivers and Samborombon bay, in the North part of the Pampean region. Boscá Casanoves, first curator of the collection, performed several paleontological studies (Boscá Casanoves 1899, 1902, 1917, 1919, 1921, 1923 a and b; among others). The collection is composed of different species such as *Smilodon*, Mylodontidae, Glyptodontidae, and Notoungulata, among others (Figure 3.7). It also includes important human remains, named as the "Samborombón skeleton", used by

Ameghino in his discussion of the first American peopling (Martel San Gil & Aguirre Enríquez 1964; Salinas Jaques 2001; Catalá Gorges 2004, 2011; Belinchón et al. 2009).

Figure 3.7. Different Mylodontidae humerus from MCNV, Valencia.

3.1.1.3. France

The South American collection housed in *Muséum National d' Histoire Naturelle* (MNHN) (Figure 3.8) has different origins:

(i) The Dupotet Collection originated when Juan Manuel de Rosas, governor of Buenos Aires, gave it to Dupotet, a French admiral, in 1846. The material was originally excavated by Muñiz, around the locality of Luján (Podgorny 2001a). The collection is composed of species such as Mylodontidae, *Macrauchenia patachonica* or *Megatherium americanum*.

(ii) The Seguin Collection is composed of two selling (1850 and 1867) that this collector made to the Muséum (Podgorny 2009). Mylodontidae, *Macrauchenia patachonica* are among the identified species. The collection of 1867 included human remains and stone tools, extracted from Carcaraña River in Santa Fé (Ameghino 1915 [1880]). The material comes mostly from Santa Fé or Río Salado.

(iii) Another provider identified was Teodoro Vilardebo. He was a Uruguayan medical doctor that was a fossil merchandiser. One of his providers was de Angelis, a Neapolitan traveller that found a way of living by selling Pampean bones (Podgorny 2011). The material was excavated around 1841 and arrived to París in 1847 (Podgorny 2011). Some labels indicate that the collection originated in Buenos Aires, even though they could be related with the excavation that de Angelis realized in Salto

(Podgorny 2011). Different Glyptodons, Mylodontidae, *Megatherium americanum* or Notoungulates such as *Toxodon platensis* are some of the species identified in this collection.

(iv) Other providers were Bonnement, who brought fossils from La Plata locality, and Castelnau. Part of the collection has the Museo de La Plata label adhered, while other fragments do not have identification of the collector or provider (some of them are from Rio de La Plata). Part of this material could belong to the collection that Bravard sold to this institution (Podgorny 2001a). August Bravard was a French naturalist contracted by the *Gobierno de Buenos Aires* and the *Confederación Argentina* to record the natural resources of Argentina (Tonni et al. 2008; Podgorny 2009) and at the same time he sold collections to different European museums (Podgorny 2001a).

Figure 3.8. Skeleton of Megatherium americanum exposed in MNHN, Paris.

3.1.1.4. England

In the Natural History Museum, London (NHM), it is housed part of the Darwin collection. This material was send by the time he was travelling in the Beagle, and was originally deposited at the

Royal College of Surgeons. Richard Owen identified and described all the specimens such as the *Macrauchenia patachonica*, *Mylodon darwini* or *Toxodon platensis* (Figure 3.9). After the bombing of the Second World War, the remaining material was relocated in this museum (Podgorny 2001a; Fernicola et al. 2009). Even though part of this collection comes from Puerto San Julian in Patagonia, it was included given the historical importance of this collection.

There is also part of the Bravard collection, sold to this institution in 1854 (Podgorny 2001a). Nevertheless, most of the material could not be identified with a specific provider. The localities registered in the labels were La Plata, Rio Carcaraña or Rio de La Plata.

Figure 3.9. Toxodon platensis head housed in MHN, London (Darwin Collection).

3.1.1.5. Switzerland

In this country two collections sold by Roth were visited. One is housed in the *Muséum d'Histoire Naturelle de la Ville de Genève* (Geneve) (MHNVG) and the other in *Paläontologisches Institut und Museum* (Zurich) (PIMUZ). Santiago Roth was born in Switzerland, but arrived to Argentina in 1866 with his family (Marchon 1925; Bond 1999a). In the next decades he started to collect and sell Quaternary mammals collections to different European museums. Although he didn`t had an academic formation, he achieved several charges in the *Museo de La Plata*, between 1895 and his dead in 1924. Before arriving to this institution, in 1880 makes a first selling to Geneve and latter, in 1889 to Zurich (Marchon 1925). In MHNVG, the most important groups identified were different species of Glyptodontidae, *Toxodon* and *Megatherium americanum* (Figure 3.10). Some bones referred to Punta Santa Elena. In PIMUZ, the collection is composed of different Xenarthra, Ungulates and Carnivores remains, coming from different localities of the Northwest of Buenos Aires and South of Santa Fe province (Figure 3.11). Along with mammal fauna, Roth sold humans rests currently known as “Hombre de Pontimelos” (Bond 1999a).

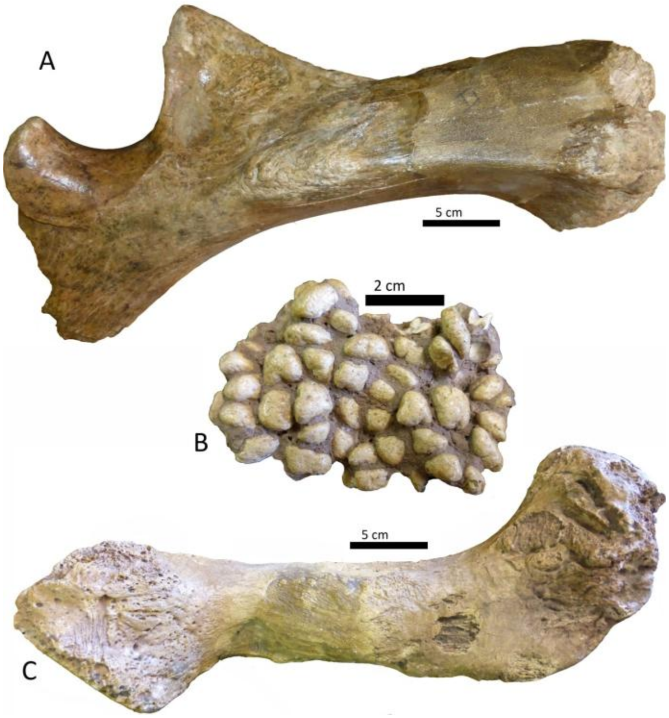


Figure 3.10. MHNVG collection, Geneve: A. Ulna of Toxodon, B. Osteoderms of Mylodon, C. Clavicle pathology of Megatherium americanum.

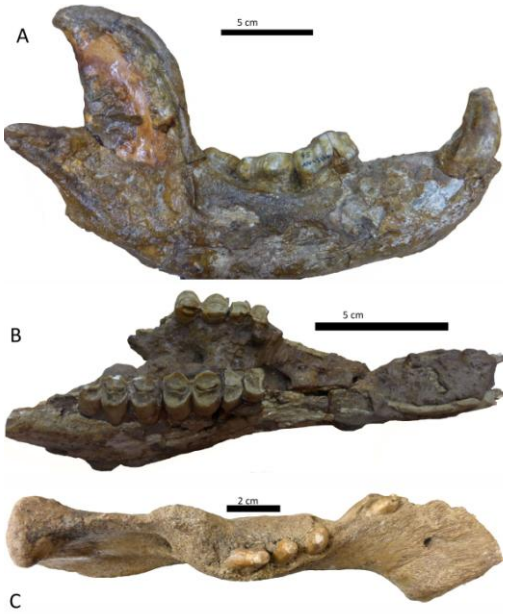


Figure 3.11. Mandibles from PIMUZ, Zurich: A. Ursus (notice restoration), B. Lama (with concretions) C. Juvenil Mylodon.

3.1.1.6. Austria

In the *Naturhistorisches Museum Wien* (NMW) there is a collection sold by Krncsek, in 1908. Sofonías Krncsek was school director in Mercedes that used to collaborate with Ameghino (Lanzelotti and Acuña Suarez 2014). *Megatherium americanum*, Mylodontidae, Glyptodontidae and Ungulates composed this assemblage. It is remarkable also one *Smilodon populator* skeleton in the permanent exhibition that presents several pathologies (Drexler and Zapfe 1956) (Figure 3.12).

Figure 3.12. Smilodon populator with pathologies exposed in NMW, Vienna.

3.1.1.7. Germany

In the *Museum für Naturkunde*, Berlin (MN), there is a mounted hindlimb and some elements of *Glyptodon* (Figure 3.13). Nevertheless this museum possesses an important collection of Cueva del Mílodon in the Chilean Patagonia. Even though several carnivore interventions were detected in this assemblage, it will not be discussed here, given it is out of the studied region of this work.

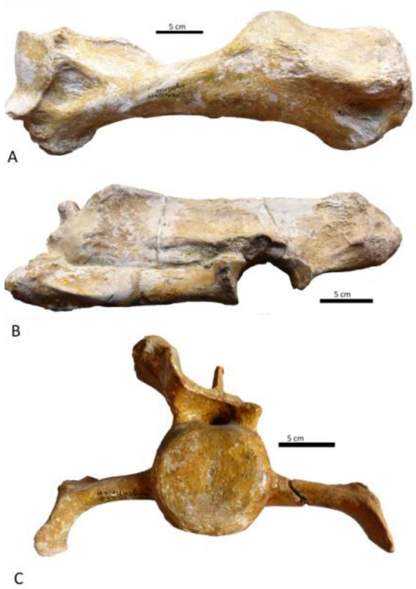


Figure 3.13. Glyptodontidae remains of MN, Berlin: A. Humerus, B. Radio Ulna, C. Vertebra.

3.1.1.8. Denmark

Another important collection of South American megafauna is the Lausen Collection housed in the *Statens Naturhistoriske Museum (Zoologisk Museum),* Copenhagen (ZMK) (Figure 3.14). Valdemar Lausen was a Danish doctor that worked in Buenos Aires for several years. He bought fossil assemblages to several providers to be donated to this museum (Lykke Hansen 2014 pers. comm.). Roth sold the most important part of the assemblage in 1878 (Bond 1999a). As in the PIMUZ case, this part of the collection comes from different localities of the Northwest of Buenos Aires and South of Santa Fe province. It is composed, as in the other museums, of different native American groups. Other two providers were Angelis and Larroque. The first one can be de Angelis, the same provider of Vilardebo named before. This assemblage is composed of *Megatherium americanum* bones with several pathologies. Larroque was a collector from Mercedes and Ameghino´s friend (Lanzelotti and Acuña Suarez 2014).This collection dates from 1889 and is composed of *Megatherium americanum*, different Mylodontidae, Glyptodontidae and Ungulates.

Figure 3.14. Skeletons of Megatherium americanum and Glyptodon exposed in ZMK.

3.1.2. ARGENTINEAN COLLECTIONS

3.1.2.1. Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN)

This institution is a standing point in Argentinean scientific discipline. Originally created as the *Museo Público de Buenos Aires*, its rise is linked with the revolutionary period of independence this country passed between 1810 and 1816 (Perazzi 2008). Nevertheless its importance and development started to grow up after the half of the 19th century. The European influence, the incorporation of new lands that allowed realizing scientific exploration along the country, and its nationalization in 1884 positioned this institution as one of the most prestigious at that time (Perazzi 2008). Germám Burmeister was contracted as the first director in 1862 and Ameghino was his director between 1902 until his dead in 1911 (Perazzi 2008). The material reviewed here is composed of a heterogeneous assemblage of different providers. In order to have a general panorama of the material housed in this institution, a selection of different taxa groups was realized (Figure 3.15).

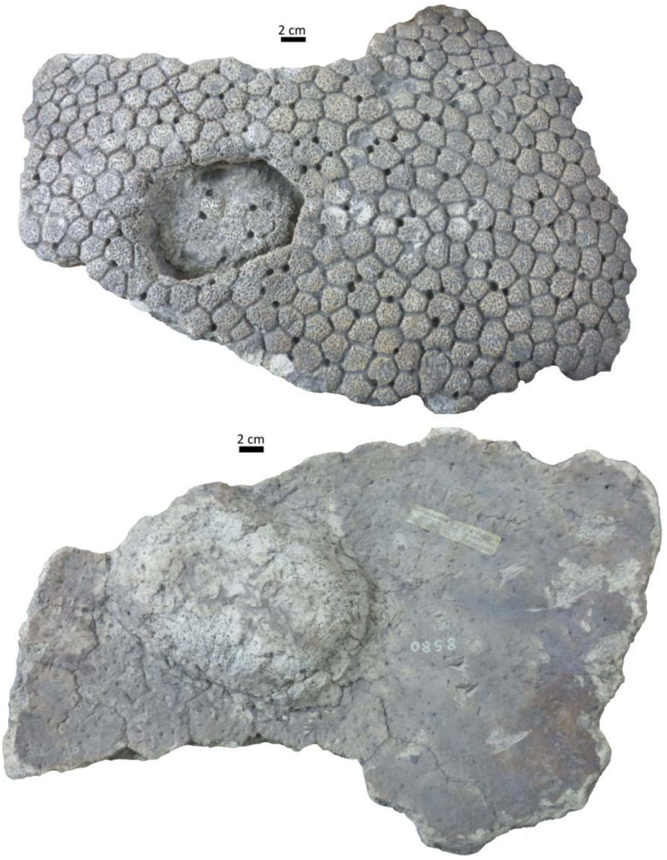


Figure 3.15. Glyptodon carapace with pathology from MACN, Buenos Aires.

3.1.2.2. Museo de La Plata, La Plata (MLP)

Along with the former, is one of the funding stone of natural science development in this country. It was created in 1884, based in the personal collections of Francisco Pascasio Josué Moreno that was its first director (Farro 2008). The first decades were used to collected fossils from South American megafauna (Figure 3.16). Thanks to the different exploration research, the museum housed a diverse type of geological, paleontological and anthropological material from the entire country (Farro 2008). A selection of these old collections was reviewed, and also two collections described by Ameghino were considered. One is housed in the *División de Paleontología* and is from Middle Pleistocene, named here as MLP Ameghino (paleont. Coll.). In his work "*Los mamíferos fósiles de la República Argentina, Parte 1*" (Ameghino 1916 [1889]), he assigned the fractured bones to human intervention. The other is in the *División de Arqueología* (named as MLP Ameghino (archaeo. Coll.)) and described by Ameghino in "*La Antigüedad del Hombre del Plata*" Ameghino (1915 [1880]). This material proceeds from different sites used by Ameghino for probing the convivence of humans and megafauna (Lanzelotti and Acuña Suarez 2014).

Figure 3.16. Macrauchenia patachonica skeleton exposed in MLP, La Plata.

3.1.2.3. Museo Municipal de Ciencias Naturales Carlos Ameghino, Mercedes (MCA)

In this museum are housed different fossil assemblages from the surrounding of Mercedes city. Given the earlier works of Ameghino in the region, and of the different assemblages sold to European museums from this locality, a part of the collections was reviewed. It was inaugurated in 1947 by the palaeontologist José Bonaparte (Lanzelotti and Acuña Suarez 2009) and its heritage is composed by a rich paleontological and archaeological collection (Figure 3.17).

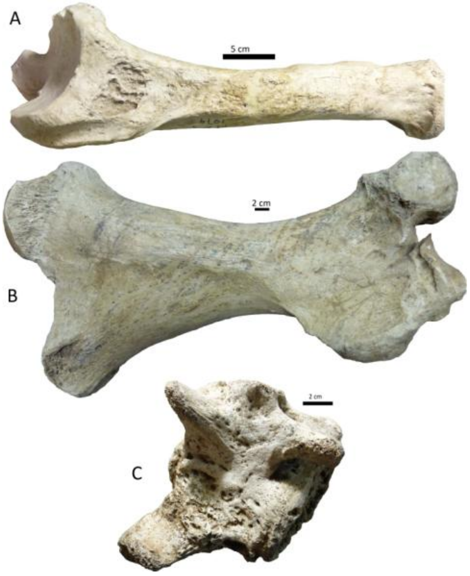


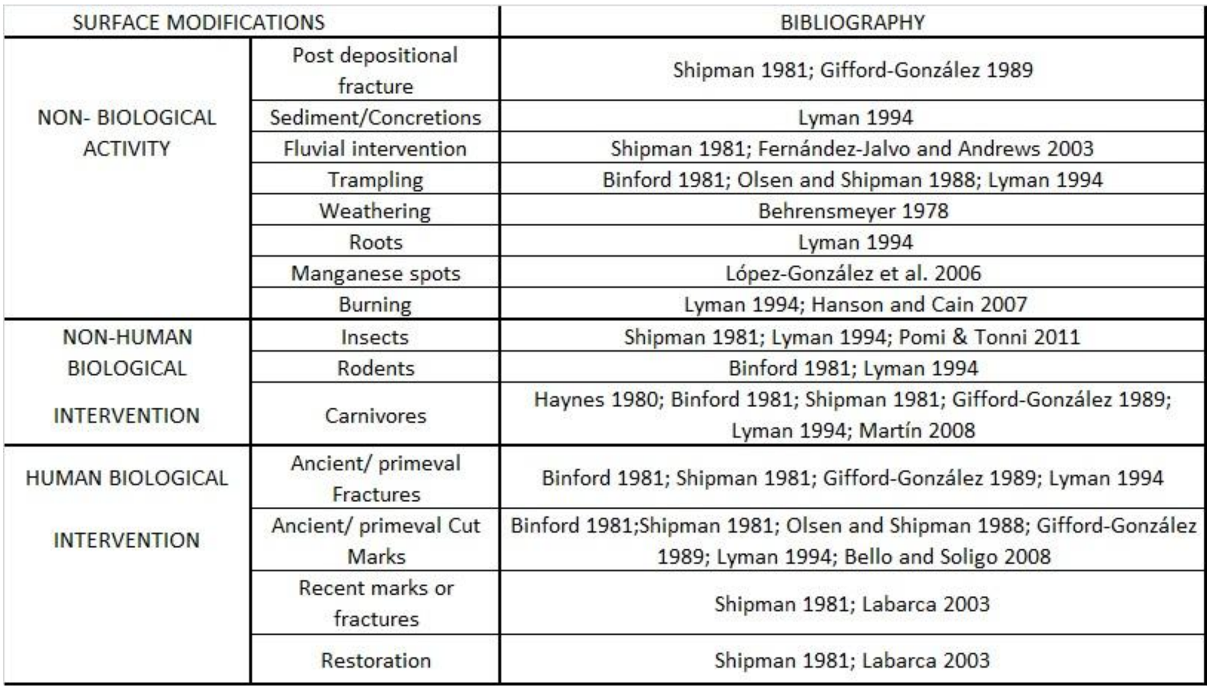
Figure 3.17. Bones from MCA: A. Radio of Toxodon with pathology, B. Femur of Toxodon, C. Vertebra of Glyptodon with pathology.

3.2. METHODS

Taphonomical procedures were used to confront the material in order to differentiate the several surface modifications of osseous material passed through after animals' dead (Behrensmeyer 1975; Shipman and Rose 1983a; Andrews and Cook 1985; Bonnichsen 1989; Fisher 1995; Selvaggio and Wilder 2001; Faith et al. 2007; Fernández-Jalvo and Andrews 2016). Efremov (1940, 1953) had established the general basis of Taphonomy. Along these last decades this discipline had made several progresses. From a theoretical point of view, it is considered that postdepositional factors add information regarding the history and sequence of formation of the deposits, and of the sequence of deposition of each of the modifications. They are also indicators of the environment to which the bones were subject to, and indirectly, this information can be useful to realize paleoecological and paleoenvironmental interpretations. Unlikely, in the past, they were considered as blurring processes that affected assemblage composition (Behrensmeyer and Kidwell 1985; Kidwell and Behrensmeyer, 1988; Bonnichsen 1989; Cutler et al. 1999; Martin 1999; Fernández-López 2000; Fernández-Jalvo et al. 2011; Denys and Patou-Mathis 2014). Actualistic research and technological devices have contributed to have a corpus of control information of how difference surface modifications are acting over bones (Lyman 1994; Denys 2002; James and Thompson 2015; Fernández-Jalvo and Andrews 2016). These studies were realized in the paleontological and archaeological fields not only to understand the different agent that can affect the sites, but also to distinguish anthropic and/or carnivore intentionality.

Nevertheless in this work, this corpus of knowledge was used to analyze decontextualized material. Factors working in the biostratinomy and fossildiagenessis stages were taken into account. The first one comprise the ones that affects bony remains from the dead of the animal until its burial, while the second one are produced when the material is buried until the discovery (Fernández-López and Fernández-Jalvo 2002). In this work they were used to analyze the modification that had affected bone surfaces and thus distinguish biological intervened bones.

The surface modifications considered were separated by: non-biological activity, non-human biological intervention and human biological intervention (Table 3.2). Although we briefly have explained them in the published papers, we refer to each of them in the following sections. Especially for the first ones, we exemplified with the material from the different museums visited.



SURFACE MODIFICATIONS		BIBLIOGRAPHY
NON- BIOLOGICAL ACTIVITY	Post depositional fracture	Shipman 1981; Gifford-González 1989
	Sediment/Concretions	Lyman 1994
	Fluvial intervention	Shipman 1981; Fernández-Jalvo and Andrews 2003
	Trampling	Binford 1981; Olsen and Shipman 1988; Lyman 1994
	Weathering	Behrensmeyer 1978
	Roots	Lyman 1994
	Manganese spots	López-González et al. 2006
	Burning	Lyman 1994; Hanson and Cain 2007
NON-HUMAN BIOLOGICAL INTERVENTION	Insects	Shipman 1981; Lyman 1994; Pomi & Tonni 2011
	Rodents	Binford 1981; Lyman 1994
	Carnivores	Haynes 1980; Binford 1981; Shipman 1981; Gifford-González 1989; Lyman 1994; Martín 2008
HUMAN BIOLOGICAL INTERVENTION	Ancient/ primeval Fractures	Binford 1981; Shipman 1981; Gifford-González 1989; Lyman 1994
	Ancient/ primeval Cut Marks	Binford 1981;Shipman 1981; Olsen and Shipman 1988; Gifford-González 1989; Lyman 1994; Bello and Soligo 2008
	Recent marks or fractures	Shipman 1981; Labarca 2003
	Restoration	Shipman 1981; Labarca 2003

Table 3.2. Surface modification considered.

3.2.1.Non-biological activity

This item refers to surface modifications over bones not realized by biological causes (e.g. carnivores/humans) but have their origin in the "natural forces" of the environment. Briefly, the following non-biological activities considered for this work were:

3.2.1.1. Post-depositional fracture

Unlike fresh bones, dry bones fractures produces transverse breaks or rectangular/triangular borders (Shipman 1981a; Villa and Mahieu 1991; Lyman 1994; Fernández-Jalvo and Andrews 2016) (Figure 3.18).

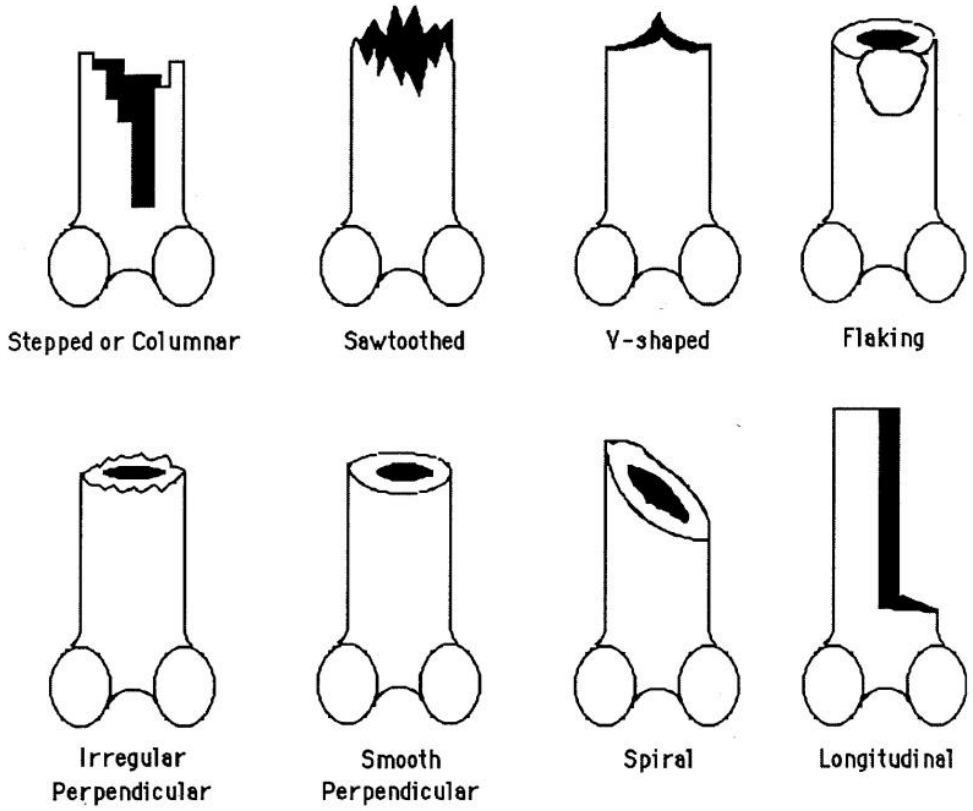


Figure 3.18. Different types of fractures (from Lyman 1994: 319). Stepped and/or longitudinal types of breakage are related with dry bones, while spiral ones with green/fresh bone.

Lack of the collagen that tempers the impacts (Fernández-Jalvo and Andrews 2016) implies that they do not have the plasticity and flexibility of fresh bones and fractures generally follow the internal mineral structures (Alcántara 2006). Borders will tend to be irregular and rough, with straight angles and without impact points (Alcántara 2006; Fernández-Jalvo and Andrews 2016). Fractures can be caused by natural process such as trampling (see below), sediment movement, compaction (Andrews and Cook 1985; Lyman 1994; Haynes and Krasinski 2010; Fernández-Jalvo and Andrews 2016) or temperature conditions (Karr and Outram 2012). Nevertheless frozen conditions can also produce spiral fractures in dry bones that can mimic biological intervention (Karr and Outram 2012) (Figure 3.19).They can also be produced by excavation activities or museum manipulation (see below). When broken edges do not suffer of other postdepositional process unlike the rest of the bone, it indicates that fracturing was produced in advances stages of deposition (Fernández-Jalvo and Andrews 2016).

Figure 3.19. Two examples of post depositonal fracture. A. Mylodon rib with spiral fracture from MCA, Mercedes (Notice trampling also), B. Tibia of Cervidae with irregular/rectangular fracture from MCNV, Valencia, notice sediment.

3.2.1.2. Sediment/Concretions

Burial can produce a series of diagenetical changes in bones. Soil composition, microbial activity and state of the bone interplay in long term producing chemical and/or physical modification in its structure, such as loss of collagen, changes in porosity; recrystallization or incorporation of mineral as carbonate deposition or organic particles, producing permineralized/ mineralized or petrified bones and/or changes in the colour (Behrensmeyer 1975; Lyman 1994; Lawson et al. 2000; Nielsen-Marsh and Hedges 2000; Rodríguez Suárez 2005; Smith et al. 2005, 2007; Ceccanti et al. 2007; Nielsen-Marsh et al. 2007; Fernández-Jalvo and Andrews 2016). When bones are buried in moist sediments, the humid conditions of the soils can produce corrosion over the bones, the macroscopic consequence is the loss of tissue in all the exposed surfaces (Fernández-Jalvo and Andrews 2016). However, local sedimentary context of burial is highly variable and can alter differently even bones from the same assemblage (Nielsen-Marsh and Hedges 2000; Rodríguez Suaréz 2005). Weigh of sediments can also produce deformation without breakage of the bones (Lyman 1994; Fernández-Jalvo and Andrews 2016).

It was also considered into this type of modification, presence or absence of sediments and/or concretions that can coverage part or totally bone´s surface, hindering the detection of biological interventions (Figure 3.20).

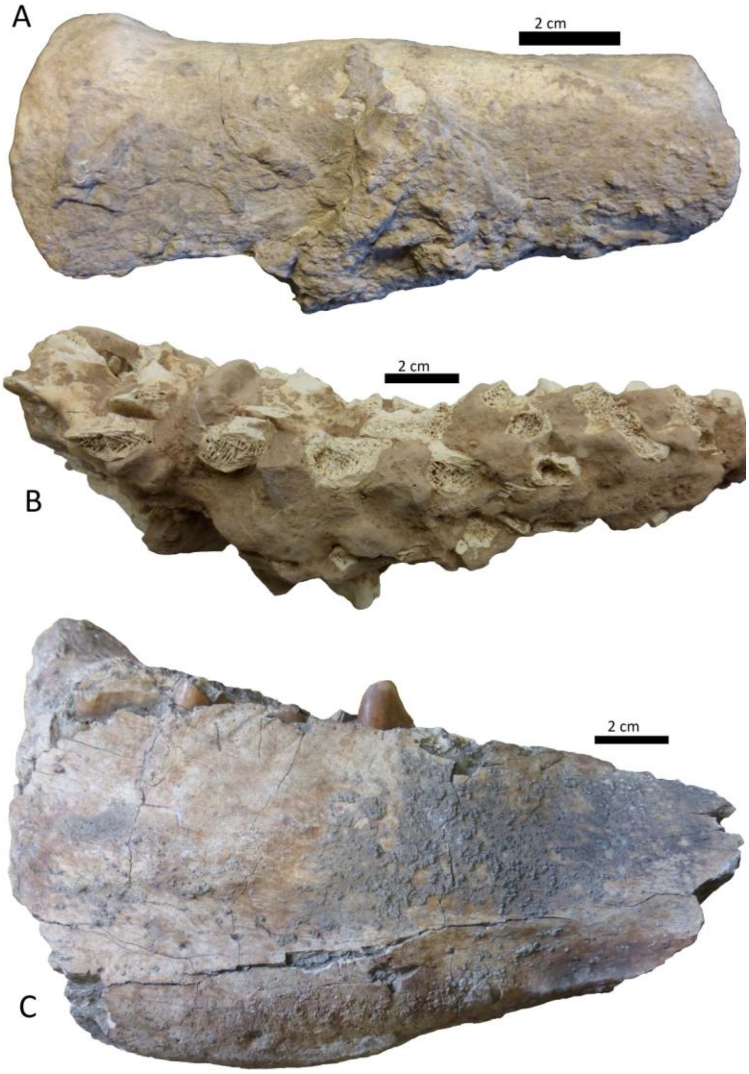


Figure 3.20. Different types of sediment coverage. A. Equus tibia from NMW, Vienna, B. Eutatus vertebrae from PIMUZ, Zürich, C. Scelidotherium leptocephalum mandible from MNHN, Paris.

3.2.1.3. Fluvial Intervention

Water can influence in several ways to bones assemblages. Fluvial erosion and transport by water streams can produce changes in bone's surface in dependence of the type of bone, type of sediment and the energy and/or time that are subject to (Korth 1979; Shipman and Rose 1988; Fernández-Jalvo and Andrews 2003, 2016; Thompson et al. 2011). The effects can go from fissures, pitting and ablation to rounding, polishing or degree of brightness (Fernández-Jalvo and Andrews 2003, 2016; Thompson et al. 2011) (Figure 3.21). This type of action can produce confusion between fluvial eroded bones and anthropically polished bones (Shipman and Rose 1988) but fluvial action will tend to erode the whole bone (Lyman 1994; Fernández-Jalvo and Andrews 2016). It is also different of eolic erosion that will generally affect distinctively the bone, in relation with the exposed surface (Fernández-Jalvo and Andrews 2016).

Figure 3.21. MLP Ameghino (paleont. Coll.), La Plata. Bones with fluvial action: A and B Metapodioum Equidae, C. Metapodium Lama, D. Humerus diaphysis, E. Rib fragment. Notice polish and brightness in A, B and C, and scratches and pitting in D and E. They also show post-depositional fracture.

Water stream action can also produce transportation of objects depending on different factors such as density, type and shape of the bone, if they are articulated or not and also if they are dry or fresh. It also depends on water conditions, as size of sediment particle, energy of current or topography among others (Behrensmeyer 1975; Korth 1979; Lyman 1994; Coard 1999; Fernández-Jalvo and Andrews 2003, 2016). Similar orientation of bones assemblage can be related with water transport, even though it can change with post-action disturbance (Toots 1965; Lyman 1994; Fernández-Jalvo and Andrews 2003). In 1969, Voorhies had classified in five groups the transportability of bones in a flume. This organization was subsequently modified by different researchers (Behrensmeyer 1975, Boaz and Behrensmeyer 1976; Korth 1979; Lyman 1994; Coard 1999).

This type of action can mix bones from different origins, consequently introducing bias for doing paleoecological assumptions, but also can be a good indicator of the depositional history of bone assemblage (Fernández-Jalvo and Andrews 2003).

3.2.1.4. Trampling

Abrasion of sediments over bones, product of the movement of animals and/or humans, can produce lines and scratches that can be confused with cut marks (Korth 1979; Shipman and Rose 1983a; Olsen and Shipman 1988; Fiorillo 1989; Behrensmeyer et al. 1986; Domínguez-Rodrigo et al. 2009; Haynes and Krasinski 2010) (Figure 3.22).

Some characteristics to differentiate trampling from cut marks are:

> (i) They will tend to be randomly oriented, this means they are not related with anatomical areas for butchering (Andrews and Cook 1985; Olsen and Shipman 1988; Lyman 1994; Domínguez-Rodrigo et al. 2009), in convex surface (Fernández-Jalvo and Andrews 2016) or in the shafts (Fiorillo 1989; Fernández-Jalvo and Andrews 2016). In this last case, they will present a transverse orientation in relation with the long axis, following the rotation movements of bones as they are trampled (Andrews and Cook 1985; Fernández-Jalvo and Andrews 2016).
>
> (ii) They are shallower and have a more open section than cut marks (Andrews and Cook 1985; Olsen and Shipman 1988; Fiorillo 1989; Lyman 1994; Domínguez-Rodrigo et al. 2009; Fernández-Jalvo and Andrews 2016).
>
> (iii) Surface present general polishing (Olsen and Shipman 1988) and microabrasion in the form of shallow stria randomly distributed or crossing obliquely to trampling marks (Domínguez-Rodrigo et al. 2009).
>
> (iv) Trampling marks will be present more abundantly in number than the discrete patches of cut marks (Andrews and Cook 1985; Olsen and Shipman 1988; Fernández-Jalvo and Andrews 2016).

Some features that trampling can share with cut marks are:

> (i) The presence of microstration in the internal walls. Nevertheless, they will tend to have a non-straight trajectory and probably be non-continuous (Andrews and Cook 1985; Domínguez-Rodrigo et al. 2009, 2010)
>
> (ii) As is the case for cut marks, trampling marks can have symmetrical or asymmetrical grooves. This is related with the type and/or orientation of sediment particles (Andrews and Cook 1985; Domínguez-Rodrigo et al. 2009)
>
> (iii) Sometimes trampling marks can have a straight orientation as cut marks (Domínguez-Rodrigo et al. 2009; Fernández-Jalvo and Andrews 2016) or V shape cross section. In this

case they will be shallower and narrower than cut-marks (Andrews and Cook 1985). Another similarity notice is that they can even be present as patches of parallel marks (Behrensmeyer et al. 1989).

In one of the last revisions realized about this subject, Fernández-Jalvo and Andrews (2016) have highlighted that the basic differences with cut marks is that trampling marks will tend to be less deep, shorter, more frequent, not related with muscle attachments and preferentially with transversal orientation to long bones axis.

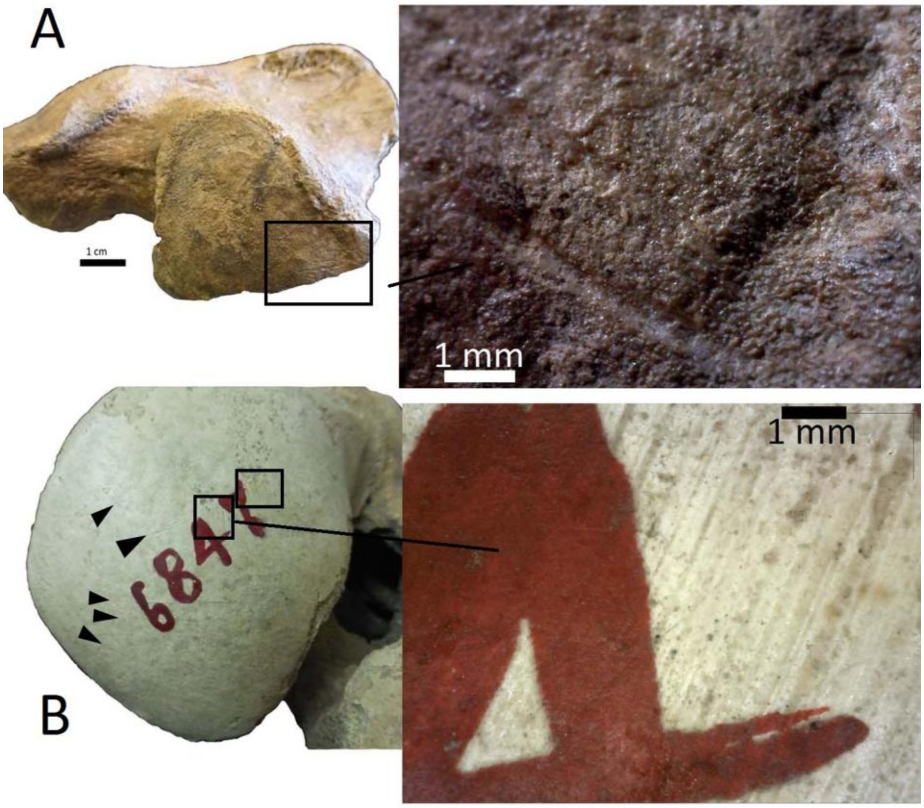


Figure 3.22. Two trampling's examples. A. Axis of Scelidotherium sp. from MHNVG, Geneve, with trampling in the articular surface. Even though they have parallel orientation, it can be observed in the magnification they superficial and have U shape section, B. Distal femur of Toxodon from MACN, Buenos Aires, with different sets of trampling: long ones indicated by the arrows and shorter and parallel with different orientation in the rectangles. The magnification of one of these patches reveals they are superficial and width.

3.2.1.5. Weathering

Exposed bones to aerial conditions can provoke changes in their superficial aspect (Fernández-Jalvo and Andrews 2016). Sun, wind or contrasting temperatures can result in cracking, exfoliation, flaking, splittering and in later stages, the decomposition (Behrensmeyer 1975, 1978; Lyman and Fox 1989;

Fisher 1995; Stiner et al. 1995; Fernández-Jalvo and Andrews 2016). Environment can also alter the organic matrix, losing the collagen and facilitating dissolution and remineralization (Fernández-Jalvo and Andrews 2016). Total or partial burial can affect in different ways parts of the same bone (Fernández-Jalvo and Andrews 2016). As defined by Behrensmeyer (1978) weathering is a continuous process throught time. For Southern Kenya, she defined a series of 6 stages, each of them describing the accumulative degrading process of the microstructure destruction of bones components. Consequently weathering can be an indirect indicator of its time of exposal before burying (Behrensmeyer 1978) (Figure 3.23). Nevertheless, this process will not be straightforward, as it will depend on local conditions, burial element, taxon or size of the specimen, bone element and duration of the process involved (Behrensmeyer 1978, Brain 1981; Andrews and Cook 1985; Lyman and Fox 1989; Tappen 1994, 1995; Andrews and Armour-Chelu 1998; Fernández-Jalvo and Andrews 2016; Otaola and Tripaldi 2016). The important aspect to be highlight here is that this effect can obscure the recognition of cut marks (White 1992; Bello et al. 2009; Fernández-Jalvo and Andrews 2016). Nevertheless, when weathering cracks do not cross through supposed cut marks, it can be indicating that they would probably be trampling marks (Fernández-Jalvo and Andrews 2016).

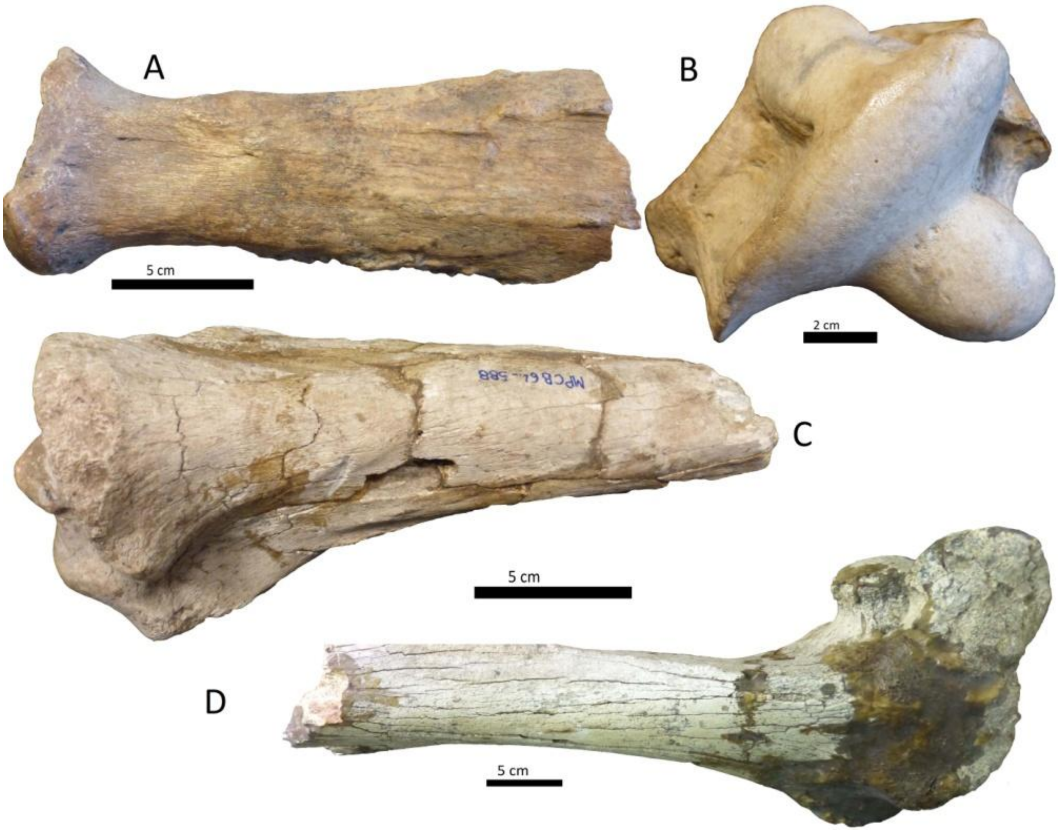


Figure 3.23. Bones showing different degrees of weathering stages. A. Radio of Lestodon from MNW, Vienna, B. Talus of Lestodon from MNW, Vienna. They have been minimum affected by environmental condition and can be related with weathering stages 1 or 2 of Behernsmeyer scale, C. Tibia of Equidae from MCNV, Valencia, D. Femur of Toxodon from MACN, Buenos aires. The presence of deeper fissures indicates longer time of subaerial

exposition. Both with weathering stages 3 or 4 of Behernsmeyer scale. Notice restoration work in C and D and post-depositional fracture in A, C and D.

3.2.1.6. Roots

Acids contain in roots can gnaw bones, producing thin, shallow lines, pits or dendritic patterns over their surfaces (Figure 3.24). When attacking the bone, they can change the colour of the surface where they pass through (Domínguez-Rodrigo and Barba 2006; Domínguez-Rodrigo and Martínez-Navarro 2012; Fernández-Jalvo and Andrews 2016). In more advanced stages they can produce fissures in the inner part of the bone (Fernández-Jalvo and Andrews 2016). In extreme cases, they can make bones more fragile or even fracture them (Behrensmeyer 1978; Binford 1981; Lyman 1994; Fernández-Jalvo and Andrews 2016). Scratches are U shape with concave contours and they differentiate from cut marks in the fact that can have a straight shape only for some millimetres, given that they are generally present as branches (Fernández-Jalvo and Andrews 2016).

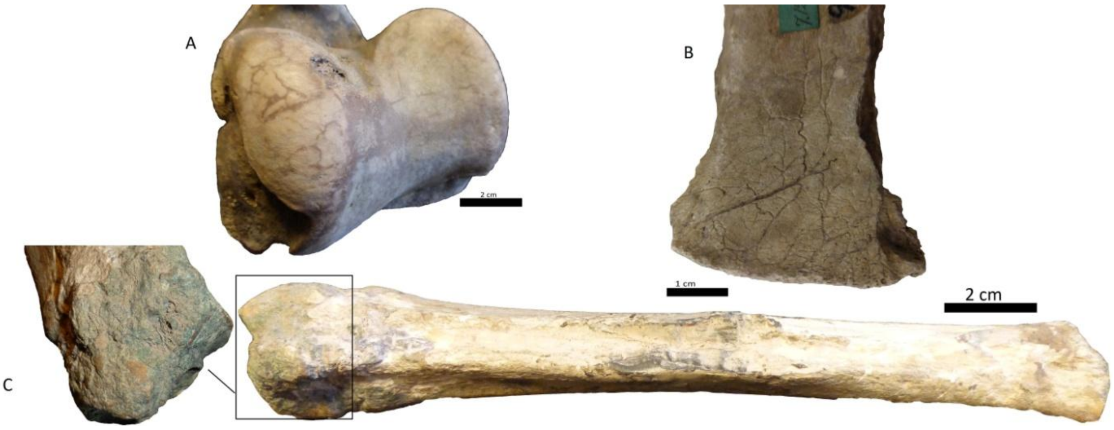


Figure 3.24. Different degrees of root affecting bones. A. Talus of Lomaphorus elevatus from NMW, Vienna, with superficial coloration of roots. B. Rib from Glyptodon from ZMK, Copenhaguen with deep marking. C. Metatarsal of Auchenia (Lama) with rest of roots from NMW, Vienna.

3.2.1.7. Manganese Spots

This type of modification black-colours bones and can be easily confused with the action of fire (López-González et al. 2006). The origin of this type of coverage is a consequence of manganese-oxidising bacteria contained in different types of burial conditions (humid, lime-stone bedrock or alkaline conditions, reducing environment or oxidizing and microorganism actions) (López-González et al. 2006). Manganese coverage can be a good indicator of the sequence of deposition of the deposit: when covering other biological marks, indicates the sequence of the different bone's modification action and/or if they are absence in articular surfaces can be indicating that the skeleton was still in anatomical position when manganese deposition started. Also variable black-coloring of the same bone, indicates heterogeneity of the sedimentary infill (López-González et al. 2006). They can also present as a dendritic/branching pattern over the bone (Fernández-Jalvo and Andrews 2016) (Figure 3.25).

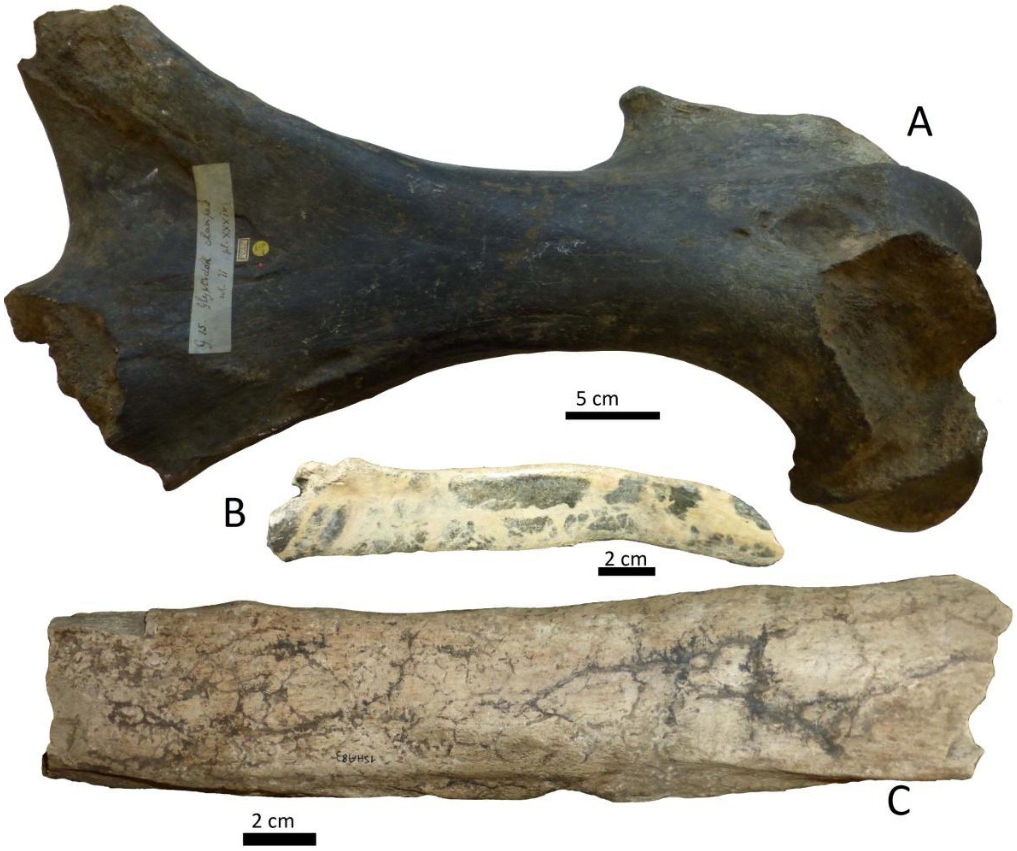


Figure 3.25. Different types of manganese over bones. A. Femur of Glyptodon clapives from NHM, London, with complete coverage of manganes over the bone. B. Mylodon rib from MCA, Mercedes, with spots of manganese. C. Megatherium rib from MGGCB, Bologna, with dendritic pattern.

3.2.1.8. Burning

Studies of fire are always related with finding anthropical intentionality on the burning of bones, even though is difficult to distinguish natural fire from human made one (Shipman et al. 1984; Nicholson 1993; Bennett 1999). Burning was considered as a non-biological activity in this work given that the decontextualized nature of the samples studied cannot allow distinguishing the anthropic origin of this type of modification (Stiner et al. 1995). Another question that complicates detecting burned bones in these collections is that sediment, organic acid, and manganese dioxide can affect surface bone's, giving a similar aspect to burned bones (Shipman et al. 1984; Nicholson 1993; Hanson and Cain

2007). Also recristallization can be due to causes as weathering and in-situ diagenesis other than burning (Stiner et al. 1995; Hanson and Cain 2007). On the other side, given that burned bones are more easily broken than non-burned ones (Stiner et al. 1995), the probability to find these types of fragments in the collection is especially low (Figure 3.26).

Figure 3.26. Box containing rest of burned Megatherium americanum ribs from MCSNM, Milano.

The final aspect of burned bones can be influenced by several variables as type of bone, collagen content (fresh or dry bone), time and degree of exposition to fire or even its position within the fireplace (Nicholson 1993; Bennett 1999; Hanson and Cain 2007; Fernández-Jalvo and Andrews 2016). Consequently burned bones can have a highly variable appearance. The easiest recognizable bones that suffered this type of process are the charred or calcinated bones (Nicholson 1993; Whyte 2001; Walker and Miller 2005; Hanson and Cain 2007). Macroscopically, at lower degrees of temperature bones that had suffered a burning process can present black or brown colours and the cortical surface is unaltered. At higher temperatures polygonal cracking can occurred and they will tend to have white or light gray colour (Shipman et al. 1984; Nicholson 1993; Hanson and Cain 2007). Nevertheless colour and temperature are not straightforward (Shipman et al. 1984; Nicholson 1993; Whyte 2001; Walker and Miller 2005) or cracking can be due to other causes (Hanson and Cain

2007). Consequently this type of macroscopically recognition has to be followed by other technological devices such as SEM, X-ray diffraction, infra-red spectroscopy or histological analysis that has given crucial information for determination of the characteristics of burned bones (Shipman et al. 1984; Fiorillo 1989; Stiner et al. 1995; Hanson and Cain 2007). Consequently, considering this type of modification for collection material is not simply. It was taken into account when the collections were reviewed, although its contribution is limit for this type of analysis.

3.2.2.Non-human biological intervention

This type of surface modification is related to all the biological interventions realized by biological causes other than humans. A cautionary note must be introduced here. Most of the actualistic research was realized with current American, European or African species that have their correlate in the past. Most of South American fauna does not have similar correlates in the present, and as biological intervention can vary depending in the microstructure of the bone of different taxa (Archer and Braun 2013) all these types of modification are taken as a general reference framework.

3.2.2.1. Carnivores

Studies of carnivore marks over bones were originally developed to separate it from human modification/accumulation (Haynes 1983a; Capaldo and Blumenschine 1994; Blumenschine et al. 1996; Brugal and Fosse 2004; Yravedra et al. 2011, 2014; Sala and Arsuaga 2016). Nevertheless this type of modification had started to have its own importance, independently if there was human intervention associated or not. Carnivores' marks per-se is a way to confront biological interactions among species, and to analyze paleoecological conditions (Haynes 1980; Gifford 1981; Blumenschine and Marean 1993; Domínguez-Rodrigo 1999a; Blumenschine et al. 1996; Brugal and Fosse 2004; Borrero et al. 2005; Faith et al. 2007; Pobiner 2008; Kaufmann et al. 2016). Consequently, as morphometrical studies, biomechanical reconstructions or isotopes analysis, carnivores' marks is an indication of carnivore-herbivore relationships and can be confronted with human-herbivore interactions.

Different types of marks can be left by carnivores when attacking bones (Binford 1981; Shipman and Rose 1983a; Haynes 1983a and b; Lyman 1994; Sala and Arsuaga 2016). The conspicuous marks considered here are:

(i) *pitting and/or punctures*: They result from pressure of the cusp teeth when biting the bone (Maguire et al. 1980; Binford 1981; Shipman 1981b; Haynes 1983a; Blumenschine 1988; Lyman 1994; Pobiner 2008; Delaney-Rivera et al. 2009; Fernández-Jalvo and Andrews 2016).

Pittings are shallower while the punctures can be more profund and they can be related with the different density of epiphyses/diaphyses of the bone (Binford 1981; Shipman 1981b; Pobiner 2008; Fernández-Jalvo and Andrews 2016; Sala and Arsuaga 2016) or the size of the animal (Fernández-Jalvo and Andrews 2016) (Figure 3.27A). Even though sizes of the pit/puncture cannot be useful to differentiate among types of carnivore, small and large taxa can be differentiate (Gifford-González 1989; Selvaggio and Wilder 2001; Domínguez-Rodrigo and Piqueras 2003; Pickering et al. 2004; Delaney-Rivera et al. 2009; Andrés et al. 2012; Fernández-Jalvo and Andrews 2016; Sala and Arsuaga 2016).

(ii) *scratches or scores*: They are the result of the teeth dragging the surface of the bone. They are superficial elongated marks that can have U sections and have diverse orientation, even though generally are perpendicular or transverse to the long axis of long bone. They can have internal exfoliation at both sides of the score and be present as a set of parallel marks or with different orientation (Maguire et al. 1980; Binford 1981; Shipman 1981b; Shipman and Rose 1983a; Lyman 1994; Domínguez-Rodrigo and Barba 2006; Pobiner 2008; Fernández-Jalvo and Andrews 2016; Sala and Arsuaga 2016). When they are positioned at the edge of the bone, they can have a wither dimension (Fernández-Jalvo and Andrews 2016).

(iii) *furrowing*: Reefers to extraction of cancellous tissue of long bone ends (Binford 1981; Haynes 1983a; Domínguez-Rodrigo et al. 2012; Sala and Arsuaga 2016). Pressure of teeth over the bone when biting can leave a crenulated edge on the border (Maguire et al. 1980; Binford 1981; Lyman 1994). This type of intervention by itself can be confused given the different biostratinomic and diagenetic process that can mimic it (Domínguez-Rodrigo et al. 2015). Consequently they must be accompanied by other types of marks or diagnostic characteristic in order to differentiate it.

(iv) *spiral fractures*: When carnivores break bones to access inner content they generally start by the epiphysis given they are softer than the shaft (Binford 1981; Haynes 1983a and b; Eickhoff and Herrmann 1985). Instead, when these ones are broken to reach the marrow content (Binford 1981; Blumenschine 1987; Sala and Arsuaga 2016), the intervention can leave spiral or curved fractures with smooth walls. The pressure can also leave spiral cracks along the bone wall without break it (Maguire et al. 1980; Haynes 1983b; Fernández-Jalvo and Andrews 2016; Sala and Arsuaga 2016) (Figure 3.27B). Also carnivores, when bitting, statically pressure over bone’s shaft can produce notches. They are negative scars on the medullar section, produced as a consequence of detached bone flakes. They have semicircular shape and cross perpendicularly the wall of the bone (Brain 1981; Bunn 1981; Haynes 1982; Capaldo and Blumenschine 1994; Lyman 1994; Fisher 1995; Domínguez-Rodrigo and Barba 2006; Fernández-Jalvo and Andrews 2016). Nevertheless not all long bones are easily broken. Big mammals are less prompted of carnivore fracturing (Binford 1981; Haynes 1983b). On the other side, spiral fractures can also be done by other forces as trampling or weathering (Binford 1981; Haynes 1983b, 1988; Fernández-Jalvo and Andrews 2016). Consequently, for the assemblages review, this type of intervention was not considered, except for the Ameghino's collection from MLP, due to the more general context of the sample.

By the way, different works have tried to adjudicate bone intervention to the different carnivores that inflicted damage. Bone marking by different taxa will be influenced by a series of variables such as bone element and density, size of pack hunting group, carnivore competition, herbivore size, season of dead or abundance of prey among other factors (Brain 1967, 1969; Haynes 1980, 1983a and b; D'Andrea and Gotthardt 1984; Blumenschine 1987; Pobiner and Blumenschine 2003; Faith and Behrensmeyer 2006; Faith et al. 2007; Pobiner 2008; Yravedra et al. 2011; Domínguez-Rodrigo et al. 2015). Currently, it is still difficult to link carnivore's marks with the animal that produced them, or to clearly differentiate between hunting or scavenging (Fernández-Jalvo and Andrews 2016). In this sense, marks left by different carnivores can have certain degree of overlap. However actualistic research is progressing in recognizing some types of differentiation of the intervention left among them (Haynes 1983a; Domínguez-Rodrigo 1999b; Selvaggio and Wilder 2001; Delaney-Rivera et al. 2009; Andrés et al. 2012; Domínguez-Rodrigo et al. 2012, 2015; Sala and Arsuaga 2016). Consequently different features were recognized for linking carnivore to damage found in each collection. Ursids, canids and felids were the considered groups of carnivores for inflicting the marks (as hyenas were not present in the Americas).

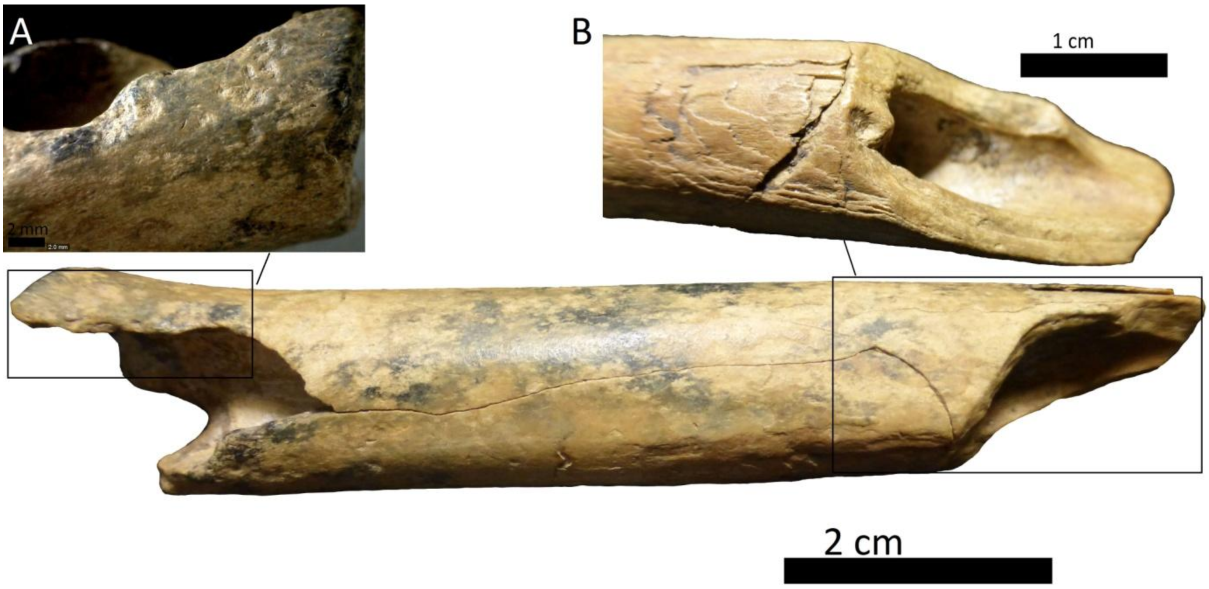


Figure 3.27. Indeterminate diaphysis from MCA, Mercedes with carnivore pitting (A) and fracture (B).

(i) *Ursids*: They tend to leave lighter types of bone modification marks (Haynes 1983a; Saladié et al. 2013). Cheek teeth are used to grind down and crush trabecular bone (Haynes 1983a, 1985). Pits, punctures and scores are the most characteristic intervention realized (Pinto and Andrews 2003; Burke 2013; Saladié et al. 2013; Arilla et al. 2014). Flat-bottom type of imprints teeth and superficial sets of parallel short to long scratches are other types of marks left (Haynes 1983a; Saladié et al. 2013). These scratches can have irregular walls and bottoms (Saladié et al. 2013). The shape of the tooth will tend to be square or rectangular (Haynes 1983a). Even though they could have been capable of breaking bones, it is not a general behaviour in this group (Haynes 1983b; Sala and Arsuaga 2013) but they tend to furrow epiphyses (Saladié et al. 2013; Arilla et al. 2014; Sala and Arsuaga 2013, 2016).

(ii) *Felids*: In general are less prone of bone modification in comparison with other taxons (Haynes 1983a; Brugal and Fosse 2004; Domínguez-Rodrigo et al. 2012, 2015; Fernández-Jalvo and Andrews 2016; Sala and Arsuaga 2016), even though they can leave several types of marks as pits and scores (Domínguez-Rodrigo et al. 2012), or large grooves (Haynes 1983a). Scratches will tend to be perpendicular to the long axis of the bone (Haynes 1983a). Teeth shape will be “axe-edge” or elongated V shape (Haynes 1983a). They can also furrow spongy parts of long bone ends (Haynes 1983a).

(iii) *Canids:* They can have important participation in inflicting marks over bone surfaces (Sala et al. 2014; Sala and Arsuaga 2016). They can produce important furrowing, exposing trabecular bone while removing patches of the long bones ends. In advances stages of modification they can leave only cylinders (Haynes 1980, 1983a; Sala et al. 2014). Scratches will be present in the zones near to bone extraction (Haynes 1983a). They can also leave important scores and punctures and/or pitting (D’Andrea and Gotthardt 1984; Burke 2013; Sala et al. 2014; Sala and Arsuaga 2016). Some canids, as wolves, can have a similar capacity modification as hyenids (Domínguez-Rodrigo et al. 2012; Sala et al. 2014) as they are capable of breaking the shafts (Binford 1981; Haynes 1983a and b, 1985; Yravedra et al. 2011; Sala et al. 2014; Sala and Arsuaga 2016), specially when they are in homesites or scavenging sites (Haynes 1983b). Impression will be wide and deep, with cone or truncated cone shape (Haynes 1983a). Nevertheless differences exist among the different types of canids. Wild African dog, for example, will tend to consume less amount of bone, thus modification of them will be lighter (Yravedra et al. 2014).

In relation with the consumption sequence, there is a general agreement that in first access scenario, carnivores start to consume from ventral section, up to the ribs, the hindlimbs and the forelimbs or directly from hindquarter to forequarter. Hard parts as lower limbs (distal tibia, metapodiums, phalanx) and head contents are left or can be accessible latter on, given they are harder or have small amount of meat to offer (Blumeschine 1986, 1987; Stiner 1991; Lyman 1994; Brantinham 1998; Domínguez-Rodrigo 1999b; Brugal and Fosse 2004; Haynes and Krasinski 2010; Kaufmann et al. 2016; Sala and Arsuaga 2016).

3.2.2.2. Rodents

Rodens' marks are distinguished by being parallel, reflecting the continuous dragging of the incisors onto bone's surface. The marks are generally on margin areas, or spongy portions of fresh bones (Binford 1981; Eickhoff and Herrmann 1985; Haglund et al. 1988; Pobiner 2008; Fernández-Jalvo and Andrews 2016). They are broad, flat-bottomed and occur in regular rows (Bunn 1981; Brain 1981, Johnson 1985; Shipman and Rose 1983a; Fiorillo 1989) (Figure 3.28).

Figure 3.28. Rodent marks in an indeterminate rib from MCA.

3.2.2.3. Insects

Different types of insects, such as Dermestidae, Tenebrionidae, tineid moths and termits can attack bone surface producing marks such as holes, pits, grooves and scratches (Behrensmeyer 1978; Shipman 1981; Lyman 1994; Kaiser 2000; Di Donato and Del Papa 2010; Pomi and Tonni 2011; Fernández-Jalvo and Andrews 2016). Their presence is an indicator of habitats and paleoenvironmental conditions, such as temperature and moisture (D'Andrea and Gotthardt 1984; Pomi and Tonni 2011). Their position over fissures indicates the sequence of different surface modifications that bone pass through (Pomi and Tonni 2011).

Even though more research is needed for understanding this type of modification, it was considered in order to differentiate it from carnivores marks (Figure 3.29).

Figure 3.29. Scelidotherium leptocephalum bones from PIMUZ with probable insects perforations.

Marks left by other fauna as avianfauna were not considered given they can be confused with marks left by other types of mammalian animals (Domínguez-Solera and Domínguez-Rodrigo 2011). However they would have probable been an important group that had feed on native fauna. Current studies are producing reference marks to understand accumulation and bone modification as the eagles, vultures and caracaras (Ballejo et al. 2016; Montalvo et al. 2016).

3.2.3.Human biological intervention

3.2.3.1. Ancient/Primeval fractures and cut marks

Animals are process by humans (e.g. cutting and fracturing the bones) in order to extract the different resources (Guilday et al. 1962; Binford 1981; Lyman 1994). Bones can subsequently be used to produce different types of instruments and tools (Johnson 1985, 1989; Lyman 1994).

As happens for carnivores, humans fracture bones in order to access the marrow (Binford 1981; Lyman 1994). Nevertheless, studying anthropically fracture bones can be complex. As pointed before, fresh fractured bones will tend to have spiral morphology with smooth surface (Villa and Mahieu 1991; Capaldo and Blumenschine 1994; Lyman 1994; Johnson 1985, 1989; Outram 2002; Alcántara et al. 2006; Fernández-Jalvo and Andrews 2016). When they have human origin, they result from dynamic loading of a stone over the bone. The impact of lithic tools can produce notches (Binford 1981; Brain 1981; Johnson 1985; Noe-Nygaard 1989; Capaldo and Blumenschine 1994; Fisher 1995; Galán et al. 2009) although they will be broader and shallower than carnivores ones (Capaldo and Blumenschine 1994) and can be superficial or deep, depending the part of the bone (Fernández-Jalvo and Andrews 2016). Nevertheless recent experiments have shown that anthropic notches can also be confused with carnivores ones (Galán et al. 2009). Percussion pits can accompany these notches. They are characterized as pits or grooves with or without associated microestriation, internal crushing and/or flacking (Blumenschine and Selvaggio 1988; Fisher 1995; Outram 2002; Domínguez-Rodrigo and Barba 2006; Pickering and Egeland 2006; Galán et al. 2009; Fernández-Jalvo and Andrews 2016). When internal microstriation is absent, it can be confused with carnivore pitting (Fisher 1995; Galán et al. 2009). As in carnivores' case, flakes can be detached from this action (Blumenschine and Selvaggio 1988; Fisher 1995; Galán et al. 2009) and they can leave extractions in the cortical or medular faces. Sometimes, the bone presents a semicircular, depress area with fissures in the cortical part called the impact or loading point (Johnson 1985; Lyman 1994). As notice for fracture realized by carnivores, bones with spiral fractures only indicates that the bone was fresh-broken, not anthropically broken (Binford 1981; Johnson 1985; Lyman 1994; Fernández-Jalvo and Andrews 2016). Thus considering this type of anthropic intervention can be difficult without having more complete information. Only in Ameghino´s collection from MLP the different bone breakage patterns were considered as more contextual information was obtained from this sample.

Bone surface modification as cut marks are one of the most direct way to analyze past human exploitation of the carcasses and reconstruct ecological contexts (Shipman and Rose 1983a; Capaldo and Blumenschine 1994; Fisher 1995; Lyman 2005; Bello and Soligo 2008; Fernández-Jalvo and Cáceres 2010). In stripping the muscles packages away, humans can produce marks onto bone's surfaces. Not all the strokes will leave marks in the bone (Egeland 2003; Lyman 2005; Fernández-Jalvo and Cáceres 2010) given that they are not done with intention, but are subproducts of the processing activities (Lyman 1992; 2005; Fernández-Jalvo and Cáceres 2010). Classically it was proposed that cut marking was avoided to save cutting edge attrition (Bunn 2001). Nevertheless cut marking is a consequence of different factors such as technology used, raw material of the lithic, numbers of butchers', condition of the carcasses, intensity of processing, stage of the butchering process, skeletal element process and presence/absence of muscles and tendons among others factors (Binford 1981; Shipman and Rose 1983a; Lyman 1992, 2005; Domínguez-Rodrigo 1997, 1999a; Egeland 2003; Greenfield 2006; Dewbury and Russell 2007; Fernández-Jalvo and Cáceres 2010; Merrit 2012, 2015).

In the case of the megafauna, the probability of marking a bone is related with its size and hard periosteum, consequently few marking will be produced (Shipman and Rose 1983b; Frison 1989; Gifford-González 1989; Scott 1989; Lyman 1992; Fisher 1995; Haynes and Krasinski 2010; Domínguez-Rodrigo and Yravedra 2009). It was also proposed that larger animal will tend to present larger patches of marks than smaller ones. Cuts can be deeper given that muscles to be detached are bigger and more input force is needed (Bello et al. 2009; Merrit 2015).

Given the complexity surrounding the debate about the definition of cut marks (Domínguez-Rodrigo and Yravedra 2009; James and Thompson 2015) in order to confront the collections, a series of morphological and configurational features (Fisher 1995) were taken into account.
Among the morphological features considered were:

- Elongated/ straight, narrow type of linear incision: In general cut marks follow this type of shaping, given the way of cutting motion (Shipman and Rose 1983a; Lyman 1994; Fisher 1995; Greenfield 2006; Domínguez-Rodrigo et al. 2009; Fernández-Jalvo and Cáceres 2010), even though longer linear marks can be curved (Fernández-Jalvo and Andrews 2016). Also the width and the deep of the mark can be broader related among others with the instrument used, raw material, pressure and angle of application (Walker and Long 1977; Shipman and Rose 1983a; Greenfield 2006; Bello et al. 2009; Domínguez-Rodrigo et al. 2009; Fernández-Jalvo and Cáceres 2010; Haynes and Krasinski 2010; Merrit 2012; Fernández-Jalvo and Andrews 2016). These marks can be accompanied by shoulder effect (small and parallel marks), barbs (positioned at both ends of cuts) or splitting effect (several lines originated from the main one) (Shipman and Rose 1983a; Eickhoff and Herrmann 1985; Fisher 1995; Domínguez-Rodrigo et al. 2009). Besides linear incisions, other types of marks related with the different processing action are scrape marks, sawing marks and chop marks (Noe-Nygaard 1989; Fernández-Jalvo and Andrews 2016).
- Walls with V shape and internal microstriations (Olsen and Shipman 1981; Shipman and Rose 1983a; Noe-Nygaard 1989; Lyman 1994; Fisher 1995; Greenfield 2006; Fernández-Jalvo and Cáceres 2010). Cross section shape sometimes can be U and not V, and this is generally related with the type of bone and raw material used (Fernández-Jalvo and Andrews 2016). Microstriations is one of the most classical features to define a cutmark although latter experiments have shown that trampling can also have internal microstriations (Andrews and Cook 1985; Behrensmeyer et al. 1986; Fiorillo 1989; Oliver 1989; Lyman 1994; Fisher 1995; Domínguez-Rodrigo et al. 2009) or are also left in carnivores's scores (Eickhoff and Herrmann 1985; Lyman 1994). Microstriations can be easily lost by post-depositional factors (Eickhoff and Herrmann 1985; Behrensmeyer et al. 1986). Consequently it can be expected that several cut marks will lack this feature (Domínguez-Rodrigo et al. 2009). When microestriation are present, will tend to be continuous (Domínguez-Rodrigo et al. 2009).
- Cut marks will preferentially show oblique/transversal or perpendicular orientation to the axis of the bone (Behrensmeyer et al. 1986; Olsen and Shipman 1988; Domínguez-Rodrigo et al. 2009).

- Grooves can be symmetrical or asymmetrical, depending on the tool's inclination (Walker and Long 1977; Andrews and Cook 1985; Domínguez-Rodrigo et al. 2009; Fernández-Jalvo and Andrews 2016).
- Raised shoulder edge can be present. These are produced by the pressure of the lithic that can move upward the borders of the groove (Bello et al. 2009; Domínguez-Rodrigo et al. 2009). Bromage and Boyde (1984) identified this feature as bone smears.
- Lithic touching the bone can produce several micromorphological features such as Hertzian Cone or faulting that can indicate directionality of the cut mark (Bromage and Boyde 1984; Fernández-Jalvo and Andrews 2016). These were also considered even though their presence can be relative and not easy to find in all the marks (Fisher 1995; Bello et al. 2009).

As the above features are not enough to contrast human origin of cut marks, it is important to consider the configurational features (Fiorillo 1989; White 1992; Fisher 1995; Domínguez-Rodrigo et al. 2010; Merrit 2015) that are related with the general position over bones. Cut marks have to be present as patches or cluster of marks with parallel or similar orientation among them (Merrit 2015) and have to be related with specific anatomical position (Andrews and Cook 1985; Eickhoff and Herrmann 1985; Behrensmeyer et al. 1986, 1989; Bunn and Kroll 1986; Fiorillo 1989; Oliver 1989; Lyman 1992; Domínguez-Rodrigo et al. 2009). Even though, sometimes they can be done randomly (Pickering and Egeland 2006; Domínguez-Rodrigo et al. 2009) they will be generally distributed accordingly with muscles and tendons (Guilday et al. 1962; Binford 1981; Olsen and Shipman 1988; Fiorillo 1989; Gifford-González 1989; Noe-Nygaard 1989; Lyman 1994; Domínguez-Rodrigo 1999a; Galán and Domínguez-Rodrigo 2001; Pickering and Egeland 2006; Domínguez-Rodrigo and Barba 2006; Fernández-Jalvo and Andrews 2016). Binford (1981) was one of the first researchers that studied cut marks distribution in relationship with the different anatomical features. Consequently they can be classified according the different processing stages realized over animal's carcasses:

(i) Skining: These one will generally be positioned were the skin is firmly attached like over metacarpals and metatarsals, carpals and tarsals, or mandible and cranium (Binford 1981; Noe-Nygaard 1989; Lyman 1994; Galán and Domínguez-Rodrigo 2013).

(ii) Disarticulation/Dismembering: As these marks are done with the purpose of separating the different body parts, they will be related with articulation points (Binford 1981). These are on joint surface or near long bone end, in vertebrae and pelvis parts (Binford 1981; Olsen and Shipman 1988; Noe-Nygaard 1989; Lyman 1994; Domínguez-Rodrigo 1999a; Galán and Domínguez-Rodrigo 2013) and have an oblique or parallel orientation to bone axis (Olsen and Shipman 1988; Galán and Domínguez-Rodrigo 2013). They can be deeper, broader and have great inclination than the other ones (Noe-Nygaard 1989; Bello et al. 2009).

(iii) Filleting/Defleshing: They result from the act of subsequently separation of muscles from bones or processing meat packages (Binford 1981). They are produced cutting perpendicularly to bone axis in near-epiphyses of long bone ends and/or in the mid-shafts (Binford 1981; Noe-Nygaard 1989; Lyman 1994; Domínguez-Rodrigo 1999a; Galán and Domínguez-Rodrigo 2013) and are present as short series of parallel marks in the anterior or posterior faces of these bones (Binford 1981).

According to Binford (1981) the sequence of disarticulation involves first the separation of the head from the rest of the post-cranial skeketon. Latter on hindlimbs and forelimbs are separated from the axial skeleton and when dismembering the vertebrae, part of the rib can be attached. Nevertheless, different variables play into the processing action, as number of participants, distance from base camp, size of the animal, among others (Gifford-González 1989) thus, this process is not always straightforward.

It was also considered intentional modification of the bone for further utilization. This could be identified from general shaping, which differentiates it from carnivore and natural agency (Johnson, 1989). To consider a bone anthropically produced it was taken into account that the high variability of broken shapes can be the result of post-depositional fragmentation (Haynes and Krasinski 2010). Fractured bones can be used for a function without further alteration or can be subsequently modified. These extensively modified bones can be distinguished as anthropogenically altered because of their sophisticated shapes (Lyman 1994). They will result from systematically and repetitive action to conceive a specific shape for a certain purpose (Lyman 1994). Given the decontextualized origin of the collection, only clear, pattered modification over bones (Johnson 1985; Lyman 1994) can be assigned to human purpose in this work.

3.2.3.2. Recent marks or fractures

During excavation instruments can produce modern marks or fractures over bones and this can be confused with old cut marks (White and Toth 1989; Fernández-Jalvo and Andrews 2016). The basic difference with these ones is that they will have lighter colour of the surrounding surface and cross over primeval surface modifications (Shipman and Rose 1983a and b; Fisher 1995) (Figure 3.30). Nevertheless, sometimes the tool did not penetrate enough to expose subcortical bone (Fisher 1995). Consequently morphological and configurational features exposed above are taken into account to identify old cut marks.

3.2.3.3. Restoration

As with recent marks, museums manipulation, storage and cleaning procedures can add more modern marks (Shipman and Rose 1983a and b; Behrensmeyer et al. 1989; Fisher 1995; Fernández-Jalvo and Marin-Monfort 2008; Haynes and Krasinski 2010; Fernández-Jalvo and Andrews 2016) and application of different substances to reconstruct bones can also cover old ones (Scott 1989) (Figure 3.30).

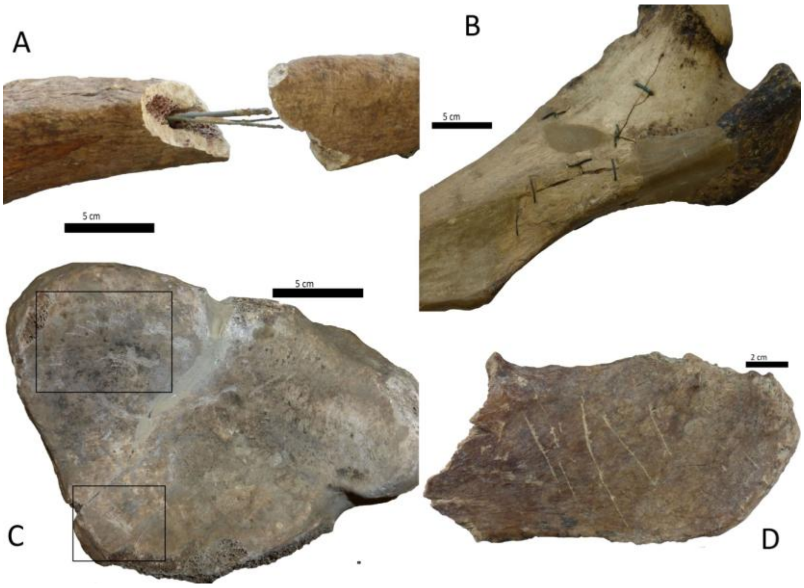


Figure 3.30. Recent anthropic intervention in bones. A. Megatherium americanum rib from MCNV, Valencia, with an inside metal in order to unify a recent fracture. B. Macrauchenia patachonica femur from NHM, London (Darwin Collection), with metal and gypsum. C. Proximal epiphysis of radio of Megatherium americanum from MNHN, Paris, with gypsum and indication of marks realized during excavation. D. Mylodon transversal apophysis from ZMK, Copenhaguen, with recent marks.

3.2.4. Technical aspects of the analysis

Considering the non-contextualized characteristic of the sample, only the clearer biological interventions were evaluated as the result of carnivore and/or human intervention. Anthropic marks had to present the following characteristics:

1. Marks had to have some of the morphological features described above. Their V-shape cross section, microstriations or elongated shape are the most cited features in the bibliography to define its anthropic origin. Summing to this, they have to be crossed by other non-biological activity described before and have to have the same colour that the surrounding surface (Shipman and Rose 1983a and b; Fisher 1995).
2. Marks have to fulfil the characteristics of the configurational features: being related with bony sections susceptible of being mark in the butchering process and be present as groups with parallel orientation

This work is aware that equifinality can be present when interpreting cut marks (Domínguez-Rodrigo et al. 2010; Merrit 2015) especially when context lacks. Nevertheless our proposition intended to control the different variables that can affect them. For carnivore marks at least two of the described interventions have to be presented in order to consider them as with this type of intervention.

It was selected bones with taxon and element identification. Indeterminate fragments and plates were left aside given that they yield scarce information and to not increase total number of the reviewed material. Nevertheless, considering that both Ameghino's collection from MLP has more contextual information than the others, indeterminate material was included. The different surface modifications were registered in an excel form, detailing which of the non-biological activity and biological intervention were observed. Here also the different surface modifications were annotated plus the presence of pathologies, recent marks and restoration (Appendix Table 2). In order to have the general composition per order or family of the different collections, zooarchaeological measurements such as NISP (Number of Identified Specimens) and MNI (Minimum number of individuals) were applied. The first one was used to count the number of skeletal element of identified and indeterminate material (Grayson 1984c; Mengoni Goñalons 1988; Lyman 1994). The second one was used as an approach to account for the minimum number of identified species (Grayson 1984c; Mengoni Goñalons 1988; Lyman 1994). To calculate it, age and laterality were considered.

Regarding the technical treatment of the samples, different technological procedures have been applied along these decades to detect and describe non-biological activity and biological interventions. From early pioneer SEM analyses to Alicona 3D Infinite Focus that makes 3D images of the marks (Shipman 1981b; Shipman and Rose 1983a and b; Andrews and Cook 1985; Fernández-Jalvo and Andrews 2003, 2016; Greenfield 2006; Bello and Soligo 2008; Bello et al. 2009) each decade advance to obtain better ways to go further in the definition of the biological modifications. Scanning electronic microscope has been criticized for practical questions, it is especially time-consuming, expensive, it can damage bones and only emphasizes in the micromorphology of the marks (Eickhoff and Herrmann 1985; Fisher 1995; Blumenschine et al. 1996; Domínguez-Rodrigo et al. 2009). Instead, some authors suggested that magnifying glasses of low magnifications can be a very good approach for detecting cut marks (Blumenschine and Selvaggio 1988, 1991; Olsen 1988; Fisher 1995; Blumenschine et al. 1996; Domínguez-Rodrigo et al. 2009).

In view of the special context in which this work has been developed (the studying of different museum's collections) from the array of technologies developed, the most practical ones were selected in order to properly analyze each of the assemblages. Considering the necessity of using some type of magnification technology (Blumenschine et al. 1986; Domínguez-Rodrigo et al. 2009) different technological devices were selected for detecting the morphological attributes that cannot be recognized only with naked eye. In this sense, the material was reviewed with magnifying glasses (3'5 X and 12 X). An initial test was also done with SEM S4100 housed in the Universitat de Valencia at the beginning of this research with the MCNV material. Casting was realized with silicon RTV 901. Nevertheless this procedure was rejected given the time-consuming aspect of this technology (Blumenschine et al. 1996). A model Dinolite microscope AD4113T model with magnifications upt to 120x and its software (Dinolite 2.0) was then used. This microscope has the advantage of its high resolution quality, which allows observing details and photographing microstriations and cut shapes as well as for taking small measurements. Its USB connection makes it an ideal instrument for transportation and analyzing material in the field or different museums. This instrument was used in other taphonomical works as Domínguez-Solera and Domínguez-Rodrigo (2011), Dantas Trindade et al. (2012); Scheifler (2014); Álvarez (2015); Kaufmann et al. (2016) among others.

In addition some bones were selected for casting to be reviewed with a Hirox KH-8700 digital microscope (Boschin and Crezzini 2012). The material used for casting was Provil Novo Light for the negative and Polyvinylsiloxane for the positive. A caliper was used to take general measurements. A Panasonic Lumix DMC-TZ35 camera up to 20x Full HD was used for general photographs.

After describing the regional setting and its geological conformation, the collections analyzed and the general methodology used, the next chapter will deal with the theoretical framework in order to interpret the results obtained.

4. THEORETICAL FRAMEWORK: *HOMO SAPIENS* AS AN INVASIVE SPECIES IN THE AMERICAS

This chapter deals with the ecological framework this work is based. Concepts explained here will be useful to latter discuss humans-native fauna relationships based on the evidence found in the different collections.

Some propositions have been focussing in human dispersion in the Americas as with invasive species characteristics (Barnosky et al. 2004; Lanata et al. 2008a and b; Lanata 2011; Pitblado 2011; Marean 2015; Goldberg et al. 2016). Invasive species, alien species or non-native species are different ways to denominate organisms that introduce in non-original, new territories. They are characterized by a high demographic rate and fast expansion through the different environments that compose the novel space (Shea and Chesson 2002; García-Ramos and Rodríguez 2002; Cadotte et al. 2006; Murphy et al. 2006; Blackburn et al. 2011). Their spreading will follow connectivity axis, overcoming geographic and/or biological barriers (Mooney and Cleland 2001; Cadotte et al. 2006; Murphy et al. 2006; Blackburn et al. 2011). Non-native species process of expansion has been characterized as a series of stages to analyze their evolution. They migrate using different aquatic or terrestrial vectors and arrive into new territories. When they establish they will be faced to biotic interaction with native species. In this early stage, non native species have the advantage of not having direct competition or that their prey are not used to the newcomers. This situation feedbacks growing demographic rates, and as a consequence, spreading beyond the original entry point will follow (Cadotte et al. 2006; Davis 2009). Invasive species have a successful trend of dispersion and permanence along time, but also have deleterious effects in the new environment (Davis 2009).

Several concepts of this ecological scenario can be applied to analyze humans' dispersion in the Americas. Especially important are the trophic relationships and niche concepts, given that the hypothesis proposed, links humans and native fauna in the DLPB under this concept. Related with this is the situation of humans as a new species in an unfamiliar territory, and the consequences this produce in the megafauna and in the dispersion over the new land. At last, it is also highlight its fast dispersion rate and the usage of connection axis such as corridor that would have facilitated movements across different environments.

4.1. TROPHIC RELATIONSHIP/NICHE

One of the key aspect of this process is that the introduction of new species in an ecosystem can substantially change native trophic relationships and the niches they conformed (Mooney and Cleland 2001; Shea and Chesson 2002; Kondoh 2006; Murphy et al. 2006; Duffy et al. 2007; Wilson and Wolkovich 2011).

Trophic relationships are the complex way different species interplay among them (Polis 1991; Boege and del Val 2011). Intra and inter-species interactions shape ecological communities, structuring feeding guilds within resource-partitioning system (Brantingham 1998; Duffy et al. 2007; Moleón et al. 2014). They act as top-down control of communities and their alteration by external causes can promote different adaptational answers and influences in related organisms (Mooney and Cleland 2001; Duffy et al. 2007; Boege and del Val 2011; Wilson and Wolkovich 2011; Moleón et al. 2014). Consequently, describing trophic relationships are necessary for understanding the evolution of ecosystems. They can be represented in food webs that are a simplified way of organizing the complexity behind organisms' interactions at multiple trophic levels (Pimm and Lawton 1977; Paine 1980; Polis 1991; Brown and Gillooly 2003). They hieratically rank the decreasing amount of energy flowing from downwards to upwards levels (Pimm and Lawton 1977; Paine 1966, 1980). For understanding human involvement with native American species, two types of trophic relationships are considered here:

- Competition: It is a horizontal relationship established by two intraspecific and/or interspecific organisms that exploited the same resources in a determined area and time (Paine 1980; Domínguez-Rodrigo 2001; Shea and Chesson 2002; Boege and del Val 2011; Pan et al. 2014). According to the distribution of energy in the different trophic levels, two species with similar requirements cannot occupy the same niche (named as the Competitive Exclusion Principle by Gause, 1934) (Hardin 1960; Leibold 1995; Mooney and Cleland 2001; Pan et al. 2014). Overlapping can have different consequences in the structuring of communities involved: displacement, migration or even extinction are the principal regulatory consequences to balance this situation (Brantingham 1998; Mooney and Cleland 2001; Duffy et al. 2007; Pan et al. 2014). As for humans involvement, different authors have already focused in the competitive character of humans and carnivores at different situations in the past (Brantingham 1998; Domínguez-Rodrigo 2001; Stiner 2002; Brugal and Fosse 2004, Martín 2008; Moleón et al. 2014; Villavicencio et al. 2016).
- Predation: it is a vertical relationship established when a prey is killed and subsequently consumed by the predator (Boege and del Val 2011; Wilson and Wolkovich 2011). In food web conceptualizations carnivore-herbivore ratio tends to be equilibrated, with higher species diversity of preys than predators. This situation enhances specialization and fitness on the lower trophic levels and brings down sympatric adaptations among predators (Paine 1966;

> Pimm and Lawton 1977; Paige 1992; Duffy 2002; Duffy et al. 2007; Domínguez-Rodrigo 2001; Boege and del Val 2011). Predation will be influenced by degree of dietary generalism/specialization (Vázquez 2006; Duffy et al. 2007). Specialized consumers will tend to reduce species richness or have narrow migration ranges for finding food. Instead generalists have a broad ample prey choice and/or ample mobilization rates (Vázquez 2006; Duffy et al. 2007). In this sense, generalist predators tend to be more successful in spreading into new environments and/or support different climatic conditions (Vázquez 2006). On the other side, adding and/or subtracting top-predators on the top of the pyramid can affects the variety of prey biomass and produces cascading effects in the ecosystem (Duffy 2002; Duffy et al. 2007). Predation has more negative impacts over the lower levels of trophic web, producing demographic changes or extinctions (Mooney and Cleland 2001; Duffy et al. 2007; Wilson and Wolkovich 2011) while extinction by competition can be a much slower process (Mooney and Cleland 2001). Humans have been related to this trophic relationship, given the invasion of the predatory guild since at least 2MA ago (Brantingham 1998; Moleón et al. 2014).

Considering that in human dispersal competition and predation relationships have been established with the native fauna across the different environments, they both can be analyzed within the hunting and/or scavenging niches from the carnivore trophic level. Consequently, focusing in humans as with invasive species dynamic in this new continent, allows analyzing its behaviour at different positions into the carnivore guild, within the multiple participating species and the variable ways of relationships established with native fauna.

In this sense, trophic relationships are included in the niche that defines the position of the animals and plants in the ecological community (Leibold 1995; Brantingham 1998; Shea and Chesson 2002). Niches are the one to one interaction that fauna or plant established with the physical and biological components of the environments (Leibold 1995; Shea and Chesson 2002; Martínez-Meyer et al. 2004). Evolutionary trends will tend to produce diversification of species so they can occupy the different niches (Sodhi et al. 2009) that will tend to be conservative across time (Martínez-Meyer et al. 2004). However resources, natural enemies and physical environment are conditions that can promote better dynamics of invasive species in a given niche, having better adaptation to exploit natural resources than native ones (Mooney and Cleland 2001; Shea and Chesson 2002). As mentioned before, alien species can modify or colonize niches occupied by other vertebrates, they can fulfil empty niches or they can even construct new ones (Shea and Chesson 2002; Odling-Smee et al. 2003). In this last case, some species can produce persistent modification in their surroundings that has an evolutionary effect in long term, and consequently, create new adaptation trends (Odling-Smee et al. 2003). Humans were characterized as having a high capacity of niche construction along its evolutionary history, creating novel ways of relation with the environment, as the agriculture or urbanization, but also, a high degree of alteration of the biodiversity related with its Pleistocene expansion, and its exploitation system (Day et al. 2003; Odling-Smee et al. 2003; Moleón et al. 2014; Marean 2015; Boivin et al. 2016).

4.2. EXOGENUS SPECIES

Given the novelty of humans in the Americas, two considerations must be highlighted:

On one side, animals were not adapted to *Homo sapiens* predation. Nevertheless smaller mammals have high reproductive systems and habitudes that made them survive humans' predation (Cione et al. 2009, 2015). As was seen in Chapter 2, naivety is one of the arguments used for understanding megafaunal extinction by human causes. Naivety is highlight in ecology as a factor that intermediates between the new predator and native fauna (Kondoh 2006). They will have success predation over native species as the failure in recognition of this ones, does not allow recognizing new predator as a thread. Lack of visual contact or behavioural patterns produce lack of adequately answers in these situations. On the other side, invaders will not have natural enemies (known as the Enemy Release Hypothesis) as native predators do not recognize newcomers as a potential prey (Kondoh 2006). Nevertheless, this situation depends of the capability of reaction of the prey-predators involved and also it will be more effective in early stages of invasion, when alien species are still not abundant in the landscape (Kondoh 2006). Americas would have presented a complex situation. Megafauna was not abundant and humans had broad-diet systems, where this resource would not have been the principal one as observed in Chapter 2 (Haynes 2007, 2009a; Surovell and Waguespack 2009). As already pointed there, non-continuous, but also, non-interrupted exploitation of megafauna by humans would have extended for several millennia. This particular situation, would have not allowed to develop the necessary anti-predator system to reject human intervention (Koch and Barnosky 2006; Fernandez 2016; Surovell et al. 2016).

On the other side, humans did not know the territory where there entered to. In this sense, resources, information and knowledge of the territory, must have been constructed from the first initial stages of exploration and also, each time groups moves to new patches of resources (Borrero 1989-90; Meltzer 2002; Rockman 2003; Miotti 2006). Development of confrontation systems in unfamiliar landscapes was necessary to manage risks and unpredictions, derived from climate instability but also from ignorance of the distribution of resources or raw materials (Kelly 1999; Meltzer 2002; Rockman 2003). This would have influenced in the mobility, social organization and the construction of social networks, so information about resources, flows among populations (Meltzer 2002; Rockman 2003; Dillehay 2014). The entrance to an unknown land also implied that humans in the Americas lack of the presence of similar species, as happened in Eurasia and African continents, where *Homo erectus*/

Homo antecessor/ *Homo neanderthalensis* must have been potential competitors for the same resources as *Homo sapiens* (Hortolà and Martínez-Navarro 2013; Marean 2015).

4.3. FAST DISPERSION/ CORRIDORS

This situation in the early entrance stage of humans must have influenced for a fast dispersion over the continent (Kelly 1999; Meltzer 2002; Hazelwood and Steele 2004; Lanata et al. 2008a and b; Lanata 2011; Goldberg et al. 2016). Recent simulation have calculated the expansion across the Americas lasted between 2.800 to 2.200 years (Lanata et al. 2008a and b; Lanata 2011) that is accordance with genetic evidence (Tamm et al 2007). This timing dispersion is even faster than dispersal in the Old World, where for example, the spreading of the Aurignacian, associated with *Homo sapiens*, in Europe and Middle East dates from approximately 40.000 to 30.000 AP (Otte and Kozlowski 2003; Maíllo-Fernández 2006; Nigst et al. 2014; Liu et al. 2015; Soler and Soler 2016).

This situation could have been influenced by the ignorance of the territory that must have power the usage of distinct corridors. Coasts and mountains like the Andes are generally the principal named axis of expansion (Fladmark 1979; Anderson and Guillam 2000; Kelly 2003; Surovell 2003; Miotti 2006; Lanata et al. 2008a and b; Lanata 2011; Dixon 2013). Human dispersal must have been patchy, with some areas colonized latter than others, while some regions would have remained empty until late Holocene (Anderson and Guillam 2000; Miotti 2006; Lanata et al. 2008a and b; Borrero 2009; Lanata 2011). In this sense, most favourable patches and/or ecotones must have been occupied and used before moving to others (Anderson and Guillam 2000; Kelly 2003; Lanata et al. 2008a and b; Lanata 2011). The most beneficial places could be understood as “hot spots”, where more intensity of interaction among organisms is expected (Smith et al. 2011). These ones could have fuelled demography and at the same time motorize subsequent dispersion across the continent (Lanata et al. 2008a and b; Lanata 2011).

Understanding humans as an invasive species, allows getting deep into the diversity of relationships established among native fauna and the new arriving species. The degree of different trophic levels and resource-partitioning would have been altered with human entrance. This situation is particular to post Last Glacial Maximum, given that previous invasions, during GABI event, has not produced the same type of extinction without replacement of the empty niches (Patterson and Pascual 1968; Mooney and Cleland 2001).

The ecological concepts presented here were generally linked to understand American situation. Nevertheless in the Discussion they will be used again to analyze the results found in the different collections. Next, the results will be presented.

5. RESULTS

This chapter is divided in several parts. The first one is dedicated to describe the species over which antrophic and/or carnivore intervention was found. They belong to native South American orders Xenrthra and Notoungulata. Reference to other species belonging to these orders will be mention to appreciate the variability of native fauna composing these clades. In the second part of the chapter a general presentation of the species analyzed in each museum is presented. In the third part the published/accepted papers are showed. At last the still not published material will be described and a revaluation of the material from MCNV will be presented.

5.1. DESCRIPTION OF SPECIES WITH BIOLOGICAL INTERVENTION

5.1.1.XENARTHRA

Magnorder Xenarthra Cope, 1889

Most of the animals found with biological intervention belong to the Magnorder Xenarthra Cope, 1889. This native placental clade, conforms a monophyletic group and is the most characteristic and successful of South America (Patterson and Pascual 1968; Hoffstetter 1981; Bargo et al. 2000; Bargo 2003; Gaudin and McDonald 2008; Milne et al. 2009; Carlini and Zurita 2010; Pujos et al. 2012; Fariña et al. 2013; Straehl et al. 2013) with an important Tertiary radiation (Delsuc et al. 2004). It comprises 31 extant species grouped in 14 genera and more that 150 extinct genera (Fariña et al. 2013; Straehl et al. 2013) divided in Cingulata and Pilosa (de Paula Couto 1979; Vizcaíno et al. 2006; Bargo and Vizcaíno 2008; Gaudin and McDonald 2008; Carlini and Zurita 2010; Fariña et al. 2013) (Figure 5.1). Present day species of Xenarthra, such as the living tree sloths (Tardigrada), the anteaters (Vermilingua) or the armadillos (Cingulata) (Figure 5.1 to Figure 5.4) are a relictual group of a past well diversified magnorder (Delsuc et al. 2004; Gaudin and McDonald 2008; Pujos et al. 2012) with ample range of adaptations, covering different South American environments (Pujos et al. 2012). Consequently extinct species have no living counterparts, since survivors have few resemblances with those ones (Bargo 2003; Delsuc et al. 2004; Gaudin and McDonald 2008; Pujos et al. 2012).

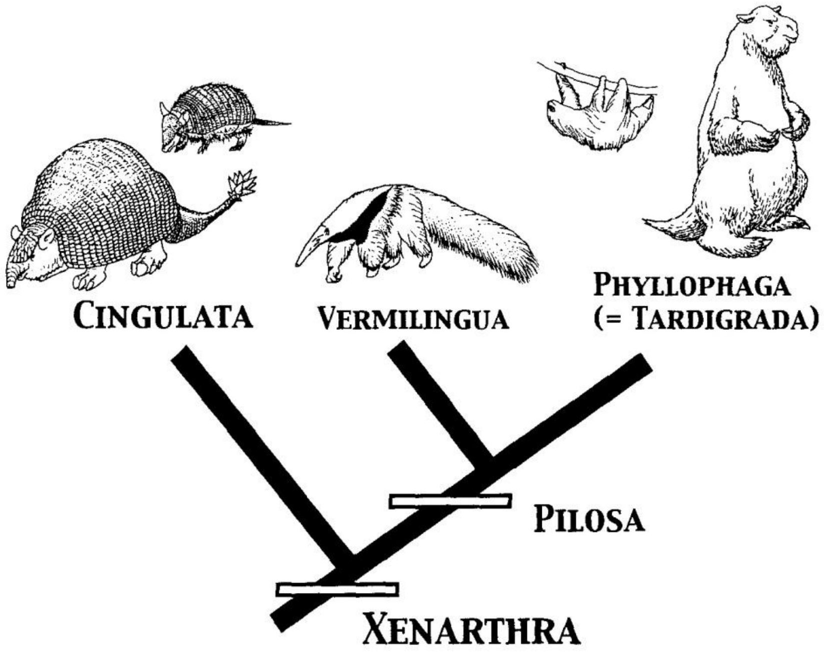


Figure 5.1. Phylogenetic relationships among extinct and extant groups of Xenarthra (From Gaudin and McDonald 2008).

Figure 5.2. Armadillo Dasypus novemcinctus (from Wikimedia Commons).

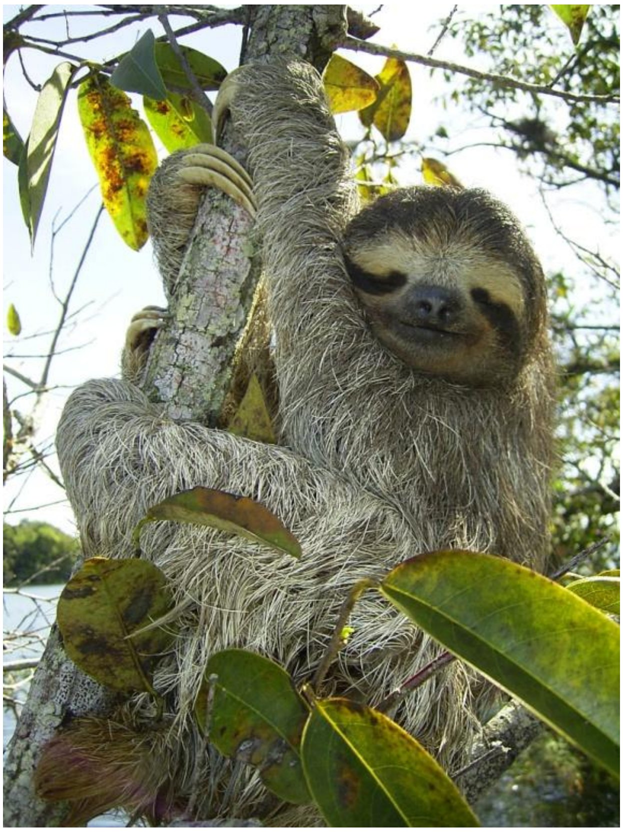


Figure 5.3. Sloth Bradypus tridactylus (from Wikimedia Commons).

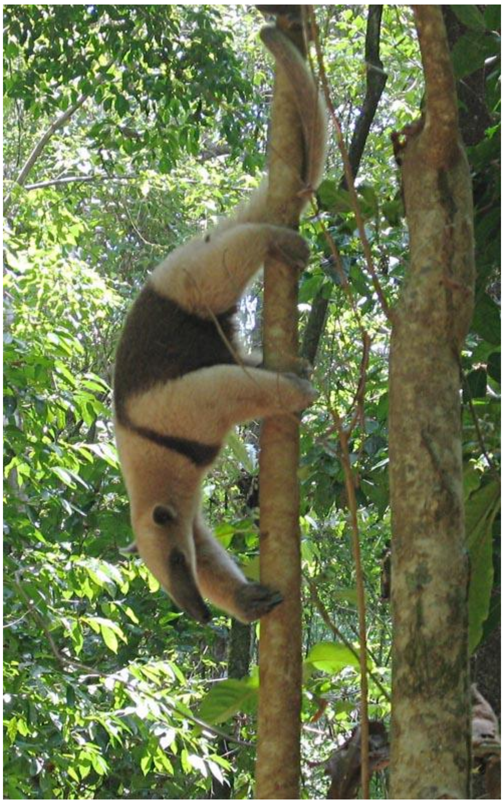


Figure 5.4. Anteater Tamandua mexicana (from Wikimedia Commons).

One of the characteristics that originally was used to separate this varieted group of animals is the presence of additional vertebral apophyses in the dorsolumbar vertebrae (de Paula Couto 1979; Gaudin 1999; Delsuc and Douzery 2009; Carlini and Zurita 2010; Fariña et al. 2013). The original name of "*Desdentados*", that means toothless, was given because of their simplified type of tooth (de Paula Couto 1979; Fariña et al. 2013), although only the Vermilingua group lack them (Carlini and Zurita 2010). Nevertheless Xenarthra dental morphology is almost unique (Bargo et al. 2000; Vizcaíno et al. 2006). Their main characteristic are that they have homodont teeth, reduced in number, without incisive and canines, with hypselodont enamel (ever growing and high-crowned) (de Paula Couto 1979; Bargo 2001; Vizcaíno et al. 2006). Other characteristics used to describe this order are its low metabolism and locomotion (McDonald 2005; Straehl et al. 2013). Recent studies in the bone miscrostructure have revealed that is composed of a mixture of woven, parallel-fibered and lamellar tissue with different degrees of remodelling and compactness (Straehl et al. 2013). Higher remodelling index in extinct species could probably be related with prolonged life span and increased size in extinct forms. Compactness would have been related with the locomotion and life habits (e.g. more humeral compactness in relation with digging activities) (Straehl et al. 2013).

Order Cingulata Illiger, 1811

This is a highly diversified order characterized for having an exoskeleton in the form of a carapace (de Paula Couto 1979; Milne et al. 2009; Carlini and Zurita 2010; Soibelzon et al. 2010; Fernicola and Porpino 2012; Fariña et al. 2013; Straehl et al. 2013) (Figure 5.5 and Figure 5.6). This one is composed of dermal scutes covered with epidermal scales with variable attachment among them (Gaudin and McDonald 2008; Milne et al. 2009). This protection covers the body, the head and the tail (de Paula Couto 1979; Milne et al. 2009; Carlini and Zurita 2010; Soibelzon et al. 2010; Fariña et al. 2013). Unlike the other members of this Magnorder, the backbones had a series of modifications in order to support the carapace. Except for the atlas, the cervical vertebrae are fused having the name of mesocervical vertebrae. Thoracic and lumbar vertebrae are also fused among them and to the carapace, forming large tubes, and the sacro is fused to the pelvis (de Paula Couto 1979; Gaudin 1999; Fariña et al. 2013; Zamorano et al. 2014a).

For this work two species are highlighted: *Doedicurus* sp. and the *Panochthus tuberculatus*. Fernicola (2008) was followed the taxonomic classification.

Suborden Glyptodontia Ameghino, 1889
Infraorden Glyptodontoinei Gray, 1869
Superfamily Glyptodontoidea Gray, 1869

Generally known as Glyptodons, they are one of the most frequent monopheletic groups of South America (Fernicola 2008; Soibelzon et al. 2010; Gaudin and McDonald 2008). They evolved in the Late Eocene in Patagonia, with the last registers in the Late Pleistocene- Early Holocene (Carlini and Zurita 2010). The ornamentation of them was generally used to classify the different species (de Paula Couto 1979; Scilliato-Yané et al. 1995; Gaudin and McDonald 2008; Soibelzon et al. 2010) although it started to be left aside in last years to benefit cladistic studies (Fernicola and Porpino 2012).

These were heavily armoured mammals, with fix, non-mobile osteoderms and were among the bigger species of this family (Patterson and Pascual 1968; de Paula Couto 1979; Fariña 1995; Fernicola 2008; Carlini and Zurita 2010; Soibelzon et al. 2010; Zurita et al. 2010; Zamorano et al. 2014a). During the Quaternary, their most outstanding sizes were reached in the Pleistocene, with forms of more than 3 m, weighing up to 2 tons (Scilliato-Yané et al. 1995; Carlini and Zurita 2010; Vizcaíno et al. 2012).

They also possessed well developed bony tails composed of 6 mobile rings that end with an important caudal tube (de Paula Couto 1979; Zamorano et al. 2012). The rings hold up a muscle of 108 kg mass used to move the distal part of the tail capable of breaking carapaces in intraspecific fights (McNeill et al. 1999). It was also used against predators, with the caudal tube ending in bosses or spikes that increased the effectiveness of this defensive weapon (Patterson and Pascual 1968; Carlini and Zurita 2010). Some relatives have also developed accessory structures in the anterolateral region and cephalic notch of the dorsal carapace as defensive strategies, especially for the neck and ventral side (Zurita et al. 2010).

They present trilobite dentition with high degree of hypsodonty (Vizcaíno et al. 2006; Fernicola 2008; Carlini and Zurita 2010; Fernicola and Porpino 2012) related with long extended oral processing (Vizcaíno et al. 2006), because of their simple digestive apparatus and the grazing habitat preferences (eg. open grassy and shrubby environments) (Fariña and Vizcaíno 2001; McDonald 2005; Vizcaíno et al. 2006; Carlini and Zurita 2010).

Family Glyptodontidae Gray, 1869
Subfamily Glyptodontinae Gray, 1869
Tribu Doedicurini Ameghino, 1889
Genus *Doedicurus* Burmeister, 1874
Species *Doedicurus* sp.

The genus appeared in the Ensenadan (Fernicola 2008). Its perforated carapace lacked of ornamentation (Scilliato-Yané et al. 1995). It would have reach 3,6 m of length and 1.400 kg (de Paula Couto 1979; Fariña 1995; Fariña et al. 1998). This species survived until Early Holocene times given that in the archaeological site La Moderna it was dated ca. 7.500 to 7.000 BP (Politis et al. 2003; Cione et al. 2009).

Family Panochthidae Castellanos 1927
Subfamilia Panochthinae Castellanos, 1927
Tribu Panochtini Castellanos, 1927
Genus *Panochthus* Burmeister, 1866

The genus appeared in the Chapadmalalan Stage/Age (Late Pliocene) and extended until Lujanian times (Zamorano et al. 2014b), reaching 1.100 kg (Fariña 1995). They had a thick carapace without ornamentation (de Paula Couto 1979; Zamorano et al. 2012).

Contrasting with the Glyptodons, Dasypodidae or armadillos (Figure 5.2), have a mobile carapace, and the osteoderms are presented as transversal united belts that allows these animals to wrap as a ball (de Paula Couto 1979). They also characterized by possessing digging behaviour as they have fossorial habits (de Paula Couto 1979; Milne et al. 2009; Fariña et al. 2013).

Figure 5.5. Different types of Cingulata. From left to right: Glyptodon, Neosclerocalyptus and Eutatus (From Belinchón et al. 2009, design realized by Mauricio Antón).

Infraorder Pilosa Flower, 1883

This infraorder is divided in the Vermilingua and Tardigrada [Tardigrada (=Phyllophaga=Folivora)]. The late group known as sloths (Fariña et al. 2013) have a wide array of adaptation, from acuatical or terrestrial, in several past species, to arboreal in the extant ones (Canto et al. 2008; Amson et al. 2015). The reduction in the number of teeth (5/4) is a particular formula exclusive of the extinct group (Gaudin and McDonald 2008; Straehl et al. 2013).

Some linkages had subcutaneous osteoderms characterized by small cylindrical bones (de Paula Couto 1979; Brandoni et al. 2008). They divided into several Subfamilies (de Paula Couto 1979) that could be related with the filling different past niches (Bargo et al. 2006a; Bargo and Vizcaíno 2008). Here the family Megatheriidae and the family Mylodontidae are highlight.

Superfamily Megatherioidea Gray, 1821
Family Megatheriidae Owen, 1843
Subfamilia Megatheriinae Gill, 1872
Genus Megatherium Cuvier, 1798
Species *Megatherium americanum* Cuvier 1796.

This specie was one of the most symbolic and representative of the South American fauna since its discovery in 18th century (Bargo 2001; Brandoni et al. 2008) (Figure 5.6). The family appeared in the Middle Miocene in Patagonia (Brandoni et al. 2008) although it is in the Bonarean and Lujanian where its record becomes more abundant (Soibelzon et al. 2010).

Its estimate body mass has been calculated between 3 to 6 tonnes converting it in the bigger of this community (Bargo 2003; Fariña et al. 1998, 2013). Skull shape differs from other sloths in that the cranial and rostral regions are narrow and the ventral part has a bulge to accommodate the teeth (Bargo 2001). This group was characterized by prismatic-quadrangular molars with bilophodont form and extreme hypsodonty (de Paula Couto 1979; Casinos 1996; Bargo 2001) with a vertical movement and cutting capacity (Bargo 2001, 2003; Bargo and Vizcaíno 2008). They had a narrow-muzzle configuration, with a prehensile upper lip probably adapted to eat turgid or moderate to soft tough food and were generalized browser eating leaves, fruits and shrubs (Bargo 2001, 2003; Bargo et al. 2006a; Bargo and Vizcaíno 2008). Consequently they had better oral processing than Mylodons, related to their low fermentation rate or lower metabolic requirements (Vicaíno et al. 2006; Bargo and Vizcaíno 2008). It was also proposed that could have been an opportunistic scavenger (Fariña and Blanco 1996). Anatomically this is related with the capacity of fast extension and speed that had in the forearms (Fariña and Blanco 1996; Bargo et al. 2000; Bargo 2003) and the powerful claws that could have been involved this task (Fariña and Blanco 1996; Bargo 2003), thus adopting a bipedal position (even though it also had a quadruple one) (Casinos 1996). This more dynamic description contrast with earlier suppositions that assumed that the bipedal position would have been useful to consume the leaves from the trees using its long tail as a tripod (de Paula Couto 1979; Fariña et al. 2013) and using the claws to extract roots (de Paula Couto 1979; Fariña et al. 2013). This species survived until Early Holocene times given that in the archaeological site Campo Laborde was dated ca. 8.800 to 7.700 BP (Politis and Messineo 2006; Cione et al. 2009).

Superfamily Mylodontoidea Gill, 1872
Family Mylodontidae Gill, 1872

They have prismatic or cylindrical tooth, reduced in number (5/4) (de Paula Couto 1979; Bargo et al. 2006b; Bargo and Vizcaíno 2008). The anteromedial mastication movement was probably related with a poor capacity in extensive oral food processing (Vizcaíno et al. 2006; Bargo and Vizcaíno 2008). Thus their main activity would have been for crushing with less capacity of gridding (Bargo and Vizcaíno 2008). This would have been compensate with a high fermentation rate due to better developed digestive system, low metabolic requirements, or both (McDonald 2005; Vizcaíno et al. 2006; Bargo and Vizcaíno 2008). The members were short, tibia and fibula not fused and also possessed claws (de Paula Couto 1979). Two subfamilies were recorded in the different collections.

Subfamily Mylodontinae Gill, 1872

It appeared in the Early Miocene in Patagonia (de Paula Couto 1979). The skull was prismatic-rectangular and anteriorly widened (Bargo 2001; Bargo and Vizcaíno 2008). Humerus did not possessed the entepicondiloide foramen (de Paula Couto 1979). From the different species composing this Subfamily, *Glossotherium robustum* is highlighted here.

Genus Glossotherium Owen, 1840
Species *Glossotherium robustum* Owen, 1842

It was one of the biggest of this group. Different mass estimation had been calculated for it: 500 to 1.000 kg (Christiansen and Fariña 2003; Fariña et al. 2013), 1.200 kg and 1.500 kg (Bargo et al. 2000; Bargo 2003; Fariña et al. 2013) and between 1 to 2 tonnes (Fariña et al. 1998, 2013). Its digging capacity would have been related to the construction of paleoburrows, currently registered in the pampean region (Bargo et al. 2000; Vizcaíno et al. 2001; Bargo 2003; Fariña et al. 2013), but also for searching food (Bargo and Vizcaíno 2008). They would have been mainly grazers and bulk-feeders of turgid food (Bargo 2001, 2003; Bargo et al. 2006b; Bargo and Vizcaíno 2008) with low degree of hypsodonty (Bargo and Vizcaíno 2008). In their wide-muzzeled configuration, the lips and the tongue would have been used together to pull out the vegetation (Bargo et al. 2006a; Bargo and Vizcaíno 2008).

Subfamily Scelidotheriinae Ameghino, 1904

This was a smaller group than Mylodontinae. They had a narrow, tubular and elongated skull and the tooth were transversally compressed (Bargo 2001; Miño-Boilini and Carlini 2009; Fariña et al. 2013). It became an endemic group of South America, given that it not participated in the GABI event (Miño-Boilini 2012). Two genera are recognized:

Genus Scelidotherium Owen, 1839

The most studied species in this group is *Scelidotherium leptocephalum*. It was recorded during the Bonarean and Lujanian of the Pampean region (Miño-Boilini 2012), with a body mass estimated between 600 kg and 1 tonne (Fariña et al. 1998, 2013; Bargo et al. 2000). Even though they had a high degree of hypsodonty, they would have been selective feeder (Bargo et al. 2006a). As with *Glossotherium*, its digging capacity would have been not only for burrowing activity, but would have also been used for searching underground food. Consequently, soils particles contained in their ingested food can partially explain their hypsodonty (Bargo 2003; Bargo et al. 2006b; Bargo and Vizcaíno 2008; Fariña et al. 2013). The narrow-muzzled configuration would have contained a prehensile lip to select certain types of plants (Bargo et al. 2006a; Bargo and Vizcaíno 2008). A recent dating of 7.615±85 yrBP has shown that survived until Early Holocene times (Prado et al. 2015).

Genus Scelidodon Ameghino, 1881

It was recorded since the Deseadan until the Lujanian (Miño-Boilini 2012) being scarce in the Pampean region (Miño-Boilini and Carlini 2009). Recent analysis has proposed that this group can be included in the *Scelidotherium* genus, as the haplotype seems to be a juvenile species of *Scelidotherium leptocephalum* (Miño-Boilini et al. 2014).

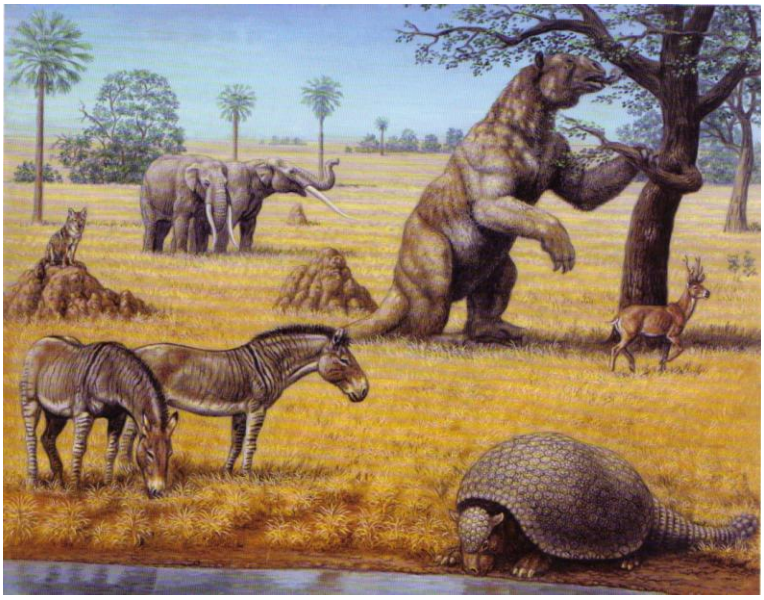


Figure 5.6. Some species described: In the front Glyptodon and Equus. Backwards Megatherium americanum with an erect posture, behind a group of two Proboscides (From Belinchón et al. 2009, design realized by Mauricio Antón).

5.1.2.NOTOUNGULATA

The other important South American group in this work is the South American ungulate named Notoungulata Roth, 1903 (Figure 5.7). It originated in the Palaeogene (Welker et al. 2015) and evolved in isolation from other known ungulates (Fariña et al. 2013), being taxonomically assigned into the supraorder Meridiungulata (McKenna 1975; McKenna and Bell 1997; Fariña et al. 2013; Welker et al. 2015). A recent protein study had placed them as a sister group of the Perissodactyla, thus integrating it in the Pan-perissodactyla taxon (Welker et al. 2015).

Notoungulates were a very successful order (Patterson and Pascual 1968), given the abundance and diversity recorded among the South American ungulates (Bond et al. 1995; Fariña et al. 2013; Elissamburu 2012; Welker et al. 2015). At least 108 genera are recognized for this order (Elissamburu 2012).

Suborder Toxodonta Scott, 1904
Family Toxodontidae Gervais, 1847
Subfamily Toxodontinae Trouessart, 1898
Genus *Toxodon* Owen, 1837

In the Pleistocene of the Pampean region this Suborder is a relictual group, with the survival of one family, being *Toxodon platensis* the typical species (Bond et al. 1995). Nevertheless other species of the Quaternary times were *Toxodon ensenadenseis*, *Toxodon darwini*, *Toxodon gezi* or *Toxodon burmeisteri* among others, although they are probably synonyms of the first one (Bond et al. 1995, Bond 1999b; Miño-Boilini et al. 2006). The genus evolved in the Pliocene and survived until Early Holocene times (Bond et al. 1995). Its mass was calculated more than one tone (Fariña et al. 1998, 2013) and around 3,5 m of large (Forasiepi et al. 2007).

This monophyletic group is generally compared with hippos or rhinos because of their appearance and griding pattern of their molar crowns (de Paula Couto 1979; Fariña et al. 2013). In fact it is characterized by its voluminous body and short limbs (Forasiepi et al. 2007). These ones were developed for supporting the weight and some locomotion activity (Elissamburu 2012) given that they would had had a more erect and log time standing up position (Fariña and Álvarez 1994; Shockey 2001). It had a robust head with large and width premaxilar that could be related with the presence of a prensil lip (Forasiepi et al. 2007). They had ever-growing, high-crowned (hypselodont) teeth (MacFadden 2005). This morphological configuration could have been related with the abrasive type of food intake (Forasiepi et al. 2007). Isotopic studies from exemplars of the Pampean region have reveal they had mixed C_3 grazer and/or browsing diet, living in grasslands and/or mixed forested and grasslands habitats (MacFadden 2005). This supposed an ample capacity for adapting to the different vegetational patches (MacFadden 2005) even though were classically described as being adapted from semi-aquatic environments (de Paula Couto 1979; Bond et al. 1995; MacFadden 2005). In the archaeological site Campo Laborde 2 AMS dates over this species have given dating ca. 11.750 (Steele and Politis 2009).

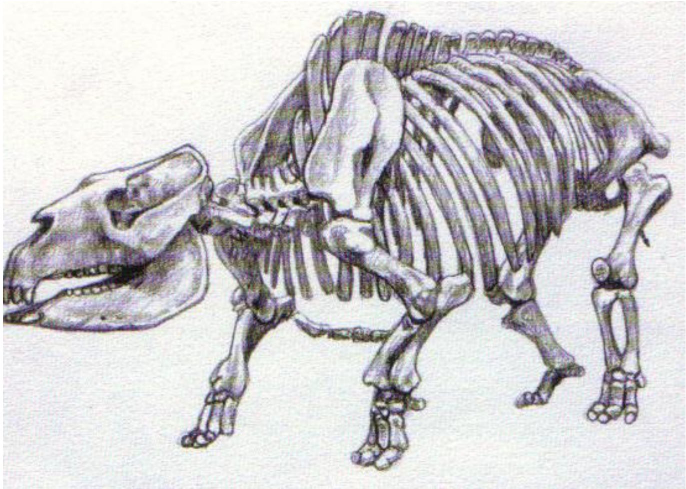


Figure 5.7. Toxodon image (From Belinchón et al. 2009).

Other important high diversified group into the Notoungulate order is the Litopterna. In the Quaternary, this group suffered of the declination of the species. In Lujanian times *Macrauchenia patachonica* is the most known species (Bond et al. 1995; Fariña et al. 2013). The more conspicuous characteristic is the retraction of the nasal bones that was interpreted as a result of the development of a trunk (Bond et al. 1995; Fariña et al. 2013). It was distributed along different South American regions that indicate an adaptation to different environments (Bond et al. 1995; Fariña et al. 2013). It weighed around one tonne, and had a system of swerving and dodging in order to escape from predation (Fariña et al. 2005).

5.2. GENERAL PRESENTATION OF THE COLLECTIONS

Representation of NISP and MNI in the different taxa per museums is represented in Figure 5.8 and Figure 5.9, and in Table 5.1 to Table 5.4. It can be observed that groups belonging to Xenarthra (Xenarthra, *Megatherium*, Mylodonidae, Glyptodontide and Dasypodidae) are the most abundant ones in European and Argentinean museums. This can be related with the fact that Xenarthra order was a novelty for paleontological research during that time. Especially for European museums the percentage of NISP is higher than Argentinean ones (64.20% in the first one versus 21.54% in the second one) (Table 5.2). Considering the European collections were formed during 19th century, when the discovering and enthusiasm for this group was in its maximum rank, classification trend could have influenced in the interest of the museums for having more skeletons of this group to study its anatomy and creating new species. Nevertheless it has to be also considered that current abundance of this order can be reflecting the past predominance this group had in the region, given their ample capacity of diversification to the several environments (Pujos et al. 2012; Fariña et al. 2013). It can be observed in Figure 5.8 and Figure 5.9 and Table 5.1 to Table 5.4 that at both sides of the Atlantic a similar trend was detected in the NISP and MNI: Mylodontidae and Glyptodontidae are the most abundant fossil assemblages followed by *Megatherium*. As seen above, both Mylodontidae and Glyptodontidae are the most variable and diversified groups, with several subfamilies, families, genera and species. Thus it has not to be discarded that collectors would have mostly found these taxa in their excursions. From both groups, Mylodontidae has a better representation that could be related with the decision of not including the plates of *Glyptodon* for this analysis.

On the other side, *Megatherium americanum*, the most emblematical specie from the region during 19th century, is less represented than the other groups, although it is better represented in European collections than in Argentinean ones (percentage of NISP 14.38% in Europe and 0.82% in Argentina, Figure 5.8 and Table 5.2). Nevertheless, when considering the percentage of MNI (Figure 5.9 and Table 5.4) this difference is more equated: 6.15% in Europe and 2.98% in Argentina.

Dasypodidae presents higher percentage of NISP in Argentinean than in European collections (0.49% in Europe and 2.06% in Argentina, Figure 5.8 and Table 5.2). Nevertheless when considering the percentage of MNI, European collections present more quantity of individuals (1.23% in Europe versus 0.52% from Argentina, Figure 5.9 and Table 5.4). This is related with the MACN sample that only represents three individuals, while the less amount of NISP in the European collections belongs to different individual.

Megatherium, Mylodontidae and Glyptodontidae were present in all the European collections expect for MM that only house Glyptodontidae, and MSNF, that only has *Megatherium*. MCNV has the best representation of Mylodontidae and Glyptodontidae (percentage of NISP 13.60% for the first one and 3.70% for the second one, Table 5.2). Nevertheless when considering the percentage of MNI, Glyptodontidae remains from MCNV equates to MNHN (2.63% in both institutions, representing 15 individuals, Table 5.4). This institution also follows MCNV in the representation of the percentage of MNI, with 5.27% (Table 5.4). MCSNM has better representation of *Megatherium*, with 4.43% of percentage of NISP (Table 5.2). But, considering that this collection had suffered from a bombing, more fragmentation of the material is expected, that could probably increased the NISP to 295 (Table 5.1). Taking out this collection, MCNV has the better representation of this taxon (percentage of NISP: 2.19%, Table 5.2). However when considering the percentage of MNI, ZMK has more individuals, with 2.28%, as seen in Table 5.4. Considering only percentage of NISP (Table 5.2), *Megatherium* assemblage is also important in MGGCB (1.64%) and in NMW (1.21%). Mylodontidae are more abundant in ZMK (7.59%), PIMUZ (4.15%) and NHM (2.45%). In NMW there is also an important representation of Mylodontidae (1.42%) and Glyptodontidae (2.10%) remains. Glyptodontidae is also abundant in PIMUZ (1.45%) and ZMK (1.92%). The high representation in MRSNT could be related, as in MCSNN, with a higher fragmentation due to the bombing this museum suffered. In the Argentinean institutions MLP collections are the most important for Mylodontidae (8.44%) and Glyptodontidae groups (2.40%), but it is also remarkable the amount of Mylodontidae housed in MCA (4.96%) (Table 5.2).

Notoungulates and Ungulates (*Toxodon*, *Macrauchenia*, among the first ones, and Artiodactyla, Equidae, Mastodon[3] and *Tapirus* among the second ones) are the following group that are more abundant in the collections (Figure 5.8 and Figure 5.9 and Table 5.1 to Table 5.4). In European collections the percentage of NISP is higher than Argentinean ones (8.68% in the first one, 3.099%) (Table 5.2). Artiodactyls can be more abundant given than here were included Cervids and Camelids, such as Lama and Paleolama. Toxodons, among the South American Notougulates, and Artiodactyla, among Holartic Ungulates, are the better represented in Europe (percentage of NISP of 2.30% for Toxodons and 3.65%, for Artiodactyla, Figure 5.8 and Table 5.2) than in Argentina (percentage of NISP of 0.91% for Toxodons and 1.06%, for Artiodactyla, Figure 5.8 and Table 5.2). Nevertheless,

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[3] As Mastodons bones were few, it was included into the Ungulates even though recent studies position it into the Paenungulata (Foley et al. 2016)

when considering the percentage of MNI, they both equate (for Toxodons 3,69% in Europe and 3,51% in Argentina; and for Artiodactyla 5,79% in Europe and 5,44% in Argentina; Figure 5.9 and Table 5.4). The contrary tendency is observed with Equidae. Percentage of NISP is almost the same for both Europe and Argentina (0.94% for the first one and 0.96% for the second one; Figure 5.8 and Table 5.2), but the MNI reveals a better representation of them in the Argentinean museums (2.28% in the first one and 3.33% in the second one; Figure 5.9 and Table 5.4). This is due to the better representation of this group in the MLP Ameghino (paleont. Coll.). Regarding the rest of the groups, *Macrauchenia* was most observed in European than in Argentinean collections (percentage of NISP 1.57% versus 0.12%; Figure 5.8 and Table 5.2; and percentage of MNI of 2.36% and 0.87%; Figure 5.9 and Table 5.4). Mastodonts were specially recognized in European museums (12 bones from different collections in Europe and only two bones in MCA, Table 5.1), while only one bone of Tapirus was observed in ZMK (Table 5.1).

Unlike the Xenarthra, Notungulates and Ungulates are not represented in several European museums, such as MGGCB, MRSNT, MSNF and MM. ZMK presents all the groups identified here, as happens in PIMUZ (except for Tapirus). Roth was the principal provider in both institutions, consequently, recollection filters could had influenced in this trend. Nevertheless, even in MHNVG Roth was also provider, here only Toxodons and Mastodons were recognized, being more abundant here than in the rest of the museums (percentage of NISP, 0.93% for the first one and 0.090% for the second one; Table 5.2). In the other Roth collections, Toxodons are also well represented in ZMK (0.57%), but scarce in PIMUZ (0.06%) (Table 5.2). On the other side, even though MCNV has the best representation of Artiodactyla (1.45%) and Equidae (0.45%) from all the European museums (Table 5.2), *Toxodon* is represented with only two bones (Table 5.1). *Macrauchenia* in MNHN is a better represented group (0.51%; Table 5.2) in comparison with the rest of the European institutions. In Argentinean museums Toxodons among the Notoungulata and Artiodactyla among Ungulates are the most important groups, as happens in Europe. Artiodactyla is especially better represented in MACN (0.31%) and MLP collection (summing 0.55% between the three collections of this museum, Table 5.2). At last, rodents in MACN and MNHN refer to *Hydrochoerus hidrochoerus* while in MLP is related with a mandible of micromammals that belongs to the MLP Ameghino (paleont. Coll.). The categories Megamammals indeterminate, *Mesotherium*, Carnivora and Indeterminated are only apply for Ameghino collections from MLP.

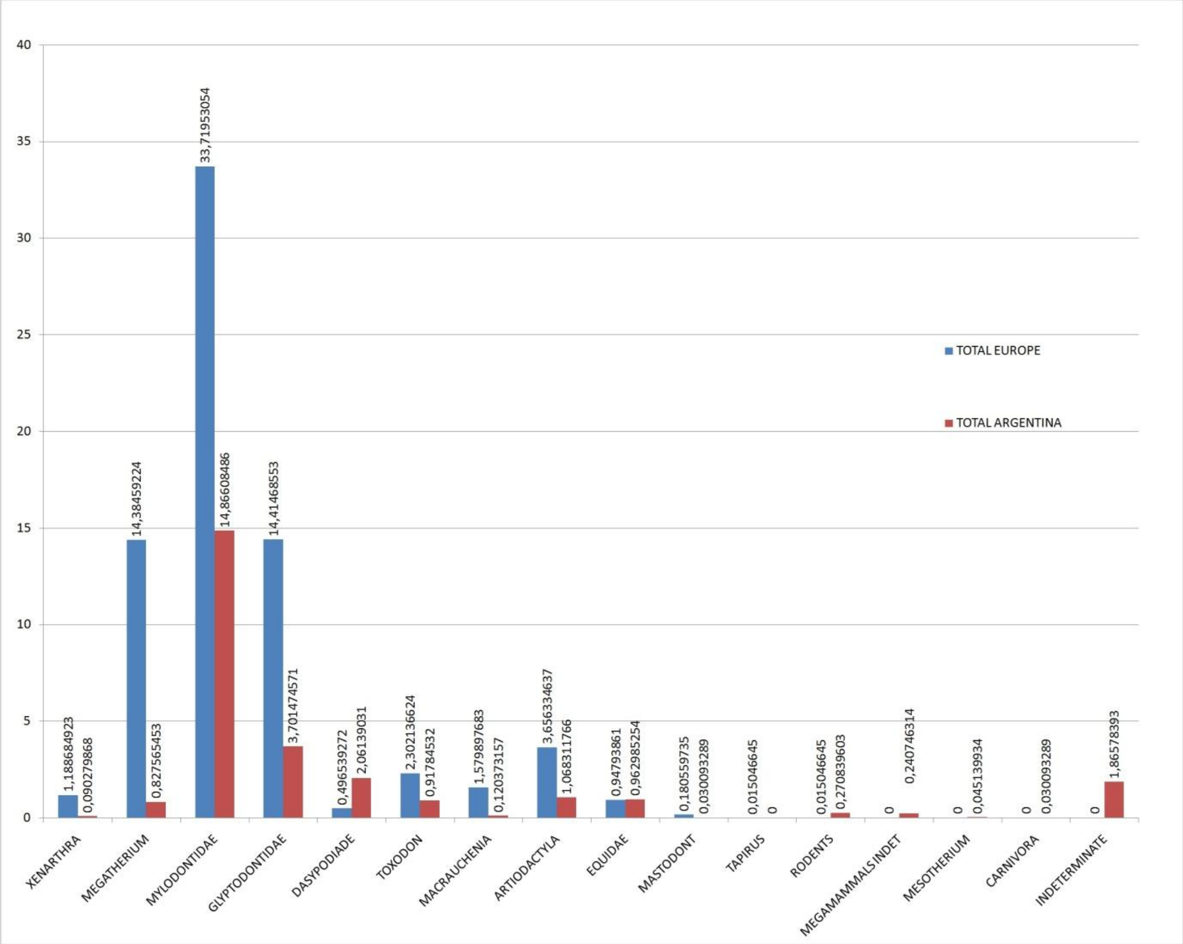

Figure 5.8. Percentage of NISP Europe and Argentina.

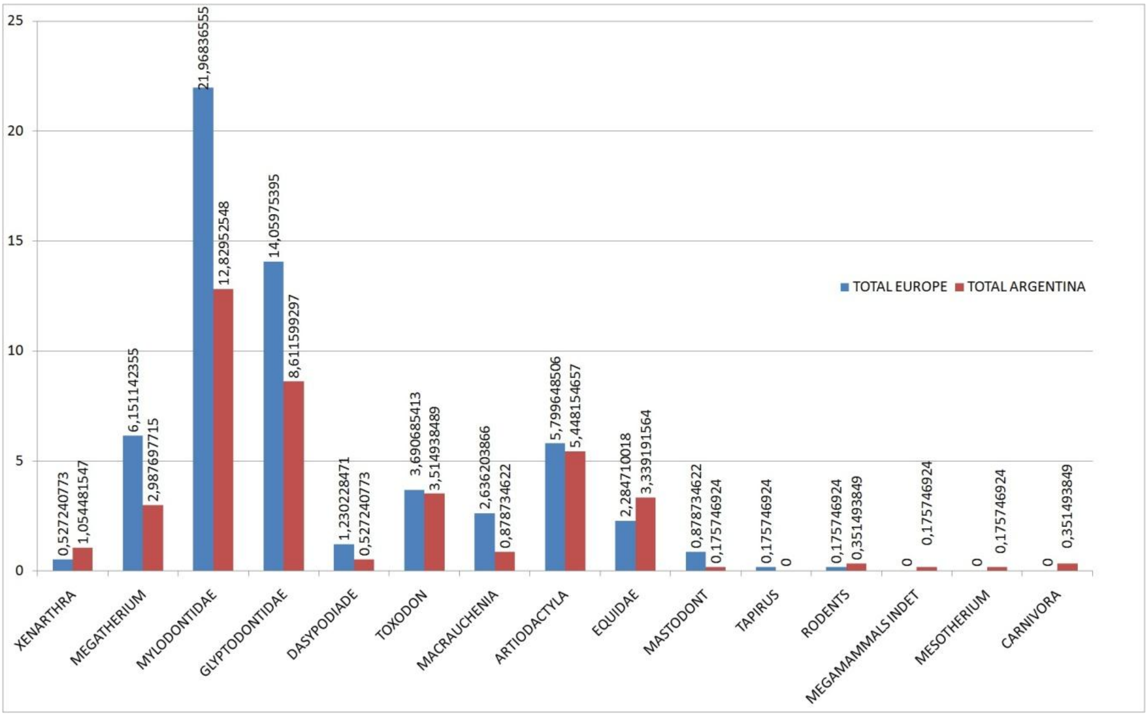

Figure 5.9. Percentage of MNI Europe and Argentina.

MUSEUMS	XENARTHRA	MEGATHERIUM	MYLODONTIDAE	GLYPTODONTIDAE	DASYPODIADE	TOXODON	MACRAUCHENIA	ARTIODACTYLA	EQUIDAE	MASTODONT	TAPIRUS	RODENTS	MEGAMAMMALS INDET	MESOTHERIUM	CARNIVORA	INDETERMINATE	TOTAL
MCNV	7	146	904	246	18	2	28	97	30	-	-	-	-	-	-	-	1478
MGGCB	-	109	95	54	-	-	-	-	-	-	-	-	-	-	-	-	258
MCSNM	69	295	11	8	-	1	-	-	-	-	-	-	-	-	-	-	384
MRSNT	-	23	-	138	-	-	-	-	-	-	-	-	-	-	-	-	161
MSNF	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30
NHM	-	30	163	22	-	6	25	14	-	-	-	-	-	-	-	-	260
MHNVG	-	12	32	59	8	62	-	-	-	6	-	-	-	-	-	-	179
PIMUZ	-	40	276	97	5	4	2	15	8	2	-	-	-	-	-	-	449
NMW	3	81	95	140	-	7	-	1	1	2	-	-	-	-	-	-	330
MM	-	-	-	16	-	-	-	-	-	-	-	-	-	-	-	-	16
ZMK	-	141	505	128	-	38	16	88	19	2	1	-	-	-	-	-	938
MNHN	-	49	160	50	2	33	34	28	5	-	-	1	-	-	-	-	362
TOTAL EUROPE	79	956	2241	958	33	153	105	243	63	12	1	1	-	-	-	-	4845
MACN	4	45	95	22	137	51	6	21	35	-	-	17	-	-	-	-	433
MCA	2	-	330	64	-	5	1	13	2	2	-	-	-	-	-	-	419
MLP Ameghino(paleont. Coll)	-	-	1	-	-	2	1	9	19	-	-	1	16	3	1	85	138
MLP Ameghino (archaeo. Coll)	-	-	1	-	-	3	-	2	-	-	-	-	-	-	1	39	46
MLP	-	10	561	160	-	-	-	26	8	-	-	-	-	-	-	-	765
TOTAL ARGENTINA	6	55	988	246	137	61	8	71	64	2	-	18	16	3	2	124	1801
TOTAL	85	1011	3229	1204	170	214	113	314	127	14	1	19	16	3	2	124	6646

Table 5.1. NISP of the collections.

MUSEUMS	XENARTHRA	MEGATHERIUM	MYLODONTIDAE	GLYPTODONTIDAE	DASYPODIADE	TOXODON	MACRAUCHENIA	ARTIODACTYLA	EQUIDAE	MASTODONT	TAPIRUS	RODENTS	MEGAMAMMALS INDET	MESOTHERIUM	CARNIVORA	INDETERMINATE	TOTAL
MCNV	0,105326512	2,196810111	13,60216672	3,701474571	0,270839603	0,030093	0,421306049	1,459524526	0,4514	-	-	-	-	-	-	-	22,23894
MGGCB	-	1,640084261	1,429431237	0,812518808	-	-	-	-	-	-	-	-	-	-	-	-	3,882034
MCSNN	1,038218477	4,438760156	0,165513091	0,120373157	-	0,015047	-	-	-	-	-	-	-	-	-	-	5,777912
MRSNT	-	0,346072826	-	2,076436955	-	-	-	-	-	-	-	-	-	-	-	-	2,42251
MSNF	-	0,451399338	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,451399
NHM	-	0,451399338	2,45260307	0,331026181	-	0,09028	0,376166115	0,210653024	-	-	-	-	-	-	-	-	3,912128
MHNVG	-	0,180559735	0,481492627	0,887752031	0,120373157	0,932892	-	-	-	0,09027987	-	-	-	-	-	-	2,693349
PIMUZ	-	0,601865784	4,152873909	1,459524526	0,075233223	0,060187	0,030093289	0,225699669	0,12037	0,03009329	-	-	-	-	-	-	6,755943
NMW	0,045139934	1,218778212	1,429431237	2,106530244	-	0,105327	-	0,015046645	0,01505	0,03009329	-	-	-	-	-	-	4,965393
MM	-	-	-	0,240746314	-	-	-	-	-	-	-	-	-	-	-	-	0,240746
ZMK	-	2,121576888	7,598555522	1,925970509	-	0,571772	0,240746314	1,324104725	0,28589	0,03009329	0,01505	-	-	-	-	-	14,11375
MNHN	-	0,737285585	2,407463136	0,75233223	0,030093289	0,496539	0,511585916	0,421306049	0,07523	-	-	0,01505	-	-	-	-	5,446885
TOTAL EUROPE	1,188684923	14,38459224	33,71953054	14,41468553	0,496539272	2,302137	1,579897683	3,656334637	0,94794	0,18055974	0,01505	0,01505	-	-	-	-	72,90099
				TOTAL XENARTHRA	64,2040325			TOTAL NOTOUNGULATES/ UNGULATES			8,68191						
MACN	0,060186578	0,677099007	1,429431237	0,331026181	2,06139031	0,767379	0,090279868	0,315979537	0,52663	-	-	0,25579	-	-	-	-	6,515197
MCA	0,030093289	-	4,965392717	0,962985254	-	0,075233	0,015046645	0,19560638	0,03009	0,03009329	-	-	-	-	-	-	6,304544
MLP Ameghino(paleont. Coll)	-	-	0,015046645	-	-	0,030093	0,015046645	0,135419801	0,28589	-	-	0,01505	0,240746314	0,045139934	0,0150466	1,278964791	2,076437
MLP Ameghino (archaeo. Coll)	-	-	0,015046645	-	-	0,04514	-	0,030093289	-	-	-	-	-	-	0,0150466	0,586819139	0,692146
MLP	-	0,150466446	8,44116762	2,407463136	-	-	-	0,39121276	0,12037	-	-	-	-	-	-	-	11,51068
TOTAL ARGENTINA	0,090279868	0,827565453	14,86608486	3,701474571	2,06139031	0,917845	0,120373157	1,068311766	0,96299	0,03009329	-	0,27084	0,240746314	0,045139934	0,0300933	1,86578393	27,09901
				TOTAL XENARTHRA	21,54679506			TOTAL NOTOUNGULATES/ UNGULATES			3,09961						
TOTAL	1,278964791	15,21215769	48,58561541	18,1161601	2,557929582	3,219982	1,70027084	4,724646404	1,91092	0,21065302	0,01505	0,28589	0,240746314	0,045139934	0,0300933	1,86578393	100

Table 5.2. Percentage NISP of the collections.

MUSEUMS	XENARTHRA	MEGATHERIUM	MYLODONTIDAE	GLYPTODONTIDAE	DASYPODIADE	TOXODON	MACRAUCHENIA	ARTIODACTYLA	EQUIDAE	MASTODONT	TAPIRUS	RODENTS	MEGAMAMMALS INDET	MESOTHERIUM	CARNIVORA	TOTAL
MCNV	1	2	40	15	3	1	1	6	5	-	-	-	-	-	-	74
MGGCB	-	1	4	4	-	-	-	-	-	-	-	-	-	-	-	9
MCSNM	1	1	3	2	-	1	-	-	-	-	-	-	-	-	-	8
MRSNT	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	2
MSNF	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2
NHM	-	5	12	8	-	3	3	5	-	-	-	-	-	-	-	36
MHNVG	-	1	3	5	2	1	-	-	-	2	-	-	-	-	-	14
PIMUZ	-	3	5	6	1	1	1	7	1	1	-	-	-	-	-	26
NMW	1	1	4	7	-	1	-	1	1	1	-	-	-	-	-	17
MM	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
ZMK	-	13	24	16	-	9	4	9	4	1	1	-	-	-	-	81
MNHN	-	5	30	15	1	4	6	5	2	-	-	1	-	-	-	69
TOTAL EUROPE	3	35	125	80	7	21	15	33	13	5	1	1	-	-	-	339
MACN	4	11	31	12	3	13	3	16	8	-	-	1	-	-	-	102
MCA	2	-	20	11	-	5	1	7	2	1	-	-	-	-	-	49
MLP Ameghino(paleont. Coll)	-	-	1	-	-	1	1	4	3	-	-	1	1	1	1	14
MLP Ameghino (archaeo. Coll)	-	-	1	-	-	1	-	1	-	-	-	-	-	-	1	4
LP	-	6	20	26	-	-	-	3	6	-	-	-	-	-	-	61
TOTAL ARGENTINA	6	17	73	49	3	20	5	31	19	1	-	2	1	1	2	230
TOTAL	9	52	198	129	10	41	20	64	32	6	1	3	1	1	2	569

Table 5.3. MNI of the collections.

MUSEUMS	XENARTHRA	MEGATHERIUM	MYLODONTIDAE	GLYPTODONTIDAE	DASYPODIADE	TOXODON	MACRAUCHENIA	ARTIODACTYLA	EQUIDAE	MASTODONT	TAPIRUS	RODENTS	MEGAMAMMALS INDET	MESOTHERIUM	CARNIVORA	TOTAL
MCNV	0,175746924	0,351493849	7,029876977	2,636203866	0,527240773	0,175747	0,175746924	1,054481547	0,87873	-	-	-	-	-	-	13,00527241
MGGCB	-	0,175746924	0,702987698	0,702987698	-	-	-	-	-	-	-	-	-	-	-	1,58172232
MCSNN	0,175746924	0,175746924	0,527240773	0,351493849	-	0,175747	-	-	-	-	-	-	-	-	-	1,405975395
MRSNT	-	0,175746924	-	0,175746924	-	-	-	-	-	-	-	-	-	-	-	0,351493849
MSNF	-	0,351493849	-	-	-	-	-	-	-	-	-	-	-	-	-	0,351493849
NHM	-	0,878734622	2,108963093	1,405975395	-	0,527241	0,527240773	0,878734622	-	-	-	-	-	-	-	6,326889279
MHNVG	-	0,175746924	0,527240773	0,878734622	0,351493849	0,175747	-	-	-	0,35149385	-	-	-	-	-	2,460456942
PIMUZ	-	0,527240773	0,878734622	1,054481547	0,175746924	0,175747	0,175746924	1,230228471	0,17575	0,17574692	-	-	-	-	-	4,569420035
NMW	0,175746924	0,175746924	0,702987698	1,230228471	-	0,175747	-	0,175746924	0,17575	0,17574692	-	-	-	-	-	2,987697715
MM	-	-	-	0,175746924	-	-	-	-	-	-	-	-	-	-	-	0,175746924
ZMK	-	2,284710018	4,217926186	2,811950791	-	1,581722	0,702987698	1,58172232	0,70299	0,17574692	0,17575	-	-	-	-	14,23550088
MNHN	-	0,878734622	5,272407733	2,636203866	0,175746924	0,702988	1,054481547	0,878734622	0,35149	-	-	0,17575	-	-	-	12,12653779
TOTAL EUROPE	0,527240773	6,151142355	21,96836555	14,05975395	1,230228471	3,690685	2,636203866	5,799648506	2,28471	0,87873462	0,17575	0,17575	-	-	-	59,57820738
				TOTAL XENARTHRA	**43,93673111**			**TOTAL NOTOUNGULATES/ UNGULATES**			**15,4657**					
MACN	0,702987698	1,933216169	5,448154657	2,108963093	0,527240773	2,28471	0,527240773	2,811950791	1,40598	-	-	0,17575	-	-	-	17,92618629
MCA	0,351493849	-	3,514938489	1,933216169	-	0,878735	0,175746924	1,230228471	0,35149	0,17574692	-	-	-	-	-	8,611599297
MLP Ameghino(paleont. Coll)	-	-	0,175746924	-	-	0,175747	0,175746924	0,702987698	0,52724	-	-	0,17575	0,175746924	0,175746924	0,1757469	2,460456942
MLP Ameghino (archaeo. Coll)	-	-	0,175746924	-	-	0,175747	-	0,175746924	-	-	-	-	-	-	0,1757469	0,702987698
MLP	-	1,054481547	3,514938489	4,569420035	-	-	-	0,527240773	1,05448	-	-	-	-	-	-	10,72056239
TOTAL ARGENTINA	1,054481547	2,987697715	12,82952548	8,611599297	0,527240773	3,514938	0,878734622	5,448154657	3,33919	0,17574692	-	0,35149	0,175746924	0,175746924	0,3514938	40,42179262
				TOTAL XENARTHRA	**26,01054482**			**TOTAL NOTOUNGULATES/ UNGULATES**			**13,3568**					
TOTAL	1,58172232	9,13884007	34,79789104	22,67135325	1,757469244	7,205624	3,514938489	11,24780316	5,6239	1,05448155	0,17575	0,52724	0,175746924	0,175746924	0,3514938	100

Table 5.4. Percentage MNI of the collections.

5.3. PUBLISHED/ ACCEPTED PAPERS

After reviewing the collections, biological intervened bones were described and interpreted in different publications along these years. The material with anthropic intervention was presented separately in a series of reviews while the material with carnivore intervention was presented in one paper. Following the reader will find:

- In first place, a paper published in 2015 in the Spanish Journal of Palaeontology that deals with the evidence from MCNV. This first publication was related with the first revision of this collection. Consequently, the total amounts and the evidence presented is different of what was done for the second revision (e.g. consideration of indeterminate and plates).
- The second publication deals with the material rescued in MACN, MNHN and ZMK and presented in Computs Rendus Palevol. This paper is currently in press.
- The third publication presents a *Megatherium americanum* atlas with anthropic marks from MSNF in the Rivista Italiana di Paleontologia e Stratigrafia. This paper is currently in press.
- The fourth publication deals on the bones with carnivore intervention found in MCNV, MNHN, NMW and MLP. This work was send to PeerJ was accepted with minor modifications.

Other presentations realized in Congress and one additional published paper can be seen at the end of this thesis, in the section “Additional papers and presentation in Scientifics Reunions”. Also, more figures of the megamammals biologically intervented bones can be found in the section “Additional Figures and Tables.

5.3.1. SPACES AND SPECIES: THE RODRIGO BOTET COLLECTION (VALENCIA, SPAIN) AND THE PALEOECOLOGICAL RELATIONSHIPS OF EARLY HOMO SAPIENS DURING THEIR DISPERSAL IN THE SOUTHERN CONE OF SOUTH AMERICA (SPANISH JOURNAL OF PALEONTOLOGY)

SPANISH JOURNAL OF PALAEONTOLOGY

Spaces and species: The Rodrigo Botet Collection (Valencia, Spain) and the palaeoecological relationships of early *Homo sapiens* during their dispersal in the southern cone of South America

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ABSTRACT

In this paper we present the taphonomic analysis of the Rodrigo Botet Collection, an assembly of fossil bones excavated from the Region of the Pampas (Argentina) which display evidence of having been subject to anthropic action. This collection of South American mammals is housed at the Natural Science Museum of Valencia (Spain), and is the most important of its type in Europe. In order to better comprehend the evidence found in this collection a palaeoecological framework was applied. This framework was linked to the relations established between *Homo sapiens* and the native megafauna, which may have implied new forms of niche construction or colonization in South American spaces. The distribution of the different species over the landscape, the general ecological characteristics of these mammals, and the presence of possible competitors were taken into account

RESUMEN

En este trabajo se presenta el análisis tafonómico realizado en la Colección Rodrigo Botet, proveniente de la Región Pampeana (Argentina) donde se hallaron distintos huesos con evidencias de intervención antrópica. Esta colección de mamíferos Sudamericanos se encuentra alojada en el Museo de Ciencias Naturales de Valencia (España) y es la más importante de este tipo en Europa. Un marco paleoecológico fue aplicado a fin de entender la evidencia encontrada. Este se vinculó con las relaciones que *Homo sapiens* estableció con la megafauna nativa y que pudo significar la construcción y/o colonización de nichos en los espacios sudamericanos. Para analizar esta dinámica se tuvo en cuenta la distribución de las diferentes especies en el paisaje, las características ecológicas de estos mamíferos y la posible presencia de competidores. En este contexto, las poblaciones humanas se during the research. In this context we emphasise that human beings behaved as an invasive species in this continent during the first peopling of America. Special attention is also placed on comparing different early human dispersal events in different scenarios. America and Europe are exemplary case studies for making further discoveries on the several anthropic impacts that our species has exerted in different times and spaces.

Keywords: American peopling, megafauna, Pleistocene-Holocene Transition, Pampean Region, Argentina.

habrían comportado como una especie invasora durante el primer poblamiento americano. También se hace un énfasis especial en la importancia de comparar distintas situaciones de dispersiones tempranas en distintos escenarios. En este sentido, América y Europa son excelentes casos de estudio para dar cuenta de los distintos tipos de impacto que nuestra especie realizó en diferentes espacios y tiempos.

Palabras clave: Poblamiento americano, megafauna, Transición Pleistoceno-Holoceno, Región Pampeana, Argentina.

1. INTRODUCTION

The dispersal of *Homo sapiens* in Eurasia and in America has been a challenge for researchers. In both continents, the entry of our species occurred in unique palaeoecological contexts: in Eurasia, there have been pulses of colonization by species of the genus *Homo* since at least the early Pleistocene. They introduced some environmental modifications and, in the last millennium, competed with *Homo sapiens* for the exploitation of resources. This was not the case in America, since *Homo sapiens* was the first and only *Homo* species that thrived in this continent during the late Pleistocene. Specifically, in South America, the human population found a unique assortment of animals, the South American megafauna, that had developed thanks to the relative isolation of the continent during part of the Cenozoic Era until 3 Ma ago (Webb, 1978; Fariña *et al.*, 2013). In both continents, Eurasia and South America, geographical dispersal took place successfully which, as a result, affected the diversity in species and changed their native relationships. Specifically, this paper focuses on presenting how this happened in the Pampas, a nodal sector for the evolution of populations of megafauna and for the dispersal of *Homo sapiens*, since it joins the Brazilian and Guayanian regions and the southernmost part of the continent.

To further explore the matter, we studied the interaction between *Homo sapiens* and megafauna through a series of taphonomic analyses on the items in the Rodrigo Botet Collection at the Natural Science Museum of Valencia (Spain) (Chichkoyan, 2011, 2013; Chichkoyan *et al.*, 2013). This collection is the most important of its kind in Europe and has been kept in Spain since the end of the 19th century. Several fossil bones in this collection were detected to have been subject to human action. In order to analyse these results, a palaeoecological framework was applied. This approach allows for its interpretation from the general perspective of interaction. The resulting aggregate of species in the space, their ecological characteristics, like the fact that they had never before been in contact with humans or their sexual maturity and reproduction strategies and, also, the low interspecific competition among carnivores, might have favoured the creation of new paleoecological relationships, such as niche construction or colonization of those already existent. This could be related to the possible invasive nature (*sensu* Lanata *et al.*, 2008a, b) of *Homo sapiens* during their first dispersal in the Americas, destabilizing in the process of its native trophic chain.

Firstly, we will offer an explanation of the general specifications of our materials and methods and, further on, of the fauna that displayed signs of anthropic action. The following section will describe the results of the analysis. The paper ends with the discussion and conclusions drawn from these findings, integrated into a general overview of the palaeoecological interactions between human beings and megafauna.

2. MATERIALS AND METHODS

The American Southern Cone is a relevant space for the comprehension of the palaeoecological relationships established by humans with other large mammal species. Although South America, especially the Southern Cone, offers plentiful evidence of the interaction between human beings and megafauna, this information is still relative poorly understood (Borrero, 2008, 2009) and has not been integrated to the new general dispersal models of human population for different environments.

The focus here will be placed on the Pampean Region, one of the richest in megamammals during the Pleistocene. The discovery of various mammalian skeletons in this area enabled the creation of a chronostratigraphic sequence for the entire continent (Cione *et al.*, 2009). This region was characterized by an arid and dry weather, with a low vegetation strata and the predominance of open spaces. It is located between 31 degrees and 39 degrees South and is an ecotonal biotope located between two large biogeographical regions: the Brazilian Region to the North and the Patagonic Region to the South. Thus, it has always been influenced by the palaeoenvironmental changes of both regions (Rabassa *et al.*, 2005; Ortiz-Jaureguizar & Cladera, 2006; Gutiérrez & Martínez, 2008; Cione *et al.*, 2009).

South American megafaunal extinction is an issue of great relevance when dealing with these species of native fauna. However, even if it is the subject of an important academic debate, the issue will not be addressed in this paper, for our primary concern is merely to discuss human palaeoecological relationships established during the first peopling of America. A good overview of this debate can be found in Koch & Barnosky (2006), and references therein. In this sense, it is necessary to go beyond the event of extinction itself and elucidate the human migration process through the territory during niche construction. This relates to the modifications that the organism caused in the environment, disturbing or changing the relationships between organisms and bringing about evolutionary change (Odling-Smee *et al.*, 2003). As to further this line of investigation, it is necessary to incorporate archaeological information backed up by evidence provided by palaeoecology, in order to allows us to integrate historical, ecological, taphonomic and geological concepts for the better understanding of life in the past (Wing *et al.*, 1992). Therefore the evidence provided by our research will merge with the palaeoecological characteristics of the native fauna and paleontological and palaeoecological concepts. It is useful to understand the relationships in the faunal population before the irruption of human beings, the expansion of a new species into a novel environment, its interaction with the native species, the influence that it could have exerted on the environment and how it overcame natural barriers (Harding *et al.*, 2006). All these elements apply to the case of *Homo sapiens* in the New World, a *Homo* species with a more flexible capacity for adapting when compared to the last million years of its evolution (Surovell *et al.*, 2005).

In order to further the research on the palaeoecological consequences that humans caused during their dispersal in the American environment, it is necessary not only to consider the information from excavations under stratigraphic control, but also, to gather information from collections housed in different museums. Even though they lack context, this kind of material may provide important information, for they may be analysed by means of new methodologies and theoretical frameworks (Pérez de Micou, 1998; Huster, 2013) and later integrated into different studies carried out in the region. This kind of analysis is fundamentally important to the study of general patterns of human behaviour in the past and their overall relation with the different palaeoregions on a large scale. This is one of the essential objectives of this work of palaeobiological and archaeological research that at the same time also allows interregional comparison (Stiner, 1994; Gamble, 2002). Consequently, the study of this material is a key element for the advancement of current investigations, not only because it minimizes the impact that a campaign of excavation has on the environment, by avoiding the destruction of the sites, but also because the material may be re-evaluated in new studies (Goetze & Mills, 1991; Pérez de Micou, 1998; Pérez *et al.*, 2005; Huster, 2013). In addition, it integrates material into ongoing research carried out in Argentina and the rest of South America but which is kept elsewhere.

These collections are composed of fossil elements that were extracted from non-stratigraphical excavations carried out during the 19th century, when different voyagers undertook journeys to both the Pampean and Patagonian regions (Chichkoyan, 2011). They are composed of different large mammals – over 44 kg in weight – and species of megafauna – over 1,000 kg – and most of them, have never been studied from this perspective, so they may prove an important source of information. Although these 19th century collections lack a precise stratigraphic context, it is possible to obtain chronologies from bones with evidence of human activity, providing reliable evidence and enabling the contextualisation of this interaction. This can be used to generate new research expectations and/or interpretative models that integrate both archaeological and palaeoecological information.

The taphonomic study carried out on the Rodrigo Botet Collection, is an exemplary case study and relevant to this subject (Chichkoyan, 2011, 2013; Chichkoyan *et al.*, 2013). This is the most important collection of South American fossil megafauna in Europe and has been the subject of paleontological studies performed by Boscá y Casanoves, first curator of the collection (Boscá y Casanoves, 1899, 1902, 1917, 1919, 1921, 1923a, b; among others). It was donated to the Museum of Valencia by Rodrigo Botet at the end of the 19th Century and is the result of non-systematic excavations executed by Enrique de Carles in the north-eastern sector of the Pampean Region: Samborombón Bay, and different zones near the rivers of La Plata, Salado, and Samborombón (Fig. 1). The collection is composed of 29 genera and 66 species, such as *Smilodon*, Mylodontidae, Glyptodonts, and Notoungulata, among others. It was part of the first Paleontological Museum in Europe and it is characterized by the quantity and diversity of material. It also includes important human remains, such as the “Samborombón skeleton”, used by Ameghino to discuss when the first American peopling took place (Martel San Gil & Aguirre Enríquez, 1964; Salinas Jaques, 2001; Catalá Gorges, 2004; Belinchón *et al.*, 2009).

The bones of which this collection is composed were analysed by means of taphonomic methodologies. Studies on bone surfaces are useful not only to find and describe anthropic cut marks, but also to discover paleoenvironmental and ecological information (Behrensmeyer & Kidwell, 1985; Bonnichsen, 1989; Bello & Soglio, 2008). The

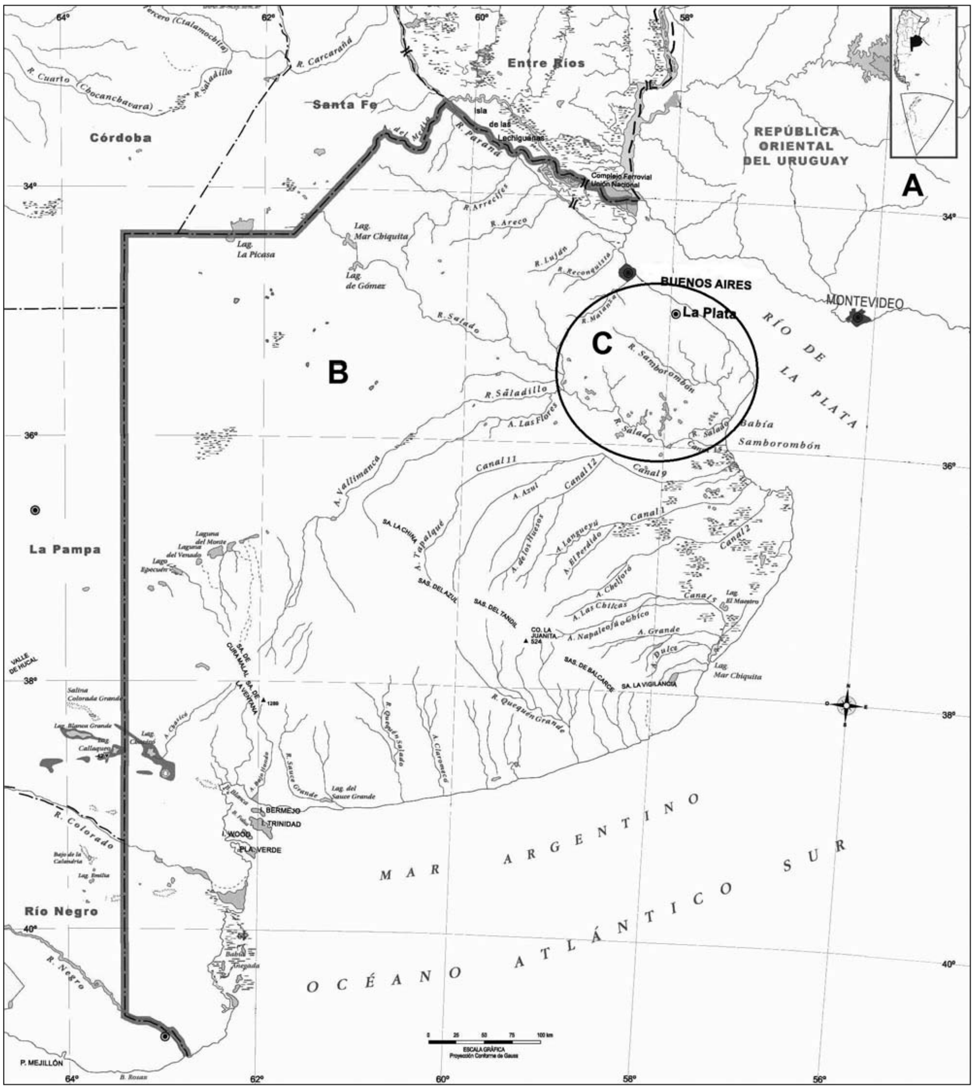

Figure 1. Geographical setting. A) Argentina. B) Buenos Aires Province. C) General provenance of the Rodrigo Botet Collection. (Modify from IGM).

traces left on bones can be linked to their causal agency and, in this way, can be used to determine the element that brought them about (Gifford-Gonzalez, 1991; Lyman, 1994). This can be put into practice not only in the case of human-made marks, but also for imprints that were caused by other natural elements (Binford, 1981; Behrensmeyer, 1991; Lyman, 1994; Coard, 1999; Fernández López, 2000; Domínguez-Rodrigo *et al.*, 2009). Therefore, the taphonomic history of the bones housed in the museums, which lack any sedimentary context, may be interpreted.

For this work, 11,466 bones over 2 cm long, with their cortical surface in an adequate state of preservation were selected. Firstly, they were analysed with the aid of magnifying glasses and stereoscopic microscopes

– Olympus SZ-PT – in order to differentiate any bone presenting human action from those affected by eroding agents such as carnivores, roots, weathering, trampling, wind or fluvial transport and any other natural factor (details in Chichkoyan, 2011). Currently, new studies and new methodologies are being applied on the material. It has been re-viewed with the aid of microscopes equipped with 6.4, 16 and 40X magnification lenses – Wild Heerbrugg M3B –, and other processing methodologies will also be applied in the future in order to retrieve the maximum information possible from the sample or improve previous results derived from the collection.

However, the material will be presented in the same fashion as in previous works (Chichkoyan, 2011, 2013; Chichkoyan *et al.*, 2013). Only bones that display signs of human intervention and have been assigned to a taxonomic group are presented in this study. Although other researchers describe and classify the cut marks (Walker & Long, 1977; Abe *et al.*, 2002; Bello & Soglio, 2008; Bello *et al.*, 2009; De Juana, 2010; among others) we considered that any bone that displayed V-shaped markings in areas consistent with the process of butchering, and which had occurred prior to any other type of post-depositional process, such as weathering, trampling, deterioration by the action of roots, manganese stains or other eroding factors like water or wind, would have been subject to anthropic action (Binford, 1981; Shipman, 1981; Lyman, 1994; Bunn, 1999; Fernández López, 2000; Domínguez-Rodrigo *et al.*, 2009). Several elements of the collection that had been subject to human action could be the result of intentional patterns created as a result of anthropic polish. Markings were described in terms of orientation, general position on the bone, and their relative position with other marks derived from non-human activity, plus any other information considered relevant, not only of the mark itself but also of its surrounding context. This allowed for the understanding of the taphonomic history of the different bones with cut marks. In addition, the species on which these were found offers information on the ecological characteristics, chronology and distribution of these populations. The relative position of the markings on the bone grants insight on the general butchering process and stages of the animal's exploitation by human beings.

In the following section, the general characteristics of the species that have been subject to human intervention in the Rodrigo Botet Collection are described. And later on, the results of the analyses will be presented and discussed.

3. SYSTEMATICS

Phylum CHORDATA Bateson, 1885
Class MAMMALIA Linnaeus, 1758
Order XENARTHRA Cope, 1889
Family **Mylodontidae** Gill, 1872

Mylodons (Fig. 2) are part of the Order Xenarthra, which originated in South America. This order is divided into Cingulata – an explanation will be offered later on – and Pilosa, which is in turn divided into Vermilingua or anteaters and the Folivora or Tardigrada, better known as sloths (Vizcaíno *et al.*, 2012). Mylodontidae is a member of the latter group along with three other families – Megalonychidae, Nothrotheiidae and Megatheriidae –

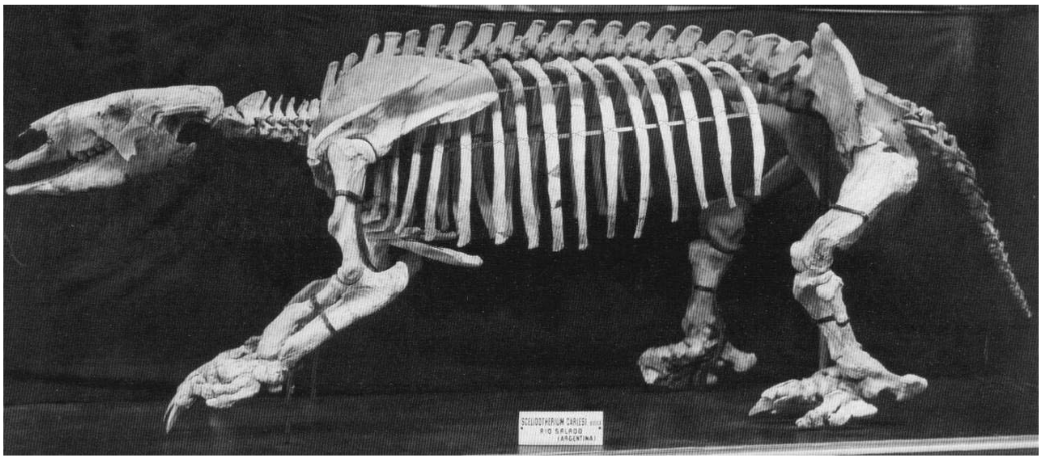

Figure 2. *Mylodon* (*S. carlesi*) from the Rodrigo Botet Collection (from Belinchón *et al.*, 2009).

(Fariña *et al.*, 2013). Mylodontidae in turn is composed by two clades: Mylodontinae – the *Glossotherium*, *Mylodon* and *Lestodon* genera – and Scelidotheriinae – the *Scelidotherium*, *Scelidodon*, *Catyonyx* and *Valgipes* genera – (Fariña *et al.*, 2013). This family is comprised of megamammals that are over 1 tonne in body mass, although some species such as *Scelidotherium leptocephalum* were smaller, with an average weight of 633 kg (Fariña *et al.*, 1998, 2013); in other cases, like *Glossotherium robustum,* some specimens weighed less than 1 tonne, which is explained by sexual dimorphism in the species (Christiansen & Fariña, 2003; Fariña *et al.*, 2013). This group was adapted to live in cold and dry environments, such as the Pampean Region during the Pleistocene. During this period of time savannah-grassland habitats developed, which allowed for the diversification of this family. It became extinct by the early Holocene, after a change in the climate conditions (Deschamps, 2005; Ortiz-Jaureguizar & Cladera, 2006; Prevosti & Vizcaíno, 2006; Miño-Boilini & Carlini, 2009). These animals had a set of molariform, hypsodont teeth, intimately related to their different consumption habits (Paula de Couto, 1979; Fariña *et al.*, 2013).

Phylum CHORDATA Bateson, 1885
Class MAMMALIA Linnaeus, 1758
Order XENARTHRA Cope, 1889
Family **Megatheriinae** Owen, 1842
Genus *Megatherium* Cuvier, 1796

This group, member of Tardigrada, is related to the Mylodontidae but is characterized by its enormity. In fact, the largest specimens belong to this clade, such as the well-known *Megatherium americanun*, which could weigh over 4 tonnes (Fig. 3). As was the case with Mylodons, this group also thrived in open spaces and was typical of the Pampean Region, although it expanded as far as the region of Ecuador, by using the Andes as a corridor as did many other species (Pujos, 2008). They developed an herbivorous diet which was probably complemented with animal protein derived from scavenging or maybe even predatory activity (Fariña, 1996; Fariña & Blanco, 1996; Pujos, 2008). This animal was typical of the Pleistocene period and was especially abundant during the Lujanian period (Brandoni *et al.*, 2008; Pujos, 2008).

Phylum CHORDATA Bateson, 1885
Class MAMMALIA Linnaeus, 1758
Order XENARTHRA Cope, 1889
Family **Glyptodontidae** Burmeister, 1879
Genus *Neosclerocalyptus* Paula Couto, 1957

In previous research, the provenance of the material that belonged to this family – an osteoderm – could be determined only as far as family level. In this second round of revision, we were able to identify the genus it belongs to. The families Glyptodontidae and Dasipodidae – which are the following to be explained – are part of the Cingulata. Although their general appearance differs from that of the Tardigrada, the presence of an extra joint in their vertebrae and their low basal metabolism are a characteristic feature of this order; and in addition, they are also K-selected animals when it comes to reproduction strategy (Gaudin, 1999; McDonald, 2005; Fariña *et al.*, 2013). A remarkable feature of these animals was that they were covered with a hard shell that protected their entire body and part of their extremities. This exoskeleton was characterized by its fixed osteoderms (Fig. 4). Glyptodons also presented a merged spinal cord to support the weight of their shell (Gaudin, 1999). The *Neosclerocalyptus* sp., in turn belonged to the subfamily Hoplophorinae, and was

Figure 3. *Megatherium americanum* currently exhibited at the Natural Science Museum of Valencia (from Chichkoyan, 2011).

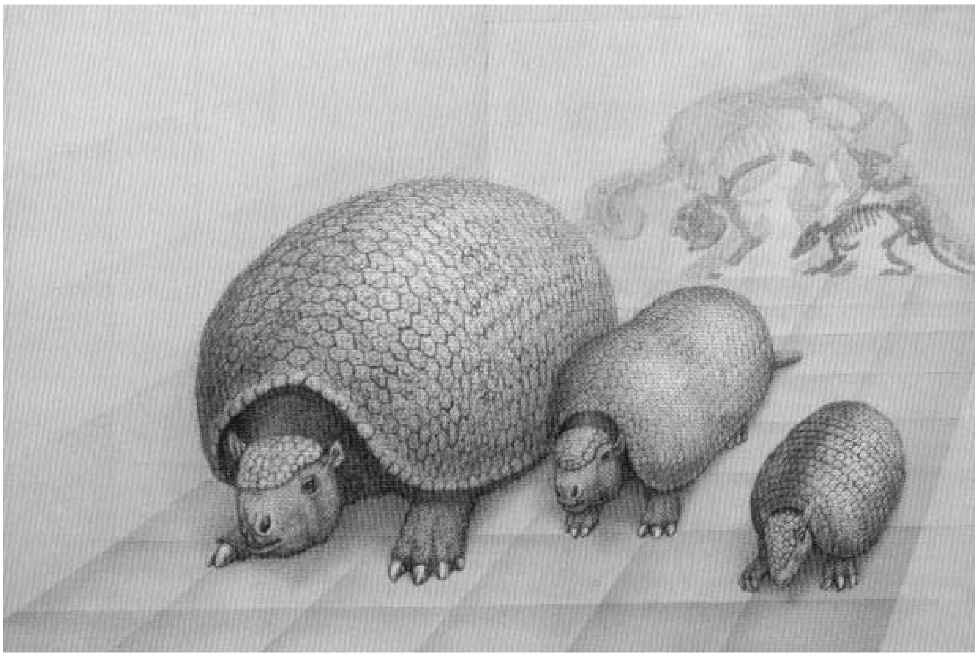

Figure 4. Several reconstructions of Cingulata, by Mauricio Antón. From left to right: *Glyptodon*, *Neosclerocalyptus* and *Eutatus* (from Belinchón *et al.*, 2009).

one of the smallest species of the Family Glyptodontidae (Fariña *et al.*, 2013). This family survived until the early Holocene and some species were part of human exploitation activities in the Pampean region, such as the *Doedicurus clavicaudatus*, that was excavated from La Moderna (Gutiérrez & Martínez, 2008; Gutiérrez *et al.*, 2010; Soibelzon *et al.*, 2012).

Phylum CHORDATA Bateson, 1885
Class MAMMALIA Linnaeus, 1758
Order XENARTHRA Cope, 1889
Family **Dasipodidae** Bonaparte, 1838
Genus *Eutatus* Gervais, 1867

Eutatus is also a member of the Cingulata, and belonged to the Family Dasipodidae (Vizcaíno & Bargo, 1998). These members of the group are characterized by their smaller size, 50 kg in body mass, and mobile osteoderms (Vizcaíno & Bargo, 1998; Krmpotic *et al.*, 2009; Fariña *et al.*, 2013). In contrast with other members of this order, it is suggested that this family was characterized by an R-select reproduction strategy (McDonald, 2005). Although its body size does not qualify for it to be considered megafauna, this species belongs to the Order Xenarthra, of which there is anthropic evidence, and survived until recent times, as opposed to the rest of the megamammals, that were hardly able to survive the Pleistocene-Holocene boundary (Krmpotic *et al.*, 2009; Gutiérrez *et al.*, 2010) (Fig. 4).

Phylum CHORDATA Bateson, 1885
Class MAMMALIA Linnaeus, 1758
Order LITOPTERNA Ameghino, 1889
Family **Machraucheniidae** Gill, 1872
Genus *Machrauchenia* Owen, 1839

Macrauchenia patachonica Owen, 1839

Along with the Order Xenarthra, Litopterna is a group native to South America. This order was very diverse, as a result of its extensive evolution that dates back to the late Paleocene (Vizcaíno *et al.*, 2012). *Macrauchenia patachonica* weighed over 1 tonne and the shape of its body was similar to that of a camel or a horse (Fariña *et al.*, 1998, 2005) (Fig. 5). It emerged during the Ensenadan and Lujanian ages and was typical of arid climates (Bond *et al.*, 1995). Although its size was a natural defence against predatory attacks, it has been suggested that this animal also adopted swerving and dodging strategies to avoid falling prey to predators (Fariña *et al.*, 2005).

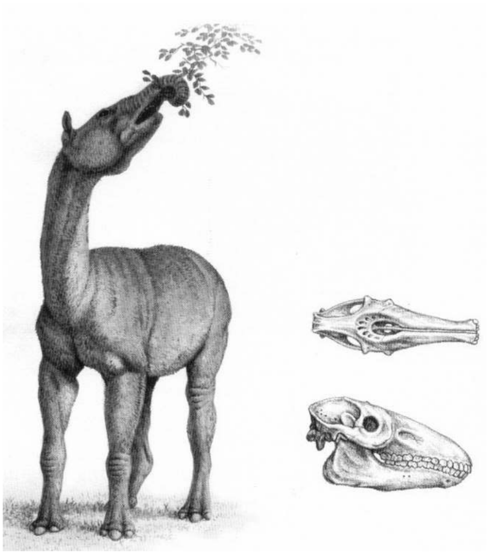

Figure 5. *Macrauchenia patachonica* by Mauricio Antón (from Belinchón *et al.*, 2009).

4. RESULTS

Ten elements from different species displayed traces of different types of anthropic action (Chichkoyan, 2011): four elements belonged to *Mylodon*, one rib to *Megatherium* sp., another two ribs to *Macrauchenia patachonica* and three osteoderms, one of them belonging to *Neosclerocalyptus* sp. and another two to *Eutatus* sp. Thanks to the new technologies in use, one of the bones of *Macrauchenia patachonica* previously reported to bear cut marks, is currently under process of study in order to determine the origin of the marks it display. The number of markings and their distribution can be viewed in Table 1.

The diversity of the species evidencing human intervention in the collection is a very good sample of the fauna native to South America that once lived in the region and disappeared upon human arrival – with the only exception of *Eutatus* sp., which survived until more recent times (Chichkoyan, 2011, 2013; Chichkoyan *et al.*, 2013). This fauna was very diverse throughout the Quaternary. The Ensenadan and Bonarean ages – during the early and middle Pleistocene – show an abundant and assorted fauna, for both extant and extinct species were detected in the biostratigraphical units. However, at the end of the Lujanian age – 130,000 to 7,000 B.P. – especially between 21,000 to 10,000 B.P., at least 52 species and 38 genera went extinct in South America: particularly, large animals and megamammals (Lessa & Fariña, 1996; Lessa *et al.*, 1997; Cione *et al.*, 2009). This coincided with the rise in temperature and the wetter conditions that followed the Last Glacial Maximum – 20,000/16,000 B.P. (Rabassa *et al.*, 2005) – which was, in general terms, essentially similar to the interglacial periods that characterized the Pleistocene.

Table 1. Material with anthropic traces found in the Rodrigo Botet Collection.

SPECIES	TYPE OF BONE	SIZE (mm)		
		length	width	high
Mylodontidae	Rib	105	10	35
Mylodontidae	Scapula	180	40	70
Mylodontidae	Cervical vertebrae	105	140	95
Mylodontidae	Metatarsal	30	35	95
Megatherium sp.	Rib	1000	55	70
Macrauchenia patachonica	Rib	480	15	40
Macrauchenia patachonica	Rib	460	15	30
Neosclerocalyptus sp.	Osteoderm	20	10	20
Eutatus sp.	Osteoderm	15	5	10
Eutatus sp.	Osteoderm	15	5	15

With regard to the species that display anthropic action, we have noticed that out of all the groups that present anthropic cut marks, marks on the Family Mylodontidae are the most abundant in the collection; the bones bearing marks include: one rib fragment, one scapula, a fragmented cervical vertebrae and a metatarsal. The rib shows three transversal cut marks in the shaft sector; it has some manganese stains along its entire surface (Fig. 6). The scapula has one transversally oriented cut mark 11 cm from the glenoid cavity (Fig. 7). This element was highly affected by taphonomic agents such as roots and trampling, but the resulting imprints were left over the cut mark, indicating that the human activity occurred prior to these agents affecting the bone. The same was observed when examining the cervical vertebrae (Fig. 8), which had cut marks on its dorsal surface that were inflicted before the occurrence of trampling and manganese stains. The last of the Mylodontidae items that displayed signs of human intervention was a metatarsal (Fig. 9). Its level of preservation was quite good and the cut marks were identified on its distal epiphysis. An insect hole could also be observed in some of these marks, indicating that the cut marks happened prior to its deposition (Chichkoyan, 2011; Chichkoyan *et al.*, 2013). The amount of cut marks in Mylodontidae bones may be related to the fact that this type of animal was the most abundantly identified in the collection – N: 1.124 or 25, 12 % of the material identified. However, it could also be related to its characteristic

Figure 6. Mylodontidae rib with anthropic cut marks. Detail of the middle incision viewed with 40X magnification factor.

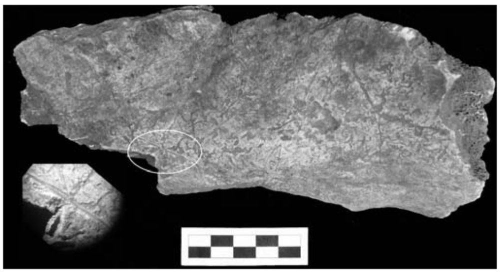

Figure 7. Mylodontidae scapulae with anthropic cut marks. Detailed view, 6.4X magnification factor.

Figure 8. Mylodontidae cervical vertebrae with anthropic cut marks. The two surfaces where they were detected are shown: **1)** From below: a general view of the incision. From above: Detailed view. 40X magnification factor. **2)** From above: Distribution of the cut marks over the right dorsal tuberculae. From below: Detailed view, 6.4X magnification factor.

Figure 9. Mylodontidae metatarsal presenting anthropic cut marks. Close up view of the distal epiphysis and detailed view, 16X magnification factor.

distribution, since it was one of the most abundant taxa in the Pampean region, as we have mentioned previously.

Another fossil with cut marks, which also belongs to the Order Xenarthra, was a rib belonging to *Megatherium* sp. In this case, the first time it was studied, we detected that the bone had four cut marks in its distal sector with some original sediment still attached to part of the cut mark cavity. Three of them are in the shape of an inverted N and the other is spaced apart from these. This element had been weathered and is missing part of its cortical tissue; it also presents some old restoration work carried out at the museum. Other materials belonging to this order which have been subject to human activity were osteoderms of *Neosclerocalyptus* sp. and *Eutatus*. They present what may probably be anthropic polish on their sides, although one of them was also affected by fluvial erosion that rounded the item's shape. In the case of the osteoderm of *Neosclerocalyptus* sp., it shows trails of manganese stains along two contiguous surfaces, which would indicate that this agent developed after human intervention. In addition striations derived from polishing were also detected (Fig. 10) (Chichkoyan, 2011; Chichkoyan *et al.*, 2013).

Finally, cut marks were identified on two ribs belonging to *Macrauchenia patachonica*. One set of marks were near the distal side of the rib, and the other was under the old restoration work (Fig. 11), however, given the general pattern of these markings it is possible they were the result of human intervention. The other rib that was originally presented is currently being studied.

We also observed the skeletal elements of specimens that presented anthropic action. Regarding the chances of detecting this kind of evidence, it is generally assumed that larger animals have reduced chances of tools coming into contact with their skeleton (Borrero, 2001; Pérez *et al.*, 2005; Borrero & Martín, 2012) as is the case for big mammals such as Proboscideans (Gaudzinski *et al.*, 2005) although the authors also point out that anthropic marks can also be detected in rhinoceros. In Áridos 2, for example, a middle Pleistocene site from Spain, bones belonging to elephants were found to display cut marks (Yravedra *et al.*, 2010). Therefore, the record of cut marks on skeletal elements is intimately related to way in which the animal was processed. In our case, most of the material corresponds to parts of the axial skeleton: four ribs and one cervical vertebrae. This could be linked to the fact that these parts are closer to the skin and a tool will more readily make contact with the bone. However, only two items of the appendicular skeleton were found to possess cut marks: the scapula and the metatarsal. The larger size of the appendicular skeleton must have hampered transporting the whole limb, and therefore, it seems more probable that only portions of meat were extracted. As a result there would be fewer marks present in these parts, and also, given the amount of muscles present, it is less probable that lithic tools would touch the bone.

Figure 10. Glyptodontidae osteoderm. From above: detailed view of two surfaces where continuous manganese stains are visible. From below: Detailed view of the area where the parallel striations resulting from polish were detected. 40X magnification factor.

Figure 11. Rib of *Macrauchenia patachonica*. **1)** Detailed view of the cut mark beneath the restoration work and **2)** Possible cut mark on its the distal section. 40X magnification factor.

5. DISCUSSION

The cut marks on the material of the Rodrigo Botet Collection are good indication of the various large animals and megamammals that were consumed by human beings during their first dispersal in the Pampean Region. Although other animals could have well been the base of human diet, such as the *Lama guanicoe* (Politis *et al.*, 2004; Cione *et al.*, 2009), this does not imply that other species, such as the megafauna mentioned in this paper, were not consumed. There is enough evidence supporting that human beings have exploited megamammals as a natural resource in the past.

However, the possibility that human beings only scavenged meat from animals killed by other carnivores or other natural causes must still be taken into consideration, especially if we bear in mind these events happened during a moment of paleoenvironmental change. An interesting fact related to this option is that carnivores in the ecological scenario of the Pampean region had a low predatory activity (Fariña, 1996), although they may have been an important factor in other regions such as the Patagonia (Borrero & Martín, 2012) or Chile (López Mendoza, 2007). This is consistent with fact that there were large quantities of herbivorous biomass and that Carnivora made a late arrival into the environment. The latter occurred in the late Pliocene when the two Americas were united by the Isthmus of Panama (Lessa & Fariña, 1996; Soibelzon & Prevosti, 2008; Woodburne, 2010). Although the imbalance hypothesis has been reassessed, and a more balanced ecological scenario has been suggested for the Pampean region, the fact remains that only *Smilodon populator* and eventually *Panthera onca*, *Puma concolor* and *Canis nehringi* were capable of predation on megammamals (Prevosti & Vizcaíno, 2006) and it is also probable that *Megatheium americanum* could have had access to animal proteins, although this would have occurred as a result of its activity as an opportunistic scavenger (Fariña, 1996; Fariña & Blanco, 1996). The size of these animals (Lessa & Fariña, 1996) rendered them inaccessible to carnivores, the same way other large animals are inaccessible to predators in other environments around the globe. Lions, however, occasionally kill large prey, such as giraffes, buffalos or rhinoceros. Regardless, for this to happen, they must hunt cooperatively given the strain of bringing large prey down (Schaller, 1972; Bertram, 1979; Hayward & Kerley, 2005). Therefore, the chances of human beings scavenging animals killed by other carnivores are reduced. It is also relevant to note that until now, no evidence of attacks by other carnivores could be found on any of the items of the collection. However, it is also important to consider that the sudden arrival of *Homo sapiens* could have significantly reduced the availability of prey for the native carnivores and therefore had a negative effect on their survival (Cione *et al.*, 2009). The great capacity to modify their environment and adapt, plus the ability to produce weapons, rendered *Homo sapiens* the most formidable predator for both herbivores and carnivores alike, either directly or indirectly. However, another possibility is that humans benefitted from animals that had perished due to natural causes. Finding archaeological evidence of this is considerably more complicated since the material we studied lacks context.

Nevertheless, we may provide arguments that have been put forward to help analyse the issue. Generally speaking, it is always complicated to prove a certain animal was being hunted by human beings in the absence of direct evidence, such as a piece of lithic lodged in a bone of an animal, like the one found at Taima Taima in Venezuela (Borrero, 2009). We consider that this idea is supported by the information drawn from several stratigraphically controlled sites in the northern and southern Pampean region, which indicates human beings directly predated on megafauna. Sites such as La Moderna, Campo Laborde, Paso Otero or Cueva Tixi, in the South, have revealed that activities took place which hint towards the species *Doedicurus clavicaudatus*, *Megatherim americanum, Equus neogeus*, *Hippidion* sp. or *Eutatus seguini* being accessible to human beings. In the first of these sites, elements pertaining to *Doedicurus clavicaudatus* were associated with quartz tools. The animal's mandible, its axial parts, and its carapace had not been removed from the site grounds. In Campo Laborde, a rib belonging to *Megatherium americanum* displaying cut marks was found, and meat and viscera of the animal had seemingly been transported elsewhere, away from the carcass of the animal. In addition, the bones of megafauna had been used as fuel for kindling, for burnt bones were found at the site Paso Otero 5. In Cueva Tixi, three phalanx bones and six osteoderms belonging to *Eutatus seguini* had been burnt and found near what used to be a fireplace (Mazzanti & Quintana, 1997; Politis & Gutiérrez, 1998; Gutiérrez & Martínez, 2008; Politis & Messineo, 2008). Other important findings related to human-megafauna interaction have also been reported from Arroyo del Vizcaíno, Uruguay, located in the northern sector of the region. Here a non-contextualized clavicle belonging to *Lestodon* displayed cut marks as the result of human activity. In addition, several other bones from stratigraphically controlled excavations also presented several types of incisions (Arribas *et al*., 2001; Fariña, 2002; Fariña & Castilla, 2007; Fariña *et al*., 2014). The anatomic positions of the cut marks on fragments of the animal's skeleton seem to indicate that human beings had direct access to different types of megamammals.

In this particular case, the information drawn from the analysis of the markings reveals that some elements are consistent with the first stages in animal processing proposed by Binford (1981). Even though this model is based on butchering procedures for medium-sized animals, the author does point out that the basic patterns of dismemberment are common for most animals since these procedures depend on the generalised anatomy of the skeleton. While the animals referred to in this work are larger in size, the general procedures for the separation of the axial and appendicular parts of the body are useful to understand how butchering of the animal could have taken place. The presence of cut marks on the cervical vertebrae, for example, is related to the process of separating the body from the skull, one of the first actions carried out during the processing of the animal (Binford, 1981). In addition, the evisceration of the carcass and skinning is also one of the first stages of the process (Binford, 1981). These actions usually cause marks on the ribs, such as those detected on several ribs of Mylodon, *Macrauchenia patachonica* and *Megatherium* sp. in the Rodrigo Botet Collection. The polishing we noticed on the osteoderms of Glyptodontidae and *Eutatus* is also worth discussing. This kind of activity must have been carried out on fresh material; if the osteoderm had been polished after it had fossilised, the lack of collagen in the item would have caused it to break. The rest of the material in the Rodrigo Botet Collection subject to human activity is harder to relate to any other particular stage of the processing of an animal; although the markings on the scapula belonging to Mylodontidae, since they are located close to the joint, could be attributed to the action of separating the appendicular hind limb from the rest of the body, which could also be consistent with the stages of dismemberment proposed by Binford (1981). Even though affirming that *Homo sapiens* had had direct access to these species of megafauna might be premature at this stage, evidence suggests that human beings were actually present from the very first stages of the process of butchering (Chichkoyan, 2011, 2013; Chichkoyan *et al*., 2013). Since the specimens lack any context, elucidating whether the animal was hunted or scavenged after a natural death is still complicated.

Having reached this point, it becomes relevant to relate this information to the paleoecological context of these species and the environment they inhabited. This will contextualize and aid us as we interpret the material in the Rodrigo Botet Collection in the context of different ecological settings. This information was provided by several research papers that grant us insight on how these species lived in the past. Therefore, non-contextualized cut marks can be integrated into a general framework of interaction between human beings and native fauna. Two issues are worth highlighting: on the one hand, the general ecological characteristics of the native fauna, such as their naivety in relationship with an invader species and their reproduction strategy; and on the other hand, the distribution of the species over the terrain.

Firstly, it is necessary to note that none these of species had ever come into contact with human predation previously (Cione *et al*., 2009). The lack of contact with an invading species contributes to the success of the invasion and destabilizes the established trophic chain (Kondoh, 2006). Given the relatively late arrival of our species to the continent, these species were not prepared to survive predation by the hand of a super social, technological and carnivorous primate such as *Homo sapiens*. The several taxa that indeed did survive the presence of human beings were those adapted to survive in areas that were not accessible to humans, such as wetlands, mountainous areas, or forests (Cione *et al.*, 2009). The same circumstance still applies to the distribution of proboscideans nowadays that inhabit tropical forest biomes in Africa and Asia, areas where human populations hardly ever settle (Surovell *et al.*, 2005). Other species with speedier reproductive cycles, such as guanacos (*Lama guanicoe*) and smaller species have been able to survive over time (Cione *et al.*, 2009). Consequently, the lack of natural defences against a technologically superior predator such as *Homo sapiens*, could have favoured the decline of these slow and naive populations of megafauna.

Secondly, the rate at with which these animals became extinct varied in accordance to the speed of their sexual development and reproductive strategy (Cione *et al.*, 2009). Megafauna, such as *Megatherium* sp., Mylodons, or *Macrauchenia patachonica* followed K-selected reproductive strategies or had low basal metabolisms, this meant they had fewer offspring per individual (Johnson, 2002; McDonald, 2005; Cione *et al.*, 2009; Souza Lima-Ribeiro & Felizola Diniz-Filho, 2013). In this sense sporadic killings of members of these species would have negatively affected birth rates for its entire population, let alone continuous depredation. Consequently, this meant several taxa would become extinct in a relatively short time period, as is the case of those species that barely passed the Pleistocene-Holocene boundary. Their situation differs from that of *Eutatus*, for example, which due to its great reproductive capability (McDonald, 2005) and plentiful numbers, survived until more recent times (Krmpotic *et al.*, 2009). These circumstances also applied to other smaller mammals, such as *Lama guanicoe* (Cione *et al.*, 2009). Material belonging to genus *Eutatus* other than that of the collection also evidence anthropic action, for example the material found in the depths of the Cueva Tixi (Mazzanti & Quintana, 1997).

The distribution of these animals over the terrain must also be discussed and, although additional information is still required as to gain full understanding of their distribution, some insight on interesting issues has been gained this work of research and other related publications. Given the evidence collected from several Pampean sites and the evidence gathered during the analysis of the Rodrigo Botet Collection, we may suggest that the population density of these species in this region must have been higher than that of, for example, the Patagonia. Altogether, migrations, distribution, and population density must have been dependent on climatic forces, among other factors (Bennet & Provan, 2008) and caused the differential spreading of the species. In this case, the Pampean Region, from where the Rodrigo Botet Collection originates, may have functioned as an shelter area (Bennett & Provan, 2008) where these animals could have converged due to the cold and dry climatic conditions that prevailed throughout of the Pleistocene (Cione *et al.*, 2009). During this period of time, climatic fluctuations influenced the expansion and dwindling of the native populations of fauna, but never caused the total extinction of taxa (Cione *et al.*, 2009). Consequently, their numbers must have been less plentiful when *Homo sapiens* arrived, their population being denser in the more adequate areas for their survival. In addition to fewer species being present throughout the terrain, a new and unique, technologically superior predator such as *Homo sapiens* was added to the equation. Additionally, this uneven distribution may have caused heterogeneous dispersal among regions and consequently the differential access of human beings to them.

Therefore several variables influenced the development of the new palaeoecological relationships caused by the novel presence of *Homo sapiens* (Martínez *et al.*, 2013). New approaches on the subject consider the arrival of *Homo sapiens* in America a “species invasion” (*sensu* Lanata *et al.*, 2008a, b; Lanata, 2011) since they focus on the high demographic levels of human dispersal in different environments. This is related to the distribution of available resources, which must have created a hierarchy of spaces. Thus, they would have influenced the dynamics of their dispersal, resulting in “hot and cold spots” (Smith *et al.*, 2011). Palaeoecological guidelines relate these variable resources to different scenarios of niche construction or colonization. If these modifications are persistent throughout a certain period of time, they could bring about evolutionary change during the lifespan of the species (Odling-Smee *et al.*, 2003). In this sense, the colonization of South American environments by *Homo sapiens* might have been an important factor in the destabilisation of the natural adaptations that the native prehistoric fauna had developed to face the climatic oscillation typical of the Pleistocene (Cione *et al.*, 2009; Martínez *et al.*, 2013). This would have meant that humans had occupied, displaced, and created new positions of predation in the trophic chain, and developed new forms of niche construction or colonization. Simultaneously, this type of activity probably brought about the extinction of certain taxa both directly and indirectly (Cione *et al.*, 2009; Martínez *et al.*, 2013) for they altered the established palaeoecological relationships. The consequences of the invasion by *Homo sapiens* varied from area to area, and several factors have to be taken into account in order to fully comprehend this process. In this study, we took into consideration the distribution of the different species over the terrain, the ecological characteristics of the megafauna, such as the K-selected strategies of reproduction and their vulnerability before the novel presence of a highly superior predator like *Homo sapiens*, or the low level of competition with other carnivores. The predation on a native fauna with these characteristics would have affected the ability for survival of the population of megafaunal species and this implies new forms of niche construction.

In more general terms, the influence that human presence exerted on the prehistoric native fauna in South America can be considered part of the Sixth Great Extinction (Molina, 2008). Although this event is geologically recent and specific to mammals and megafauna (Molina, 2008; Femias Gual & Colino Polo, 2011), it has been thoroughly studied since it is intimately related to the arrival of *Homo sapiens* and anthropic activity, which was highly destructive for the environment (Molina, 2008; Hortolà & Martinez-Navarro, 2012). Consequently, it is important to advance in an interdisciplinary line of research that contemplates the dispersal of *Homo sapiens* in different environments as a complex process and the various consequences that this must have brought about. America and Europe are excellent case studies, especially the Southern Cone of South America and the Iberian Peninsula. These are two regions characterized as being the last portion of a larger continental mass to be colonized by human beings during their initial dispersion. However, the first takes place in a latitudinal direction and is located in the Southern Hemisphere whilst the second extends in a longitudinal fashion and occurred in the Northern Hemisphere. This implies that the first arrivals of *Homo sapiens* in both continents occurred in a context of generalized palaeoenvironmental diversity. Ensuing work will offer information on the chronologies of the material that was presented in this paper. Other techniques for the study of the material are and will continue to be applied in order to detect cut marks and this new information will improve the results obtained so far. These will also reveal evidence in other specimens for the better understanding of the first dispersal of human beings and their impact on both continents.

6. CONCLUSIONS

The findings drawn from the analysis of the Rodrigo Botet Collection and their integration with a palaeocological theoretical framework support the notion that human beings colonized different geographic and palaeoecological zones during the first peopling of America. Some of them, such as the Pampean Region, would have turned into a shelter zone for the survival of megamammals throughout the Pleistocene. This would have allowed significant human predation on the native fauna, which was affected by the palaeoenvironmental changes of this period (Cione *et al.*, 2009). Thus, the irruption of *Homo sapiens* in the region could have disrupted the natural state of equilibrium in the ecosystem. This can be interpreted as a phenomenon of “species invasion” (*sensu* Lanata *et al.*, 2008a, b; Lanata, 2011) where, in the context of fast dispersion, several processes of niche construction or colonization would have taken place due to the new palaeoecological relationships established by the arrival of *Homo sapiens*.

This paper is just an example of the several interdisciplinary studies that are being conducted in order to understand the dispersal of *Homo* spp. in different spaces. The Southern Cone of South America is an example of how our species has altered native palaeoenvironments. In Europe, other scenarios might have occurred since the early arrival of several species of *Homo* spp. The final invasion of *Homo sapiens* – which has also been characterized as an invasive species in this palaeolandscape – must have destabilised the structural relations among these first *Homo* species and the rest of the populations of fauna, resulting in the loss of biodiversity and extinction of several species, including *Homo neandertalensis* (Hortolà & Martinez-Navarro, 2012). It is important to study in detail both continents as case studies, where different situations developed, and thereby understand the impact caused by human beings in different spaces throughout time.

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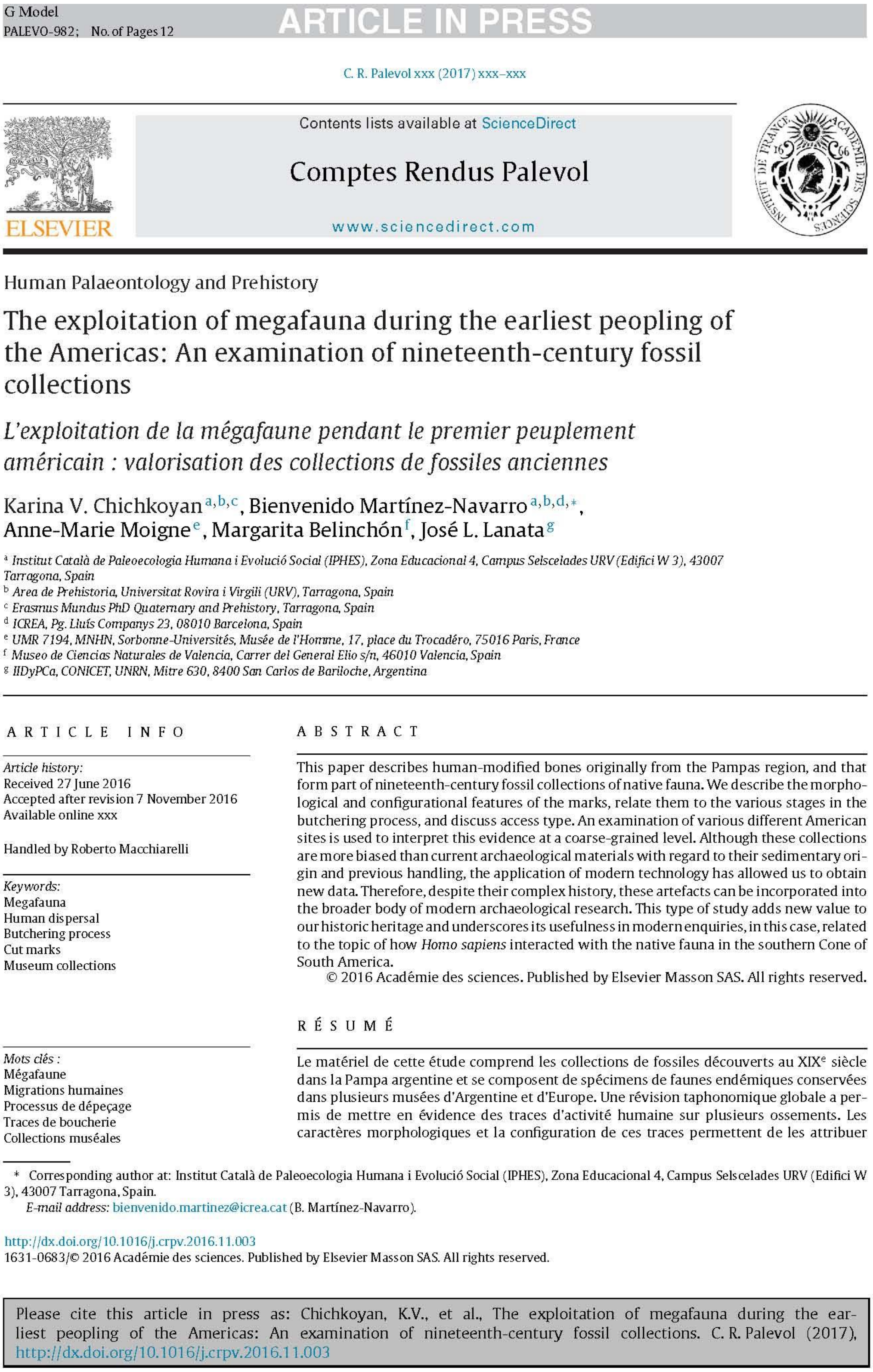
5.3.2. THE EXPLOITATION OF MEGAFAUNA DURING THE EARLIEST PEOPLING OF THE AMERICAS: AN EXAMINATION OF NINETEENTH-CENTURY FOSSIL COLLECTIONS (COMPUTS RENDUS PALEVOL)



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Human Palaeontology and Prehistory

The exploitation of megafauna during the earliest peopling of the Americas: An examination of nineteenth-century fossil collections

L'exploitation de la mégafaune pendant le premier peuplement américain : valorisation des collections de fossiles anciennes

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ABSTRACT

This paper describes human-modified bones originally from the Pampas region, and that form part of nineteenth-century fossil collections of native fauna. We describe the morphological and configurational features of the marks, relate them to the various stages in the butchering process, and discuss access type. An examination of various different American sites is used to interpret this evidence at a coarse-grained level. Although these collections are more biased than current archaeological materials with regard to their sedimentary origin and previous handling, the application of modern technology has allowed us to obtain new data. Therefore, despite their complex history, these artefacts can be incorporated into the broader body of modern archaeological research. This type of study adds new value to our historic heritage and underscores its usefulness in modern enquiries, in this case, related to the topic of how *Homo sapiens* interacted with the native fauna in the southern Cone of South America.

Mots clés :
Mégafaune
Migrations humaines
Processus de dépeçage
Traces de boucherie
Collections muséales

RÉSUMÉ

Le matériel de cette étude comprend les collections de fossiles découverts au XIXᵉ siècle dans la Pampa argentine et se composent de spécimens de faunes endémiques conservées dans plusieurs musées d'Argentine et d'Europe. Une révision taphonomique globale a permis de mettre en évidence des traces d'activité humaine sur plusieurs ossements. Les caractères morphologiques et la configuration de ces traces permettent de les attribuer

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à des étapes du processus de boucherie. Ces collections fossiles souffrent, plus que tout autre matériel archéologique, de nombreux biais liés à leur origine sédimentaire et à leur historique. Néanmoins, les observations microscopiques et l'étude des traces à partir des données de scanner surfaciques ont permis d'argumenter et de confirmer ces interprétations. Malgré leur histoire compliquée, ces collections peuvent ainsi être intégrées à un corpus archéologique et étudiées selon ce nouvel axe de recherche. Ce type d'étude permet de revaloriser un patrimoine historique en montrant l'intérêt de ces collections dans des problématiques actuelles telles que la question de l'interaction d'*Homo sapiens* avec les mégafaunes endémiques du cône austral d'Amérique du Sud.

1. Introduction

Unlike on other continents, anatomically modern humans were the first and only *Homo* species that dispersed from high latitudes to lower ones and again to higher latitudes in the Americas (Lanata, 2011). Although these first populations used a diverse array of resources in the different paleoenvironments (Lanata, 2011), their exploitation of native megafauna has been one of the most widely debated topics. The arrival of humans coincides with the extinction of this native fauna and the paleoenvironmental changes that affected them during the Late Pleistocene-Early Holocene. Thus, humans, climate and/or a combination of these would have driven these animals to extinction (Barnosky et al., 2004; Borrero, 2009; Cione et al., 2009; Graham and Lundelius, 1984; Grayson and Meltzer, 2015; Hubbe et al., 2013; Lanata, 2011; Martin, 1973; Monjeau et al., 2015; Surovell et al., 2016; among others). Archaeologically, it is difficult to prove the extent of the human influence. One of the main problems is the scarcity of early archaeological sites and the weak association or absence of cut marks. This would suggest a human influence that was minor and opportunistic (Arribas et al., 2001; Borrero, 2009; Grayson and Meltzer, 2015; Hubbe et al., 2013). However, from a paleontological point of view, humans were an important biological factor that affected this native community (Cione et al., 2009).

Cut marks are the most direct way to analyse the past exploitation of fauna by humans, but the megamammal species tend to have few such marks because their size, skin and the periosteum mean that their bones are not easily modified (Crader, 1983; Yravedra et al., 2011; Haynes and Klimowicz, 2015). Additionally, in the case of the Americas, the density of early sites would have been lower than on other continents due to the recent arrival of humans (Surovell and Grund, 2012). Preservation processes, the construction of cities, and even early uncontrolled excavation shave all contributed to the loss of this type of data (Fucks and Deschamps, 2008; Surovell and Grund, 2012).

In relation to this last point, the megamammal collections currently housed in many natural science museums stem from major fossil trafficking operations that took place between Argentina and Europe in the 19th century (Podgorny, 2011). The revision of these collections in search of evidence of biological intervention (both human and carnivore) constitutes an alternative method for uncovering new information. Museum collections are one of the most important means of preserving information about past and present life, and fossil collections, which are archives of past diversity, are especially valuable (de Renzi, 2002; Suarez and Tsutsui, 2004). The study of this information currently contributes to a wide range of disciplines, including palaeontology, genetics, biology and even the study of global climate change. Furthermore, the incorporation of this information into new studies can save money and time (Suarez and Tsutsui, 2004). Within this context, fossil collections can be very useful in the field of archaeology, and the revision of different paleontological and historical collections has yielded new data due to the discovery of human and carnivore biological intervention (Chichkoyan et al., 2015; Dowd and Carden, 2016; Labarca, 2003; Martín, 2008; Perez et al., 2005; Prous, 1986; Redmond et al., 2012; Saunders, 2007; Saunders and Daeschler, 1994). The revision of some of the collections mentioned in this paper has already revealed the presence of cut-marked bones (see details in Toledo, 2009). Thus, the components of these historical collections are a tool that can potentially provide new data to help us better understand human behaviour with regard to past fauna communities at a regional level.

The biggest drawback with this kind of record is the lack of context information (Turvey and Cooper, 2009) because archaeology is a context-dependent discipline (Schiffer, 1983). Fossil collections are an artificial selection filtered by biostratinomy, fossildiagenesis, excavation, merchandising and restoration processes. The first two filters are common with past and present collections of materials. In general, paleontological and archaeological records are biased representations of the living past because natural and/or anthropic actions have dispersed, destroyed and modified primary deposits (Schiffer, 1983). But they have also undergone historical-cultural selection (Turvey and Cooper, 2009), as they are the result of what excavators deemed worthy of rescue, what was offered by commercial sponsors and what museums wanted to buy (de Renzi, 2002; Podgorny, 2011; Turvey and Cooper, 2009). Collectors often attempted to complete specimens with bones from different individuals, and museums generally wanted the largest and most complete skeletons (de Renzi, 2002; Podgorny, 2011). For all of these reasons, 19th-century fossil collections represent a more biased record than materials collected today.

That being said, a weak context does not necessarily equal a complete lack of information. The advancement in these last decades of our ability to interpret bone

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modifications (Fariña et al., 2014b) has meant that we can now delve deeply into this non-traditional source of information for the field of archaeology. The definition of attributes for the detection of carnivore and anthropic cut marks, and the introduction of technological devices like microscopes have allowed us to identify materials bearing evidence of biological intervention. This information is useful to distinguish the various stages of the butchering process, discuss different exploitation scenarios, and make comparisons with evidence from controlled excavations at a coarse-grained scale. Radiocarbon data can provide information regarding when these interactions occurred. In short, fossil collections are a valid record with less specific information. The presence of various natural and anthropic filters does not mean that these collections should be ignored for use in current archaeological research.

This study presents the results of a revision of some Argentinean and European fossil collections. This is part of an ongoing project that is reviewing contextualised and decontextualised 19th-century collections to detect human and carnivore biological intervention in different skeletal elements of native fauna (Chichkoyan et al., 2015). Four cut-marked bones were recovered: a left humerus from a *Doedicurus* sp. from the “Museo Argentino de Ciencias Naturales Bernardino Rivadavia” (MACN), a right ulna from a *Megatherium americanum* from the “Muséum national d’histoire naturelle” (MNHN) and two caudal vertebrae from *Panochthus tuberculatus* from the Statens Naturhistoriske Museum (Zoologisk Museum) (ZMK). The low number of materials presented here is even more significant when the above-mentioned filters and the general American scarce recording of human traces are taken into account. The recovery of a few bones with cut marks is just an inkling of the irrecoverable information lost in these earlier campaigns. So, this type of material is highly relevant not only for its scientific value, but also because it represents the importance of the contribution of historic fossil collections.

2. Material

The collections come from diverse excavations that took place at different points in the area surrounding the Río de la *Plata basin*, which is currently part of Buenos Aires Province, Argentina. It corresponds to the Pampa Region, a fertile plain that is favourable to urban concentrations and agricultural activities (Fucks and Deschamps, 2008). It was subject to Quaternary loess deposition and environmental changes. This involved a complex geomorphologic formation with different regression and transgression events. The late Pleistocene-early Holocene period was characterised by the fluvial deposits formed during the transgression (subsequent to the Last Glacial Maximum) and the pedogenetic event at the beginning of the Holocene. Arid and dry paleoenvironment, redeposition of sediments and drastic climatic oscillations were typical during this period (Cione et al., 2009; Fucks and Deschamps, 2008).

We studied the following collections:

- the material housed at the MACN is labelled as MACN PV 6071. It comes from Arroyo Grande, Balcarce, located in southeast Buenos Aires Province at approximately 37°50′ S 58°15′ W. It comes from the late Pleistocene-early Holocene Luján Formation. The assemblage, assigned to *Doedicurus* sp., consists of a right mandible, a fragment of an ulna and some plates, in addition to the humerus presented here;
- the Vilardebó Collection housed at the MNHN. The *Megatherium americanum* ulna studied here is labelled as MNHN.F.PAM 751 and comes from the Pampean formation. In the 19th-century different naturalists, including D’Orbigny, Darwin, Doering and Ameghino, have defined this formation. In general terms, it referred to the sediments deposit during the Pleistocene until early Holocene periods (Tonni and Pasquali, 2006). de Blainville included this element in his fourth volume of ‘Ostéographie’ (1839–1864) (Planche III, Fig. 6 and 6′);
- the Lausen Collection housed at the ZMK. The material presented here proceeds from the town of Mercedes (34°39′ S 59°25′ W) and it is labelled ZMK 38/1889. It is an assemblage comprised of 11 more vertebrae, two patellae, a mandible, a chevron, a caudal tube and several fragments of *Panochthus tuberculatus* plates in addition to the vertebrae presented here.

The species named here belong to the diversified native South American group corresponding to the order of the Xenarthra, which is divided into Cingulata and Pilosa. The family Glyptodontidae belongs to the former, which includes the *Doedicurus* sp. and the *Panochthus tuberculatus*. This is a monophyletic group, characterised by a hard shell of fixed osteoderms (Zurita et al., 2010). *Doedicurus* sp. could have weighed up to 1400 kg, and the *Panochthus tuberculatus* could have weighed up to 1100 kg (Fariña et al., 1998). Pilosa includes the *Megatherium americanum* in the Megatheriidae family. It is the largest animal in this order, as it could weigh from four to over six tonnes (Fariña et al., 1998). According to the biochronological framework (Tonni, 2009), *Doedicurus* sp. appears in the *Mesotherium cristatum* biozone, and *Panochthus tuberculatus* and *Megatherium americanum* in the *Megatherium americanum* biozone that began at 400,000 BP. They all became extinct in the *Equus (Amerhippus) neogeus* biozone, which lasted until the early Holocene.

3. Methodology

Bones from the appendicular and axial skeleton of identified species and skeletal elements were reviewed. The different bone surface modifications were documented, such as post-depositional fractures, the presence of original sediments or concretions, fluvial erosion, trampling, weathering, roots, manganese spots and burning traces (Behrensmeyer, 1978; Binford, 1981; Fernández-Jalvo and Andrews, 2003, 2016; Lyman, 1994; Olsen and Shipman, 1988; Shipman, 1981; among others). Distinguishing these different alterations is necessary in order to evaluate the conditions to which the bones were subjected in the past and to identify possible human biological intervention.

Ancient cut marks macroscopically will have the same appearance of the rest of the bone and may have post-depositional agents on top of them (Dowd and Carden,

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2016; Labarca, 2003; Perez et al., 2005; Prous, 1986; Redmond et al., 2012; Saunders, 2007; Toledo, 2009). These characteristics differentiate them from fresh marks or fractures made during excavation or handling at the museums. Such marks or fractures are different in colour from the surrounding cortical tissue (Fisher, 1995) because they were not exposed to the same post-depositional agents that affected the bones in the past. Nevertheless, sometimes the tool did not penetrate enough to expose subcortical bone (Fisher, 1995), and therefore morphological and configurational features (sensu Fisher, 1995) can be useful to identify past human intervention and consequently further inform our determinations. Among the morphological features, we looked at elongated transversal or longitudinal marks with a V cross-section and internal microstriations in their walls, or microscopic features such as smears (Bello et al., 2009; Binford, 1981; Fernández-Jalvo and Andrews, 2016; Lyman, 1994; Shipman, 1981). Configurational features, like the presence of several groups of marks with a parallel or semi-parallel orientation, were also taken into account (Binford, 1981; Fernández-Jalvo and Andrews, 2016; Lyman, 1994; Olsen and Shipman, 1988). These groups of marks had to be located in parts of the bone related to the different butchering stages as defined by Binford (1981). Cut marks made during the disarticulation of the limbs or filleting stages are diagnostic, as they will probably coincide with long bone ends (Galán and Domínguez-Rodrigo, 2013).

The material was reviewed with the naked eye and then with 3.5× and 12× magnifying glasses. A 4113 model Dinolite microscope and its software were also used. High-resolution digital images were taken using a Panasonic Lumix DMC-TZ35 camera. On MNHN and ZMK, bone casts were also taken to be reviewed with a Hirox KH-8700 digital microscope at IPHES. The material used for casting was Provil Novo Light for the negative and Polyvinyl Siloxane for the positive.

4. Results

A NISP of 943 bone remains have been analysed: 433 elements from the MACN, 51 elements from the MNHN and 459 from ZMK:

- in the left humerus from the *Doedicurus* sp. (MACN PV 6071) (Figs. 1 and 2), two groups of possible cut marks were detected. They are located on the anterior and posterior faces on the epicondylar medial side of the distal metadiaphysis region. One group is located on the anterior-medial face, obliquely oriented in relation to the long axis of the bone, over the epicondylar crest (Figs. 1A and 2A). This group is comprised of at least three long cut marks of approximately 2 cm in length, and two shorter marks measuring about 0.5 cm. The other group is located on the posterior face near the distal articular border. It is oriented perpendicularly in relation to the long axis of the bone (Figs. 1B and 2B). It is made up of five long marks measuring approximately 1.5 cm;
- the right ulna of the *Megatherium americanum* (MNHN.F.PAM 751) housed at MNHN has a set of cut marks on the proximal metadiaphysis of the bone in the posterior-medial position under the coronoid process. They are located perpendicularly to the long axis of the bone, and comprise a complex grouping of long and short marks that run parallel to one another. From the external border to the interior, the set was divided into four parts (Fig. 3). The first (Fig. 3A) is a group of seven short marks, measuring from 0.3 to 0.5 cm in length and situated 0.2 to 0.5 cm apart. On the distal part of this set there is a longer mark measuring 1.2 cm. Very near this mark, there is another grouping of four long marks (Fig. 3B) measuring approximately 2 cm in length and located 0.2 to 0.3 cm apart with a slightly concave orientation. This group also contains approximately located 3 cm cut mark with a more rectilinear orientation. Immediately next to this group, there are four marks measuring approximately 0.5 cm, with a V cross-section and superposed by a weathering crack (Fig. 3C). Finally, a group of two to four marks measuring approximately 1.5 cm in length is located on the posterior face of the bone (Fig. 3D). This last group is almost invisible and discontinuous, as if the pressure applied here was less intense than at the beginning of the mark. In the same position, but near the lateral side of the bone, at 6 cm from the end of this group of marks, there are three slight marks measuring approximately 0.5 cm in length and separated by 0.1 cm. They are as weak in appearance as the main mark described in the last set. The weathering cracks that crosscut these cut marks, the fossilised sediment inside of them, and their similar appearance to the rest of the bone indicates that the marks were not produced posterior to excavation. Three casts were made of the main cut mark. Acetone was used to clean inside and around the cut to remove the attached sediment. Of the three casts, the first two were taken for the same purpose. The third cast was analysed using the Hirox KH-8700 digital microscope. Although the pieces were thoroughly cleaned, the remnants of old sediments were firmly attached. A special effort was made during the cleaning procedures to remove the sediment without damaging the bone. Only at the beginning of the short cuts in the first set described (Fig. 3A) was it possible to appreciate one of the cut mark's walls with microstriations (Fig. 4). In the rest of the cast, the cut marks presented smooth walls. This was probably due to the attached sediment left in the groove;
- one of the *Panochthus tuberculatus* vertebra (ZMK 38/1889) from the ZMK presents a set of eight possible cut marks on the dorsal side of the right transversal process. They have the same oblique orientation in relation to the medial axis of the bone. They were divided into two groups. The first four cut marks form a group positioned on the anterior-medial side of the transversal process. They are short and superficial (from 1 to 2 cm in length) and do not touch the anterior edge of the transversal process (Fig. 5). The other four marks are posterior-laterally positioned, touching the posterior edge of the transversal process and are deeper. This group is comprised of one longer cut mark measuring 3 cm and the others measuring 1 and 2 cm. The marks have smears in both walls and asymmetric grooves (Fig. 5). Concretions of sediments were documented covering and surrounding some

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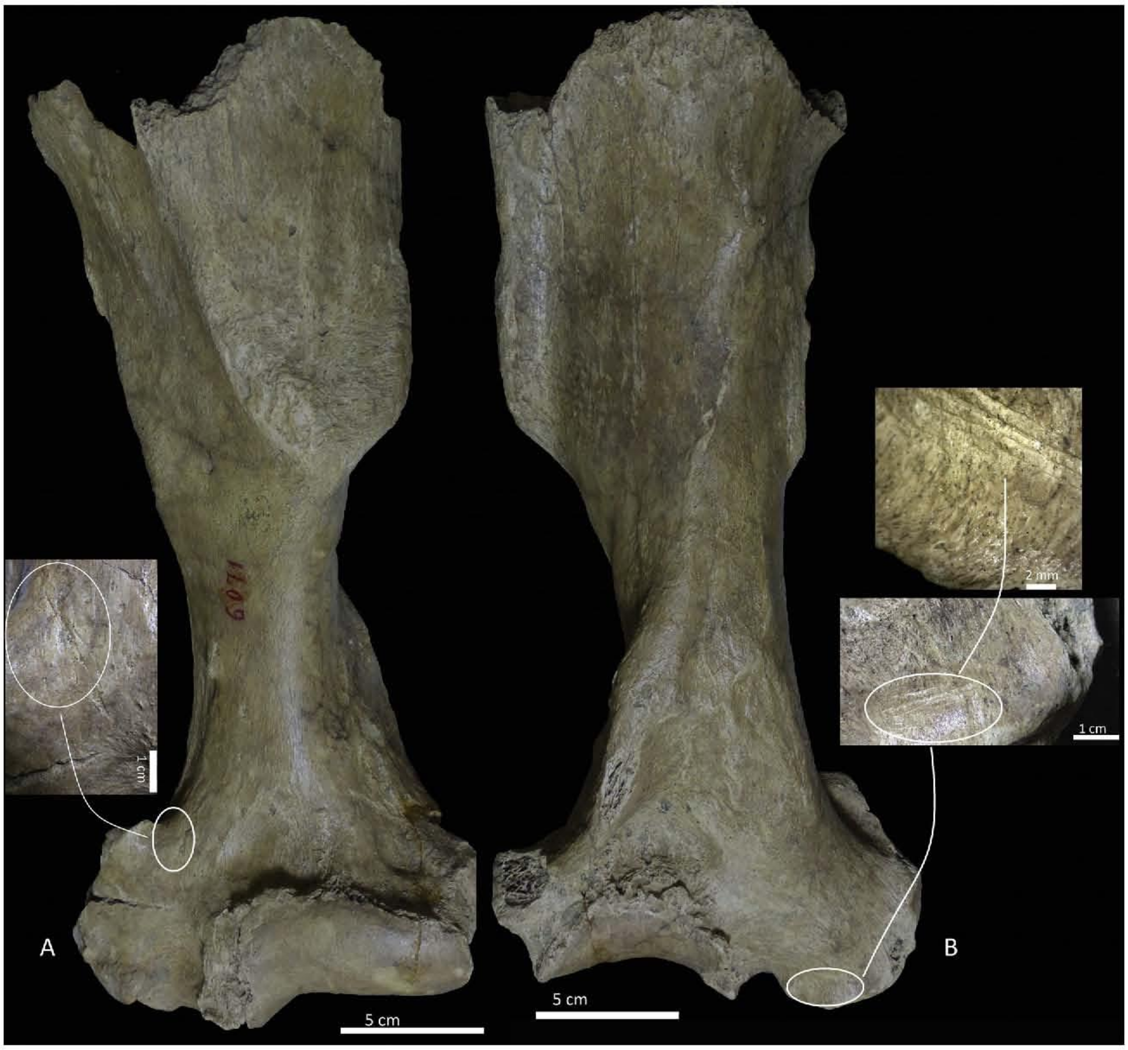

Fig. 1. Left humerus of *Doedicurus* sp. MACN PV 6071, A. Anterior face and B. Posterior face, in the circle, amplification of the cut marks.
Fig. 1. Humérus gauche de *Doedicurus* sp. MACN PV 6071, A. Face antérieure et B. Face postérieure ; les stries de boucherie sont visibles dans les cercles.

parts of the marks. This indicates that the marks occurred before the action of this agent. A sample of this vertebra was sent for dating to the 'Centre for Isotope Research' (Groningen), but regrettably was out of collagen. The other vertebra contains four grooves on the same side of the transversal process and in the same distribution. There are two superficial anterior-medially positioned marks measuring 1 and 3 cm. The other two are anterior-laterally positioned. As in the other case, this group is in contact with the border and the marks are deeper. One mark measures 4 cm in length and the other 1 cm. The grooves are wider and covered with sediment. The vertebrae underwent the same cleaning procedure and four casts were made. Microstriations and V shape were observed in the larger mark of the external group of the first described vertebra (Fig. 6).

The basic morphological characteristics of cut marks as described in the bibliography were documented, some of the most important of which are elongation, the presence of microstriations, a V-shaped cross-section and smearing. Configurational features, such as the presence of groups of marks of similar characteristics on specific parts of the bone, strongly suggest an anthropogenic origin. The fact that evidence of anthropic intervention is found underneath other natural traces such as sediments, manganese and weathering cracks, and that they have the same condition that the rest of the cortical surface indicate that they

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Fig. 2. Schematic drawing of *Doedicurus* sp. MACN PV 6071 with cut marks localization. A. Anterior face. B. Posterior face.
Fig. 2. Dessin schématique de *Doedicurus* sp. MACN PV 6071 avec les stries de boucherie. A. Face antérieure. B. Face postérieure.

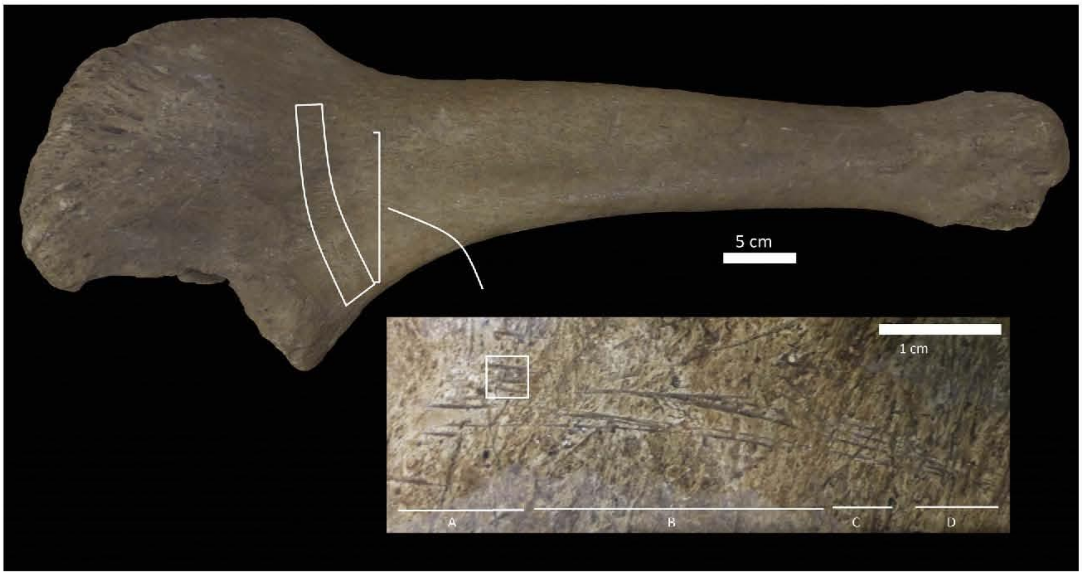

Fig. 3. Right ulna of *Megatherium americanum* MNHN.F.PAM 751, posterior-medial face with amplification of the groups of cut marks: A, B, C and D described in the text. In the rectangle: localization of Hirox image.
Fig. 3. Ulna droit de *Megatherium americanum* MNHN.F.PAM 751, face postéro-mésiale avec grossissement des groupes de stries de boucherie : A, B, C et D décrits dans le texte. Dans le rectangle : localisation de l'image de Hirox.

were probably made prior to burial and were not the result of excavation or museum handling processes.

5. Discussion

5.1. Butchering process

Because the identified cut marks are located on parts of the bone related to the epiphysis zones and or/muscle insertion points, they can be associated to the different butchering stages (Binford, 1981). These areas are the most susceptible to bearing anthropogenic traces left during the disarticulation or filleting stages (Binford, 1981; Galán and Domínguez-Rodrigo, 2013).

Both groups of marks on the *Doedicurus* sp. humerus are located in the epicondylar medial region. Different species of Xenarthra possessed complex sets of muscles and tendons, such as the triceps muscle and the anconeus in the postmedial part of the humerus, which inserts into the olecranon of the ulna (Olson et al., 2016; Toledo et al., 2013). The first muscle extends over nearly the entire surface of the distal metadiaphysis of the humerus (see Toledo et al., 2013: Fig. 5). Butchering experiments on this part have shown that processing stages will leave cuts with

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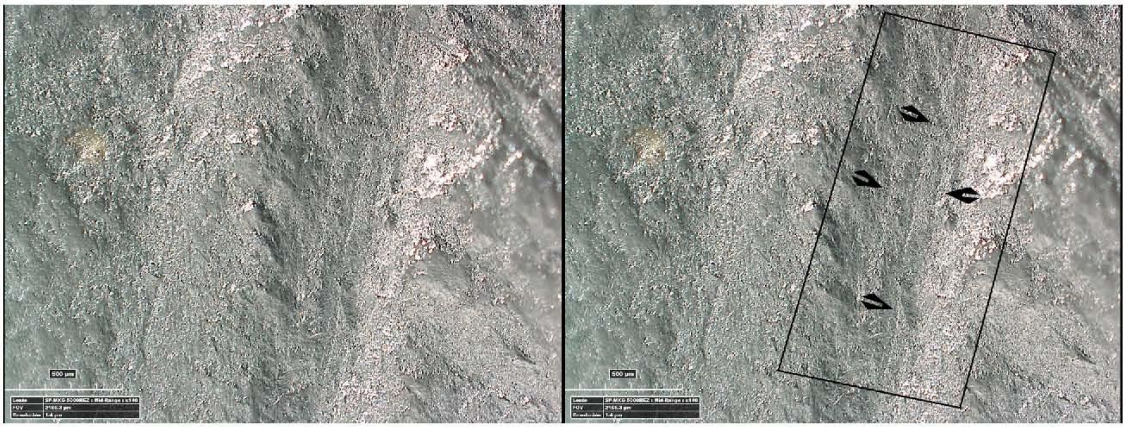

Fig. 4. Hirox image of the cast of the right ulna of *Megatherium americanum* MNHN.F.PAM 751 with indication of possible microstriations.

Fig. 4. Image Hirox des répliques des traces de l'ulna de *Megatherium americanum*, MNHN.F.PAM 751 avec les microstries.

Fig. 5. Caudal vertebra of *Panochthus tuberculatus*, ZMK 38/1889. Posterior view with amplification of the group position on the transversal process. Indication of smeared bone. In the rectangle: asymmetrical groove, microstriations and localization of Hirox image.

Fig. 5. Vertèbre caudale de *Panochthus tuberculatus*, ZMK 38/1889. Vue postérieure avec grossissement du groupe de stries situées sur le processus transverse. Notez le bord avec épaulement. Dans le rectangle: le sillon asymétrique, les microstries et localisation de l'image Hirox sont visibles.

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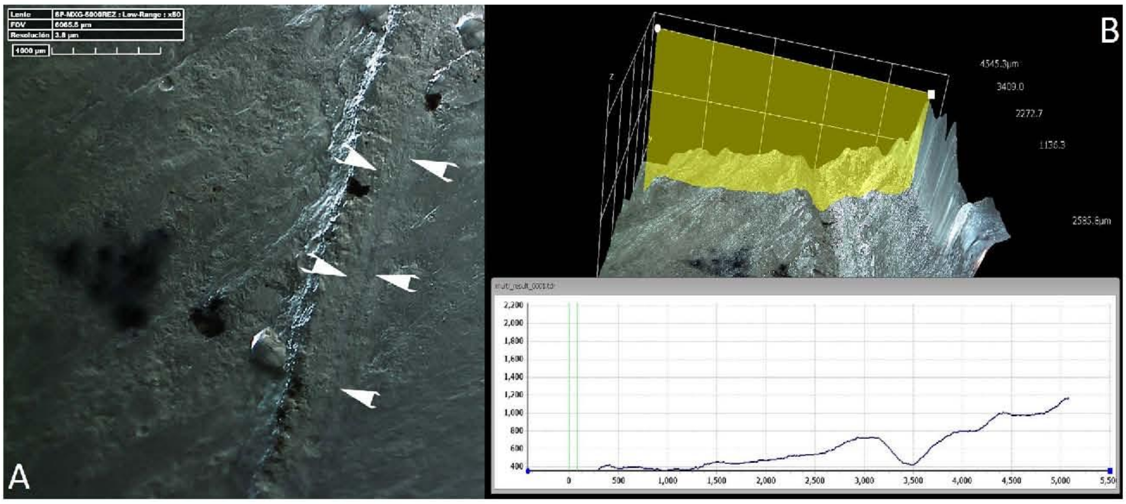

Fig. 6. A. Hirox image of the cast of the vertebra of *Panochthus tuberculatus*, ZMK 38/1889 with indication of microstriations. B. Hirox profile of the same section. Notice asymmetrical groove and V shape .

Fig. 6. A. Image Hirox des répliques de la vertèbre de *Panochthus tuberculatus*, ZMK 38/1889, présentant les microstries. B. Profil Hirox de la même section. Remarquez le sillon asymétrique et la forme en V.

an oblique and/or perpendicular orientation in the distal part (Binford, 1981; Galán and Domínguez-Rodrigo, 2013). Thus, the orientation of the cut marks and their position in similar areas of muscle or ligament insertion relates both groups of cut marks to the stages of disarticulation of the humerus from the ulna and/or the filleting of the muscle package. The marks on the *Megatherium americanum* ulna are located on the proximal metadiaphysis of the bone, under the coronoid process. This feature holds the insertion of the annular ligament, the insertion of the biceps brachii and the muscle brachialis (see Olson et al., 2016: Fig. 2; Toledo et al., 2013: Fig. 6). Furthermore, the supinator and the flexor digitorum profundus muscles are medially located (Olson et al., 2016; Toledo et al., 2013). Thus, the complex group of observed traces could be related to the intention of cutting the ligaments and separating the ulna from the humerus in a disarticulation stage or to fillet the different muscle groups. The different pressure executed at the beginning and the end of the cut mark are associated with the cutting edge of the instrument when this action was carried out or with the position of the animal during butchering. Also, the presence of the coronoid process might involve more pressure applied here than in the rest of the cutting motion. Finally, in the case of the *Panochthus tuberculatus* caudal vertebra, the cut marks are located on the transversal process. They can be related to the action of removing the muscle pocket contained in the tail (McNeill et al., 1999). This can be compared with the filleting process of tenderloin and sirloin extraction in the thoracic and lumbar vertebra. In these elements, the marks are elongated and transversally oriented to the dorsal spine (Binford, 1981) as they are here.

Thus, the presence of cut marks on the epiphyses would have served to cut ligaments, separate distal and proximal forelimb parts, or, as in the case of the vertebra, to extract different muscles in the disarticulating or filleting butchering stages of meaty segments. The forelimb of a three tonne animal can yield 50 kg of meat (Arribas et al., 2001), while the muscle in the tail of a Glyptodons can weigh 108 kg (McNeill et al., 1999). This evidence coincides with general American record. In fact, different sites along the continent have revealed evidence of butchering marks on the bones of the megafauna species cited here (humerus, ulna and vertebra) (see detail in Table 1). Anthropic manipulation is present in the form of cut marks, crescentic gouges, chopping, fracturing, impacts or were transported elements (see detail in Table 1). In those sites, these interventions were related to either disarticulation or filleting processing actions as it is proposed for the evidence presented here.

5.2. Access type

These traces could have been produced as the result of hunting or scavenging activities. At many sites throughout the Americas, most marks were created during scavenging activities. However, at other sites such as Murray Springs, Pleasant Lake, El Vano and Campo Laborde, hunting would have been the method of procurement (Casamiquela, 1979; Dillehay, 1997; Fisher, 1984; Hannus, 1989; Hemmings, 2007; Jackson et al., 2011; Jaimes Quero, 2005; Johnson, 1976; Martín, 2008; Prous, 1986; Saunders, 2007; Saunders and Daeschler, 1994). Both modalities of exploitation have been recorded at Pampas sites that contain the species of the same Order as discussed in this work (Fariña et al., 2014a; Politis and Gutiérrez, 1998; Politis and Messineo, 2008; Steele and Politis, 2009; Suárez and Santos, 2010). It should be noted also that in this region these species beside consumption have been exploited for bone technology and fuel (Politis and Messineo, 2008; Steele and Politis, 2009) (see detail in Table 1).

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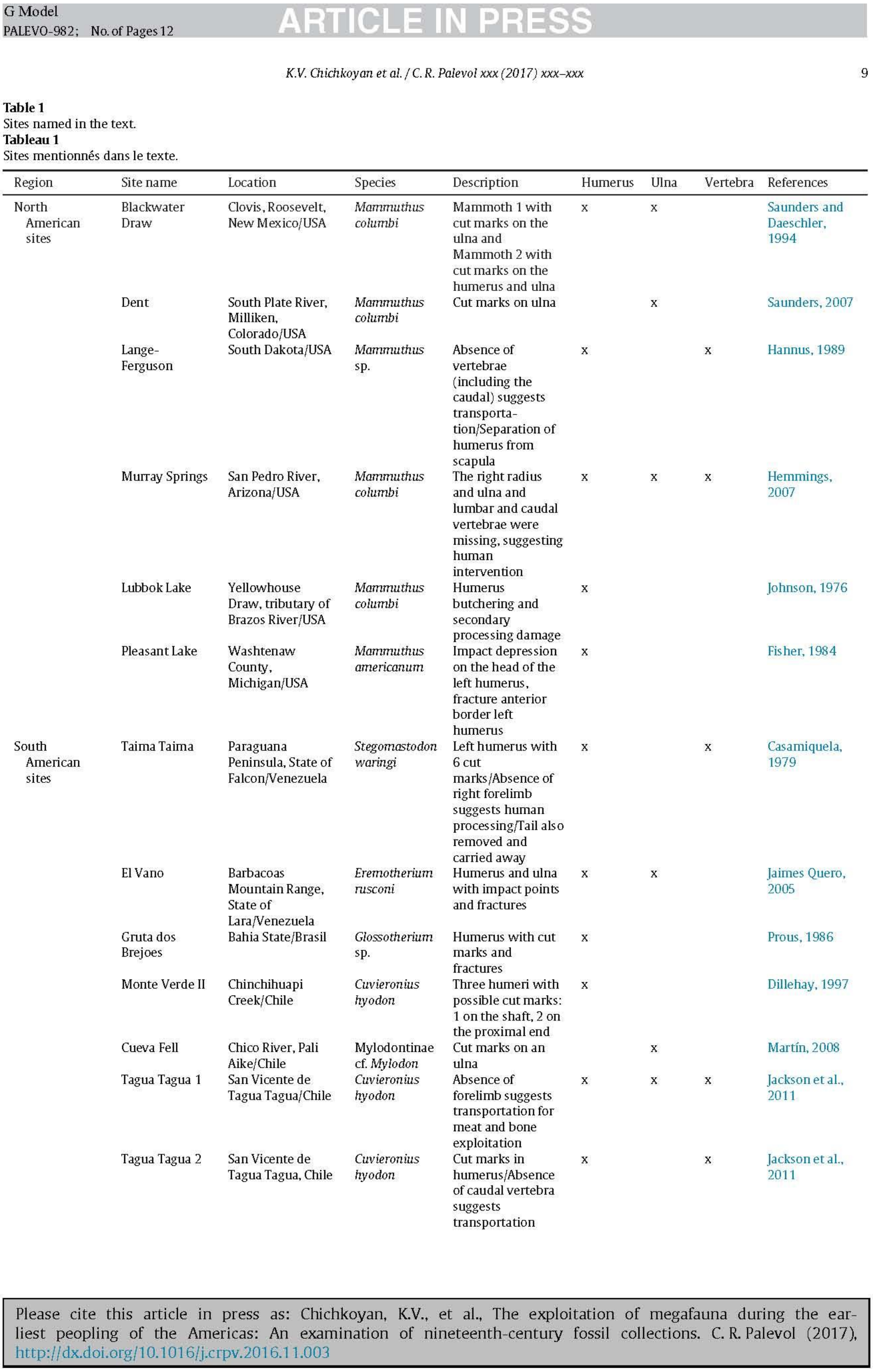

Table 1
Sites named in the text.
Tableau 1
Sites mentionnés dans le texte.

Region	Site name	Location	Species	Description	Humerus	Ulna	Vertebra	References
North American sites	Blackwater Draw	Clovis, Roosevelt, New Mexico/USA	*Mammuthus columbi*	Mammoth 1 with cut marks on the ulna and Mammoth 2 with cut marks on the humerus and ulna	x	x		Saunders and Daeschler, 1994
	Dent	South Plate River, Milliken, Colorado/USA	*Mammuthus columbi*	Cut marks on ulna		x		Saunders, 2007
	Lange-Ferguson	South Dakota/USA	*Mammuthus* sp.	Absence of vertebrae (including the caudal) suggests transportation/Separation of humerus from scapula	x		x	Hannus, 1989
	Murray Springs	San Pedro River, Arizona/USA	*Mammuthus columbi*	The right radius and ulna and lumbar and caudal vertebrae were missing, suggesting human intervention	x	x	x	Hemmings, 2007
	Lubbok Lake	Yellowhouse Draw, tributary of Brazos River/USA	*Mammuthus columbi*	Humerus butchering and secondary processing damage	x			Johnson, 1976
	Pleasant Lake	Washtenaw County, Michigan/USA	*Mammuthus americanum*	Impact depression on the head of the left humerus, fracture anterior border left humerus	x			Fisher, 1984
South American sites	Taima Taima	Paraguana Peninsula, State of Falcon/Venezuela	*Stegomastodon waringi*	Left humerus with 6 cut marks/Absence of right forelimb suggests human processing/Tail also removed and carried away	x		x	Casamiquela, 1979
	El Vano	Barbacoas Mountain Range, State of Lara/Venezuela	*Eremotherium rusconi*	Humerus and ulna with impact points and fractures	x	x		Jaimes Quero, 2005
	Gruta dos Brejoes	Bahia State/Brasil	*Glossotherium* sp.	Humerus with cut marks and fractures	x			Prous, 1986
	Monte Verde II	Chinchihuapi Creek/Chile	*Cuvieronius hyodon*	Three humeri with possible cut marks: 1 on the shaft, 2 on the proximal end	x			Dillehay, 1997
	Cueva Fell	Chico River, Pali Aike/Chile	Mylodontinae cf. *Mylodon*	Cut marks on an ulna		x		Martín, 2008
	Tagua Tagua 1	San Vicente de Tagua Tagua/Chile	*Cuvieronius hyodon*	Absence of forelimb suggests transportation for meat and bone exploitation	x	x	x	Jackson et al., 2011
	Tagua Tagua 2	San Vicente de Tagua Tagua, Chile	*Cuvieronius hyodon*	Cut marks in humerus/Absence of caudal vertebra suggests transportation	x		x	Jackson et al., 2011

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Table 1 (*Continued*)

Region	Site name	Location	Species	Description	Humerus	Ulna	Vertebra	References
Pampean region sites	Arroyo Vizcaíno	Canelones/Uruguay	*Lestodon armatus*	Cut marks on an ulna		x		Fariña et al., 2014a
	Pay Paso 1	Quarai River/Uruguay	*Glyptodon* sp.	Glyptodon scutes in association with lithic artefacts				Suárez and Santos, 2010
	La Moderna	Azul, Buenos Aires/Argentina	*Doedicurus clavicaudatus*	Transport of meaty elements like forelimbs	x	x		Politis and Gutiérrez, 1998
	Arroyo Seco 2	Tres Arroyos, Buenos Aires/Argentina	*Megatherium americanum*	Tibia with helical fracture				Steele and Politis, 2009
	Campo Laborde	Olavarria, Buenos Aires/Argentina	*Megatherium americanum*	One rib with cut marks, one rib helically fractured, one rib transformed into informal tool				Politis and Messineo, 2008
	Paso Otero 5	Necochea, Buenos Aires/Argentina	*Megatherium americanum*	Burned bone used as fuel				Steele and Politis, 2009

If previous carnivore activity had occurred in the cut-marked bones described above, exploitable tissues would still have remained. Disarticulation or filleting marks indicating the presence of meat pockets at the time of human access. Though still scarce, the direct evidence of carnivore predation in the region (Scanferla et al., 2013), the variability of this native fauna implies that an important niche must have developed around this resource (Fariña, 1996). Carnivores may have accessed these animals by hunting or scavenging. However, these herbivores possessed defence systems that make the first option unlikely. Glyptodontidae coverage and accessory structures evolved as a defensive strategy to prevent carnivore predation (Zurita et al., 2010). *Megatherium americanum* could have been scavenged by canids like *Protocyon* (Prevosti and Schubert, 2013) or could have been sporadically hunted by *Smilodon*, especially juveniles (Prevosti and Vizcaíno, 2006). However, the increasing body size of herbivores recorded during the Pleistocene was a defence system that evolved in response to carnivore diversification (Vizcaíno et al., 2012). Thus, as in the scavenging activities of megamammals that occurred in African or European environments, Pampas carrion would have sustained different carnivore groups, to which humans must be added, at the end of the Pleistocene (Borrero, 2009; Crader, 1983; Fariña, 1996; Haynes and Klimowicz, 2015; Yravedra et al., 2011). Humans also applied new ways of exploiting this resource, like direct hunting with novel technology (Cione et al., 2009).

6. Conclusions

Different types of evidence were considered to define the origins of the described anthropogenic alterations. Their general morphology was analysed with different magnifying glasses and microscopes, which allowed us to recognise several of the attributes defined for cut marks. Configurational features such as the presence of groups of similar marks with the same orientation led to the suspicion of anthropogenic origin. Additionally, all of the marks are, in general, related to the location of the epiphyses or to muscle/ligament attachments. This information supports the relation of these marks to specific butchering stages, such as the separation of limbs or muscles, as observed in other American sites. This may have been the result of hunting and/or scavenging activities and would have implied that humans competed with Pampas carnivores for megamammal carcasses. At a coarse-grained level, this information adds to the body of knowledge on the relation between *Homo sapiens* and native species, and provides greater insight into paleoecological relationships (Chichkoyan et al., 2015).

The record of human biological marks on material collected during the 19th century means that these collections potentially contain archaeological information to be investigated. These collections are not only archives of the past, but also represent unrecoverable deposits that have to be explored in order to resolve modern enquiries. Consequently, these kinds of studies can not only increase the value of such fossil collections for the field of archaeology, but can also reveal information on the region and raise questions for future lines of research.

Acknowledgments

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5.3.3. DESCRIPTION AND INTERPRETATION OF A *MEGATHERIUM AMERICANUM* ATLAS WITH EVIDENCE OF HUMAN INTERVENTION (RIVISTA ITALIANA DI PALEONTOLOGIA E STRATIGRAFIA)

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DESCRIPTION AND INTERPRETATION OF A *MEGATHERIUM AMERICANUM* ATLAS WITH EVIDENCE OF HUMAN INTERVENTION

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Key words: Megafauna; Human dispersal; Pampean region; Taphonomy; Museum's collection.

Abstract. This paper discusses a *Megatherium americanum* atlas from the Pampas region of Argentina, which is currently housed at the Museo di Storia Naturale di Firenze, Italy. Traces of anthropic cut marks were found on the dorsal and ventral faces of the posterior part, in articulation with the axis. This is the first time that this type of evidence has been documented on this element of this species. The position of these marks suggests that they resulted from the act of separating the head from the postcranial skeleton. They were therefore most likely made in an effort to exploit the contents of the head. Current research focusing on museum collections employing modern methods can provide new and valuable information, despite the general lack of contextualization of these pieces. In the case studied here, these methods have allowed us to delve deeper into the first dispersal of *Homo sapiens* and their interaction with the native fauna in the South American Southern Cone.

INTRODUCTION

Early human dispersal in the Americas is a much debated topic. The routes of entry, the regions humans moved into, the kind of demographic growth they experienced, the resources they used and the impact they had on the environment have been extensively discussed in recent decades (Martin 1973; Graham & Lundelius 1984; Anderson & Gillian 2000; Barnosky et al. 2004; Brook & Bowman 2004; Koch & Barnosky 2006; Lanata et al. 2008; Cione et al. 2009; Lanata 2011; Pitblado 2011; Borrero & Martin 2012; Fariña et al. 2014; Abramson et al. 2015; Grayson & Meltzer 2015; Monjeau et al. 2015; Goldberg et al. 2016; among others).

Human impact seems of singular importance due both to the profound changes in the landscape since the mid-19th century (Grusin 2015) and the characteristic distinctiveness of Quaternary American environments. In fact, unlike other land masses, this continent remained virtually isolated except during certain periods when North America and Eurasia were connected. South America remained separated from North America until approximately 3 million years ago (Fariña et al. 2013). This particular feature gave rise to a unique pace in the evolution of life, such as the development of a native paleo-environment that did not interact with our species after the last glacial maximum, when *Homo sapiens* came onto the stage (Martin 1973; Cione et al. 2009; Lanata 2011; but see also Toledo 2005; Azcuy et al. 2011; Boëda et al. 2014; Fariña et al. 2014; for discussions of earlier human entries). Megafauna weighing more than 44 kg were the masters of this landscape and particularly species weighing over 1000 kg. These had unique and diverse biological characteristics and particularities different to northern or Holarctic fauna and they disappeared after the Pleistocene-Holocene transition (Cione et al. 2009; Fariña et al. 2013). Thus, current American

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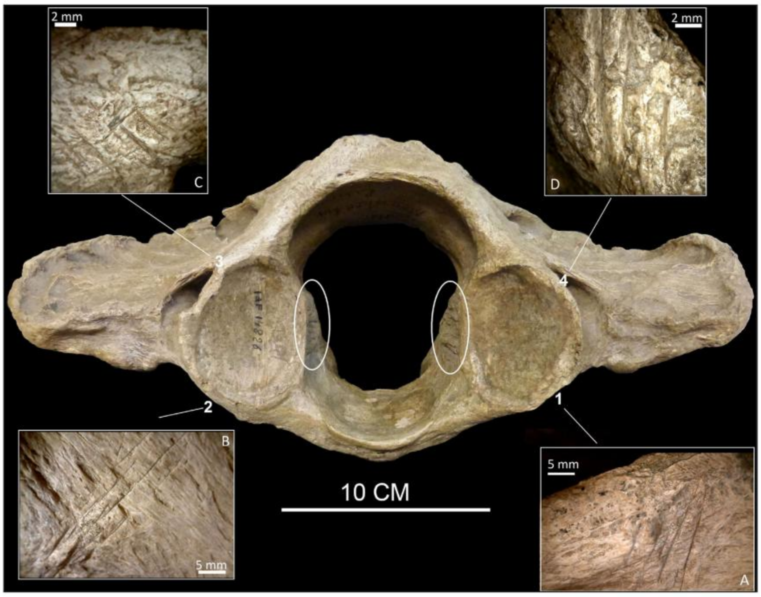


Fig. 1 - Atlas of *Megatherium americanum* (IGF 14826). The position of the numbers indicates the position of the different groups of anthropic cut marks described in the text. In the circles, the bony regrowth.

environments exhibit a stark contrast to the paleobiological development this continent underwent in the past (Cione et al. 2009).

As a result, South America is a paradigmatic case in understanding the evolution of native species and in appreciating how anatomically modern humans interacted with them. The dispersal of *Homo sapiens* coincides with the climate fluctuations characteristic of the Pleistocene-Holocene transition. Because of this, the debate has generally focused on analyzing the extent to which human intervention could have affected megafauna extinction during this period (Graham & Lundelius 1984; Barnosky et al. 2004; Koch & Barnosky 2006; Politis & Messineo 2008; Cione et al. 2009; Lanata 2011; Borrero & Martin 2012; Martínez et al. 2013; Fariña et al. 2014; Grayson & Meltzer 2015; Monjeau et al. 2015; among others). The scarcity of early archaeological sites and slight and weak association with or direct evidence of native fauna predation would suggest that human intervention on these species was minor and opportunistic (Arribas et al. 2001; Borrero & Martin 2012; Hubbe et al. 2013; Grayson & Meltzer 2015). However, from a paleontological point of view, humans seem to have been a considerable biological factor in the demise of megafauna (Cione et al. 2009).

In the Pampas region, different archaeological sites have yielded evidence of megafauna exploitation, in what are currently the countries of Uruguay and Argentina (Steele & Politis 2009; Suárez & Santos 2010; Martínez et al. 2013; Fariña et al. 2014; among others). Research in different parts of the world has started to incorporate paleontological collections and collections from old excavations housed in various museums (Prous 1986; Saunders & Daeschler 1994; Labarca 2003; Perez et al. 2005; Martin 2008; Fisher 2009; Toledo 2009; Krasinski 2010; Redmond et al. 2012; Chichkoyan et al. 2015; Dowd & Carden 2016). The biological interventions (either carnivore or human) that may have affected bone surfaces can potentially provide information to help advance our understanding of paleoecological relationships between different species (Chichkoyan et al. 2015).

To this end, this paper discusses an atlas from a *Megatherium americanum* (IGF 14826) bearing anthropic cut marks, which is currently housed in the Museo di Storia Naturale di Firenze (MSNF) (Fig. 1). This is part of a research project that is reviewing 19th century collections to find evidence of biological interventions on different elements of native fauna (Chichkoyan et al. 2015; Chichkoyan 2016). The MSNF collection has only 30 bone elements

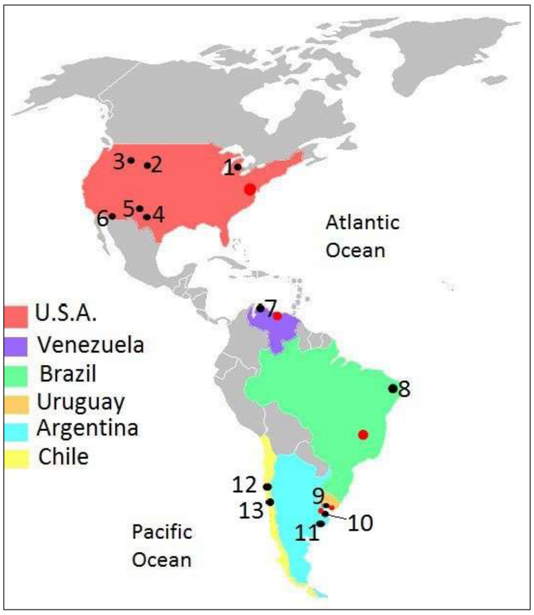


Fig. 2 - Principal American sites named in the text: 1 - Pleasant Lake and Sheathelm, 2 - Lange/ Ferguson, 3 - Colby, 4 - Lubbok Lake, 5 - Blackwater Draw, 6 - Murray Springs, 7 - Taima Taima and El Vano, 8 - Poço Redondo, 9 - Arroyo del Vizcaino, 10 - Río de la Plata, 11 - Arroyo Seco, Campo Laborde and Paso Otero, 12 - Quereo II, 13 - Tagua Tagua. Red points indicate Capital Cities of each country (Modified from Wikimedia Commons).

from this species, making it one of the smaller collections of this type in Europe. Nevertheless, this atlas is one of the most diagnostic elements with evidence of anthropic intervention found. It is the first time that these types of traces have been detected on an atlas of this species. By reviewing collections housed in museums, new information can be obtained, and these materials can regain their investigative value for inclusion in current research topics.

In the coming sections, we will delineate the regional context as well as the materials and methods used in this analysis, followed by a precise description of the traces on the atlas. In order to discuss this evidence, we will compare this case with other American sites in which the heads of megafauna have been exploited. This will offer insight into the possible purpose of the marks on the piece under study. We will also briefly discuss types of access. Finally, in the conclusions, we will mention the usefulness of undertaking this type of work with museum collections.

REGIONAL SETTING AND MATERIALS

The collection housed at the MSNF comes from the Pampas region, Río de La Plata, Buenos Aires province, Argentina (Fig. 2, number 10). The Pampas region is a vast plain composed of different subunits differentiated by geomorphology, soils, vegetation, and drainage, among other characteristics. The area that lies along the Río de la Plata is part of the northern rim of the geological region called the Salado Basin. The area was subject to various different marine regression and transgression events (Cavallotto 2002), and one such event occurring after the Last Glacial Maximum was particularly important in terms of sediment deposition. Different paleoclimatic pulses and eolian and fluvial contributions point to complex geological processes at the end of the Pleistocene (Cavallotto 2002; Toledo 2005; Cione et al. 2009; Zárate et al. 2009).

The discovery of the *Megatherium americanum* in 1787 at the Luján River and Darwin's visit to the region revealed the novelty of South American fauna to the scientific community. Consequently, during the 19th century, a complex fossil trafficking network developed between Argentina and different European countries like England, France, Spain or Italy. This was related to European colonization and expansion policies, as well as to Argentina's need to be involved in this new economic and political system (Podgorny 2001).

In this context, the MSNF's Pampas collection belongs to the museum's former collections. According to the historical catalogue currently housed in the Museo di Storia Naturale La Specola, the Megatheriidae collection was bought in 1850. In 1871 some Glyptodontidae remains (labeled "near Buenos Aires") were added. The museum was opened to the public in 1775 by Granduca Pietro Leopoldo of Tuscany before Firenze became the capital of Italy (from 1866 to 1871). Thus during the first half of 19th century this museum, as the ones in Paris and London, was pioneer in the development of natural scientific research (Cioppi & Dominici 2010). The acronym IGF before the catalogue numbers stands for Instituto Geologico di Firenze, today the MSNF.

This material was not extracted in the way that methodological excavations are completed today. Although some general information about locality and stratigraphic position was sometimes re-

Fig. 3 - Right *Megatherium americanum* clavicle (IGF 14824). Bony regrowth can be seen in the scapular end.

corded, the specific position and associated context was not always documented. This was the way that excavations were done in the 19th century, when the procurement and description of the most complete skeletons was the ultimate objective (Turvey & Cooper 2009).

The collection is mainly made up of appendicular bones (one tibia, two humeri, one femur, one ulna, one radius and five bones from the foot). From the axial skeleton, in addition to the atlas, there are 12 caudal vertebrae and three fused dorsal vertebrae with exostosis. The presence of three clavicles with bony regrowth on the scapular end indicates the presence of at least two individuals in this collection. The clavicle IGF 14824 (Fig. 3) was sent for AMS ^{14}C dating to the University of Berkeley (California) but it did not contain collagen. Besides the *Megatherium americanum*, the Pampas collection consists of four fragments of Glyptodontidae plates. Restoration activities at the time of recovery were not clearly documented. Some bones have minimal restoration or reconstruction material with gypsum, and only old glue was applied. Macroscopically, the whole collection appears similar to the atlas, which will be described in detail below.

Megatherium americanum belongs to the Xenarthra order, a diversified South American native order. It is part of the Megatheriidae family that evolved in the Middle Miocene (Brandoni et al. 2008). It is characterized by its enormity, with weights ranging from four to six tons. Like most of the extinct families of this order, it has no current-day counterpart (Fariña et al. 2013). It had a cylindrical skull and a mandible with a prominent bulge to accommodate the hypsodont and bilophodont teeth. It had a browsing diet but also ate moderate to soft tough foods and it may have been an occasional carrion feeder (Bargo 2001; Fariña et al. 2013). Its anatomical configuration would have allowed it to stand on its hind limbs (Fariña et al. 2013). From a biostratigraphic point of view, this taxon first appeared in the region in the *Megatherium americanum* biozone that starts at 0.4 MA and it was last recorded in the *Equus (Amerhippus) neogaeus* biozone that extended until 8000 yr BP (Tonni 2009).

METHODS

Different surface modifications have been documented including non-biological activity, and non-human and human biological interventions (Tab. 1). The former were useful to analyze what general processes had affected the bone and to partially reconstruct the lost context of the bony elements. Furthermore, they were useful in ruling out any type of activity that might have mimicked cut marks, and thus allowed us to distinguish between non-biological activity and biological intervention. Several studies have been conducted in this field over the past few decades, but due to spatial constraints, only some of the most significant and classical of these works are mentioned here (Tab. 1).

Non-biological activity. The non-biological activity considered included: 1) postdepositional fracture, which is produced when the bone has already lost its organic content (Shipman 1981; Gifford-González 1989); 2) presence of original sediment or concretions, as this is sometimes attached to bones (Lyman 1994); 3) fluvial erosion, which scrapes the surface and, in the long term can cause rounding to the bones (Shipman 1981; Fernández-Jalvo & Andrews 2003); 4) trampling, which occurs when sediments scrape the bones. Trampling often leaves signs that can be confused with cut marks; however, one basic difference is that trampling marks are generally random and undulating (Binford 1981; Olsen & Shipman 1988; Lyman 1994); 5) degree of weathering, caused by exposure to en-

Tab. 1 - Classification of the different surface modification and some of the most important works that explain them.

SURFACE MODIFICATIONS		BIBLIOGRAPHY
NON- BIOLOGICAL ACTIVITY	Post depositional fracture	Shipman 1981; Gifford-González 1989
	Sediment/Concretions	Lyman 1994
	Fluvial intervention	Shipman 1981; Fernández-Jalvo & Andrews 2003
	Trampling	Binford 1981; Olsen & Shipman 1988; Lyman 1994
	Weathering	Behrensmeyer 1978
	Roots	Lyman 1994
	Manganese spots	López-González et al. 2006
	Burning	Lyman 1994; Hanson & Cain 2007
NON-HUMAN BIOLOGICAL INTERVENTION	Insects	Shipman 1981; Lyman 1994; Pomi & Tonni 2011
	Rodents	Binford 1981; Lyman 1994
	Carnivores	Haynes 1980; Binford 1981; Shipman 1981; Gifford-González 1989; Lyman 1994; Martín 2008
HUMAN BIOLOGICAL INTERVENTION	Ancient/ primeval Fractures	Binford 1981; Shipman 1981; Gifford-González 1989; Lyman 1994
	Ancient/ primeval Cut Marks	Binford 1981;Shipman 1981; Olsen & Shipman 1988; Gifford-González 1989; Lyman 1994; Bello & Soligo 2008
	Recent marks or fractures	Shipman 1981; Labarca 2003
	Restoration	Shipman 1981; Labarca 2003

vironmental conditions, which can give an approximate idea of the time of burial (Behrensmeyer 1978); 6) presence of roots (Lyman 1994); 7) presence of manganese spots (López-González et al. 2006); 8) and burned bones due to exposure to fire (Lyman 1994; Hanson & Cain 2007).

Non-human biological intervention. Insect perforation, rodent and carnivore marks were considered among possible types of non-human biological intervention (Binford 1981; Shipman 1981; Lyman 1994; Pomi & Tonni 2011). It is especially important to identify carnivore marks in order to determine whether any type of non-human carnivore may have exploited the carcasses of these animals. Imprints, grooves, perforations, castings and fractures were taken into account (Haynes 1980; Binford 1981; Shipman 1981; Lyman 1994; Gifford-González 1989; Martin 2008).

Human biological intervention. In examining museum pieces, the extraction methods used in the past and the manner in which the museums handled or restored the objects have to be considered. These processes can cause marks or fractures, both at the time of excavation and in the reconstruction and restoration of the fossils in the lab (Shipman 1981; Labarca 2003). Two differences distinguish these fresh traces from the original marks on the piece: fresh cut marks are the color of the subcortical bone and they interrupt postdepositional factors, such as weathering fissures, manganese or trampling (Labarca 2003; Perez et al. 2005; Toledo 2009; Redmond et al. 2012; Dowd & Carden 2016). As these marks are made during and after excavation, they are not subject to postdepositional factors that affected the bone in the past. This explains the different color of newer cut marks and their interruption of past non-biological activity imprinted on the cortical surface.

The definition and differentiation of all these type of processes allows us to identify and determine ancient or primeval human anthropic actions on bones. The cut marks must exhibit the general classical features compiled by different researchers over the years (Binford 1981; Shipman 1981; Olsen & Shipman 1988; Gifford-González 1989; Lyman 1994; Bello & Soligo 2008; among others): they must be elongated with a transversal or longitudinal orientation, have a V-shaped cross-section, and feature parallel striations on their walls. The types of cut marks are related to the amount of force applied, the quantity of remaining meat, the presence of tendons, ligaments or skin, and the instruments used. They are also associated with the anatomical features related to the butchering of the animal (Binford 1981; Gifford-González 1989; Borrero & Martin 2012; Redmond et al. 2012). Once cut marks are identified, they can be related to different butchering stages during the processing of the animal (Binford 1981; Lyman 1994), which allowed the humans to manipulate and access the different organs and pockets of meat inside the animals (Bunn et al. 1988; Lyman 1994).

The material was reviewed with the naked eye and with magnifying glasses (3.5 X and 12 X). A Dinolite microscope 4113 model with magnifications of 20x to 200x and its software (Dinolite 2.0) was also used. This instrument is useful for detecting details and photographing microstriations and cut shapes as well as for taking small measurements. A caliper was used to take general measurements. A Panasonic Lumix DMC-TZ35 camera up to 20x Full HD was used for general photographs.

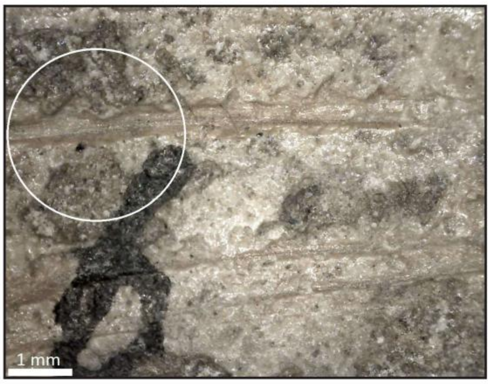


Fig. 4 - Magnification of excavation mark located on the left articulate axis facet of the atlas. The circle indicates the interruption of the manganese spot. 50 x magnifications.

Results

Non-biological activity. The atlas measures 30.5 x 13 x 11 cm. It belongs to an old individual, as evidenced by osteolith regrowth in the foramen (Fig. 1). The atlas bears minor postdepositional fractures, and is well conserved with no adhered concretions or fluvial erosion. Its level of weathering is 1 on the Behresmeyer scale with minimum weathering fissures (1978). This reflects fast burial after the animal's death. There is no evidence of modifications caused by roots or trampling, and only a few manganese spots were found.

Non-human biological intervention. No carnivore or any other kind of non-human biological intervention was detected.

Human biological intervention. The atlas exhibits excavation marks in the left articulation facet. What is relevant about these marks is that they are lighter in color than the surrounding bone and they crosscut manganese spots (Fig. 4). Thus, they must have been made when the material was excavated or during handling at the museum.

The ancient human traces are distributed in four groups, comprised of three to six cuts each. Two are situated on the ventral face and two on the dorsal face, surrounding the facets that articulate with the axis, the second cervical vertebra. They are transversally oriented to the sagittal plane. The groups were numbered from 1 to 4 (Fig. 1).

Group 1 (Fig. 1A, Fig. 5) is on the right part of the ventral face. It is comprised of five marks, two of them measuring approximately 2 cm and the other three between 0.5 and 1 cm. Some weathering fissures and manganese spots cross these cut marks. Thus the marks where made before deposition (Fig. 5A). Near the largest marks, some Hertzian cones were observed as well as internal microstriations (Fig. 5A and B). These marks are deeper than those in group 2, on the left side of the same face (Fig. 1B, Fig. 6). Here, at least three main, more superficial cut marks were counted. One of these measures 3 cm and the others 2 cm in length. Smaller cut marks were detected parallel to these or partially crossing the main marks (Fig. 6A). They are especially abundant near the articular facet and are separated by 0.2 to 0.3 cm. Manganese spots crossing the marks were also documented (Fig. 6B). The traces in these two groups run parallel to one another.

Groups 3 and 4 are situated on the dorsal face, on the left and right side, respectively. In these cases, the marks extend between the border of the articular surface and the posterior alar foramen, which allows the passage of the second spinal nerve (Owen 1861). Group 3 (Fig. 1C, Fig. 7) is made up of 6 main marks measuring approximately 1 cm, oriented parallel to one another and separated by 0.2 cm. They are situated in the medial section of

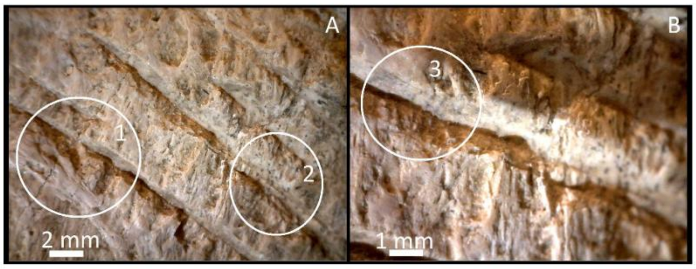
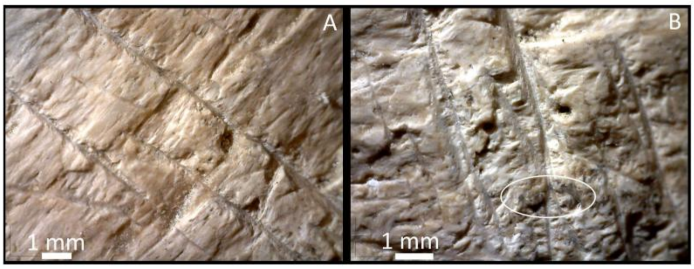


Fig. 5 - Magnification of cut-mark group 1. A - Circle 1 indicates weathering fissures crossing several cut marks and a possible Hertzian cone, circle 2 indicates manganese spots crossing several cut marks. 20 x magnifications. B - Circle 3 indicates internal microstriations. 40 x magnifications.

Fig. 6 - Magnification of cut-mark group 2. A - Detail of long and short marks. 35x magnifications. B - Detail of another section of the marks. In the circle, manganese spots crossing several cut marks. 45 x magnifications.



the posterior alar foramen. At a distance of 2 cm from this group, on the dorsal face, two additional cut marks were documented, measuring approximately 1 cm. These cuts lie next to the posterior alar foramen, which allows the occipital artery to pass (Owen 1861). Group 4 consists of six marks (Fig. 1D, Fig. 8), deeper than those in group 3. They also measure approximately 1 cm with a separation of 0.2 cm between them. They appear slightly more perpendicular in relation to the sagittal plane than the rest of the groups. There are manganese spots both on the bone surface and the cut marks. In this case, two additional marks cross between the two foramens and are parallel to the sagittal plane of the bone.

Discussion

General examinations of the marks. We documented a general regularity in the location of the marks, which surround the facets of articulation with the second vertebra both on the dorsal and ventral faces. Only on the dorsal surface were some additional traces detected farther from the facets, but in these cases, they were near the posterior alar foramen which leaves a passage for the occipital artery. They exhibit the same type of fossilization as the rest of the bone, with manganese and weathering fissures that, in some cases, cross these marks. This implies that they were already present befo-

Fig. 7 - Group number 3 of cut marks, dorsal view.

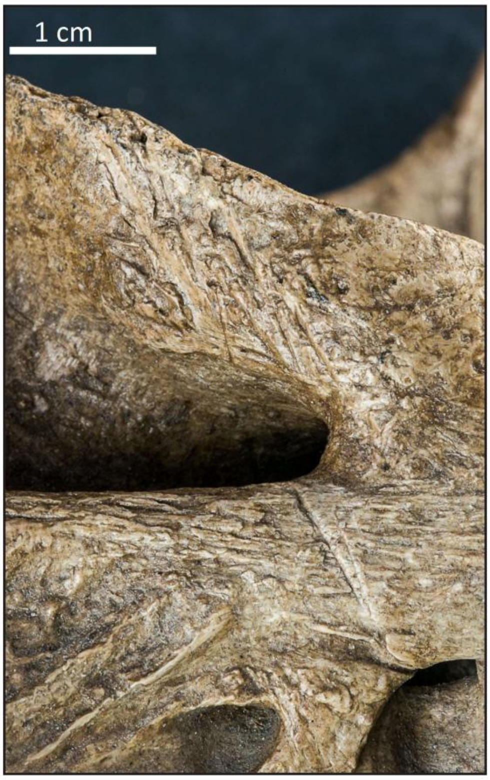


Fig. 8 - Group number 4 of cut marks, dorsal view.

REGION	SITE NAME	LOCATION/ COUNTRY	SPECIE	DESCRIPTION	REFERENCES
NORTH AMERICAN SITES	Blackwater Draw	Clovis, Roosvelt, New Mexico/ USA	*Mammuthus columbi*	Scavenging of the head in 2 mammoths	Saunders & Daeschler 1994
	Colby	Wyoming/ USA	*Mammuthus columbi*	Probable intentional anthropical transportation of skulls	Jones 1991
	Lange/Ferguson	South Dakota/ USA	*Mammuthus columbi*	Separation of the head between 4th and 5th cervical vertebra	Hannus 1989; Jaimes Quero 2005
	Lubbok Lake	Yellowhouse Draw, tributary of Brazos River/ USA	*Mammuthus columbi*	Cut marks and fracture on an immature mandible for probable exploitation of marrow and tongue	Johnson 1976
	Murray Springs	San Pedro River, Arizona/ USA	*Mammuthus columbi*	Possible consumption of brain and tongue in Area 3 (one cranium collapsed and disarticulation of the mandible. Absence of hyoid arch)	Hemmings 2007
	Pleasant Lake	Washtenaw County, Michigan/USA	*Mammut americanum*	Separation of the head by presence of cut marks between atlas and axis	Fischer 1984
	Quagaman	Michigan/USA	*Mammut* sp.	Only head	Fischer 2009
	Sheathelm	Michigan/USA	*Mammut* sp.	Only head	Fischer 2009
	St. Johns	Michigan/USA	*Mammut* sp.	Palate with upper cheek tooth dentition and basicranium	Fischer 2009
SOUTH AMERICAN SITES	Quereo II	Los Vilos/ Chile	*Cuvieronius hyodon*	Cut marks in the occipital condyle of the atlas	Labarca 2003
	Tagua Tagua 1	San Vicente de Tagua Tagua/ Chile	*Cuvieronius hyodon*	Presence of basal cranium for probable brain consumption	Jackson et al. 2011
	Tagua Tagua 2	San Vicente de Tagua Tagua, Chile	*Cuvieronius hyodon*	Ten broken skulls for probable brain consumption	Nuñez et al. 1994
	Taima Taima	Paraguana Peninsula,State of Falcon/ Venezuela	*Stegomastodon waringi*	Transportation of the head with cervical vertebrae for brain consumption/ Processing of the mandible near the site to extract the tongue	Casamiquela 1979
	El Vano	Barbacoas Mountain Range,State of Lara/ Venezuela	*Eremotherium rusconi*	One right mandible with cut marks in the buco lingual region	Jaimes Quero 2005
	Arroyo del Vizcaíno	Canelones/ Uruguay	*Lestodon armatus*	Stylohyal bone with cut marks for consumption of the tongue	Tambusso et al. 2015
	-	Poço Redondo, State of Sergipe/ Brazil	*Eremotherium laurillardi*	Polished tooth with anthropogenic marks and triangular shape	Dantas Trindade et al. 2014
PAMPEAN REGION SITES	Arroyo Seco 2	Tres Arroyos, Buenos Aires/ Argentina	*Megatherium americanum*	Tibia with helical fracture	Steele & Politis 2009
	Campo Laborde	Olavarria, Buenos Aires/ Argentina	*Megatherium americanum*	One rib with cut marks, one rib helically fractured, one rib transformed into informal tool	Politis & Messineo 2008
	Paso Otero 5	Necochea, Buenos Aires/ Argentina	*Megatherium americanum*	Burned bone used as fuel	Martínez et al. 2013

Tab. 2 - Sites named in the text.

re laboratory handling. They are thin and elongated and present internal microstriations or possible Hertzian cones. These marks also form groups with similar numbers of marks and similar separation distances between them. The systematic localization and orientation of the four groups of marks does not correspond to random trampling marks.

Group 1 on the ventral face and group 4 on the dorsal face of the right side are slightly deeper than those situated on the left side. This implies that a more forceful cutting motion was used on the right side. Although this might be discussed in terms of the presence of attached muscles and ligaments, the fact that the same anatomical features are present on the left side rules out this explanation. The evidence here does not allow inferences to be drawn about this difference. However, it might be suggested that the position of the animal at the time of the butchering or the sharpness of the instrument involved in the task could have influenced the different pressure applied when cutting the right and the left side of the vertebra. Although little can be said about the tools involved in this task, some of the instruments associated with megafauna recorded at other sites in the region include flakes, tools such as knives or scrapers and fishtail projectile points. Among the most commonly used raw materials were orthoquartzite, quartz and silicified sandstone (Suárez & Santos 2010; Fariña et al. 2014; Messineo 2015). Therefore, these types of materials might well have been used to process this vertebra.

The marks on the ventral face are longer than those on the dorsal face. This may be related to the presence of the posterior alar foramen on the latter. Additionally, these marks may be related to the act of cutting the arteries and the nerves that pass through these foramens. The presence of additional cut marks near the posterior alar foramen on the dorsal face supports this hypothesis. The cut marks on the ventral side may be longer because no foramens are present on this part of the bone.

Consequently, the four groups of cut marks surrounding the articular facets and the additional dorsal cut marks can be related to one of the dismembering stages that separate the different parts of the animal (Binford 1981; Lyman 1994). They would have been made to separate the first cervical vertebra from the second, with the intention of splitting the head from the postcranial skeleton (Binford 1981). This separation would have been oriented to process the various contents of the head. The most exploited organ here is the brain (Stiner 1991). However, the head also contains other exploitable tissues, such as the tongue and the marrow, or even the teeth, as observed at other American sites with evidence of megamammal exploitation (Tab. 2), which we will briefly discuss below.

American sites for comparison. In order to appreciate the different resources that can be obtained from the exploitation of the head, some of the most significant American sites with this type of evidence were selected for comparison (Tab. 2 and Fig. 2). Sites where the authors suggest any kind of human activity in the head, either based on direct cut marks or contextual interpretation, were taken into account. At North American and South American sites, the most abundant extinct megafauna remains of a size similar to *Megatherium americanum* are the Proboscidea (*Mammuthus, Mammut* and Gomphotheriidae), but evidence of *Eremotherium* and *Lestodon armatus* in South America was also examined. The former belonged to the same family as *Megatherium americanum* (Megatheriidae) and the latter, *Lestodon armatus,* belongs to Mylodontidae. We also considered three important sites in Argentina that present evidence of *Megatherium americanum* exploitation, although none directly related to the consumption of the head.

Different types of references to head exploitation can be seen in Tab. 2, either because of the general pattern of the site, or through direct evidence such as cut marks or fractures. The first case can be observed in Blackwater, Colby and Taima Taima where interpretations were oriented to either the scavenging of the skull in situ (Blackwater), or to the transportation of the element to another location (Colby and Taima Taima) (Casamiquela 1979; Jones 1991; Saunders & Daeschler 1994). In this regard, Fisher (2009) suggests that findings of isolated heads or basicrania, like at Sheathelm, Quagaman and St. Johns, may have resulted from human activity.

Other sites provide insight into how butchering may have been done. This is the case of Lange-Ferguson (separation of the head from the cervical vertebra four and five) (Hannus 1989; Jaimes Quero 2005), Pleasant Lake (cut marks on the first and second vertebrae) (Fisher 1984), and Quereo II, where Labarca (2003) studied old collections from Quereo and found cut marks on the anterior part of an atlas. It should also be mentioned that in Taima Taima the last cervical vertebra must have been separated from the thoracic vertebra, as no cervical vertebra was found (Casamiquela 1979).

In addition, cut marks can be associated with the consumption of the tongue and the marrow, as suggested at Lubbock Lake (Johnson 1976), the cut marks found on mandibles at El Vano (Jaimes Quero 2005) and Taima Taima (Casamiquela 1979), and the hyoid cut mark at Arroyo del Vizcaíno. In this last site, the cut would have been made in order to extract the 10 kg tongue of a *Lestodon armatus* (Tambusso et al. 2015). At Taima Taima, only the mandible was found near the site, which might be due to the process of extracting the tongue (Casamiquela 1979). In other cases, the skulls were crushed to extract the brain, like at Tagua Tagua 1 and 2 (Nuñez et al. 1994; Jackson et al. 2011). Meanwhile, at Murray Springs, one cranium was found crushed for brain consumption and the mandible was disarticulated to better access the tongue (Hemmings 2007). Finally, in Poço Redondo, Brazil, another type of evidence was found: A polished, triangular shaped tooth of *Eremotherium laurillardi* suggests that not only were the tissues of the head exploited, but the teeth may also have been sought out as a raw material (Dantas Trindade et al. 2014).

In Argentina, exploitation of *Megatherium americanum* has been documented at three sites. At Arroyo Seco 2, exploitation of this taxon included one helically fractured tibia (Steele & Politis 2009), while at Campo Laborde, three ribs exhibit evidence of human intervention in the form of cut marks or bone technology (Politis & Messineo 2008). In Paso Otero bones of this species and others were used as fuel (Steele & Politis 2009; Martínez et al. 2013).

Purpose of the marks and access scenarios. These different American sites show that the contents of the head were deemed useful throughout the continent. Considering all of the above examples, the most plausible explanation for the described cut marks is that they were made to remove the head and possibly exploit the contents of the head of an old *Megatherium americanum* individual. The brain and tongue may have been the most sought after organs. The brain of a *Megatherium americanum* was half the size of a modern-day elephant's (Owen 1861), which weighs approximately 4 kg

(Agam & Barkai 2016). On the other hand, like the *Lestodon armatus*, these animals also had voluminous tongues that could have been consumed. It is also possible that marrow and even teeth may have been resources extracted from the head. In the Pampas region, this species was not only a source of edible tissues, but the bones were also used for tool production or even fuel (Politis & Messineo 2008; Martínez et al. 2013). Hence, the high processing cost can be compensated by the complete use of the animal's skeleton.

The head contents of this animal could have been exploited in a primary or secondary access scenario.

Primary access can imply either hunting or early access to an animal that died of natural causes. Binford (1981) refers to the separation of the head as one of the first processing actions taken when dismembering an animal. This can be done between the occipital condyles and the first vertebra, between the first and the second vertebra, or from the consecutive cervical vertebrae (Binford 1981; Bunn et al. 1988; O'Connell et al. 1990; Lupo 1994). The separation of the head, at least at the sites reviewed here, can be done in other ways as well, as at times the first cervical vertebrae was involved and at other times the last vertebrae were cut to separate the head and the neck. In the case presented here, the position of the four groups of cut marks implies that in this *Megatherium americanum* individual, the separation of the exploited head also included the first vertebra. This skeletal component is sometimes transported or may be eaten at the kill spot, depending on the animal, the number of people in the carrying party, and the distance from the base camp, among other factors (Binford 1981; Bunn et al. 1988; O'Connell 1990). In the vertebra studied here, the lack of context does not allow us to determine whether transportation occurred. Among the above-cited American sites, transportation was only detected at Colby and Taima Taima (Casamiquela 1979; Jones 1991).

The head contents may have been exploited in a secondary access scenario. In this case, the exploitation of the head would have been related to scavenging (Blumenschine 1986; Stiner 1991). It was recently noted, however, that the use of the head is not always related to a marginal scavenging tendency. Although hard and heavy, the rich protein content of the head justifies its intentional transport and high processing costs (Agam & Barkai 2016), especially when the head contains all the tissues intact, as the fleshy parts of the head can be eaten faster than the brain because the skull is difficult to break for carnivores (Blumenschine 1986; Haynes 1988). However, as proposed earlier, if the cut marks described above were made for the purpose of exploiting the various contents of the head, this would imply that no part of the head had previously been consumed by carnivores. As suggested by the presence of elephant heads in Paleolithic sites (Agam & Barkai 2016), this could have been an intentional behavior, even in a scavenging scenario. Consequently, the human scavenging of megafauna carrion would have been added to an already existing scavenging niche in the Pampas region. Direct evidence of megafauna exploitation by carnivores in the region is scarce. Although one cf. *Eosclerocalyptus lineatus* (Hoplophorini) neurapophysis from the Pliocene was scavenged by *Chapalmalania* (Procyonidae) (de los Reyes et al. 2013). Therefore, as observed in European and African environments, the wide array of megafauna in the region would have been exploited by different types of carnivores, including humans (Blumenschine 1986; Stiner 1991; Arribas & Palmqvist 1999; Fariña et al. 2013, among others).

CONCLUSION

The atlas from a *Megatherium americanum* individual housed at the MSNF presented anthropic cut marks. They comprise four groups of traces on the ventral and dorsal faces, surrounding the facets that articulate the axis. The aim of the action that created these marks would have been to separate the head from the postcranial skeleton in an old *Megatherium americanum* individual. This action may have occurred in a primary or secondary access scenario, possibly to exploit the various different resources contained in the head. This is the first time that this type of human intervention has been documented on this element of this species.

This research, like similar studies carried out on museum collections all over the world (Prous 1986; Saunders & Daeschler 1994; Labarca 2003; Perez et al. 2005; Martin 2008; Fisher 2009; Toledo 2009; Krasinski 2010; Redmond et al. 2012; Chichkoyan et al. 2015; Dowd & Carden 2016), constitutes a complementary, but very useful way to search for new information. The discovery of biological marks (left by both humans and carnivores) on material collected during the 19th century means that these collections potentially harbor important information to be investigated. Though there is neither contextualization nor association with other materials, the application of new techniques developed in these last decades combined with an interdisciplinary perspective allows researchers to maximize the information obtained. It also allows us to integrate and compare this new data from an interdisciplinary point of view and at a coarse-grained level with information from other sites in order to better interpret the evidence. Consequently, the study of these old collections provides new information regarding the behavior of early human populations and their paleoecological relationships with fauna (Chichkoyan et al. 2015).

This makes old museum collections a complementary resource to information obtained from archaeological records coming from stratigraphically controlled excavations. Archaeological data is a non-renewable resource (Pérez de Micou 1998), so looking for new sources of information like that considered here is a productive way to obtain new information. It reduces research costs and the anthropogenic modification of the landscape (Pérez de Micou 1998). But to work with these kinds of samples, the researcher must also bear in mind that this material is part of a biased record, in which only certain bones and species, or only the most visible pieces, would have been chosen (Turvey & Cooper 2009). When these types of caveats are taken into account, bone remains recovered in museum collections constitute a significant contribution. Research at other museums will allow more information like this to be recovered. The dating of that material will help to establish a referential chronology of when these interactions occurred. This information can be combined with current research programs to develop new axes of study.

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5.3.4. DIRECT EVIDENCE OF MEGAMAMMAL-CARNIVORE INTERACTION DECODED FROM BONE MARKS IN HISTORICAL FOSSIL COLLECTIONS FROM THE PAMPEAN REGION

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Abstract

Pleistocene South American megafauna has traditionally attracted the interest of scientists and the popular media alike. However, ecological interactions between the species that inhabited these ecosystems, such as predator-prey relationships or interspecific competition, are poorly known. In this regard, carnivore marks imprinted on the fossil bones of megamammal remains are very useful for deciphering biological activity, and hence, potential interspecific relationships among taxa. In this article, we look at historical fossil collections housed in different European and Argentinean museums that were excavated during the 19th and early 20th centuries in the Pampean region, Argentina, in order to detect carnivore marks on bones of megamammals and provide crucial information on the ecological relationships between South American taxa during the Pleistocene. Our results indicate that the long bones of megafauna from the Pampean region (e.g., the Mylodontidae and Toxodontidae families) exhibit carnivore marks. Furthermore, long bones of smaller species and indeterminate bones also present punctures, pits, scores and fractures. Members of the large-carnivore guild, such as ursids, canids and even felids, are recognised as the main agents that inflicted the marks. We hypothesize that the analysed carnivore marks represent the last stages of megaherbivore carcass exploitation, suggesting full consumption of these animals by the same or multiple taxa in a hunting and/or scavenging scenario. Moreover, our observations provide novel insights that help further our understanding of the palaeoecological relationships of these unique communities of megamammals.

Key Words
Historical collections – Pleistocene - Taphonomy - Pampean Region - Carnivores

Introduction

Reconstructing the biological interaction between extinct animals, including competition or predator-prey relationships, is extremely difficult. This is particularly true when the information available from living analogues is limited (Figueirido, Martin-Serra & Janis, 2016). This is particularly true in the case of ancient South American ecosystems, as members of the megafauna became extinct during the latest Pleistocene-early Holocene, and these groups of mammals have no living counterparts (Cione, Tonni & Soibelzon, 2009; Fariña, Vizcaíno & de Iuliis, 2013). Located in the southern portion of this continent, Pampean (Argentinean) megamammals have fascinated scientists since the 18th century, nevertheless, attempts to understand their palaeoecology are much more recent (e.g., Fariña, 1996; Bargo, 2003; Prevosti, Zurita & Carlini, 2005; Prevosti & Vizcaíno, 2006; Figueirido & Soibelzon, 2010; de los Reyes et al., 2013; Fariña, Vizcaíno & de Iuliis, 2013; Scanferla et al., 2013; Soibelzon et al., 2014; Bocherens et al., 2016). To this end, carnivore marks preserved on the fossil bones of megaherbivores constitute an important source of information as they represent direct evidence of predator-prey relationships, or alternatively, of scavenging activity by top predators such as strictly flesh-eating and/or bone-cracking hypercarnivores (e.g., Haynes, 1982; Marean & Ehrhardt, 1995; Pobiner & Blumenschine, 2003; Pickering et al., 2004; Palmqvist et al., 2011; Espigares et al., 2013). Consequently, detecting the marks of biological activity preserved on the bone surfaces of Pampean megamammals, by means of detailed taphonomic investigations and using next-generation techniques, is crucial in deciphering the ecological relationships between Pleistocene South American palaeocommunities.

Previous studies of bone surfaces performed on fossil collections housed in various museums in the Americas have revealed carnivore activity, and hence animal interaction (Haynes, 1980; Martin, 2008, 2016; de Araújo Júnior, de Oliveira Porpino & Paglarelli Bergqvist, 2011; Dominato et al., 2011;

Labarca et al., 2014). In South America, carnivore marks have been reported from different locations (Fig. 1). Specifically in the Pampean region, there is a neural apophysis of a glyptodont cf. *Eosclerocalyptus lineatus* (Glyptodontidae, Hoplophorini) from the Pliocene (Olavarría) with a clear carnivore tooth imprint, attributed to a giant *Chapalmalania* (Carnivora, Procyonidae) procyonid (de los Reyes et al., 2013). Recently, a taphocoenosis from the margins of the Salado River, comprising remains of the equid *Hippidion principale* (Perissodactyla, Equidae) and some indeterminate bones with carnivore marks, was associated with the dirk-toothed sabre cat *Smilodon* sp. (Carnivora, Felidae, Machairodontinae) (Scanferla et al., 2013). At the archaeological site Arroyo Seco 2, bones of extinct horses such as *Equus* sp. (Perissodactyla, Equidae) show carnivore marks (Politis et al., 2016). In Patagonia, the jaguar *Panthera onca mesembrina* (Carnivora, Felidae, Pantherinae) was reportedly responsible for interventions involving the ground sloth Mylodontidae (Xenarthra, Tardigrada) and *Hippidion* groups (Martin, 2008, 2016), and a member of Felidae produced marks on mastodont (Mammalia, Proboscidea; Gomphotheriidae) bones (Labarca et al., 2014) during the late Pleistocene. In Brazil, two sites have been described where the small canid *Protocyon troglodytes* (Carnivora, Canidae) presumably scavenged the carcasses of two mastodons, *Notiomastodon platensis* (Proboscidea, Gomphotheriidae), the giant ground sloths *Eremotherium laurillardi* (Tardigrada, Megatheriidae) and *Glossotherium* (Tardigrada, Mylodontidae) (de Araújo Júnior, de Oliveira Porpino & Paglarelli Bergqvist, 2011), and *Haplomastodon waringi* (Mammalia, Proboscidea) in the Pleistocene (Dominato et al., 2011).

In this article, we study, for the first time, carnivore marks on megamammal (>1000 kg; Cione, Tonni & Soibelzon, 2009) remains from different fossil collections recovered from the Pampean region and now housed in various institutions in Europe and Argentina. Our goal is to identify potential biological activity using taphonomic methods in order to understand predator-megaherbivore interaction within Pleistocene South American mammalian communities from the Pampean region.

Materials & Methods

In order to identify those bones showing evidence of carnivore intervention, we examined 1,976 bones belonging to the following four collections (Table 1): (i) 1,478 bones from the Rodrigo Botet collection, housed at the *Museo de Ciencias Naturales de Valencia* (MCNV; Spain) that are the result of excavations undertaken by Enrique de Carles in the Northeast of the Buenos Aires province (Belinchón et al., 2009); (ii) 30 bones from the Dupotet collection, housed at the *Muséum National d' Histoire Naturelle* (MNHN; Paris, France), of Pampean age from Luján City; (iii) 330 bones from the Krncsek collection, housed at the *Naturhistorisches Museum Wien* (NMW; Austria) that proceed from the Luján River in Mercedes City and are identified as “Diluvium-Upper Pampean”; and (iv) 138 bones from the Canal de Conjunción collection (La Plata), housed at the *Museo de La Plata* (MLP), and which were extracted from a 20 m stretch along both sides of a water channel (Ameghino 1916 [1889]:128- 129).

These collections were generated during various non-systematic excavations carried out in the Eastern region of what is currently Buenos Aires province, in the Pampean region (Argentina), during the 19th and early 20th centuries. This is an extensive, flat geomorphological unit located in the central area of Argentina. The Quaternary was characterised by loess deposition, with different regressive and transgressive events (Fucks & Deschamps, 2008; Cione, Tonni & Soibelzon, 2009). The early and middle Pleistocene corresponds to the Ensenadan and Bonaerian Stages/Ages that were characterised by a cold and arid environment (Fucks & Deschamps, 2008; Cione, Tonni & Soibelzon, 2009). An important faunal turnover marks the boundary between the two stages, at *ca.* 0.5 Ma (Cione, Tonni & Soibelzon, 2009). The late Pleistocene-early Holocene corresponds to the Lujanian Stage/Age. Significant palaeoenvironmental oscillations, aeolian pulses, fluvial process and various pedogenetic events influenced this period (Tonni et al., 2003; Fucks & Deschamps, 2008; Cione, Tonni & Soibelzon, 2009). When the collections analysed in this study were originally collected, these units were included in the “Pampean Formation” (Tonni, 2011). Current biostratigraphical information (Tonni, 2009) allows the material from MCNV to be assigned to the Ensenadan to Lujanian, Stage/Age and the material from MNHN and NMW to the Bonaerian and Lujanian Stages/Ages. Furthermore, in the NMW collection, the old reference to Upper Pampean is currently equivalent to the Bonarian Stage/Age (Tonni, 2011). The last record of these mammal groups comes from the Guerrero Member of the Luján Formation, deposited between 21,000 and 10,000 ^{14}C years BP. (Tonni, 2009). In the case of the MLP assemblage, the presence of the notoungulate *Mesotherium cristatum* (Notoungulata, Mesotheriidae) among the identified species means this material can be dated as Ensenadan (Cione, Tonni & Soibelzon, 2009) (Fig. 2 and Table 1).

To understand the natural burial conditions of the remains, we considered different types of bone surface modifications such as post-depositional fractures, the presence of original sediment or concretions, fluvial erosion, trampling, weathering, root growth, manganese spots and burning traces (e.g., Behrensmeyer, 1978; Binford, 1981; Shipman, 1981; Olsen & Shipman, 1988; Lyman, 1994; Fernández-Jalvo & Andrews, 2003, 2016). These allowed us to discard any type of intervention that could simulate carnivore activity or, if superimposed onto carnivore marks, could have indicated a previous carnivore intervention.

We used the literature to identify whether bone marks were the result of carnivore activity (e.g., Haynes, 1980, 1982, 1983; Binford, 1981; Capaldo & Blumenschine, 1994; Lyman, 1994; Domínguez-Rodrigo & Piqueras, 2003; Pickering et al., 2004; Domínguez-Rodrigo et al., 2012; Delaney-Rivera et al., 2009; Sala, Arsuaga & Haynes, 2014; Sala & Arsuaga, 2016). Digested remains were not considered in the analysis. Large mammal bones do not often display the effects of digestion as they are too large to be ingested whole (Fernández-Jalvo & Andrews, 2016). Small bones tend to be splintered by the teeth of predators, making them impossible to classify either anatomically or taxonomically (Fernández-Jalvo & Andrews, 2016). This type of fragmented material was not included in our review, as a lack of context made it difficult to assign biological marks to specific taxa. The exception to this were the indeterminate and smaller bones from the MLP collection where part of the original association was conserved. Coprolites were absent in the reviewed collections.

We classified the bone marks potentially produced by carnivores into four categories (Table S1): (i) pitting and/or punctures, (ii) u-shaped elongated scratches or scores, (iii) furrowing; and (iv) spiral fractures. To explore the body size of the carnivores that potentially inflicted the marks, we used a box plot diagram (Hammer, Harper & Ryan, 2001) to compare the size of the pitting and/or punctures from the MCNV, MNHN and MLP specimens with those published by Pickering et al. (2004) (various bones), de los Reyes et al. (2013) (bone specimen Xen 30-12), and Martin (2016) (various bones); the material from NMW was excluded as the marks were too few to calculate the log area (Table S2 to S5). We chose the abovementioned studies as they allowed us to compare palaeontological and archaeological cases from the Pampean region, Patagonia, and one African case, and appreciate any similarities and/or differences with African ecosystems. Even though this information was still statistically poor, it allowed us to make some preliminary assumptions. Additionally, assigning a pit or puncture to a specific taxa is always problematic given the different factors involved (e.g., the part of the bone marked and the bite force of an animal) (Delaney-Rivera et al., 2009). Nevertheless, the overlapping of our data with the comparative cases allowed us to ascribe the marked bones to general carnivore size categories. Even though some authors have also included scores in their studies of body size (Delaney-Rivera et al., 2009; Labarca et al., 2013, de Araújo Júnior, de Oliveira Porpino & Paglarelli Bergqvist, 2011) we agree with Domínguez-Rodrigo & Piqueras (2003) that score marks relate not only with teeth size, but also the effect of the teeth being dragged over the bone surface; variability can therefore be expected from this type of mark.

We also systematically reviewed actualistic studies describing the marks that different carnivore taxa leave when feeding and, more specifically, recent research into marks made by the members of the large carnivore guild, such as ursids (Carnivora, Ursidae), felids (Carnivora, Felidae) and canids (Carnivora, Canidae) (Table S1). Specialised bone-breaking hyenas were not considered because they were not present in South America. Various studies report that ursids leave scarce to abundant teeth marks (Haynes, 1980, 1983; Burke, 2013; Saladié et al., 2013; Arilla et al., 2014; Sala & Arsuaga, 2016). In contrast, felids tend to make fewer marks on the bones since they feed exclusively on meat (Christiansen & Wroe, 2007; Sala & Arsuaga, 2016), although they can leave important signs of predation (Haynes, 1983; Marean & Ehrhardt, 1995; Martin 2008, 2016; Domínguez-Rodrigo et al., 2012; Kaufmann et al., 2016; Sala & Arsuaga, 2016). Finally, canids can produce a great number of intervention marks (Haynes, 1982, 1983; Yravedra et al., 2011; Burke, 2013; Domínguez-Rodrigo et al., 2012; Sala, Arsuaga & Haynes, 2014; Sala and Arsuaga 2016). Furthermore, while felids (including *Smilodon*) and ursids have straighter incisive arcades, canids have curved arcades (Biknevicius, Van Valkenburgh & Walker, 1996). This shape is useful when analysing pitting and/or puncture arrangements on bone surfaces (e.g., linear or curved rows of tooth impressions).

We examined the fossil remains of the megaherbivores present in the collections with 3.5x and 12x magnifying glasses. We also used a Dino-Lite Microscope AD4113T (at magnifications of 20x to 45x) and the software Dino-Lite 2.0. Both the length and breadth (major and minor axes) of the scores, pits and punctures were measured. Larger marks were measured using a caliper, and smaller ones were recorded with the measurement tool installed in the Dino-Lite. For each collection, high-resolution digital images were taken, in each museum, using a Panasonic Lumix DMC-TZ35 camera.

For the MLP assemblage we also applied the well-established archaeozoological variables MNI (Minimum Number of Individuals) and NISP (Number of Identified Specimens) as all the specimens are part of the same taphocoenosis (Lyman, 1994). While MNI was used to account for the minimum number of mammals with carnivore marks represented in the sample, the second informed the counting per taxa or skeletal part categories.

Results

We found four bones (0.2% of the total) of megaherbivores and 24 bones (1.24% of the total) of smaller and indeterminate species with potential carnivore intervention. In addition, a detailed description of the marks is given in the supplementary information (Data S1). Below, we give a general overview of the most important damage found in each collection (Table 2 and Table S5) and provide general observations from the box plot diagram (Fig. 3):

(i) A right tibia from the MCNV (nº 64-492) that corresponds to the ground sloth cf. Scelidotheriinae gen (Tardigrada, Mylodontidae). This bone presents important furrowing on both epiphyses and pits and scores on the distal epiphysis, as well as on the posterior and medial faces of the diaphysis (Fig. 4). In the box plot diagram it can be observed that the measurements of these pits slightly overlaps with the maximum sizes of large carnivores (and outliers) from Pickering et al. (2004) and falls conformably within the measurements presented by de los Reyes et al. (2013), but are slightly bigger than the Pampean case (de los Reyes et al., 2013). Nevertheless, this discrepancy could be due the bigger pit from MCNV that seems to be enlarged by post-depositional process (Data S1 and Fig. S1). They also coincide with the smaller sizes from Cueva del Milodón (Martin, 2016);

(ii) A left humerus of *Glossotherium robustum* labelled MNHN.F. PAM 119 from MNHN, with pits, scores and furrowing (Fig. 5). Comparing this with the other samples reveals the same trend as for MCNV. It matches with the log area of the tibia from MCNV, but also overlaps more with the specimens in Pickering et al. (2004) because of the presence of smaller pits on the MNHN bone. It also coincides with the range of Xen 30-12, but has bigger and smaller log area extremes than the

Pampean case (de los Reyes et al., 2013). In addition, it compares well with the smaller marks from Cueva del Milodón (Martin, 2016);

(iii) A left distal humerus of *Mylodon robustum* (nº 1908.XI.110) housed at MNW with furrowing and a possible puncture (Fig. 6). The furrowed border is scalloped and part of it is flaked. This species is considered to represent *Glossotherium robustum* (McAfee, 2009). Although not plotted, Table S5 shows that the log area coincides with the range for the rest of the sampled material; and

(iv) At the MLP, one femur condyle from the notoungulate Toxodontidae (MLP 15-I-20-32) (Notoungulata; Toxodonta) was found with scratches (Fig. 7). Moreover, in this collection 22 long bones of smaller species and two further indeterminate bones have fresh fractures, scratches, punctures/pits and crenulated edges (details of these marks are shown in Table S6) (Fig. 8 to 10). The box plot reveals the same trend for these pits and punctures as seen in the other cases. Nevertheless, the presence of smaller marks on this sample results in greater coincidence with the Swartkrans specimens (Pickering et al., 2004), and there is partial overlap with Xen 30-12 (de los Reyes et al., 2013). However, only the outliers from MLP coincide with the smaller sizes from Cueva del Milodón (Martin, 2016), and the plot partially overlaps with those of the material from MCNV and MNHN. The smaller pits on the MLP specimens were considered together with the bigger punctures on the two indeterminate bones. Large carnivores can generate both small and large pits and/or punctures (Delaney-Rivera et al., 2009), and this may explain the variability in the marks observed here.

Discussion

The above information suggests that the different types of bone marks found on both megamammal and small mammal remains were most likely inflicted by various large-size carnivore taxa that inhabited the Pampean region during the Pleistocene. Considering the limited evidence available from this region, the data presented here is crucial for exploring different predator-prey relationship scenarios and/or scavenging activities, at a coarse scale.

The agents: Pleistocene mammalian predators from the Pampean region

Several species of Quaternary carnivores have been recorded from the Pampean region. In the supplementary information, we offer a general description of these, along with some ecological characteristics (Data S2). These carnivores include ursids, felids and canids. The ursids comprise *Arctotherium angustidens* from the Ensenadan Stage/Age and *Arctotherium vetustum*, *Arctotherium bonariense* and *Arctotherium tarijense* from Bonarian and Early Lujanian times (Soibelzon et al., 2014; Figueirido & Soibelzon, 2010). In particular, the first species would have had an important capacity to feed on meat (Figueirido & Soibelzon, 2010). Felids are represented by three hypercarnivorous species: *Smilodon populator*, *Puma concolor* and *Panthera onca* (Christiansen & Harris, 2006; Prevosti & Vizcaíno, 2006; Bocherens et al., 2016). While the first two had some bone marking capacity, the third would have been capable of inflicting more damage (Van Valkeburgh &

Hertel, 1993; Marean & Ehrhardt, 1995; Antón et al., 2004; Martin, 2008, 2016; Muñoz et al., 2008; Binder & Van Valkenburgh, 2010; Domínguez-Rodrigo et al., 2015; Kaufmann et al., 2016). Finally, several pack-hunting and/or scavenging canids were present at the time, including *Theriodictis platensis* (and its sister taxon "*C*". *gezi*) in the Ensenadan (Prevosti & Palmqvist, 2001; Prevosti, Tonni & Bidegain, 2009), various *Protocyon* species throughout the Pleistocene (Prevosti, Zurita & Carlini, 2005; Prevosti & Schubert, 2013; Bocherens et al., 2016), *Canis nehringui* (currently recognised as a junior synonym of *C. dirus*, Prevosti, Tonni & Bidegain, 2009), and *Dusicyon avus* in the Late Pleistocene (Prevosti & Vizcaíno, 2006).

It is clear that carnivores with an important capacity for bone modification and/or consumption would have been responsible for the various marks observed. Even though felids such as *Smilodon* or *Puma* could have produced some bone-damage, as observed in some studies (Van Valkeburgh & Hertel, 1993; Marean & Ehrhardt, 1995; Muñoz et al., 2008; Kaufmann et al., 2016), their reduced bone-breaking potential rules them out as the principal generator of the feeding traces recorded. Furthermore, it is worth mentioning that the highly specialised viscera-eating dentition of the dirk-toothed *Smilodon* would have prevented this animal from feeding on carrion unlike other scimitar-toothed predators (e.g., *Homotherium*).

Identifying potential agents of the megamammal tooth-marks

Based on the box plot comparisons (Fig. 3), the marks on the samples in this study best match those made by the giant Pampean *Chapalmalania* (de los Reyes et al., 2013). This procyon had previously been compared with a bear, although according to de los Reyes et al., the cranial configuration is more similar to that of hyenas. From the information presented by Pickering et al. (2004), it seems that the damage inflicted also coincides to some degree with that made by large African carnivores, such as large canids, spotted hyenas and lions, or the smaller marks realised by *Panthera onca mesembrina* (Martin, 2016). These African species correspond to sizes 2 or 3 in the Bunn ranking (1986). Cross-referencing these sizes with the Pampean carnivores, they coincide with several ursids, felids and canids, although some Pampean species were larger, such as *Smilodon populator*, size 4, and *Arctotherium angustidens*, size 5 (Table 3). Moreover, the reports from the various South American sites involving pitting and/or punctures show a similar range of values as seen in this study (Table 4). Most of this information could not be plotted, as the number of marks found at each site was too low to be able to input them into the calculation. Nevertheless, it can be observed that the majority range from 5 to 10 mm in size (those from Cueva del Milodón are larger, as shown in the box plot). According to this data, different members of the Pampean large-carnivore guild would have produced the bone damage observed on the samples from the various museums. To determine which carnivores were involved, we must relate the marks to the types of bone damage generated by the potential ursid, felid and canid taxa.

The MCNV cf. Scelidotheriinae gen. tibia is the bone that presents the most significant carnivore interventions. A combination of pitting, scratches and important furrowing was observed, on both the epiphyses and medial faces. Even though all three groups of carnivores were capable of leaving these types of marks, certain characteristics allow us to relate this damage to ursids. In particular, the group of aligned pits imprinted on the medial rim (Fig. 4A) of the distal epiphysis is planar that could indeed have been made by the premolars or molars of ursids (Haynes, 1983). In contrast, the parallel, V-shaped tooth marks on the posterior face (Fig. 4C and Fig. 4E) could be related to a series of incisors and canines and would coincide with the dragging action of a straight incisor arcade (Biknevicius, Van Valkenburgh & Walker, 1996). On the other side, the parallel scores, like those seen on the distal metadiaphysis (Fig. 4B), are also generally characteristic of ursids (Haynes, 1983; Saladié et al., 2013). In addition, the intensive furrowing coincides with the bone-breaking capacity of this animal (Soibelzon et al., 2014). Other damage typical of ursids observed on the tibia includes the elongated gouge on the lateral side of the articular face (Fig. 4A) and the quadrangular-shaped grooves on the medial face of the diaphysis (Fig. 4D) (Burke, 2013; Saladié et al., 2013). That being said, these grooves, and the gouges observed on the distal metadiaphysis, do not have the regular walls and bottoms characteristic of ursid marks (Saladié et al., 2013). Also, according to current research, this damage should be superficial, a feature not observed on this bone (Haynes, 1983; Saladié et al., 2013). In this respect, some authors suggest that the damage produced by ursids is less intense than that inflicted by other groups (Haynes, 1983; Arilla et al., 2014; Sala & Arsuaga, 2016), a pattern not observed here. Consequently, more than one animal may have participated in imprinting the complex and producing the marks observed on this tibia. If that is the case, *Panthera onca* could have been involved, too. This species also possessed straight incisive arcades (Biknevicius, Van Valkenburgh & Walker, 1996) that could have produced the elongated V-shape marks (Haynes, 1983) on the posterior face. The important furrowing noticed at both ends of the bone is also consistent with this felid's damage-producing capacity (Martin, 2008, 2016; Domínguez-Rodrigo et al., 2015).

The humerus of *Glossotherium robustum* housed in the MNHN has suffered less bone loss than the tibia. Feeding marks on this element have several characteristics that could indicate it was damaged by *Arctotherium*. As observed on the tibia, the short, wide scratches present on the condyle and the wide, elongated, superficial pitting, agree with actualistic studies of ursid marks (Fig. 5B and Fig. 5C) (Haynes, 1983; Burke, 2013; Saladié et al., 2013). Nevertheless, the presence of V-shape punctures in the trochlea (Fig. 5B), characteristic of felids rather than ursids, means that other taxa, such as

Panthera onca, cannot be ruled out (Haynes, 1983). Both groups were capable of furrowing the epiphysis (Martin, 2008; Arilla et al., 2014; Domínguez-Rodrigo et al., 2015) as observed on the trocheal part of the bone (Fig. 5D).

The furrowing on the MNW *Glossotherium robustum* humerus is more ambiguous than the marks on the other two bones, since various taxa could have inflicted this type of damage on cancellous bone (Fig. 6A to 6D). The cusp that made the puncture could have been on a secodont tooth from a felid or canid (Fig. 6B). Both these groups have the capacity to damage and destroy cancellous tissue, although canids leave fewer marks on mammals larger than 400 kg (Yravedra, Lagos & Bárcena, 2011). Patagonian sites with important furrowing in Mylodontidae bones, attributed to *Panthera onca mesembrina*, could provide an important parallel (Martin, 2008, 2016) when considering the types of marks that jaguars can make on limb bones, as seen in this case.

The marked femur of Toxodontidae from the MLP must be integrated with the other evidence from the taphocoenosis in order to interpret which carnivore species was involved. Of the 138 bones studied from this site, 61.59% (NISP: 85) belong to indeterminate species, while the remaining 38.40% (NISP: 53) were identified to genus level. Among these, equids are the most common, accounting for 36.53% (NISP: 19) of the identified elements. Megamammal bones are the second most widely represented group, with 30.76% (NISP: 16). The assemblage predominantly comprises appendicular skeletal elements (73.92% or NISP: 102). Axial and planar bones contribute only 13.77% (NISP: 19) and indeterminate fragments account for 12.31% (NISP: 17). Of the carnivore-marked bones, 88% (NISP: 22) are indeterminate diaphysis of the long bones mentioned above (Tab. S6), coinciding with the general abundance of limb elements. Carnivore-marked bones represent only 18.11% (NISP: 25) of the total assemblage. The low proportion found at this site could have been influenced by its location in running water. As explained by Ameghino, (1916 [1889]) the material from this site was scattered along a 20 m stretch on both sides of a channel. Therefore, the current may not only have dispersed the primary association, but also mixed it with bony remains not originally consumed by the carnivore/s involved. This may also have influenced the skeletal assemblage, including the paucity of axial parts, resulting from density-mediated destruction or the winnowing of lighter axial bones. Nevertheless, the fact that 18.11% of the bones are marked by carnivores also indicates that a basic level of primary association remained when this material was collected. The presence of the Toxodontidae femur and other smaller bones with carnivore marks indicates that a MNI of 2 animals were consumed in the location itself. In addition, the dominance of fractured long bones could, partly, have been the result of carnivore activities that transported limbs to this area. Consequently, the carnivore/s involved in the formation of the collected assemblage must have had the capacity to break long bones and/or the ability to predate upon megamammals. In this sense, given the absence of specialised bone-crushers in the Americas, some type of canid may have been responsible for the described interventions. It is likely that either *Theriodictis platensis* or

Protocyon scagliorum from the Ensenadan Stage/Age generated these marks, as also inferred for the Brazilian cases (de Araújo Júnior, de Oliveira Porpino & Paglarelli Bergqvist, 2011; Dominato et al., 2011).

In any event, although the proportion of carnivore marks that we have found on bones of megamammals is relatively low, this precludes the conclusion that the sites where the remains were originally collected represented the den of a hypercarnivore or bone-cracking species.

Other potential carnivores specialising in medium-sized and/or small taxa, such as *Canis nehringui* or *Dusicyon avus,* could have fed on the megaherbivore community during the late Pleistocene (Prevosti & Vizcaíno, 2006; Prevosti, Tonni & Bidegain, 2009). At *ca.* 14.000 cal yrs BP (Politis et al., 2016) *Homo sapiens* also became part of the carnivore guild. Humans not only scavenged megamammal carcasses (Politis et al., 2016), but were also more successful hunters of these animals than the existing carnivores (Cione, Tonni & Soibelzon, 2009).

Megamammal carcass consumption during the Pleistocene

Considering the skeletal elements, bone mark locations, and the level of use of the bones, it seems most likely that these marks represent the final stages of megamammal carcass consumption.

(i) Marks on the tibia and the humeri are situated on the epiphysis, both the articular surface and metadiaphyses. In a hunting event, carnivores that have access to a large mammal usually begin to feed on the abdominal part, later moving to femoral muscle masses, leaving some marks on the distal epiphyses and diaphyses (Haynes & Klimowicz, 2015). Forelimbs are usually consumed later, since the skin is harder in these areas (Haynes, 1982; Haynes & Klimowicz, 2015). The same usually happens with lower limb bones, such as the tibia, due to their smaller quantities of meat (Haynes, 1982; Blumenschine, 1986; Haynes & Klimowicz, 2015). The intense gnawing of the cf. Scelidotheriinae gen. tibia, both on the distal epiphysis and medial face of the diaphysis, as well as, to a lesser degree, on the proximal epiphysis, implies that this element was fully exploited. The presence of marks on the diaphysis indicates that even the hardest part of the shaft was utilised. The same is true for both *Glossotherium robustum* humeri. The damage to the distal epiphyses was inflicted in subsequent stages and not at the beginning of the consumption sequence. The presence of furrowing on the three elements implies that the various carnivores involved were consuming a substantial amount of bone. In the case of the MLP assemblage, the dominance of broken long bone diaphyses indicates access to within-bone nutrients, relating to the last stages in the consumption sequence (Binford, 1981; Haynes, 1982; Blumenschine, 1987; Capaldo & Blumenschine, 1994).

(ii) Intensity of carcass use is related to resource availability (Haynes, 1980, 1982; Van Valkeburgh & Hertel, 1993; Delaney-Rivera et al., 2009), the size of the hunting pack (Van Valkenburgh et al., 2016), or multiple carnivore taxa involvement (Pobiner & Blumenschine, 2003; Delaney-Rivera et al., 2009). In general terms, large animal tissue is usually conserved for longer once dead (Blumenschine, 1987) and their bones have fewer marks than seen on bones of smaller species (Yravedra, Lagos &

Bárcena, 2011; Domínguez-Rodrigo et al., 2015). As the easy-to-access meat is consumed, carnivores tend to eat the remaining parts of the carcass and inflict more significant damage to the bones (Binford, 1981; Haynes, 1982; Blumenschine, 1986; Pobiner & Blumenschine, 2003; White & Driedrich, 2012; Haynes & Klimowicz, 2015, Sala & Arsuaga, 2016). Thus, marks on articulation surfaces could indicate that the bone held only a small amount of meat when the intervention took place. This is the case of the cf. Scelidotheriinae gen. tibia from the MCNV, the *Glossotherium robustum* left humerus from the MNHN, and the Toxodontidae femur from the MLP (along with other broken bones). The same hypothesis can be proposed for the *Glossotherium robustum* humerus from the MNW, although in this case, a lack of marks on the articulation surface could indicate that the bone was still attached to the rest of the limb. In general, the intensity of the marks and fractures observed indicates advanced stages of modification (Haynes, 1982; Sala & Arsuaga, 2016).

The described feeding traces therefore appear to indicate that during the Pleistocene, different species within the large carnivore guild would have accessed and consumed megamammal bones and/or the marrow of smaller animals, in the final stages of a consumption sequence. Although discussion of how the animals were predated is difficult without more contextual information, given the multiple possibilities for carnivore exploitation of megamammal carcases (Pobiner & Blumenschine, 2003), two possible extreme scenarios are considered here: the marks described resulted from a first access (hunting) event and/or secondary access (scavenging) activity. The first case would involve the same group of carnivores killing and consuming the edible muscle tissues and then exploiting bones and within-bone nutrients. Early access to the carcass of an animal that had died a natural death by the same carnivore group can be also included in this situation (Blumenschine, 1986). Alternatively, after the death of the animal (either from natural causes or hunting activities), various carnivore taxa could have fed on a single carcass. In this second situation, one group would have consumed the primary edible tissues of the bony elements, and, at a later stage, the bones and marrow would have been exploited by other carnivores.

These interventions resulting from hunting and/or scavenging events indicate that in both cases, megamammal carcasses were completely exploited by various members of the large-sized carnivore guild in the region. Our samples belong to different time periods within the Pleistocene (Fig. 2 and Table 1). This provides weak but positive evidence suggesting that consumption of edible tissues as well as the bony elements and/or marrow by different carnivore groups was a pattern that occurred repeatedly throughout that period. Full exploitation of carcasses is expected, at least periodically when food is scarce and/or more carnivore species are present, as has been proposed for other American ecosystems such as Rancho La Brea (Van Valkeburgh & Hertel, 1993; Binder & Van Valkenburgh, 2010; Van Valkenburgh et al., 2016). Thus, it seems likely that temporal palaeoenvironmental stressors would have influenced the richness of Pampean megamammal communities (Cione, Tonni &

Soibelzon, 2009), acting as cyclic, top-down pressures stimulating interspecific and intraspecific competition for the carcasses, resulting in the complete consumption of them.

Conclusions

Four megaherbivore fossil bones, 22 bones of smaller species, and two indeterminate bones with carnivore marks were studied from European and Argentinean collections of Pleistocene remains from the Pampean region, collected during the 19th and early 20th centuries. The marks were predominately identified on appendicular bones. After internal organs and muscles are consumed, limb bones are the richest parts with regard to within-bone nutrients, and in particular, the epiphyses are the easiest to penetrate by gnawing (Binford, 1981; Dominato et al., 2011; Labarca et al. 2014). Analysis of the punctures and pitting shows that these partially overlap with the range of bigger marks made by large carnivores from African environments, the smaller markings of *Panthera onca mesembrina*, and they are comparable with the giant *Chapalmalania* from the Pliocene of the Pampean region (Pickering et al., 2004; de los Reyes et al., 2013; Martin, 2016). Moreover, our measurements generally agree with the information reported from other South American sites (Martin, 2008; Dominato el al. 2011; Labarca et al., 2014; Politis et al., 2016). Consequently, it is likely that different members of the Pampean large-carnivore guild produced the marks described in this study. We interpret the data presented here as indicating the fact that ursids, canids, and possibly felids would have consumed the soft and hard tissues, inflicting various tooth marks, including pits, punctures, and scratches, furrowing bone epiphyses, and even breaking the diaphyses of long bones in order to access the marrow. These latter represent the final stages of carcass exploitation, given that the marks described on the epiphyses and diaphyses were not inflicted when bone still held large quantities of meat.

Considering that there is little information on carnivore marks from the region, as this type of evidence is still scarce, the few remains presented here significantly increase our knowledge of palaeoecological relationships in the Pampean region. The marked bones indicate that the megamammal carcases were fully exploited. This type of evidence has been recorded in the Pliocene (de los Reyes et al., 2013) and, according to the evidence presented here, continued periodically throughout the Pleistocene. Consequently, temporal shifts in prey availability would have influenced predator-prey and/or scavenging dynamics, increasing competition for carcasses and resulting in the consumption of bone and within-bone nutrients by the same or multiple taxa. Pleistocene large mammal communities would have developed different trophic levels with multiple competitive species, allowing them to persist through time and overcome different palaeoclimatic fluctuations. This situation lasted until the late Pleistocene-early Holocene when many megafaunal extinctions occurred (Van Valkenburgh et al., 2016).

Current taphonomic methods allow new results to be obtained from historical collections. In this study, different types of carnivore marks inflicted on megamammal and smaller mammal bones were measured and categorised. Interpreting these with the help of current ecological information sheds light onto the palaeoecological relationships of native Pampean mammal communities from the Pleistocene. This novel perspective offers new insights into the development of future systematic fieldwork. Both collection- and field-based research will provide crucial information on the evolution of the Pleistocene ecosystems of the South American Southern Cone.

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Figures

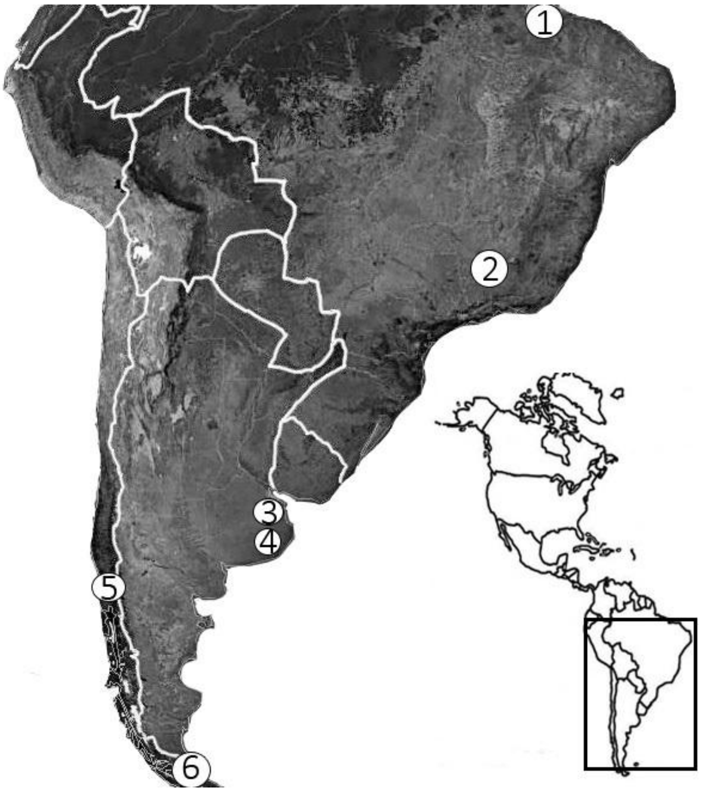


Figure 1. Map showing the general location of the sites mentioned in the text. In Brazil: 1. Tanque do Jirau and 2 Águas de Araxá. In the Pampean region: 3. Salado River and material found in different collections of this study, 4. Olavarría and Arroyo Seco 2. In the Patagonian region: 5. Pilauco, 6. Lago Sofía 4 cave, Milodón cave, Dos Herraduras rockshelter, Chingues cave, Puma cave, Fell cave, Tres Arroyos rockshelter .

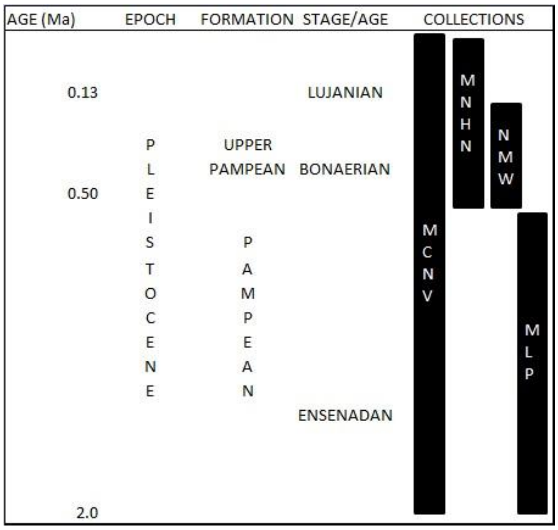


Figure 2. Pleistocene Formations, Stage/Age (not to scale) and the approximate locations of the collections in time.

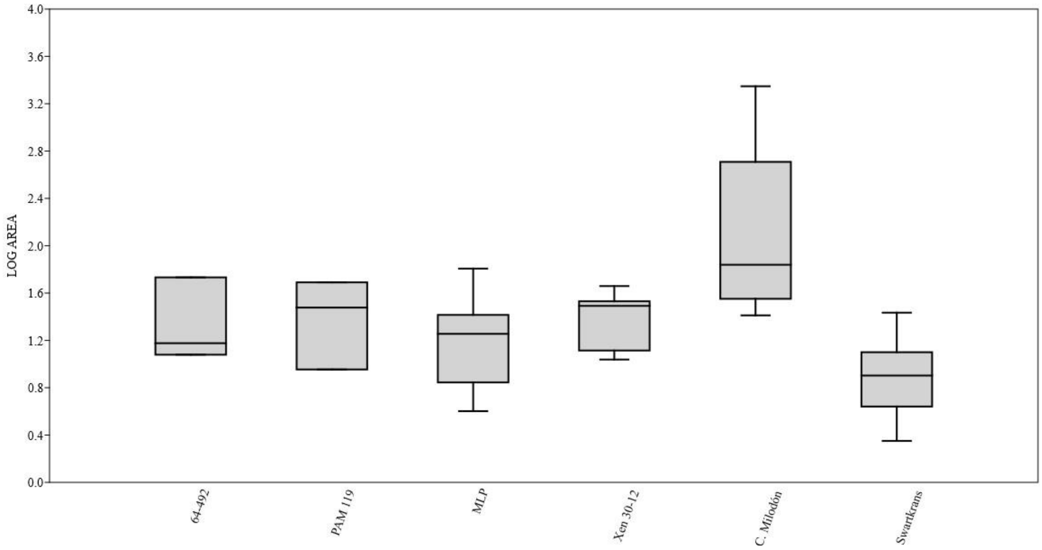


Figure 3. Box plot diagram comparing log area of the pits/punctures on the bones from MCNV 64-492, MNHN.F. PAM 119, MLP, Xen 30-12 (de los Reyes et al., 2013, Table 1), Cueva del Milodón (Martin, 2016) and Swartkrans Member 3 (Pickering et al., 2004, Appendix A, column of large mammals) (Generated using the PAST program, Version 3.14; Hammer, Harper & Ryan, 2001).

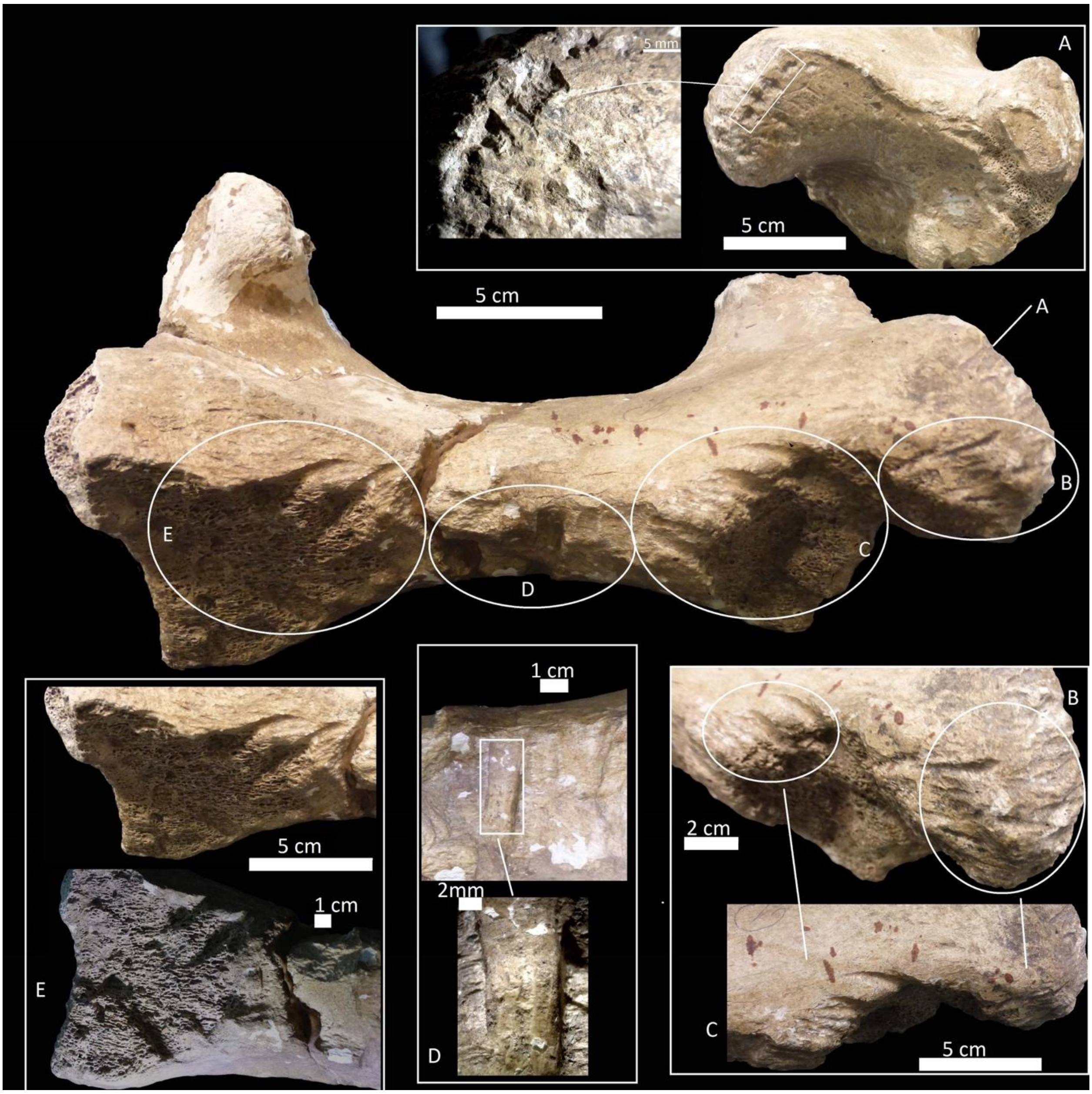


Figure 4. Right tibia of cf. Scelidotheriinae gen.,64-492 from MCNV, posterior-medial view, indicating the different marks described in the text: A) distal epiphysis, the rectangle and zoom indicate the four linearly-positioned pits; B) metadiaphysis with the U-shaped parallel scores circled; C) furrowing of the distal metadiaphysis, with a circle indicating the parallel, V-shaped teeth marks on the posterior face; D) medial face of the diaphysis with a magnified image of one of the three thick grooves; E) furrowing of the proximal metadiaphysis.

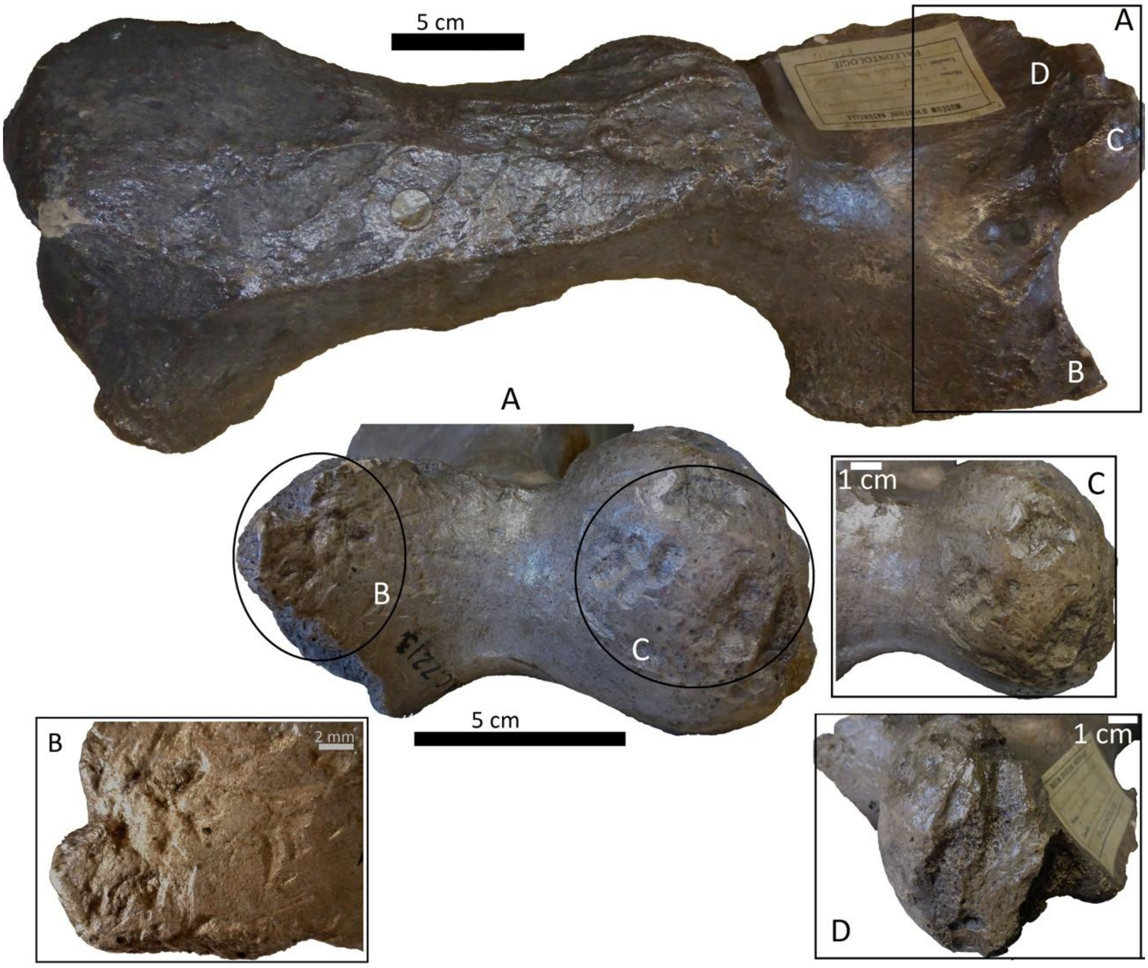


Figure 5. Left humerus *Glossotherium robustum*, MNHN.F.PAM 119 from MNHN, anterior view, indicating the different marks described in the text: A) front view of distal articular face; B) amplification of trochlear region with punctures and scratches; C) amplification of condyle with scoring; D) wide grooves on the lateral face.

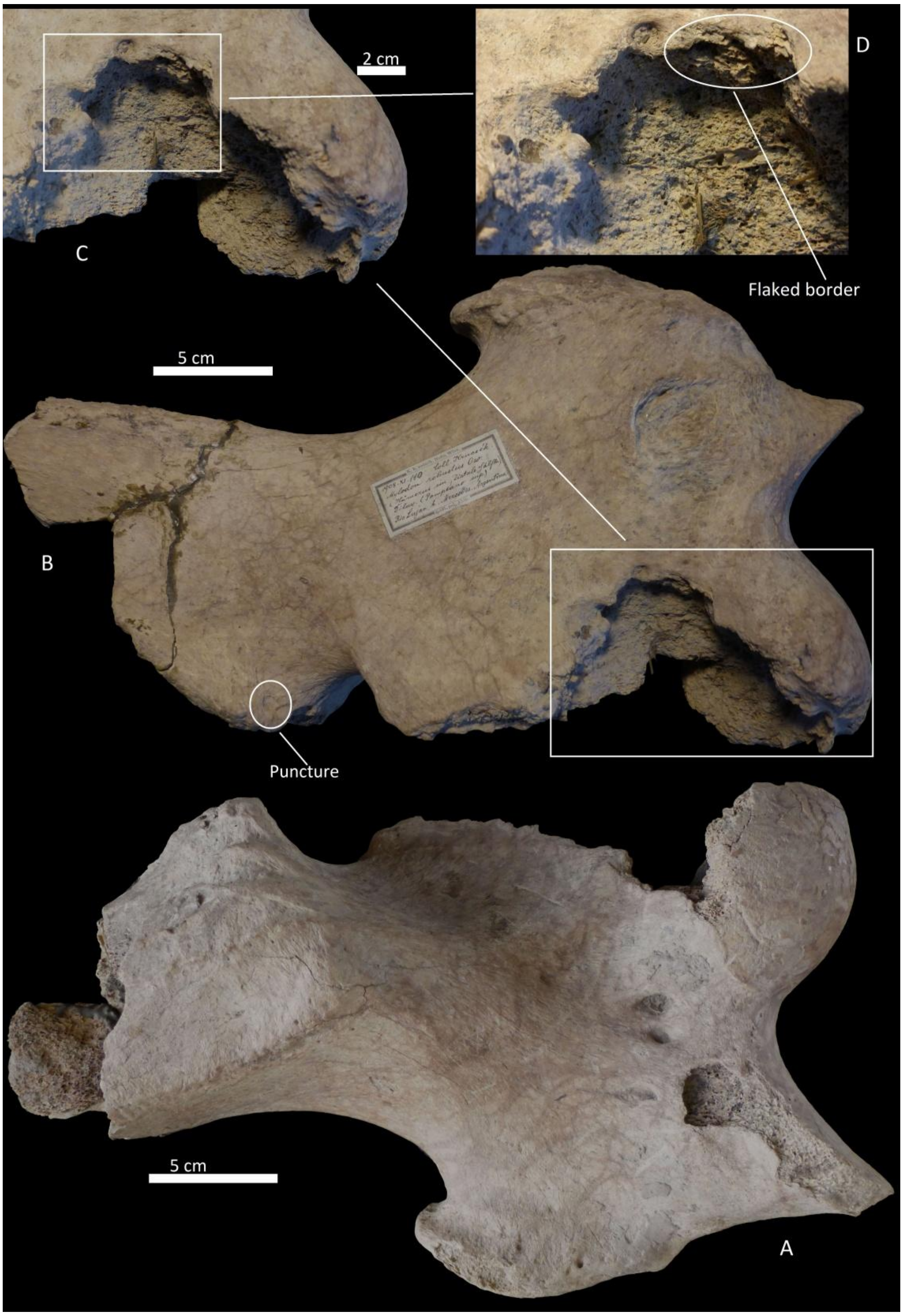


Figure 6. Left distal humerus of *Glossotherium robustum*, 1908. XI.110 from MNW: A) anterior face; B) posterior face, indicating the puncture; C) amplification of the posterior rim; and D) indication of the flaked border.

Figure 7. Condyle of distal femur of Toxodontidae, 15-I-20-32 with elongated and U-shaped scratches: A) lateral face; B) anterior view with scores; C) medial view.

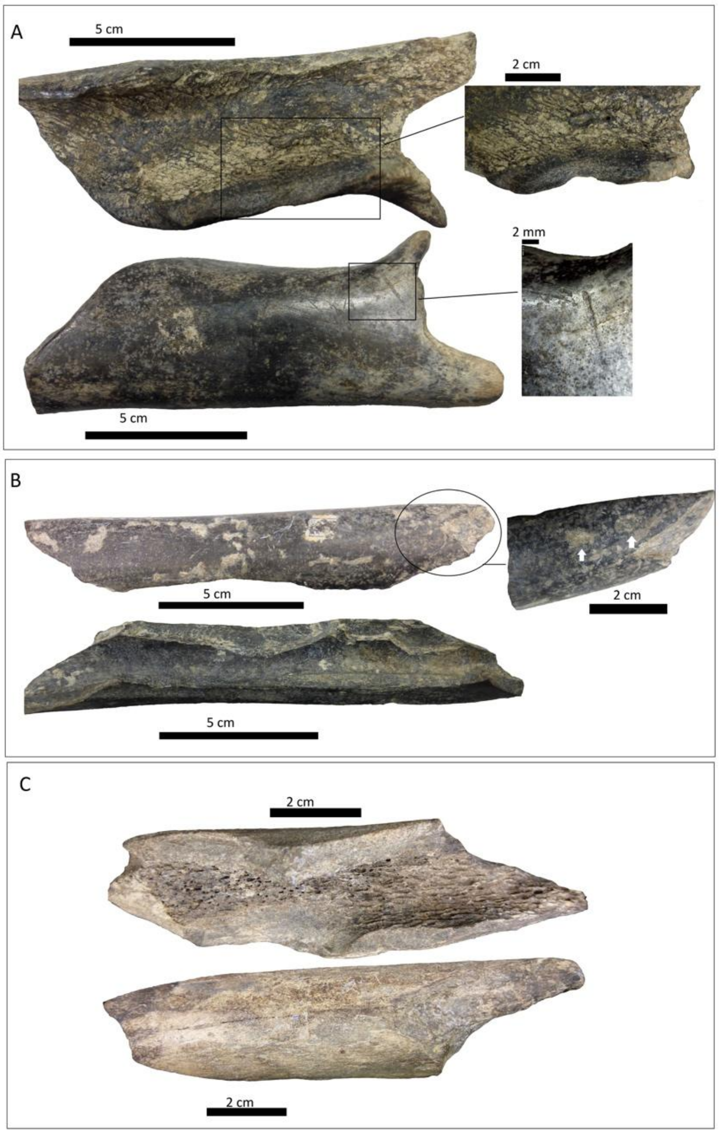


Figure 8. Bone shafts showing carnivore intervention from MLP: A) MLP 15-I-20-35 with spiral fracture, amplifications of the internal notch and the cortical face with scoring; B) MLP 15-I-20-34 with spiral fracture, notches can be observed on the medullar face, amplification of light pitting in the cortical face; C) MLP 15-I-20-33 with spiral fracture

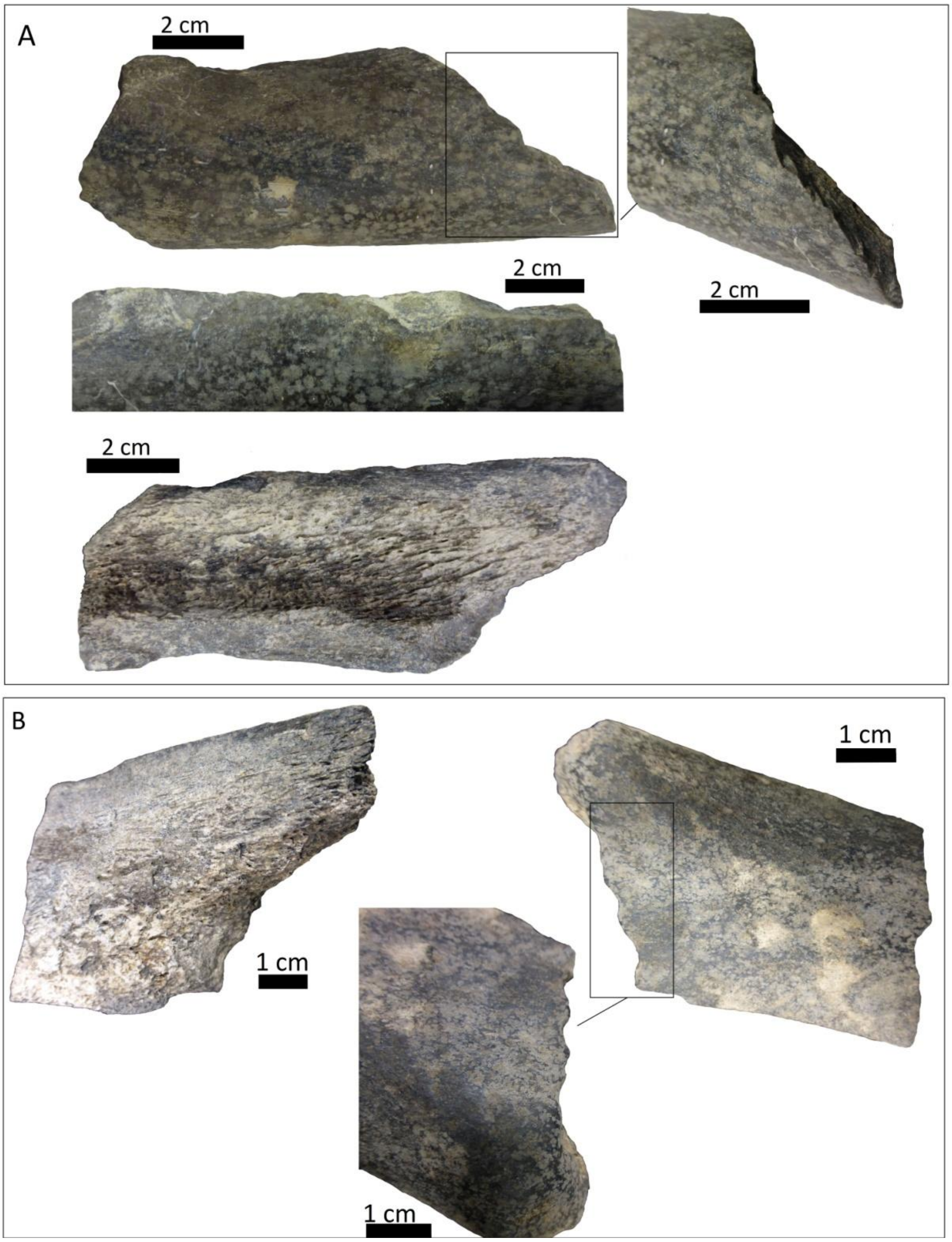


Figure 9. Bone shafts showing carnivore intervention from MLP with spiral fracture and magnification of crenulated edge: A) MLP 15-I-20-37; B) MLP 15-I-20-38

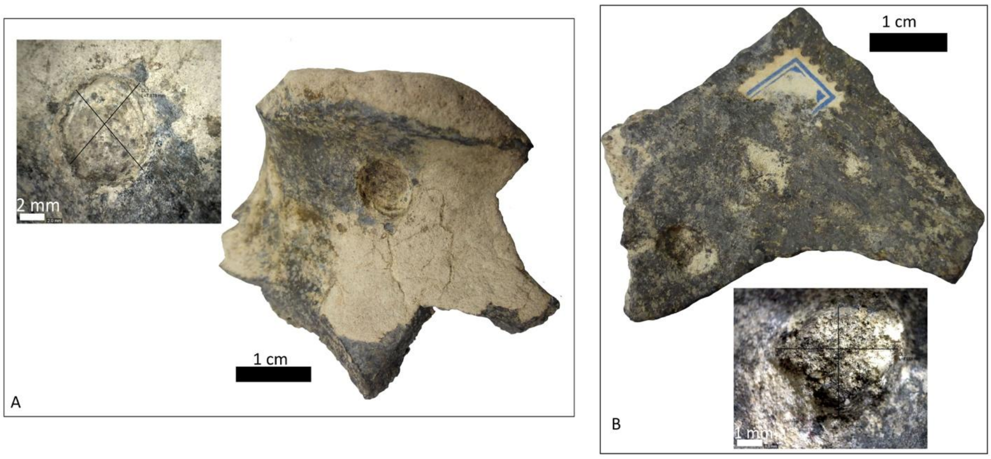


Figure 10. Indeterminate fragment of bone with puncture and amplification of the puncture with Dino-Lite measurements: A) MLP 15-I-20-36; B) MLP 15-I-20-39.

Tables

MUSEUM	MUSEUM ABBREVIATION	TAXON	MUSEUM ASIGNATION	BIOSTATIGRAPHICAL DETERMINATION
Museo de Ciencias Naturales de Valencia	MCNV	cf. Scelidotheriinae gen.	-	Ensenadan to Lujanian Stage/Age
Muséum National d' Histoire Naturelle	MNHN	*Glossotherium robustum*	Pampean	Bonarian and Lujanian Stage/Age
Naturhistorisches Museum Wien	NMW	*Glossotherium robustum*	Diluvium- Upper Pampean	Bonarian Stage/Age
Museo de La Plata	MLP	Toxodontidae	Ensenadan	Ensenadan Stage/Age

Table 1. Megamammal bones with museums assignation and current biostratigraphical determination.

MUSEUM/ SPECIMEN	SPECIES	ELEMENT	PITTING/ PUNCTURES	SCRATCHES/ SCORES	CRENULATED	FURROWING
MCNV (64-492)	cf. Scelidotheriinae gen.	Right tibia	4 x 3 mm/ 5 x 3 mm/ 9 x 6 mm/5 x 4 mm. Pittings on distal articular face, medial edge	(i) 20 x 10 mm. Score on distal articular face, lateral edge. (ii) 45 x 10 x 4 mm/ 13 x 10 mm/ 20 x 13 mm. Grooves medial face of the diaphysis (iii) 15 x 4 mm (Five marks of distal posterior face) and 15 x 5 mm (Two marks proximal posterior face).	x	x
MNHN (MNHN.F. PAM 119)	*Glossotherium robustum*	Left humerus	8 x 6 mm/ 7 x 7 mm/ 6 x 5 mm/ 3 x 3 mm. Punctures in trochlear region	(i) 45 x 10 cm groove in the condyle (ii) 10 x 7 mm/ 15 x 6 mm/ 15 x 10 mm scores in condyle	-	x
MNW (1908.XI.110)	*Glossotherium robustum*	Left distal humerus	8,5 x 6 mm	-	x	x
MLP (MLP 15-I-20-32)	Toxodontidae	Femur condyle	-	Three scratches of 40 x 5 mm/ Five scratches of 15 x 5 mm	-	-
MLP (MLP 15-I-20-36)	Indeterminate	Indeterminate	8 x 8 mm	-	-	-
MLP (MLP 15-I-20-39)	Indeterminate	Indeterminate	4,5 x 4 mm	-	-	-
MLP (MLP 15-I-20-40)	Indeterminate	Diaphysis	3.5 x 2 mm/ 6.5 x 4 mm	-	-	-
MLP (MLP 15-I-20-41)	Indeterminate	Diaphysis	2 x 2 mm	-	-	-

Table 2. Measurements of pits, punctures and scores. Presence of furrowing or crenulated edges was also indicated.

PLEISTOCENE PAMPEAN CARNIVORES	BODY SIZE (in kg.)	BODY SIZE CATEGORIES
Dusicyon avus	14	Size 1
Protocyon	20-25	Size 2
Canis nehringui	32	Size 2
Theriodictis platensis	37	Size 2
Puma concolor	47-50	Size 2
A. vetustum/ A. bonariense/ A. tarijense	110 a 140	Size 3a
Panthera onca	120	Size 3a
Smilodon populator	220-360 up to 400	Size 3b/ Size 4
Arctotherium angustidens	> 1000	Size 5

Table 3. Body size categories for Pampean carnivores (based on Bunn, 1986)

SITE	SPECIES	CARNIVORE	PUNCTURE/PITTING SIZE (in mm)	REFERENCES
Olavarría	cf. *Eosclerocalyptus lineatus* (Hoplophorini)	*Chapalmalania*	ML 8.67/ MW 4.38 / Area mm2 33.93*	de los Reyes et al., 2013
			ML 11.07/ MW 4.32 / Area mm2 45.56*	de los Reyes et al., 2013
			ML 7.98/ MW 1.95 / Area mm2 10.92*	de los Reyes et al., 2013
			ML 6.97/ MW 4.63/ Area mm2 30.98*	de los Reyes et al., 2013
			ML 8.83/ MW 1.93 / Area mm2 13.02*	de los Reyes et al., 2013
			ML 7.82/ MW 2.80 / Area mm2 17.12*	de los Reyes et al., 2013
Arroyo Seco	Equidae	-	Average: MA A (long) 7.383/ MI A (wide) 5.727	Politis et al., 2016
Mylodon Cave	*Mylodon darwini*	*Panthera onca mesembrina*	12.27 diameter	Martin, 2008, 2016
			4.34 to 9.05	Martin, 2008
			41.63 x 30.36*	Martin, 2016
			23.37 x 21.86*	Martin, 2016
			7.10 x 5.01*	Martin, 2016
			55.30 x 40.29*	Martin, 2016
			10.61 x 7.46*	Martin, 2016
			6.13 x 5.14*	Martin, 2016
			15.09 x 4.40*	Martin, 2016
			17.56 x 13.43*	Martin, 2016
			7.99 x 8.64*	Martin, 2016
			5.17 x 4.99*	Martin, 2016
			6.84 x 8.30*	Martin, 2016
Chingues Cave	*Hippidion saldiasi*	*Panthera onca mesembrina*	9 x 7.60	Martin, 2008
			8.13 x 4.79	Martin, 2008
			4.9 x 4.2	Martin, 2008
Pilauco	Gomphotheriidae	Felidae	10.24 x 11.71	Labarca et al., 2014
			8.84 x 9.71	Labarca et al., 2014
Águas de Araxá	*Haplomastodon waringi*	*Protocyon troglodytes*	Average diameter 5	Dominato el al., 2011
			Average diameter 6	Dominato el al., 2011

Table 4. South American sites with reported dimensions of pitting and/or punctures (as cited in the original publication). ML: Maximum length; MW: Maximum width; MA A: Major axis; MI A: Minor axis. Measurements marked with * were used for comparative purposes.

Data S1. Description of carnivore marks

(i) MCNV 64-492: On the right tibia of cf. Scelidotheriinae gen. the marks are concentrated on the distal epiphysis and medial face and, to a lesser degree, on the proximal epiphysis (Fig. 4). The distal epiphysis has a different groups of marks (Fig. 4A, 4B). Near the medial edge of the articular face is where most damage is observed. Here, four superficial pits are positioned linearly and surrounded by scratches (Fig. 4A). Posteriorly-anteriorly oriented, the first two pits are slightly smaller with a cuspid shape, while the other two are bigger. The pit 9 x 6 mm is almost double the size of the others. This mark was affected by post-depositional agents that probably resulted in this size increase. The manganese spot located next to the lateral side of the pit ends abruptly at the border and does not continue inside (Figure S1A). Additionally, almost in the middle, the medial border protrudes inwards, into the pit, as if the bone originally continued, separating this pit into two (Figure S1B). In consequence, it seems likely that this pit began as two, and that post-depositional events debilitated the bony separation between them. In this sense the edges of bone pits can be more affected by post-depositional conditions, as their surroundings become more susceptible to flaking and localised damage (Delaney-Rivera et al. 2009). On the lateral side of the distal articular face (Fig. 4A), a larger transverse score was detected. Parallel U-shaped scores are located over the metadiaphysis that continue beyond the rim with the four pits. One group of scores depart from the furrowing towards the articular side, while another starts from the articular side and runs towards the furrowing (Fig. 4B). They run parallel to the long axis of the bone and surround significant furrowing. This pattern implies that the *tibia caudalis* and *flexor digitorium longus* muscles were removed (Fig. 4C). Another significant furrow is present on the medial face of the proximal epiphysis (Fig. 4E); this has extracted part of the inner condyle. A crenulated rim surrounds this furrow, and there are parallel, V-shaped tooth marks over the posterior face (Fig. 4C and Fig. 4E). There is one group of five marks on the distal part and two on the proximal part, oriented posteriorly-medially. Three thick quadrangular-shaped grooves were detected on the medial face of the diaphysis (Fig. 4D). One runs along the entire face; the other two are smaller and more superficial. They start at the border of the anterior face and run up to the medial face (see Table 2 for measurements).

(ii) MNHN.F.PAM 119: The marks detected that are attributable to carnivores are on the distal epiphysis of the left humerus of *Glossotherium robustum* (Fig. 5). They are distributed on the articular face, over the condyle and trochlear regions (Fig. 5A). Near the medial side of the trochlear region, there are several V-shape punctures, surrounded by scratches (Fig. 5B). Part of the trochlea has disappeared and there are crenulated edges as a consequence of the furrowing. On the condyle, at least seven scores were detected (Fig. 5C), four of which are parallel. Superficial scratches were also observed. In the border of this region, over the lateral side, are two wide grooves (Fig. 5D) (see Table 2 for measurements).

(iii) 1908. XI.110: On the left humerus of *Glossotherium robustum* housed at the MNW, there is a corrugated fracture over the lateral face of the condyle that encompasses both anterior and posterior faces (Fig. 6A and Fig.6B). The epicondyle has been destroyed and the border has a crenulated edge. The collapsed bone is covered with sediment and the rim of the fracture is the same colour as the rest of the specimen: thus the fracture must have occurred prior to burial. Although the furrowing and crenulated edge is weak evidence of carnivore intervention (Domínguez-Rodrigo et al., 2015), the deltoid crest of the posterior face also has a possible puncture with sediment inside (Fig. 6B). Additionally, in the posterior view, the fractured border is flaked resulting from pressure exerted on it (Fig.6C and Fig.6D). The regularity of the fracturing on both the anterior and posterior faces supports the proposal that the marks on this bone could have resulted from the action of carnivores (see Table 2 for measurements).

(iv) From the megamammal bones in the MLP assemblage, a condyle of a distal femur of Toxodontidae was identified, with eight elongated, short, long and U-shaped scratches (Fig. 7). In addition, 22 bone shafts from smaller unidentified mammals display spiral fractures. Some of these also present scratches, crenulated edges or light pitting (Figs. 8 and 9). Semi-circular notches were also identified. Two indeterminate bones have bigger punctures (Fig. 10). Spiral fractures can be confused with human intervention or can occur naturally (Binford, 1981; Lyman, 1994). Nevertheless, the presence of other typical carnivore damage such as scratches and perforations, enables us to consider them as being produced by carnivore activity (see Table 2 for measurements and detail of marks in Table S6).

Data S2. Description of Pampean carnivores

(i) The ursid *Arctotherium angustidens* evolved during the Ensenadan Stage/Age. This large ‘short-faced’ bear was a member of the megafauna and recent estimations of its body mass indicate that the animal weighed more than a tonne (Soibelzon et al., 2014). Recent morphometric studies also indicate that this bear probably had an omnivorous diet supplemented by meat or carrion, as dental pathologies detected in some individuals of *Arctotherium* probably resulted from chewing bones (Figueirido & Soibelzon, 2010). Moreover, Soibelzon et al. (2014) have found biomechanical and isotopic evidence of *A. angustidens* having an omnivorous diet but with scavenging abilities. Other smaller bears that appeared later in South America, including *Arctotherium vetustum*, *Arctotherium bonariense* and *Arctotherium tarijense,* had a more plant-based diet (Figueirido & Soibelzon, 2010).

(ii) Three felids were also present in these ecosystems. The dirk-toothed sabre cat *Smilodon populator* was the top predator in this region: its estimated body mass has been calculated as being between 220-360 kg, but it could have reached up to 400 kg (Christiansen & Harris, 2006). This sabre-toothed cat may even have been capable of hunting juvenile *Megatherium americanum* (Tardigrada, Megatheriidae), with a body mass of adult individuals ranging between 4.000 and 6.000 kg (Prevosti

& Vizcaíno, 2006; Bocherens et al., 2016). However, the large sabre-like canines that it used to attack to the throat of its prey (Antón et al., 2004) precluded *Smilodon* from breaking or consuming bones regularly, although they could have inflicted important bone damage during hunting and/or soft-tissues consumption (Van Valkeburgh & Hertel, 1993; Marean & Ehrhardt 1995; Binder & Van Valkenburgh, 2010). The other two hypercarnivorous felids were *Puma concolor,* with an estimated body mass of 47-50 kg (Christiansen & Harris, 2006; Prevosti & Vizcaíno, 2006), and *Panthera onca,* weighing *ca.* 120 kg (Prevosti & Vizcaíno, 2006). Although these species would have fed on prey of *ca*. 600 kg; occasionally theses preyed on juvenile megamammals (Prevosti &Vizcaíno, 2006). The puma could have inflicted substantial mark on bone but would not usually have consumed it (Muñoz et al., 2008; Kaufmann et al. 2016). In contrast, *Panthera onca* was potentially able to break and consume bone (Martín, 2008; Domínguez-Rodrigo et al., 2015).

(iii) Hypercarnivorous canids were also present in these ecosystems at the same time. They could have cooperated in order to hunt large mammals and juvenile megamammals, and they would also have had the ability to scavenge (Prevosti & Palmqvist, 2001; Prevosti, Zurita & Carlini, 2005; Prevosti & Schubert, 2013). This may have been the case for *Theriodictis platensis*, weighing *ca*. 37 kg, which evolved during the Ensenadan Stage/Age. It could have preyed upon animals of around 600 kg, animals of extreme age classes (i.e., very old or juvenile individuals), or diseased members of the megafauna (Prevosti & Palmqvist, 2001). During the Pleistocene, there were various species of *Protocyon*, weighing between 20 and 25 kg. These could have hunted middle-sized mammals, scavenged carcasses of megamammals, and may even have competed with *Smilodon populator* (Prevosti, Zurita & Carlini, 2005; Prevosti & Schubert, 2013; Bocherens et al., 2016). *Canis nehringui,* weighing *ca*. 32 kg, was present during the late Pleistocene-early Holocene and although it would have generally fed on medium-sized mammals, pack-hunting of bigger species may have been possible (Prevosti & Vizcaíno, 2006). *Dusicyon avus*, weighing *ca*. 14 kg, would have specialised in smaller species, but consumption of larger mammals cannot be ruled out (Prevosti & Vizcaíno, 2006).

FIGURE

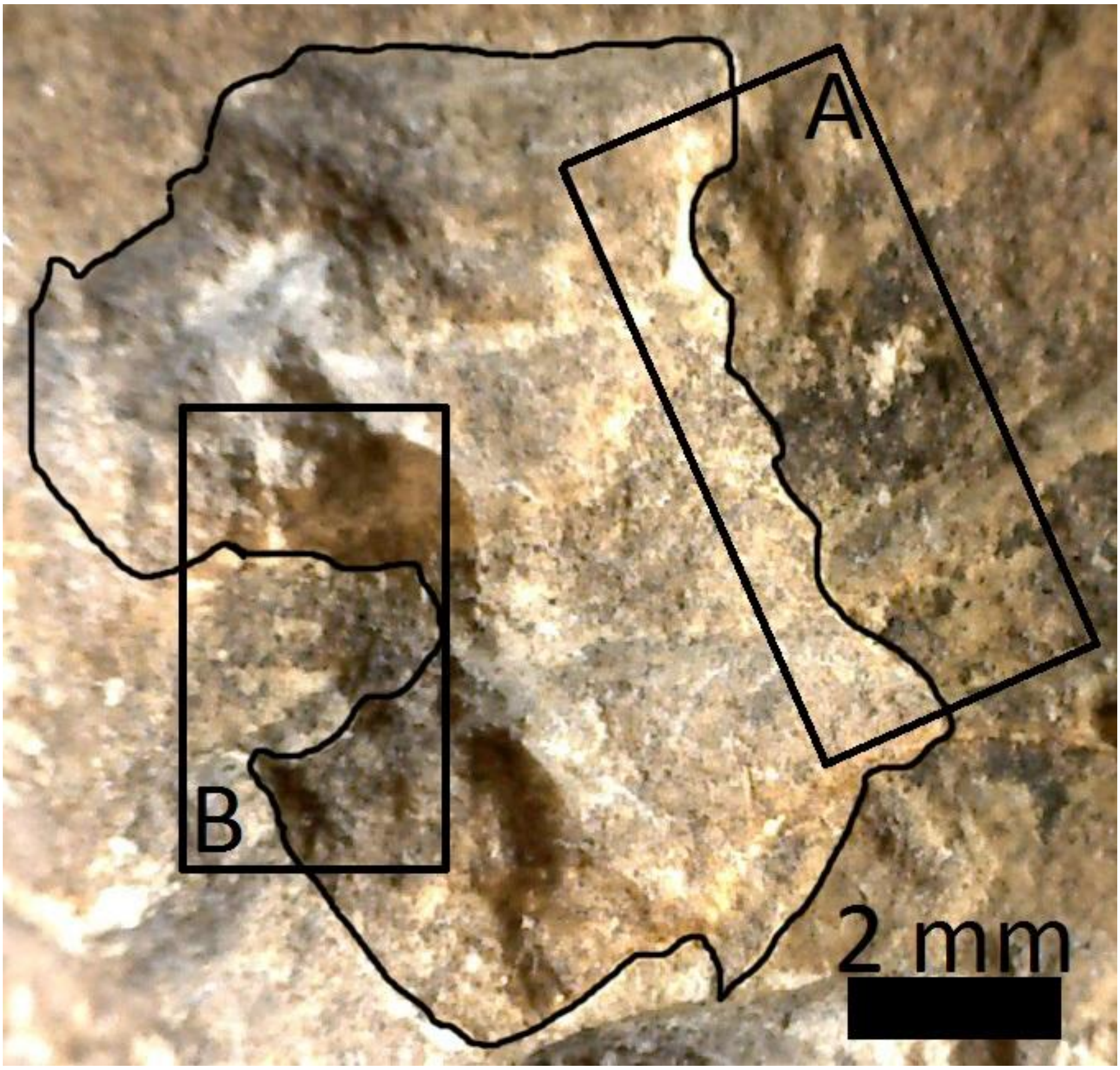


Figure S1. Pit of 9 x 6 mm located on the articular face of MCNV 64-492. A- Medial border where manganese spot abruptly ends. B- Lateral border where the pit edge protrudes inwards.

Tables

CARNIVORE MARKS	GENERAL CHARACTERISITC	CHARACTERISATION BY CARNIVORE GROUP	REFERENCES
PITTING AND/OR PUNCTURES	(i) Produced by the pressure of tooth on bone (ii) Can leave a superficial imprint (pitting) or deeper mark (puncture) (iii) Depth depends on the amount of pressure exerted and whether this occurs on the softer cancellous bone of the epiphysis or on the harder part of the shaft	URSIDS: Pitting will be planar, flat-bottomed, superficial and circular or square/rectangular.	Binford, 1981; Haynes, 1982, 1983; Lyman, 1994; Domínguez-Rodrigo and Piqueras, 2003; Pickering et al., 2004; Delaney-Rivera et al., 2009; Burke, 2013; Saladié et al., 2013; Arilla et al., 2014; Sala & Arsuaga, 2016
		FELIDS: These can inflict important teeth marks that have an “axe-edge” or elongated V-shape.	
		CANIDS: Tooth impressions tend to have a cone or truncated-cone shape.	
SCRATCHES OR SCORES	(i) U-shaped (ii) Realised when teeth are dragged over a surface (iii) Can be superficial or present as gouges	URSIDS: Characterised by short, wide, parallel groups or disordered and superimposed clusters of scratches with U-shape or, in some cases, quadrangular form. They can also leave elongated gouges.	Binford, 1981; Haynes, 1983; Lyman, 1994; Domínguez-Rodrigo and Piqueras, 2003; Pickering et al., 2004; Delaney-Rivera et al., 2009; Yravedra, Lagos & Bárcena, 2011; Burke, 2013; Saladié et al., 2013; Sala, Arsuaga & Haynes, 2014; Sala & Arsuaga, 2016
		FELIDS: Scoring will tend to be perpendicular to the long axis of the bone.	
		CANIDS: These can leave numerous scores with different orientations.	
FURROWING	(i) Cancellous bone extraction from the epiphyses (ii) This action also can leave a crenulated edge, caused by the border of collapsed bone produced by the bite having an irregular edge	URSIDS: These can crush, furrow, grind and leave crenulated edges.	Haynes, 1980, 1983; Binford, 1981; Lyman, 1994; Martín, 2008, 2016; Yravedra, Lagos & Bárcena, 2011; Burke, 2013; Saladié et al., 2013; Arilla et al., 2014; Sala, Arsuaga & Haynes, 2014; Domínguez-Rodrigo et al., 2015; Sala & Arsuaga, 2016
		FELIDS: Some groups, such as jaguars, can furrow the epiphyses.	
		CANIDS: These have ample furrowing capacity	
SPIRAL FRACTURES	(i) Fresh bone being broken due to pressure from the tooth leaving spiral borders (ii) Sometimes this action leaves notches in the wall of the bone	URSIDS: Reduced bone breaking capacity.	Binford, 1981; Haynes, 1982; 1983; Capaldo & Blumenschine, 1994; Lyman, 1994; Yravedra, Lagos & Bárcena, 2011; Domínguez-Rodrigo et al., 2012; Saladié et al., 2013; Sala, Arsuaga & Haynes, 2014; Sala & Arsuaga, 2016
		FELIDS: Reduced bone breaking capacity.	
		CANIDS: These can crush and break epiphyses and diaphyses	

Table S1. General characteristics of considered carnivore marks and their relationship with each carnivore group

De los Reyes et al., 2013 (Table 1)		
Specimen	Area mm^2	
XEN 30-12	33.93	1.53058386
	45.56	1.658583715
	10.92	1.038222638
	30.98	1.491081413
	13.02	1.114610984
	17.12	1.23350376

Table S2. Calculations using the information from de los Reyes et al. (2013).

Martin, 2016				
Specimen	Length	Breadth	Area	Log Area
94-VIII-10-1	41.63	30.36	1263.8868	3.10170818
	23.37	21.86	510.8682	2.70830887
	7.1	5.01	35.571	1.55109607
	55.3	40.29	2228.037	3.3479224
	10.61	7.46	79.1506	1.89845421
	6.13	5.14	31.5082	1.49842359
	15.09	4.4	66.396	1.82214192
94-VIII-10-96	17.56	13.43	235.8308	2.37260052
94-VIII-10-24	7.99	8.64	69.0336	1.83906052
	5.17	4.99	25.7983	1.41159109
	6.84	8.3	56.772	1.75413419

Table S3. Calculations using the information from Martin (2016).

Pickering et al., 2004 (Appendix A)				
Specimen	Length	Breadth	Area	Log Area
SWK 19683	3.2	2.7	8.64	0.936513742
	2.4	1.3	3.12	0.494154594
SWK 27684	5.3	3.3	17.49	1.242789809
	4.5	3.4	15.3	1.184691431
	3.6	2.2	7.92	0.898725182
	2.5	2.1	5.25	0.720159303
	3.1	1.8	5.58	0.746634199
SWK 287324	4.2	3	12.6	1.100370545
	2.3	1.5	3.45	0.537819095
SWK 29283	3.2	2.5	8	0.903089987
	1.9	1.8	3.42	0.534026106
	1.6	1.4	2.24	0.350248018
	2.6	1.7	4.42	0.645422269
	3	1.8	5.4	0.73239376
SWK 30555	6.8	4	27.2	1.434568904
SWK 30628	2.3	1.9	4.37	0.640481437
	2.2	1.9	4.18	0.621176282

SWK 35153	3.4	2.4	8.16	0.911690159
	3.3	3	9.9	0.995635195
SWK 36073	3.8	3.2	12.16	1.084933575
SWK 36361	4.9	4.5	22.05	1.343408594
SWK 36675	4	2.8	11.2	1.049218023
	4.1	4	16.4	1.214843848
	4.1	2.6	10.66	1.027757205

Table S4. Calculations using the information from Pickering et al, 2004.

AREA OF PITTING/PUNCTURE (in mm)				LOG AREA			
MCNV 64-492	MNHN.F. PAM 119	MNW 1908.XI.110	MLP	MCNV 64-492	MNHN.F. PAM 119	MNW 1908.XI.110	MLP
12	48	51	64	1.079181246	1.681241237	1.707570176	1.806179974
15	49		18	1.176091259	1.69019608		1.255272505
54	30		7	1.73239376	1.477121255		0.84509804
20	9		26	1.301029996	0.954242509		1.414973348
			4				0.602059991

Table S5. Calculations of area and log area for MCNV, MNHN, MNW and MLP

BOX	TAXONOMICAL DETERMINATION	ELEMENT	PITTING AND/OR PUNCTURES	SCRATCHES OR SCORES	SPIRAL FRACTURES	CRENULATED EDGES	TOTAL BONES WITH MARKS
1	Indeterminate	Diaphysis	1		8		8
4	Indeterminate	Diaphysis			1		1
6	Indeterminate	Diaphysis			1		1
8	Indeterminate	Diaphysis			4	1	4
8	Indeterminate	Diaphysis		1	1		1
8	Indeterminate	Diaphysis			1	1	1
10	Indeterminate	Diaphysis			1		1
10	Indeterminate	Diaphysis	1	1	2	1	2
12	Indeterminate	Diaphysis			1	1	1
13	Indeterminate	Diaphysis			1		1
6	Indeterminate	Diaphysis		1	1		1
5	Toxodontidae	Femur		1			1
6	Indeterminate	Indeterminate	1				1
14	Indeterminate	Indeterminate	1				1
		TOTALS	4	4	22	4	25

Table S6. Carnivore marks registered in MLP

5.4. NON-PUBLISHED MATERIAL

In this part of the chapter it will be described the still not published material. They basically consisted in one bone from NMW with artificial shape and the collection housed in the MLP (archaeo. Coll.) described the work "*La Antigüedad del Hombre en el Plata*" (Ameghino 1915 [1880]).

5.4.1.NMW

One bone from *Naturhistorisches Museum Wien* presents a probable artificial shape (Figure 5.10). This bone labelled 1908.XI.19 was originally classified as a fibula from a *Megatherium americanum*, but it is flat and has an articulation surface in one extreme of one end that could be attributable to a sternal rib. This bone has the entire surface polished and has a smooth appearance except in the epiphysis zone. The tip has a post-depositional fracture. On one of its edges, the bone has an extracted portion in the form of an L (Figure 5.10 and Figure 5.11). The longer side measures 11x3 cm and is concave in shape. Longitudinally, one border has a primary rounded concave extraction that finishes in a second, thinner worked dorsal scar (Figure 5.10A and Figure 5.11B). The reverse side has an abrupt ending (Figure 5.10B and Figure 5.11A). The shorter side of this extraction is perpendicularly oriented in relation to the long axis of the bone, measures 3x2.5 cm and has rounded borders on one side and an abrupt ending on the other (Figure 5.10A and Figure 5.11C). Fluvial erosion can be ruled out as this type of agency would influence the entire surface equally (Lyman 1994). No signs of carnivore activity were detected that could attribute this mark to such an agent. Moreover, it is highly unlikely that this complex shape could have been produced by natural agents or non-human biological action. The sediment attachment and manganese spots that cover this piece indicate that the L-shaped scars were created before burial and were not produced during excavation or museum handling.

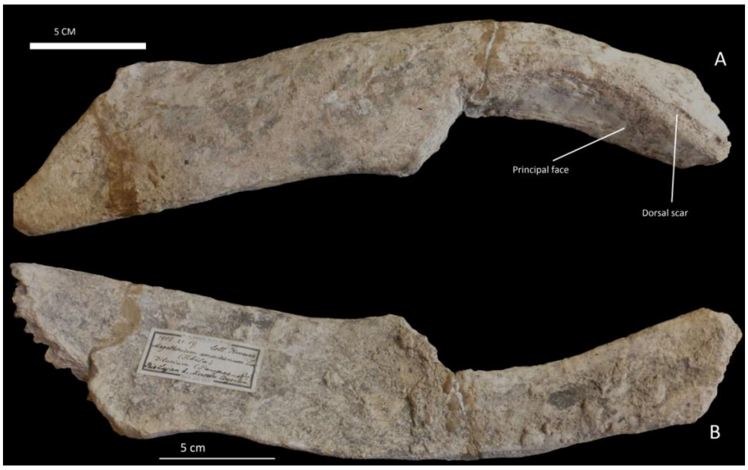


Figure 5.10. Possible Megatherium americanum rib 1908.XI.19. A) View of the principal face of extraction and the dorsal scar. B) View of the reverse abrupt ending face.

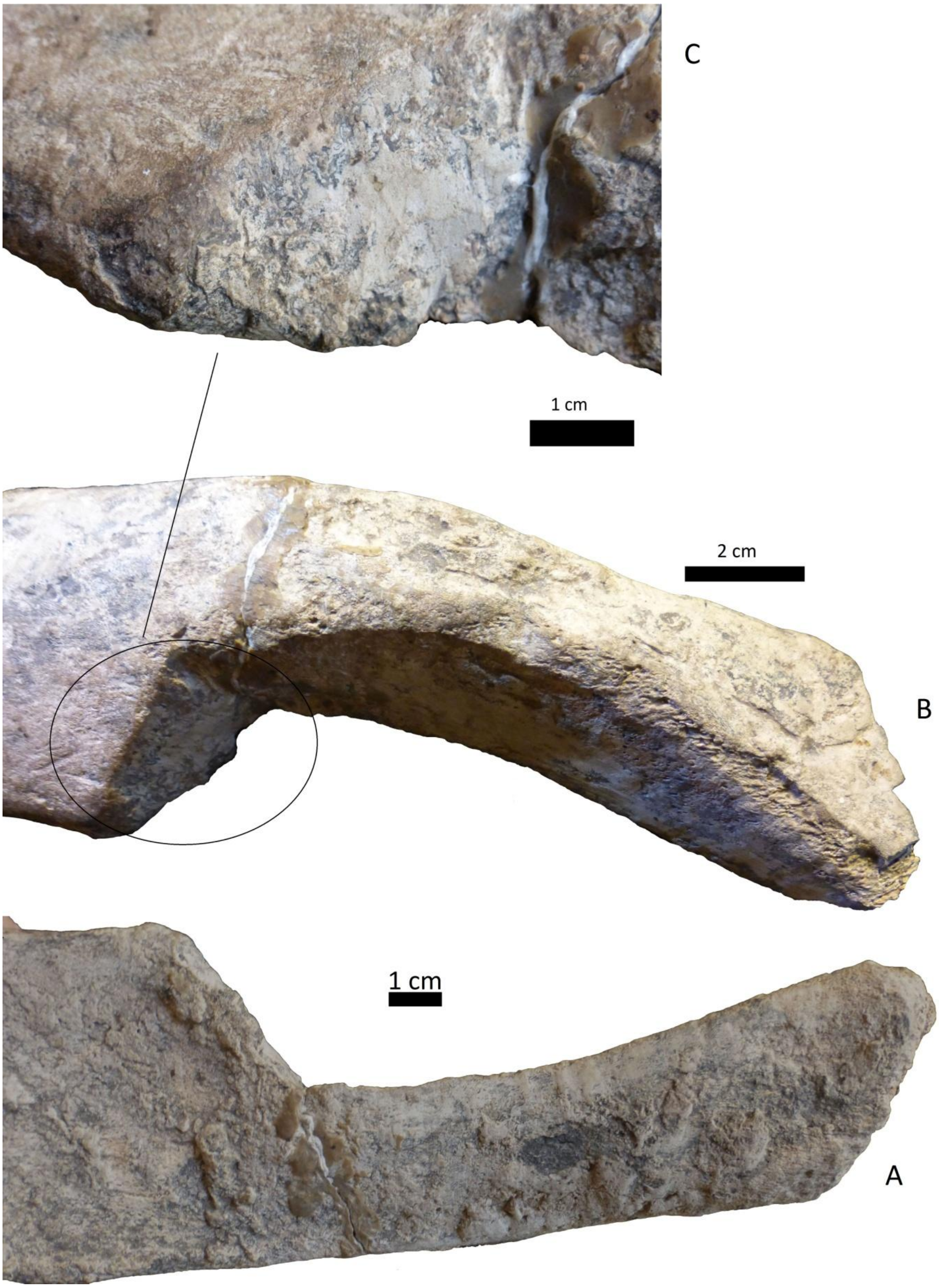


Figure 5.11. A) Detail of abrupt ending face (longer side), B) Detail of principal face (longer side), C- Detail of principal face (shorter side).

5.4.2.MLP Ameghino Collection (Archaeo. Coll.)

The Ameghino Collection housed in this section of the museum belongs to several sites (Ameghino 1915 [1880]) where Ameghino proposed the coexistence of the megafauna with humans. He presented the description of them as a series of "*Paraderos*" (archaeological sites) surrounding what currently are the Mercedes and Luján cities (Lanzelotti and Acuña Suarez 2014) (Figure 5.12). According to Ameghino´s description they were all associated with megafaunal remains. In addition, in Paradero 1, humans remains were found (Ameghino 1915 [1880]; Lanzelotti and Acuña Suarez 2014; Politis 2014).

This collection was lost for several years, and currently only a partial part was recovered. It was incorporated to this work given the supposed association with megamammals bones. Nevertheless only two bones correspond to megamammals' species (*Toxodon* and *Pseudolestodon*). This revision was also useful not only for its historical importance of the sites for the region (Lanzelotti and Acuña Suarez 2014) but also, to understand how interpretations of biological interventions were realized during 19th century.

The material analyzed here belongs to the Paraderos 1, 2, 4 and 5. In total 46 bones were reviewed, from which 38 present anthropic intervention while the rest could not be assigned to current classification of human patterns of breakage (Table 5.5 and Table 5.6).

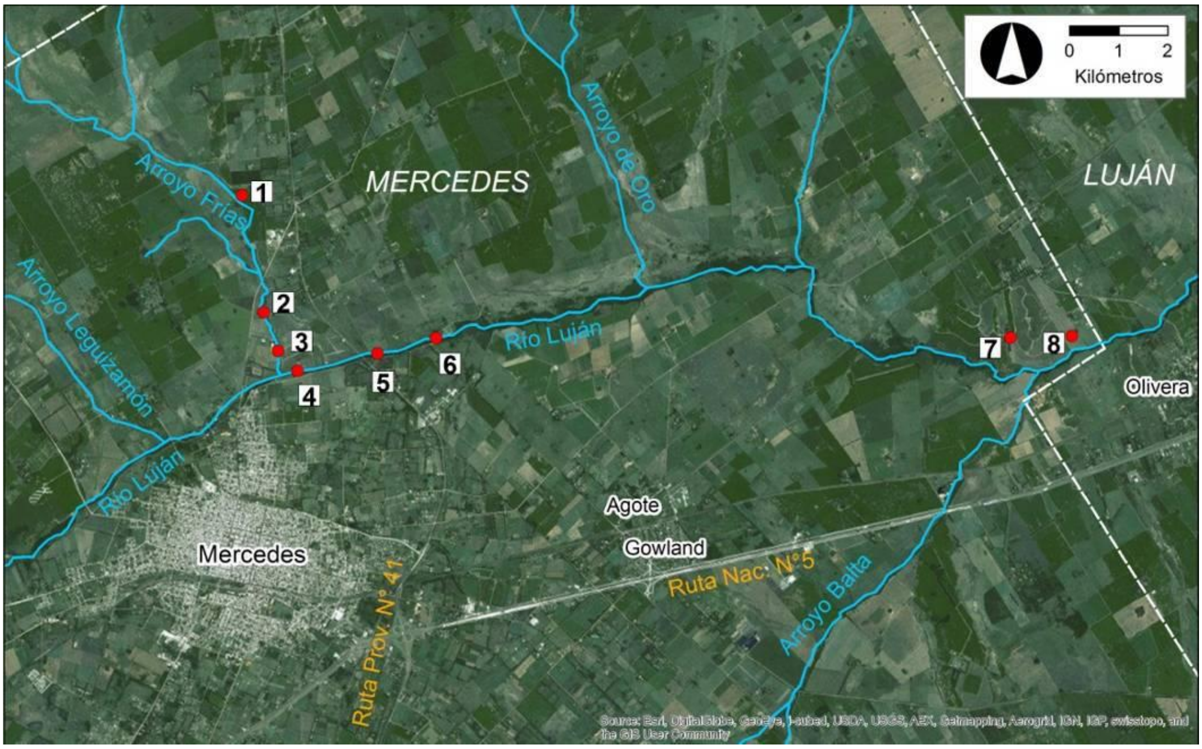
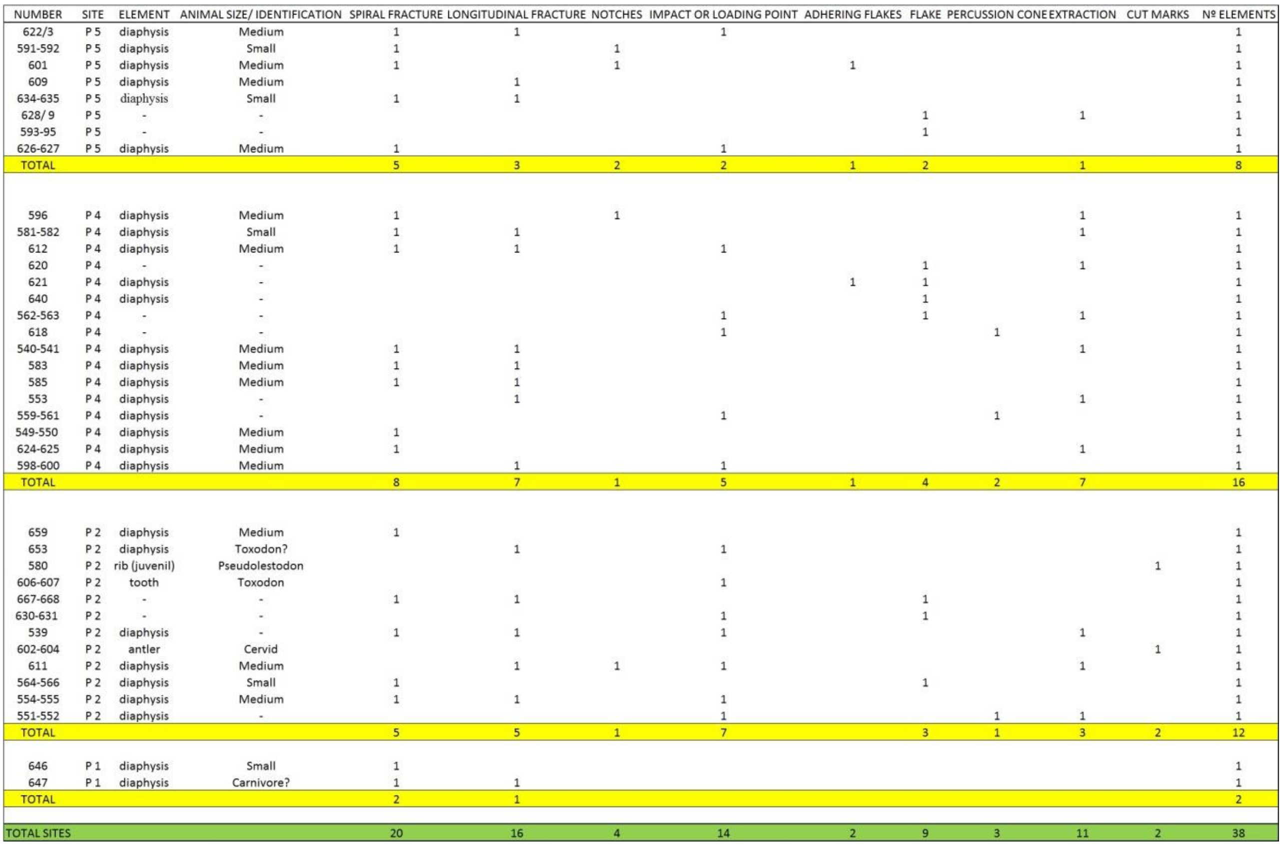
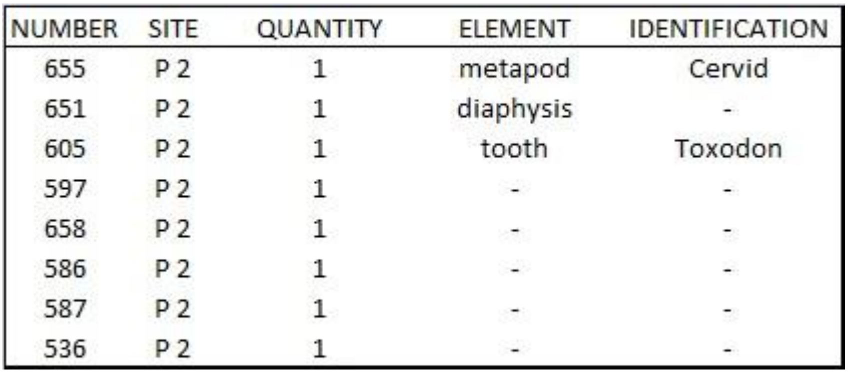


Figure 5.12. Location of the Paraderos presented by Ameghino. The material studied for this work belongs to Paraderos 1, 2, 4 and 5 (From Lanzelotti and Acuña Suarez 2014).



NUMBER	SITE	ELEMENT	ANIMAL SIZE/ IDENTIFICATION	SPIRAL FRACTURE	LONGITUDINAL FRACTURE	NOTCHES	IMPACT OR LOADING POINT	ADHERING FLAKES	FLAKE	PERCUSSION CONE	EXTRACTION	CUT MARKS	Nº ELEMENTS
622/3	P 5	diaphysis	Medium	1	1		1						1
591-592	P 5	diaphysis	Small	1		1							1
601	P 5	diaphysis	Medium	1		1		1					1
609	P 5	diaphysis	Medium		1								1
634-635	P 5	diaphysis	Small	1	1								1
628/ 9	P 5	-	-						1		1		1
593-95	P 5	-	-						1				1
626-627	P 5	diaphysis	Medium	1			1						1
TOTAL				5	3	2	2	1	2		1		8
596	P 4	diaphysis	Medium	1		1					1		1
581-582	P 4	diaphysis	Small	1	1						1		1
612	P 4	diaphysis	Medium	1	1		1						1
620	P 4	-	-						1		1		1
621	P 4	diaphysis	-					1	1				1
640	P 4	diaphysis	-						1				1
562-563	P 4	-	-				1		1		1		1
618	P 4	-	-				1			1			1
540-541	P 4	diaphysis	Medium	1	1						1		1
583	P 4	diaphysis	Medium	1	1								1
585	P 4	diaphysis	Medium	1	1								1
553	P 4	diaphysis	-		1						1		1
559-561	P 4	diaphysis	-				1			1			1
549-550	P 4	diaphysis	Medium	1									1
624-625	P 4	diaphysis	Medium	1							1		1
598-600	P 4	diaphysis	Medium		1		1						1
TOTAL				8	7	1	5	1	4	2	7		16
659	P 2	diaphysis	Medium	1									1
653	P 2	diaphysis	Toxodon?		1		1						1
580	P 2	rib (juvenil)	Pseudolestodon									1	1
606-607	P 2	tooth	Toxodon				1						1
667-668	P 2	-	-	1	1				1				1
630-631	P 2	-	-				1		1				1
539	P 2	diaphysis	-	1	1		1				1		1
602-604	P 2	antler	Cervid									1	1
611	P 2	diaphysis	Medium		1	1	1				1		1
564-566	P 2	diaphysis	Small	1					1				1
554-555	P 2	diaphysis	Medium	1	1		1						1
551-552	P 2	diaphysis	-				1			1	1		1
TOTAL				5	5	1	7		3	1	3	2	12
646	P 1	diaphysis	Small	1									1
647	P 1	diaphysis	Carnivore?	1	1								1
TOTAL				2	1								2
TOTAL SITES				20	16	4	14	2	9	3	11	2	38

Table 5.5. Detail of Ameghino Collection with human intervention.



NUMBER	SITE	QUANTITY	ELEMENT	IDENTIFICATION
655	P 2	1	metapod	Cervid
651	P 2	1	diaphysis	-
605	P 2	1	tooth	Toxodon
597	P 2	1	-	-
658	P 2	1	-	-
586	P 2	1	-	-
587	P 2	1	-	-
536	P 2	1	-	-

Table 5.6. Detail of Ameghino Collection without human intervention.

5.4.2.1. Paradero 5

Ameghino found bones of cervids, guanacos and extinct animals, plus human industry, deposited 1.5 to 2 meters below the surface. The association consisted in grooved, fractured and worked bones with quartzite instruments (Ameghino 1915 [1880]).

Eight elements were reviewed from this site, composed of diaphyses of medium and small mammals, and two indeterminate fragments that were identified as flakes. Diaphyses present spiral or longitudinal fractures and/or a combination of both. They are generally combined with other bone breakage features as notches, impact loading, extraction or even one has an adhering flake. One of the indeterminate bones identified as flake also present an extraction (Table 5.5).

Fractured bones that currently can be interpreted as for obtaining marrow, such as 591-592, 601, 609, 626-627, 634-635 were identified by Ameghino (1915 [1880]) as instruments, given their pointed aspect. According to this author they could have been used as scrapers, knifes or polishers. While the inderminated flake as 628-629 was interpreted as a possible arrow head and the 593-595 also had a possible function, although unknown. The number 622-623 was interpreted as a bone for extraction the marrow (Figure 5.13).

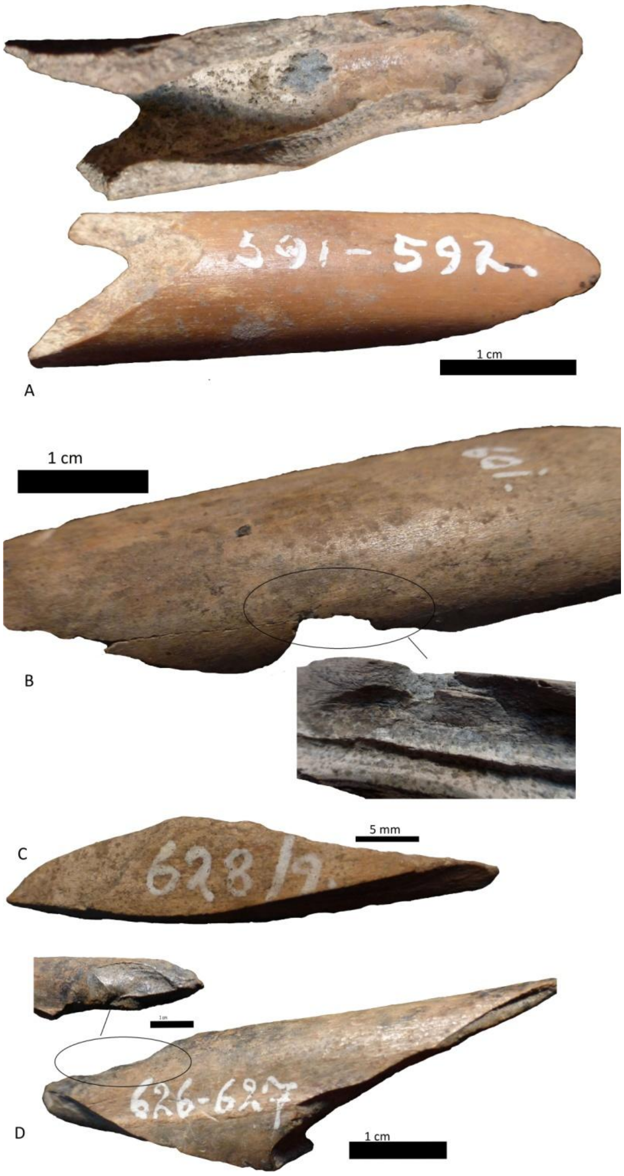


Figure 5.13. Bones of Paradero 5. A) 591-592 Diaphysis with spiral fracture and notches, B) 601 diaphysis with spiral fracture, notches and adhering flake in the internal wall, C) 628-629 indeterminate flake, D) 626-627 diaphysis with spiral fracture and impact point.

5.4.2.2. Paradero 4

Material from this site was removed from a lacustrine layer that extends until two meters under the surface. Extracted bones consisted on extinct ruminants and other mammals. From this site, 16 bones were reviewed belonging to diaphyses of medium and small mammals or indeterminated fragments. Spiral, longitudinal fractures and extraction were the most important anthropic intervention found. Nevertheless, also five bones present loading points while only one present a notch. There is also more representation of smaller bones, four interpreted as flakes (one of them with an adhering flake) and two as percussion cones (Table 5.5). Some of these indeterminate bones were also interpreted by the author as being done to be used as arrow heads (562-563, 620, 621, 640). The shape of the bones 540-541, 549-550, 559-561, 624-625 were also supposedly produced intentionally for different instruments (Figure 5.14).

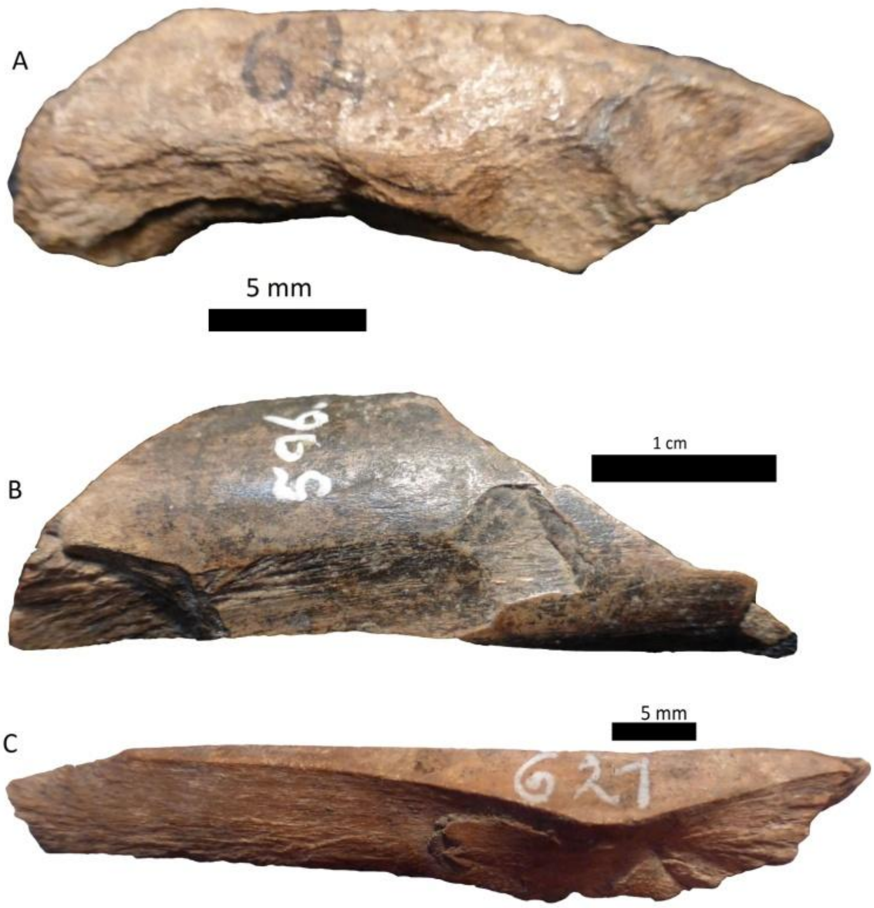


Figure 5.14. Bones of Paradero 4. A) Flake 562-563 with impact point and two successive extractions, B) Diaphysis 596 with notches and three extractions, C) Flake 621 with adhering flake.

5.4.2.3. Paradero 2

According to the Ameghino (1915 [1880]), this was one of the most important and ancient site given the big amount of bones and species identified by him. They were extracted from the Pampean layers 5, 6, and 7. Here, 20 bones were examined from which 12 present clear features of percussion marks (Table 5.5). Eight bones could not be related with specific human traces, among them, a metapod of Cervidae and a tooth of *Toxodon* (Table 5.6). Unlike the other sites, here four bones have species identification: one tooth (number 606-607) and one diaphysis (number 653) with loading point possibly of *Toxodon*, one *Pseudolestodon* rib of a juvenile individual (number 580) and one antler (number 602-604) of Cervidae with cut marks. The *Pseudolestodon* rib presents in its internal face of the diaphysis four oblique marks of 1.5 cm, approximately. Cervidae antler presents a fluvial polishing in the entire surface. It has a group of 4 oblique cut marks, two of 1 cm and one of half centimetre (Figure 5.15). Besides this material, the assemblage is composed by diaphyses of small and medium mammals. Spiral, longitudinal fractures and loading points are predominant, one also present a notch and other three extractions. Three elements (two inderminate and one diaphysis) were categorized as flakes and one diaphysis as a percussion cone.

In this site Ameghino (1915 [1880]) also interpreted some bones as instruments or worked bones, as 551-552, 554-555, 539, 630-631, 564-566 that currently were classified as with percussion marks, and 536, 586, 587, 597,658 and 587 that do not present sure features of being anthropically intervened.

Figure 5.15. Bones of Paradero 2. A) Percussion cone 551-552 with impact point and cortical extractions, B) Antler 602-604 with cut marks, C) Tooth 606-607 with impact point, D) Diaphysis 611 with magnification of notches on one side, percussion cones an extraction in the other, E) Pseudolestodon rib 580, with amplification of cut mark.

5.4.2.4. Paradero 1

Ameghino discovered this site in 1873 and given the association of human's remains with megafauna, he dedicated an special chapter in his work (Ameghino 1915 [1880]). Nevertheless, only two diaphyses with spiral and longitudinal from this site were reviewed in the collection, one of them, number 647 adjudicated probably to a carnivore (Figure 5.16).

Figure 5.16. Bones of Paradero 1A) 646, B) 647.

5.4.2.5. General observations of the sites

At the end of the 19th century, the bone breakage patterns of these sites were interpreted as instruments used for different activities. Currently, they can be reinterpreted as subproducts made by the activity of bone breakage for marrow extraction. Only teeth and antlers were modified to realize different bone tools. In the four sites, spiral and longitudinal fractures are the most represented type of anthropic intervention (Figure 5.17A and B). They are generally accompanied by other type of breakage patterns which indicated that these fractures were humanly made, and not by carnivores or other non-biological agents.

As Ameghino (1915 [1880]) indicated, Paradero 2 has a variable representation of species. Even though today only a small portion of that assemblage survived, the presence of at least three taxa identified, and the presence of small and medium size mammal indicates that at least a MNI of five animals with human traces is represented here. Besides spiral and longitudinal fractures, impact or loading point is the higher feature represented here, especially when compared with the other sites (Figure 5.17D), although notches are scarce (Figure 5.17C). In this site, most quantity of small fragments were viewed, with four fragments interpreted as flakes or percussion cone (33.33% of the total material with traces in this site), and five without clear anthropic traces. Only 25% of the material presents extractions. Bone number 611 is especially interesting given that presents two percussion cones in the lateral of the diaphysis, with an extraction following one of them, and in the other side the diaphysis presents a notch. The percussion cone 551-552 has an impact point and several cortical extractions (Figure 5.15). At last, only in Paradero 2 cut market bones were found (Figure 5.17I). Especially relevant for this work are the cut marks observed over the *Pseudolestodon* rib, indicating that consumption of juvenile individuals of megafauna occurred here. As explained, it can be observed that in this site are present all the categories of bone breakage patterns, except for adhering flakes (Figure 5.17C to E). The presence of a tooth, probably of *Toxodon*, with impact percussion and the antler of Cervidae indicate that bones were also used for tool production.

Paradero 4 is the second site where most material was reviewed. Material from this place also presents different types of humanly made traces. Beside spiral and longitudinal fractures, impact or loading points are also important (Figure 5.17A, B and D). Nevertheless bones with extraction are the most represented category than the rest of the sites, with 43.75% (Figure 5.17 H). In this category the bone 596 presents three extractions and a notch in the internal wall, while the bone 562-563 is a flake with percussion point and two extractions. In this site also the bone 621 is a flake with an adhering flake inside (Figure 5.14). Three more flakes were counted and summing with percussion cones, they represent 37.5% of the assemblage (Figure 5.17F and G).

Paradero 5 has less amount of material than the other two. Contrasting to them, notches were abundant, with 25% of representation and extractions were less (Figure 5.17C and D). This site also has one diaphysis, number 601 with an adhering flake (Figure 5.13). Even though percussion cones were not observed, two flakes and one bone with extraction were recorded (Figure 5.17F and H).

The two bones of Paradero 1 do not allows to make several observations, but to say that the only categories observed were spiral and longitudinal fractures (Figure 5.17A and B).

In conclusion, while all the sites presents spiral and longitudinal bone breakage features, in Paradero 2 more impact points were recorded, while the other categories are less represent. Unlikely, subproducts of bone percussion, as flakes, percussion cones, notches but also adhering flakes and extraction are better represented in the rest of the paraderos. This could be indicating that more processing was realized in them. Nevertheless, the biased sample prevents taking this conclusion. When excavated the sites, Ameghino observed that material was left *in situ* for future excavations (Ameghino 1915 [1880]), thus only a selected part of the material was extracted.

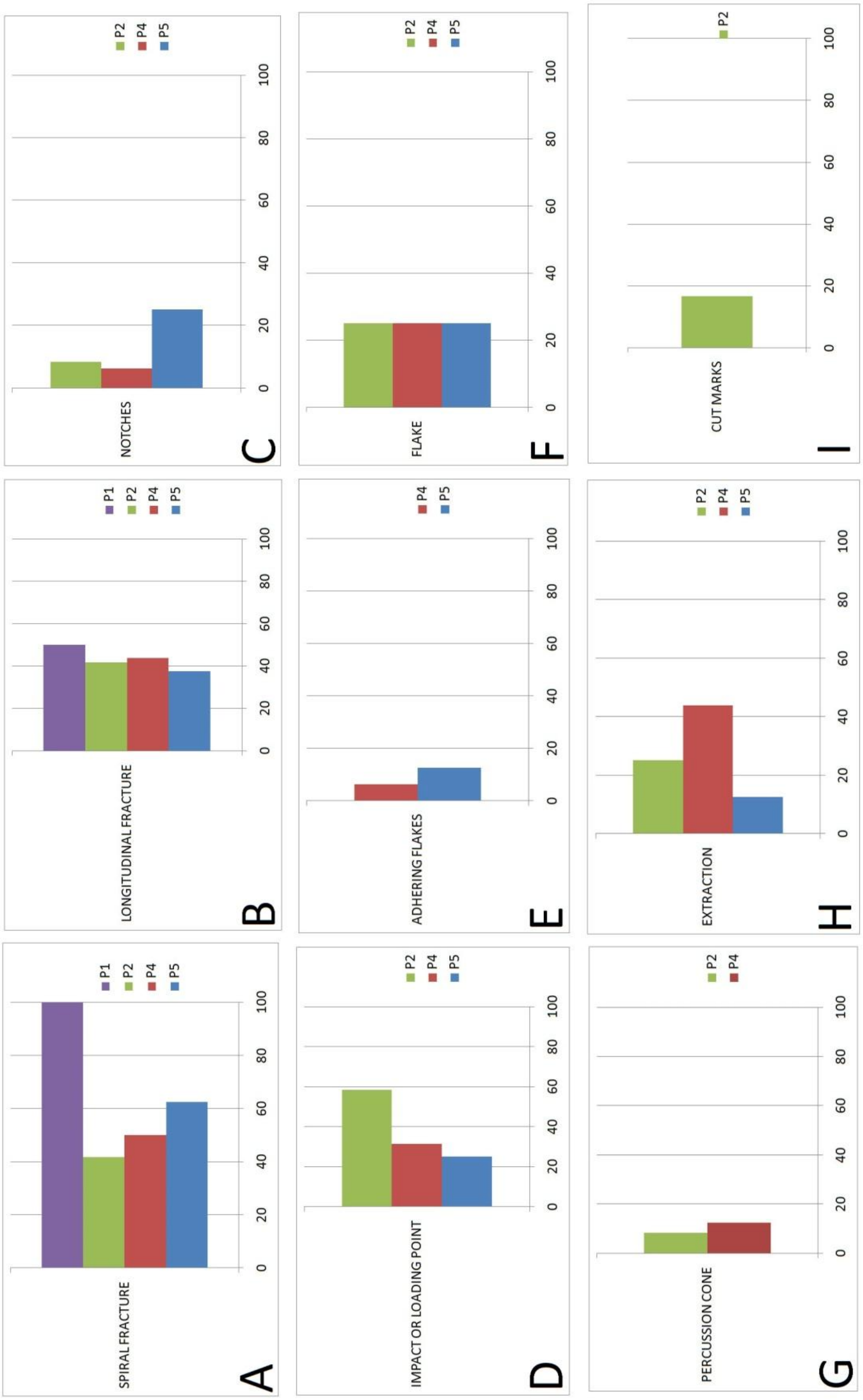


Figure 5.17. Representation of the different categories of bone breakage patterns at the Paraderos.

Also, the material was lost more than one century ago, an only a part of it have recently appeared. Thus, from the partially sample originally excavated, a smaller quantity have survived until now. In this sense, it has to be noticed that for the appendicular skeleton, diaphyses of long bone are the predominant category in the four sites while epiphyses are absent. The axial skeleton is only represented by the rib of *Pseudolestodon*, and the cranial skeleton for the tooth of *Toxodon* and the antler of Cervidae. Also more fragmentation or percussion marks are not necessarily related with more intensity of processing, but other variables can influence, as type of bone, age of the animal, presence of periostium or muscles among other (Todd and Rapson 1987; Pickering and Egeland 2006).

5.5. MCNV: A NEW REFLECTION

The material from this museum was reviewed again with the new methodologies incorporated (Dinolite and Hirox microscope). As stated befor, using SEM for two samples was time-consuming; consequently this technology was disregarded for this new revision.

Material analyzed with the new technologies allowed seeing details, such as microstriations not detected with the binocular microscope used in the first approximation realized. This is the case of the Mylodontidae rib (MPCB 64-11/12BW) that presents a V shape saw in the Dinolite microscope. Summing to this, the presence of three parallel marks allows to suspect the anthropic origin of this mark (Figure 5.18)

Figure 5.18. MPCB 64-11/12BW Mylodontidae rib with V shape. Dinolite image.

In the scapula of Mylodontidae (10-86) V shape was observed with the Dinolite microscope, while microstriations were observed with Hirox microscope (Figure 5.19 and Figure 5.20).

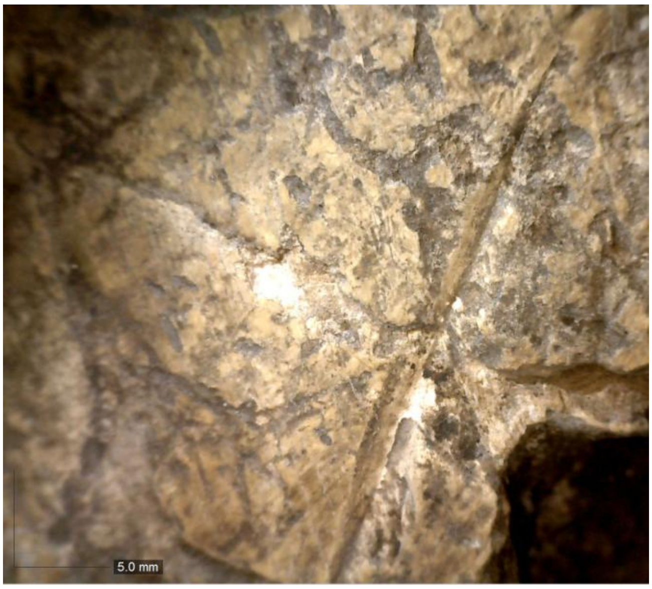


Figure 5.19. Scapula of Mylodontidae 10-86 with V shape. Dinolite image.

Figure 5.20. Negative cast of scapula of Mylodontidae 10-86 with indication of microstriation. Hirox image.

These features could not be clearly observed in the rest of the material. Consequently, given the new filters applied in this new revision, they cannot be included in the sampled material as bearing cut marks.

6. DISCUSSION

The discussion will deal with a broad-scaled analysis of the biological intervened bones. In the first part the expectations given in the introduction, will be contrasted. Latter on, some insights about the relation of humans and native fauna, considering the hypothesis, will be realized. In addition, a general comparison of the peopling of the Old World and the Americas will be done.

6.1. EXPECTATION ANALYSIS

1. To find few biological interventions over the bones. As noticed along the work, the biological intervened bones found are few. After reviewing the different collections the general departure suppositions were confirmed. Below, reference is made to each of them:

(i) As proposed in the introduction, and analyzed in the antecedents, little amount of humanly cut-marked bones is a general trend in the Americas. North America has been specially discussed as how many sites can be considered as proof of human exploitation of megafauna (Grayson and Meltzer 2002, 2015; Fiedel 2009; Haynes 2007; Surovell and Waguespack 2008, 2009) while in South America the general agreement is that the evidence is few (Roosevelt et al. 1996; Hubbe et al. 2007; Borrero 2008, 2009). In turn, as noticed in Chapter 2, this lack of evidence influenced the view that humans did little interacted with this native fauna when arriving to the Americas. Carnivore marked bones is even a more scarce record in the region. Consequently, the lack of this type of evidence did not allowed in these last decades to go further in understanding how humans/carnivores and megafauna interacted.

(ii) Low registration of biologically intervened bones was also determined by natural process (e.g. rise of sea level, post-depositional factors) and historical selection filter (early excavation system, museum requirements and restoration ways). In addition archaeological megamammals sites have generally low visibility. One animal is butchered in these types of sites, with minimum transportation of bones from kill sites/primary butchery, thus leaving most of the skeleton *in situ* (Holen and Holen 2014; Mosquera et al. 2015). For example, Hadza generally leave larger number of bones in these spots (O’Connell et al. 1992); the Kutse do not transport and/or produce heavily butchering in mega size animals (Kent 1993) and the Bisa leave almost the entire carcass in the primary butchering place (Crader 1983). Consequently given the scarce knowledge of the variability of archaeological record during 19th century, these types of archaeological sites could have been considered as paleontological one. Sites described by Ameghino (1915 [1880]) would have been easily detected given that the big amount of cut-marked bones found, gave them a higher visibility as archaeological sites. Thus, dispersed and isolated megamammals record will have low expectation of having being reported as with human marks. Current advancements in zooarchaeological and taphonomical issues, also allow having a better interpretation of the different marks that human butchering or carnivore consumption can leave over bone surfaces. Again the case of the material described by Ameghino (1915 [1880]) is an example case. The revision realized in this work over this material allows appreciating the advancement in bone interpretation during last decades. Ameghino (1915 [1880]) related almost all the bones to an intentional modification for realizing different instruments. Nowadays, it can be seen how most of them are waste of bone processing for marrow procurement. The same happens with the carnivore marked bones from MLP Ameghino (paleont. Coll.). When this material was excavated, more than a century ago, information about non-human bone modification was scant. Given the lack of knowledge of the different types of morphologies humans and/or carnivores leave over the bone, these marks were misdealing classified as with human intervention. In addition, this is an example of how historical sciences (palaeontology, archaeology, taphonomy among others) have advanced through the decades, and how with current knowledge these collections can be reanalysed, yielding new results. The poor knowledge of how biological marks could have occurred (especially regarding fragmentation of fresh bones) could have also influenced in the extraction of the materials (e.g. ignorance of small fragments or broken elements) given their low utility for commercial purpose.

(iii) At last, the general trend of low cut-marked bones in megamammal's animals is also related with their anatomy. Megamammals from controlled excavation sites such as elephants will generally bear few anthropic traces given the voluminous muscle, ligaments and perioustium difficult the contact between the instrument and the bone (Crader 1983; Gaudzinski et al. 2005; Yravedra et al. 2010; Haynes and Klimowicz, 2015) and this would have also been the case of native South American mammals such as Xenarthras (Borrero and Martin 2012). Consequently, in the case of non-contextualized collections as the one review here, this aspect must have also influenced in the low recording of traces.

2. To find different types of human intervention: cut marks and/or modified bones. Bones bearing cut marks were the type of intervention most detected in the different collections. In NMW one modified vertebra could be assigned to human intervention. In MLP Ameghino (archaeo. Coll.) different types of bone fragments produced as a consequence of bone fracturing or manufacture of bone were also found. Contrasting to the rest of the collections, given the more careful excavation of this site, implied that even smaller fragments as flakes or percussion cones were rescued. Nevertheless, in these sites, small and medium size mammals were predominant, and only a small size of tooth was adjudicated to

Toxodon. In general for the rest of the collections, as a consequence of the lack of context and the influence of natural factors that mimic human breakage pattern, clear fragments with anthropic intervention could not been detected. The difficulty of identifying anthropic activity in decontextualized collections is better understood when observing that different archaeological sites from North America have been proposed as having broken bones by human activity (e.g. Hamburguer, Shaffert, PrettyMan, Lovewell, La Sena, New Nebraska, among others; Holen and Holen 2014). But given the lack of associate lithic technology, other post-depositional process could have mimicked this type of breakage (Grayson and Meltzer 2015). Consequently, the lack of context influences negatively for detection this type of evidence in the collections. Furthermore, cultural selection could have also acted like a filter, given that smaller pieces of bones were not considered when trafficking operation took part.

3. To find cut marks in epiphysis on long bones ends and also in axial bones. Marks in both parts of the skeleton were found in the different collections (Table 6.1). Axial parts as ribs and vertebrae, and epiphyses of long bones such as ulna and humerus were the most abundant elements or where the clearest marks were found. This evidence suggests humans were exploiting different parts of megamammals' skeletons. Separation of the head from the postcranial skeleton and separation and/or filleting of appendicular parts were among the clearest activities indicated in the published papers. In addition, a rib bone could have been anthropogenically transformed. The cut marks found in the different elements are characterized by being long, between 2 to 4 cm, and some longer, as the one described in the ulna MNHN.F.PAM 751. This characteristic can be related with the fact that bigger animals will have larger and deeper marks, as muscles are bigger (Bello et al. 2009; Merrit 2015).

4. To find carnivore marks in long bone ends or fractured diaphyses for marrow extraction. Carnivore marks over megafauna bones were detected in the epiphyses of long bones (Table 6.1). Contrasting with human exploitation, no axial bone was detected with this type of intervention. In addition, in MLP Ameghino (paleont. Coll.) fractured long bones of smaller mammals were found.

5. To find different species bearing biological intervention. Except for the Toxodontidae femur, the rest of the species biologically intervened belongs to different Subfamilies of the Xenarthra Magnorder. Biological marks are especially important in different taxa of Mylodontidae group. As observed in the results, Xenarthra bones are predominant in the reviewed material, and among them Mylodontidae family the most abundant. Consequently the findings of biological marks on them could be related with these proportions. It is striking the almost absent of biological intervention in Notoungulates/Ungulates group such as *Macrauchenia*, Artiodactyla and Equidae, among the better represented bones from the different collections. The only carnivore mark in Toxodontidae proceeds from a collection where a certain degree of contextualization was conserved.

MUSEUM	NUMBER	ELEMENT	TAXON	ANTHROPIC TRACES	CARNIVORE MARKS
MCNV	MPCB 64-11/12BW	Rib	Mylodontidae	X	-
MCNV	10/86	Scapula	Mylodontidae	X	-
MLP	580	Rib	Pseudolestodon	X	-
MCNV	64-492	Tibia	cf. Scelidotheriinae gen.	-	X
MNHN	MNHN.F.PAM 119	Humerus	*Glossotherium robustum*	-	X
MNW	1908. XI.110	Humerus	*Glossotherium robustum*	-	X
MSNF	IGF14826	Atlas	*Megatherium americanum*	X	-
MNHN	MNHN.F.PAM 751	Ulna	*Megatherium americanum*	X	-
MNW	1908.XI.19	Rib	*Megatherium americanum*	X	-
ZMK	ZMK 38/1889	Caudal vertebra	*Panochthus tuberculatus*	X	-
MACN	MACN PV 6071	Humerus	*Doedicurus* sp.	X	-
MLP	MLP 15-I-20-32	Femur	Toxodontidae	-	X

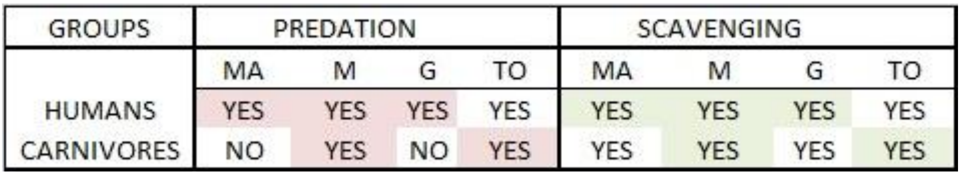
Table 6.1. Summary of the bones bearing biological marks from the different collections. Separation lines was put to visualized the different families.

6.2. SOME INSIGHTS IN THE RELATION OF HUMANS AND NATIVE FAUNA

Considering the different species bearing carnivore and anthropic mark (Table 6.1), some coarse-grained level observations can be done:

- *Megatherium americanum*: In the reviewed collections, only human's intervention was found in this taxon. Unlikely no evidence of carnivore marks was found.
- Mylodontidae: Humans and carnivore marks were detected for different taxa composing this family in the collections. While humans' marks were observed in ribs and scapula, carnivore marks were detected in appendicular elements. The presence of a juvenile rib bearing cut marks suggests that humans incorporated not only adult individuals.
- -Glyptodontidae: As *Megatherium americanum* case, only human's marks were found for this group in the different collections.
- -Toxodontidae: In the reviewed collections carnivore marks were found for this group. The bone number 653 and the tooth 606-607 identified by Ameghino as belonging to this animal and humanly intervened, cannot be currently clearly assigned to this taxon given the lack of characteristic anatomical features.

As the lack of context does not allows analyzing if the bones found were part of scavenging or hunting activities, the same status to both options is given here. In Table 6.2 both situations are considered for biologically intervened bones. Paleoecological information was included to fill in the gaps in situations where biological marks were not found (e.g. Prevosti and Vizcaíno 2006; Cione et al. 2009; Carlini and Zurita 2010; Zurita et al. 2010; de los Reyes et al. 2013; Vizcaíno et al. 2012; Pereira et al. 2013; Bocherens et al. 2016; Valkenburgh et al. 2016).



GROUPS	PREDATION				SCAVENGING			
	MA	M	G	TO	MA	M	G	TO
HUMANS	YES	YES	YES	YES	YES	YES	YES	YES
CARNIVORES	NO	YES	NO	YES	YES	YES	YES	YES

Table 6.2. Consideration of predation and scavenging scenarios for humans and carnivores in relation with the megamammal species treated here: MA) Megatherium americanum, M) Mylodontidae, G) Glyptodontidae, TO) Toxodon. In rose and green is indicated the material bearing biological intervention described in this work.

Considering biologically intervened bones presented here, humans would have predate/scavenge over three groups: *Megatherium americanum*, Mylodontidae and Glyptodontidae; while carnivore only over two: Mylodontidae and Toxodontidae. To this respect, four observations must be made:

- In a supposed predation scenario, while humans could have been able of hunting the different taxa; the members of the large-carnivore guild, such as Ursids, Felidae and Canidae could have hunt Mylodontidae and Toxodon. Even though *Smilodon populator* could have been able of hunting bigger animals such as *Megatherium americanum* (Bocherens et al. 2016), it probably attacked the juveniles of these species (Valkenburgh et al. 2016) given that the increased size of the Pleistocene communities was an antipredator system developed in response to the Holartic carnivore invasion (Vizcaíno et al. 2012). In Glyptodontidae case, the development of the carapace and tail was indicated as a defensive way to avoid carnivore predation (Patterson and Pascual 1968; Gillette and Ray 1981; McNeill et al. 1999; Carlini and Zurita 2010; Zurita et al. 2010). In fact, the evidence described by de los Reyes et al. (2013) for the neural apophysis of *Eosclerocalyptus* cf. *E. lineatus* in the Pliocene is adjudicated to a scavenging access (but see Gillette and Ray 1981 for the possible predation of a juvenile *Glyptotherium* (Glyptodontinae) in the Pliocene of Southern USA). Consequently, in a hunting scenario, humans should have established new predation ways at least for adult members of *Megatherium americanum* and Glyptodontidae groups.
- In both scenarios, there is an overlap of humans and carnivores over the exploitation of Mylodontidae species. Even though the construction of burrows by this species could have been done not only for hibernation, but to hide from the predator (Vizcaíno et al. 2001; Fariña et al. 2013; Cione et al. 2015); the presence of at least three bones bearing carnivore marks indicates that would have been a more easily prey than *Megatherium americanum* and Glyptodontidae. In spite of the sizes, *Glossotherium robustum* and cf. Scelidotheriinae gen. (between 1.000 to 1.500 kg) could have been susceptible of being hunted by top predators

such as *Smilodon populator* (Prevosti and Vizcaíno 2006; Bocherens et al. 2016). Canids such as *Theriodictis platensis* would have also predated over extreme-age (juveniles and senile individuals) or sick members of this group (Prevosti and Palmqvist 2001). Also, it cannot be discarded that they could have been hunted by groups of carnivores (Van Valkenburgh et al. 2016). Summing up to them, humans, at the last part of the Late Pleistocene would have also exploited adults and juveniles of this taxon, as noticed in the cut-marked bones.

- For the scavenging scenario, there is an overlap between humans and carnivores. Most of the carnivores have scavenging capacities (Pereira et al. 2013). In this scenario several situations could have occurred. Early or late access to animals dead by natural causes is one option, especially when considering that most of the samples analized here belong to adult members of the different groups. Scavenging over megamammals hunted by other carnivores is another option. For example, it was postulated that *Protocyon troglodytes* could have scavenged over animals hunted by *Smilodon populator* (Bocherens et al. 2016). Humans killings would have also provide a new source for carnivores that would have exploited carcasses left behind by them (Burke 2016). But also *Homo sapiens* should have also being able of using opportunistically megamammals killed by large carnivores (Ripple and Van Valkenburgh 2010). Consequently scavenging megamammals would have turned a complementary resource of other smaller and more frequent feeding resources such as camelids or deers (Borrero 1999, 2009; Messineo 2015; Martínez et al. 2016). However, anatomically modern humans had basically a hunting behaviour in the Old World, since the appearance of the Acheulian technology or even earlier (Domínguez-Rodrigo and Barba 2009; Yeshurun et al. 2007; Villa and Lenoir 2009; Bunn and Gurtov 2014; Rodríguez-Hidalgo et al. 2015; Palombo 2016; Martínez-Navarro 2016; among others). Consequently is highly disliked that *Homo sapiens* would have adopted a scavenging behaviour when entering in the New World.
- Toxodons would have only being exploited by carnivores during Middle Pleistocene. *Smilodon populator* would not have included them in their diet, given their preference for preys living in open and dry environments (Bocherens et al. 2016). Nevertheless it could have been an occasional prey for Felidae members (Prevosti and Vizcaíno 2006) or, as in Mylodontidae case, extreme-ages and disease individuals could have been more vulnerable to the predation by carnivores such as *Theriodictis platensis* (Prevosti and Palmqvist 2001) Toxodontidae bones used as fuel in the archaeological site of Paso Otero 5 (Joly et al. 2005; Martínez and Gutiérrez 2011; Prates et al. 2013) is indicating humans' exploitation of this taxa when entering to the region.

With this information the derivate hypotheses proposed in the Introduction can be analyzed:

Hypothesis 1: *Humans have modified the existing hunter/scavenger niche, establishing relationships of competition with carnivores*

Based on the interpretation realized of the biologically intervened bones presented here, a novel competitor was added to the trophic web with human's presence influencing in the intra and inter-species interactions. As a result the composition of the hunter and scavenging native niches should had been modified, as indicated for invasive species (Mooney and Cleland 2001; Shea and Chesson 2002; Kondoh 2006; Murphy et al. 2006; Duffy et al. 2007; Wilson and Wolkovich 2011):

- Carnivore predation niche should have been modified at least for species that were exploited by native carnivores, such as Mylodontidae. In the hunting niche, new competitive interactions should have been established for this taxon that was being periodically exploited by members of the large-carnivore guild before the entrance of humans. As established by the Competitive Exclusion Principle, two species with similar requierements cannot occupy the same niche. In consequence, human's novel involvement should have produced changes in its native competitors, at least for Mylodontidae prey. In addition, this novel predator should have not had natural enemies, as its novelty exluded them of being a potential prey (Enemy Release Hypothesis).
- In the scavenging access, humans should have been a novel competitor for the different megamammals' carcasses (e.g. Mylodontidae, *Megatherium americanum* or Glyptodontidae). As a consequence, native carnivores scavenging niche should have been modified, as the adittion of a new consumer would have provoque the drop off of the carcasses disponibility; decreasing the distribution of the energy among member of this guild.

Hypothesis 2: *Humans have colonized hunter niche, establishing novel relationships of predation with megafauna*

At the predation level, and after analizing the different possible scenarios, humans should have impacted at different levels of the hunting niche, according to the previous established relationship this mammal community had:

- *Megatherium americanum* and Glyptodontidae predation niches should have been colonized by *Homo sapiens*. The apparent lack of carnivore hunting over these two species along the Pleistocene was a situation that probably changed with the presence of the anatomically modern humans. Not only native fauna was not aware of the novel predator, but also the technology that humans had was more efficient to hunt animals that had developed defences for the predative behaviours of native carnivores. In consequence the vacancy of predators over these taxa should have been fullfit after human introduction.

- As Mylodontidae suffer some predation from members of the large-carnivore guild, fully colonization should not have been the case here, contrating this situation with the *Megatherium americanum* and Glyptodontidae. Nevertheless, humans' hunting supposes a change in the resource-partitioning system. Consequently, this overlapping should have implied a restructure of the predator interactions.

The different interactions that humans should have established with megaherbivores, and also with the members of the large carnivore guild entails a complex panorama. As proposed in the main hypothesis, "*Homo sapiens entry had provoked qualitative variations in the relationship among native species and consequently it had diversified its existing ecological niche*". According to this proposition, humans` novel presence must have altered the feeding guild, restructuring the established trophic levels of the native Pampean mammals' community at the end of the Late Pleistocene. Predation and competition must have been variable according to the different characteristics of the species and the previous relationships developed in this ecosystem: the predatory niche of *Megatherium* and Glyptodontidae should have been colonized by humans, Mylodontidae should have support the addition of a new predator, while carnivores should have suffer new competitive relationship at hunting and scavenging levels (Figure 6.1).

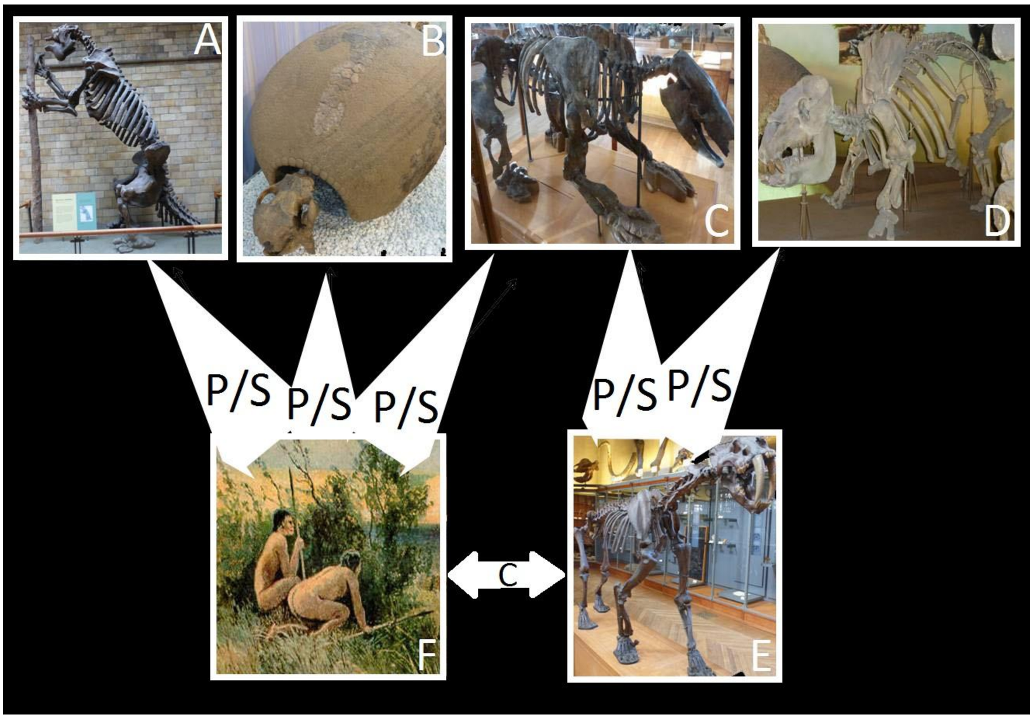


Figure 6.1. Consideration of paleoecological relationship established among humans, carnivores and megaherbivores. Homo sapiens (F) must had predate/scavenged (P/S) over species such as Megatherium americanum (A), Glyptodontidae (B) and Mylodontidae (C) species. Carnivores could have predate/scavenge over Mylodontidae or Toxodons (D). Competition (black C) between carnivore and humans must have been developed at least for some species such as Mylodontidae. A) Skeleton mounted in NHM, B) Skeleton mounted in MCNV, C

and E) Skeletons mounted in MNHN, D) Skeleton mounted in MLP, F) Figure extracted from Wikimedia Commons.

Native resource-partitioning system of the Pampean Pleistocene community probably was characterized by well developed interaction relationships across different tropic level. Holartic carnivores had an ample predation capacity, with several species competing for the resources (Prevosti and Vizcaíno 2006; Bocherens et al. 2016) and/or scavenging the carcasses at least since the Pliocene (de los Reyes et al. 2013), while some megamammals niches remained empty. Most of these herbivores, such as the Xenarthra, had been largely adapted to the different South American biomes and had survived previous invasion events by applying new antipredator strategies (Vizcaíno et al. 2001, 2012; McDonald 2005; Carlini and Zurita 2010; Zurita et al. 2010; Pujos et al. 2012; Fariña et al. 2013; Cione et al. 2015). Despite the paleoenvironmental changes of the Late Pleistocene-Early Holocene (Cione et al. 2003, 2009, 2015), at the time of humans' arrival, the native trophic web should have been highly mature and diversified, at least since the GABI event. As proposed by Valkenburgh et al. (2016:866):

"It is noteworthy that Pleistocene large mammal community composition is remarkably stable at a continental scale over at least the last 1 million years in both the Old and the New Worlds, despite glacial–interglacial fluctuations in climate. The apparently long-term and persistent stability suggests the existence of rich and complex communities that included multiple species at different trophic levels playing similar roles (redundancies), thus enhancing their resilience in the face of environmental perturbations"

In this scenario, prey-predator dynamics sustained top-down pressures regulating Pleistocene communities (Ripple and Van Valkenburgh 2010; Van Valkenburgh et al. 2016). Scavenging activities must have been also favoured given the large amount of megamammals' species during this period (Van Valkenburgh et al. 2016). According to the interpretation of the proposed working hypothesis, the scenario descibed here strongly support a situation where humans, as an invasive species, quickly disrupted this long term native ecosystem producing trophic cascades effects at various levels. As follows, existing paleoecological relationship would have drastically changed with the anatomically modern humans' presence:

- Predation: New predation opportunities arise for megamammals such as *Megatherium americanum* and/or Glyptodontidae. *Homo sapiens* presence supposed the development of new ways of top-down pressures over these communities. It also implied the summing of a new stressor over Mylodontidae community. Anti-predatory behaviours of these animals were not adapted or would have been less effective over hunting novel technologies, as already pointed by different authors (Patterson and Pascual 1968; Kay 2002; Cione et al. 2003, 2009, 2015; Surovell et al. 2005; Molina 2008; Ripple and Van Valkenburgh 2010). Consequently, the invasive species will tend to have more successful predation ways, given the naivety of native species with respect to the new predator (Kondoh 2006). This new type of predation could had had direct negative impacts, such as extinctions (Mooney and Cleland 2001).

- Competition: Competition with carnivores over same species such as Mylodontidae supposed a modification of predatory niche of this megamammal species, and an intraguild competition with carnivores. Specially at the beginning of the invasion, native predators will not recognized humans as possible competitors (Kondoh 2006; Ripple and Van Valkenburgh 2010) producing displacement of them or even extinctions, as suggested for Patagonia (Villavicencio et al. 2016). Considering that competition in open habitats is high given that the visibility permits more hunting possibilities (Domínguez-Rodrigo 2001), the open landscape such as the Pampean region would have support a dynamic interaction system among humans and carnivores. Open landscapes also favours the permanent presence of vultures that can be used as a sign for terrestrial predators (O'Connell et al. 1988; Domínguez-Rodrigo 2001; Jones et al. 2015a). Given that it was also proposed that a diverse avifauna would have exploited the Pampean megafauna (Tonni and Noriega 1998; Noriega and Areta 2005; Cenizo et al. 2015; Jones et al. 2015b), they would have also been participating in this complex trophic web. Consequently adding the anatomically modern humans, at the end of the last part of the Late Pleistocene, in this high competitive ecosystem must have produce modifications over the predatory guild of intraspecific organism. Extinctions of top-predators is a possibility in this situation (Duffy et al. 2007).
- Scavenging: Humans would have also been added to the scavenging system. Considering that periodically different paleoenvironmental stressors can produce that carcasses are fully exploited (Van Valkenburgh and Hertel 1993; Binder & Van Valkenburgh, 2010), this activity would have also been developed, at least seasonally, into a competitive context. Even though scavenging will not directly produce extinctions, the introduction of a native species can produce that native scavengers shift their diets (Wilson and Wolkovich 2011).

Human's entrance occurred in a particular changing paleoenviormental period, with higly climatic fluctuations that affected the disponibility of the *K-strategy* megamammals' communities in the paleolandscape (Cione et al. 2003, 2009, 2015; Haynes 2009a). Adding the anatomically modern humans to this feeding guild should had had deleterious effects in the niche partitioning of Pampean native communities. Therefore, the colonization and/or modification of the existing niches by this new invasive species would have been a highly disruptive factor in the native American paleoenvironments.

Humans as invasive species is a type of characterization gaining support worldwide given the general trend of humans behaviour with the past paleoenvironments (Day et al. 2003; Odling-Smee et al. 2003; Lanata et al. 2008a and b; Lanata 2011; Hortolá and Martínez-Navarro 2013; Moleón et al. 2014; Marean 2015; Dillehay 2014; Goldberg et al. 2016; Boivin et al. 2016). Still, in the Americas, the competitive scenario described did not include other *Homo* species. This situation contrast with African and Euroasiatic record. In the Old World the presence of similar *Homo* species must have implied that anatomically modern humans not only competed with carnivores but they also had an interguild competition for the same resources and/or were an ecological barrier for *Homo sapiens* dispersal (Shea 2003; Hortolá and Martínez-Navarro 2013; Liu et al. 2015).

7. CONCLUSIONS

This work tried to expand the problematic of human's dispersal in the Americas and its relation with the native fauna by considering a non-traditional source of information as historical collections. Given the samples lack of context, discussions are cautious, generated at a broad level. The focus was putted in understanding paleoecological relationships of the megaherbivore community, carnivores and humans. This is a topic not always discussed in the archaeology of the early peopling of the Americas. This is partly related with the scarce evidence of taphocenosis implicating the three (or at least two) of the agents. It was already mentioned the scarcity of early anthropic sites and this is more remarkable when sites with carnivore association is deal with. The time scale was wide, focussing on the Pleistocene, and considering humans presence was at the end of the Late Pleistocene. It is remarked the stability and the development of the ecosystem after GABI event, when several extinctions were registered after Holartic carnivores' entrance (Patterson and Pascual 1968; Webb 1978; Lessa and Fariña 1996; Woodburne 2010; Cione et al. 2015), but most of the megaherbivore community, as Xenarthras, readapted to this new situation. This scenario drastically changed after humans' entrance, with most of the extinctions grouped into the Pleistocene-Holocene transition.

Humanly made marks, even few, are informative and increase the number of human exploitation records over these mammals. They were related with human butchering system of the megamammal community, as these types of questions are lacking (Jackson et al. 2011). Anthropic separation of appendicular limbs and separation of the cranial from the postcranial skeleton were identified as the principal activities of butchering realized. Age range was predominant over adults, although juveniles individuals were also recognized. Carnivore marked bones presented here, are not only valuable given the almost null type of this evidence in the region, but also as it presented carnivore accessing to different megaherbivore community along the Pleistocene.

At a broad scale, the taxa with this type of evidence are highly useful as to compare humans and carnivores megamammals usage. Nevertheless, as the material is non-contextualized, information regarding the way of access to these animals, could not be deeply discussed. Consequently, it could not been distinguished if the biological marked bones were part of a scavenging and/or hunting event. As follows, the same importance was given to both options and the analysis of each case was done. As hunters, *Homo sapiens* presence should have colonized new niches, especially those that related with taxa that had successful defences systems developed after GABI event, such as increasing body size (e.g. *Megatherium americanum*) and/or development of defensive accessory structures (e.g. Glyptodontidae) (Zurita et al. 2010; Vizcaíno et al. 2012). Consequently, new predatory systems should have been established at least over part of the taxa. Other taxa, such as Mylodontidae, should have already accounted of carnivore predation. Therefore, humans should have established novel predation ways, modifying the existing niche of the carnivores. In this case, humans should have differently impacted in the different members of this community, considering their ecological characteristic and previous established relationships. In a scavenging case, *Homo sapiens* should have modified this scenario. In contrast to the hunting option, scavenging applies for all the species considered here, as carnivore should have also scavenged over animals that could not hunt (*Megatherium americanum*, Glyptodontidae). Nevertheless, the possibility that humans would have scavenged all the megamammals species, seems a marginal option. *Homo* species has a long way hunting tradition in the evolution of the Old World (Domínguez-Rodrigo and Barba 2009; Yeshurun et al. 2007; Villa and Lenoir 2009; Bunn and Gurtov 2014; Rodríguez-Hidalgo et al. 2015; Palombo 2016; Martínez-Navarro 2016; among others). This should have been the preferred way of accessing large mammals when specialized *Homo sapiens* entered in the Americas (Cione et al. 2003, 2009, 2015).

Carnivores should have been hunting and/or scavenging over these megafauna at least since Middle Pleistocene, as recorded here. Especially during cyclical fluctuations, when resources drop down their availability, megamammals' carcasses should have been completely consumed with more bone ingestion and or/within-nutrients (Van Valkeburgh & Hertel, 1993; Binder & Van Valkenburgh, 2010). Consequently, high interguild competition would have been the situation with humans entrance at *ca.* 14.000 BP (Politis et al. 2016) when paleoenvironment was fluctuating (Tonni et al. 2003; Zárate et al. 2009). This presence should have supposed an additional top-down pressure, in an already highly competitive ecosystem. Colonization and/or modification of existing niches should have been the principal change in a long lasting ecological ecosystem that survived previous invasion events. Human dispersal should have been fast timed, resembling an invasive species (Lanata el al. 2008a and b; Goldberg et al. 2016) not allowing the native fauna to recover from this event.

In addition, this work has been highly useful to revalorized historical collection for answering archaeological/ecological questions (since most of the research over them has been related with paleontological issues). Historical collection becomes a firsthand resource given the low record of biological marks for this time period. Usage of non-contextualized material has several debilities as already pointed. Megamammal's record was highly affected by commercial purposes, producing the lost of the primary information. Consequently, these collections had suffered more bias than other type of archaeological and paleontological material. But for fossil collections, the usage of new methodologies, considering the advances that the scientific research has realized along 20th century, and applying ecological concepts, was highly useful to detect, describe and interpret the different biological intervention. The new interpretation of Ameghino collection is an example of how the new methodologies are useful to analyze previous misleading interpretations over biological marks. Fossil collections also provided raw data to consider different possible scenarios of ecological relationships among the species.

It is also regrettably that the material sent for dating did not contain enough collagen. This did not allow providing of more information to get further insights about the chronology of the described interactions. Lack of collagen in the samples from that area was also indicated by different research works, given the poor preservation conditions of this extended open landscape (Tonni et al. 2003; Scanferla et al. 2013; Bocherens et al. 2016).

Nevertheless, in general terms, the non-traditional samples analyzed here, even few, were useful to approximate to the role of *Homo sapiens* early dispersal with native fauna in the South American Southern cone. This non-traditional question is generally left apart as the focus has been extinctions *per se* (Burney and Flannery 2005; Ripple and Van Valkenburgh 2010). As follows, new perspectives can be opened when applying new focus over old questions.

7.1. FUTURE PERSPECTIVES

Several insights are expected to be realized in future research activity:

- New dating methods are necessary to have a better and more reliable database of chronology of this fauna. Dating the bioapatite of bone is becoming an alternative solution to the collagen.
- Novel research methodologies are necessary to go into the paleobiology of the extinct megafauna. Application of stable isotope and use wear analyses over samples from historical collections will provide not only information of the diet but also of the paleoenvironment. These applications are just starting to be done over this community of megamammals. Trophic webs can be deciphered with the usage of these methodologies and this will give more contextual information as how humans have intervened in this native ecosystem. At the same time, this information can be linked with past vegetation structure and, in consequence, environment can be reconstructed.
- It is also lacking proper controlled excavations. This type of activity is urgently needed, not only to have a better control over post depositional process affecting the bones, but also to detect possible faunal associations and analyze possible biological interventions.
- Comparison with other regions, such as Patagonia, where humans' presence has the same chronology and exploitation over megafauna was also recorded, is also needed. Variability and/or similarities in ecosystems must be highlight to understand the different humans' adaptations in these initial times.

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9. APPENDIX

9.1. ADDITIONAL PAPERS AND PRESENTATIONS IN SCIENTIFICS REUNIONS

Article published in 2016 in: El poblamiento temprano en América 7. Serie: Prehistoria en América: 221-245. Editors: J.C. Jiménez López, C. Serrano Sánchez, F. Aguilar Arellano, A. González González. Morevallado Editors, México. Co-authors Profs. Cristian M. Crespo, José L. Lanata.

FÓSILES Y GENES: DATOS TAFONÓMICOS Y GENÉTICOS PARA UNA PROPUESTA ECOLÓGICA DEL POBLAMIENTO AMERICANO

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Resumen:Se realiza un breve repaso de un modelo ecológico de poblamiento americano recientemente propuesto y de dos líneas de investigación derivadas. Homo sapiens puede pensarse como una especie invasora por dos condiciones: un rápido crecimiento demográfico –tempo- y posiblemente un impacto diferencial en los paleoambientes por las características ecológicas propias de ellos –modo. Se presenta una recopilación de antecedentes desde la genética de poblaciones y de linajes maternos –ADNmt-, y nuevos análisis tafonómicos, para profundizar ambos. Se integran los resultados a estudios realizados entre las regiones pampeana y patagónica.

Comprender la dinámica de la dispersión humana es un desafío constante para la investigación actual sobre el proceso de ocupación en diferentes continentes. Cómo *Homo sapiens* colonizó las distintas latitudes del planeta, cuánto tiempo llevó la ocupación de los distintos espacios y cómo fue su interacción con el medioambiente durante este proceso, son temas de relevancia para entender nuestra historia como especie. Las características propias de las Américas -como su extensión latitudinal, el aislamiento del resto de los continentes, el hecho de no poseer incursiones homínidas previas- hacen a este continente un caso particular de estudio (Borrero, 1999; Lanata 2011). Por ello, diversas discusiones académicas, en general relacionadas al *tempo* y al modo de dispersión, analizan la cronología de esta primera entrada, los movimientos en el espacio, y la influencia que pudo haber tenido en la extinción de la fauna nativa en América, entre otras cuestiones (Anderson y Gillian, 2000; Barnosky *et al.*, 2004; Borrero, 1989-1990; Cione *et al.*, 2009; Fariña *et al.*, 2014; Graham y Lundelius, 1984; Gutiérrez y Martínez, 2008; Lanata *et al.*, 2008 a y b; Lanata, 2011; Martin, 1973; Martínez *et al.*, 2013; Martino *et al.*, 2007; Miotti y Salemme, 1999; Monjeau *et al.*, 2015; Pitblado, 2011; Prates *et al.*, 2013; entre otros). La forma en que la dispersión se produjo; colonizando ambientes de latitudes medias y altas, climáticamente variables y con cambios esperables en la biogeografía; significa entender cómo *Homo sapiens* se adaptó a situaciones fluctuantes y, logró llevar a cabo una ocupación exitosa de la región durante el Holoceno.

Recientemente, se ha sugerido que el estudio del primer poblamiento americano se puede analizar a partir de un modelo ecológico, que propone la dispersión humana en Sudamérica bajo la perspectiva de la ecología de invasiones (Goldberg *et al.*, 2016; Lanata *et al.*, 2008 a y b; Lanata, 2011; Martino *et al.*, 2007). En este modelo, *Homo sapiens* sería una especie no nativa con una dinámica de dispersión rápida -relacionado con el *tempo*- y con estrategias de explotación diferencial en las diversas regiones por donde se movilizó -relacionado con el modo. Dos líneas de investigación se desprenden de esta premisa y están siendo llevadas adelante: por un lado el *tempo*, obtenido a partir de los fechados de los sitios tempranos, en conjunción con la información obtenida del estudio e identificación genética de linajes maternos -ADN mitocondrial- realizados en poblaciones actuales y antiguas, desde el marco de la genética de poblaciones. Este tipo de información permite hipotetizar la posible dinámica de la especie invasora, establecer potenciales momentos de ingreso a través del cálculo de los tiempos de coalescencia de los haplogrupos mitocondriales e inferir cambios poblacionales mediante la frecuencia de los mismos, realizar simulaciones demográficas y evaluar, por ejemplo, el movimiento de estos grupos y las posibles rutas utilizadas, si se registran eventos de remplazo o continuidad poblacional y la evolución de las poblaciones en relación al accionar de diferentes procesos microevolutivos (Matisoo-Smith, y Horsburgh, 2012). Por otro lado, una manera de abordar el modo puede ser a través del estudio tafonómico de colecciones museísticas de faunas nativas para identificar cualquier tipo de intervención biológica -ya sea antrópica o de carnívoros- sobre las mismas (Chichkoyan, 2011). La revisión tafónomica de colecciones fósiles históricas depositadas en distintos museos del mundo aporta nuevos datos al respecto (Chichkoyan, 2011; Krasinsky, 2010; Labarca, 2003; Martin, 2008; Perez *et al.*, 2005; Prous, 1986; Redmond *et al.*, 2012; Saunders, 2007; Toledo, 2009; entre otros). Sin embargo, por un lado, la forma de extracción de las muestras que se realizaba en el siglo XIX y la descontextualización general del material (Wolff, 1975) influyen en la cantidad y tipo de información que estas colecciones pueden aportar (Chichkoyan, 2016). Pero, por otro lado también, se pueden obtener datos inéditos de una manera más rápida, directa y menos intrusiva que las excavaciones sobre el terreno (Pérez de Micou, 1998), como así plantear nuevos ejes de trabajo. Además, el integrar estas colecciones paleontológicas históricas en trabajos de investigación actuales, les otorga un valor agregado que trasciende las fronteras del "objeto de exposición" u óseos depositados en los museos (Chichkoyan, 2016). Su incorporación a problemáticas distintas a las paleontológicas significa aplicar conocimientos de distintas disciplinas, para abordar la biodiversidad pasada en general, dentro del marco de las Ciencias Naturales (Chichkoyan, 2016). Así, la detección de agentes biológicos, su análisis e integración a nivel regional para su contextualización, y su interpretación a partir de conceptos ecológicos permite analizar cómo podrían haberse relacionado las faunas nativas entre sí y con *Homo sapiens* (Chichkoyan, 2011, Chichkoyan *et al.*, 2015).

A continuación, se presentará el marco ecológico que modela la dispersión humana como una especie invasora. Posteriormente, se explican ambas líneas de evidencia: la genética y la tafonómica y los principales datos obtenidos. Finalmente se discutirán los resultados y se proponen algunas conclusiones. Debido a la complejidad y multiplicidad de conceptos que se manejan y el espacio acotado para desarrollarlos, exponemos las líneas principales de estas ideas.

Ecología de invasiones

Nuevos estudios proponen enfocar la dispersión humana como una invasión de especies en las Américas (Goldberg *et al.*, 2016; Lanata *et al.*, 2008 a y b; Lanata, 2011; Martino *et al.*, 2007). Este concepto se relaciona con la adaptabilidad y rapidez de dispersión que tiene una especie cuando se introduce en un territorio no nativo. En el caso americano, las poblaciones humanas, pasaron de paleoambientes fríos como en el caso de los 72° grados de Latitud Norte, a tropicales para luego pasar a templados y fríos en un tiempo relativamente corto si se lo compara, por ejemplo, con las primeras dispersiones de *Homo sapiens* en Eurasia (Lanata, 2011). De esta forma, para entender el carácter invasivo de la dispersión humana en América se realizaron simulaciones con distintas tasas de crecimiento anual y tomando una entrada desde Beringia hacia los 18.000 AP y el fechado de Monteverde como llegada final (Lanata *et al.*, 2008 a y b; Lanata, 2011; Martino *et al.*, 2007). A partir de esto se apreció que un crecimiento anual del 2% exige más de 20.000 años para alcanzar Tierra del Fuego desde Beringia, mientras que con un 3% tardará unos 8.900 años. Sin embargo, algo diferente sucede con una tasa de crecimiento de población anual de 4%. El intervalo de tiempo para llegar a Tierra del Fuego es de unos 5.600 años y no es muy distinto del que resulta de un crecimiento del 5%, que es de 5.100 años.

Estos dos últimos escenarios son consistentes con los primeros sitios arqueológicos de Patagonia y con una dispersión humana a partir de 18.000 AP. Esto implicaría un alto crecimiento demográfico humano, como supone uno con las características de una especie invasora. Ésta característica ecológica invasiva debe haber colaborado a que, hasta tanto se colonizasen los ambientes, las tasas de crecimiento poblacional fuesen altas. Las simulaciones muestran que a partir de tasas mayores a 3% anual, la cantidad de años parar cubrir todo el territorio americano tienden a estabilizarse. Es por ello que, la distribución poblacional no habría sido homogénea, ni que la presión demográfica habría expulsado del Norte al Sur a los humanos como postulaba el modelo de Martin (1973). Por el contrario, habría habido concentraciones poblacionales en aquellos espacios con recursos diversos y ricos -*hot spots*. E incluso regiones a las cuales los humanos habrían entrado muy tardíamente en el tiempo, habiendo ya llegado al extremo Sur continental. Por la proyección de las simulaciones y tomando en cuenta datos paleoambientales, esta rápida dispersión se habría producido por la ocupación diferencial de los ambientes, con 2 cuellos de botella importantes -Beringia y Centroamérica- ante los que se abrían amplios territorios que podrían haber agilizado la dispersión en el paisaje (Lanata *et al.*, 2008 a y b; Lanata, 2011; Martino *et al.*, 2007 y figuras allí presentadas).

Según el modelo ecológico planteado, entender a *Homo sapiens* como especie invasora permite explicar cómo habría sido la dinámica de dispersión y qué rutas podría haber tomado nuestra especie en este proceso. Los corredores en este modelo, son de importancia fundamental ya que no solamente permiten la dispersión, sino que conectan y dan acceso a distintos recursos. En especial habrían sido importantes los corredores Norte-Sur, que corre a lo largo de la faja de los Andes, y el de Oeste-Este en la Cuenca Amazónica. De esta manera, analizar los movimientos poblacionales en relación a los distintos ambientes, puede brindar información para evaluar la dinámica de la adaptación de *Homo sapiens* durante el proceso de dispersión temprana. Además, esto podría ser facilitado por una rápida colonización y/o modificación de los nichos ecológicos particulares en cada ecosistema. Así, al ocupar una región determinada, *Homo sapiens* podría generar una competencia diferencial con otros mamíferos por los mismos recursos, lo cual a su vez es ventajoso ya que muchas especies de estos mamíferos sudamericanos estaban en vías de extinción desde hacía varios milenios.

Genética

Un importante aporte y cúmulo de información generado recientemente desde la genética de poblaciones, permite estudiar algunas cuestiones relacionadas con la dispersión de *Homo sapiens* en Sudamérica. El marcador molecular más utilizado hasta el momento es el ADN mitocondrial –ADNmt- debido a sus características: posee un alto número de copias por célula, se hereda estrictamente por vía materna, no presenta recombinación y acumula secuencialmente las mutaciones a través del tiempo, las cuales pueden ser detectadas y asignadas a cada individuo o grupo. De esta manera, se pueden trazar linajes maternos e hipotetizar rutas migratorias, relaciones genéticas entre diferentes poblaciones e inferir procesos de continuidad/discontinuidad poblacional mediante la identificación de procesos microevolutivos (Matisoo-Smith y Horsburgh, 2012).

En la década de 1990, diferentes polimorfismos del ADNmt de poblaciones americanas actuales han sido identificados con el objetivo de estudiar la variabilidad y diversidad genética presente, establecer un consenso sobre las variedades presentes, y las relaciones biológicas entre las mismas. En los últimos años, gracias a la secuenciación completa del genoma mitocondrial y a la mayor cantidad de investigaciones en este campo, se logró refinar el análisis de las variedades e identificar los linajes exclusivamente americanos. Así se aumentó la resolución sobre la diversidad genética mitocondrial, la cual ha posibilitado inferir patrones filogeográficos. Actualmente, se han propuesto al menos 16 linajes fundadores derivados de las presentes en poblaciones asiáticas. Nueve de ellos, poseen una distribución pan-americana -nombrados como A2, B2, C1b, C1c, C1d, C4c, D1 y D4h3a- con tiempos de coalescencia cercanos a los 20.000 años AP, mientras que los restantes 5 -D2a, D3, D4e1c, X2a y X2g- estarían restringidos a grupos de Norteamérica (Achilli et al. 2013; Kumar et al. 2011; Perego et al. 2010; entre otros). El linaje D4h3a posee una distribución actual exclusivamente pacífica, estando presente en Norte y Sudamérica, lo cual parecería indicar que esta fue la primera ruta de dispersión de las primeras poblaciones en un evento de rápida migración (O'Rourke 2009; Perego et al. 2010, entre otros). Estos postulados fueron reforzados por la identificación de dicho linaje en diversas muestras antiguas: en el sitio On Your Knees Cave, en la Isla de Príncipe de Gales, Alaska (Kemp *et al.*, 2007), con un fechado radiocarbónico de 10.300 AP, en un individuo del sitio Anzick asignado a la cultura Clovis con una temporalidad de 10.705 años AP (Rasmussen *et al.*, 2014) y en un individuo de la Isla Lucy, Columbia Británica, Canadá (Cui *et al.*, 2013) datado en 6.200 años AP, estando los 3 sitios ubicados sobre el Pacífico.

Para Sudamérica, estudios recientes han propuesto diversos sub-haplogrupos que parecen estar restringidos al Cono Sur. Las variedades nombradas como D1g y D1j (Bodner *et al.*, 2012) parecen poseer distribuciones particulares y según los autores serían el reflejo de un rápido poblamiento costero pacífico, con posterior flujo trans-andino, generándose estas variedades mitocondriales al ingreso a la región hace unos 18.000-14.000 años AP como mínimo. El primero aparece en frecuencias considerables en poblaciones de Chile y Argentina, en ambos lados de los Andes (De Saint Pierre *et al.*, 2012 a y b; Ginther *et al.*, 1993; Moraga *et al.*, 2000). Mientras que el segundo posee distribuciones variadas, pero se encuentra presente principalmente en poblaciones del centro de Argentina (García *et al.*, 2012), lo que supone a esta región como su posible lugar de origen. Su presencia en Norpatagonia podría deberse a eventos de flujo génico Norte-Sur o al origen común de estas poblaciones. Adicionalmente se han detectado sub-haplogrupos definidos como B2i2, C1b13, C1d1b, C1d1e, en Patagonia y una alta frecuencia de los linajes fundantes B2, C1, D1, D1g, y D4h3a, siendo los tres últimos mayoritarios al Sur de la Patagonia (De Saint Pierre *et al.*, 2012 a y b). Según los últimos autores, estos resultados estarían indicando un cline Norte-Sur de los haplogrupos B2, C1b, D1y D4h3a, desapareciendo el primero e incrementándose los tres últimos en Tierra del Fuego, acompañado del linaje D1g en todas las regiones del Cono Sur. Adicionalmente el linaje fundador pan-americano D4h3 parecería estar confinado a Patagonia y Tierra del Fuego.

Sin embargo, la mayoría de la información disponible para la Patagonia argentina fue obtenida de poblaciones actuales de grupos Mapuche y Tehuelche, siendo pocos los estudios realizados sobre restos esqueletales y el intento de establecer hipótesis relacionadas con el poblamiento de la región. Diferentes proyectos en curso (Cardozo *et al.*, 2014; Crespo, 2015; Postillone *et al.*, 2014) se encuentran investigando la diversidad genética del ADN mitocondrial de poblaciones prehistóricas de diversos sectores de la Patagonia argentina. Los ejes de trabajo son: evaluar la demografía y el origen de algunas variedades mitocondriales halladas, establecer los posibles procesos microevolutivos que las mismas atravesaron, y entender la dinámica poblacional al ingreso a la región y su evolución durante el Holoceno.

En los análisis realizados en restos antiguos (García-Bour *et al.*, 2004; Lalueza *et al.*, 1997) procedentes de restos esqueletales de colecciones de museos atribuidos a grupos Aonikenk, Kaweskar, Yámana y Selk´nam, sólo detectaron los linajes C1, D1, D1g y D4h3a, estando ausente los linajes A2 y B2. Se ha adjudicado dicha ausencia a la deriva génica como principal proceso de reducción de la variación genética. Recientemente se han descripto a los linajes C1 y D4h3a en individuos prehistóricos del Holoceno tardío y en poblaciones actuales procedentes de los archipiélagos chilenos (De la Fuente *et al.*, 2015; Moraga *et al.*, 2010), adscriptos a grupos Kaweskar y Yámana. De acuerdo con estos autores, en las poblaciones antiguas estos linajes comprimen el 90% de la variabilidad genética mitocondrial, sugiriendo condiciones de extremo aislamiento y baja demografía. Sin embargo, los restos humanos analizados en el sitio Baño Nuevo 1 (Manríquez *et al.*, 2011) de la Patagonia chilena datados en 9.000 AP, demostraron la presencia de los linajes B y C, sugiriendo la continuidad y discontinuidad de algunos linajes, posiblemente producto de la deriva génica.

Para el caso de la Patagonia argentina diversas investigaciones en curso han identificado en restos esqueletales del Holoceno tardío los linajes A2, C1, D1, D1g, D1j y D4h3a, tanto en sectores cordilleranos como en la costa atlántica (Crespo, 2015; Dejean *et al.*, 2014). Se ha observado en los resultados una reducción de la diversidad genética al Sur, encontrándose sólo las variedades C1, D1 y D4h3 en Tierra del Fuego (Crespo, 2015; Postillone *et al.*, 2014) y posiblemente una modificación en la composición genética mitocondrial debido al proceso de Araucanización del Siglo XVI (Crespo, 2015). En su conjunto, los resultados obtenidos estarían indicando una baja diversidad mitocondrial en general. Estos patrones pueden deberse posiblemente a la acción de la deriva, la baja demografía y la ausencia de flujo génico con grupos distantes, portadores de linajes diferentes a los patagónicos; y que dichos linajes probablemente reflejen una continuidad poblacional sostenida, tal vez desde el comienzo de poblamiento de la región, hasta momentos históricos (Crespo, 2015).

En la región pampeana no se han realizado muestreos sistemáticos aún, pero sí se cuenta con algunos trabajos iniciales en los últimos años en diversos sectores. Se ha logrado tipificar los haplogrupos B, C y D en 8 de los 23 individuos analizados del sitio Arroyo Seco 2, con temporalidades desde los 7.500 años AP. La secuencia temporal y regional de estos resultados demuestra una continuidad poblacional de los linajes mitocondriales hasta épocas más tardías, sin mediar procesos de reemplazo (Pérez *et al.*, 2009). Recientemente se han publicado los resultados obtenidos de análisis realizados al Este y Oeste del actual territorio de Uruguay, observándose los haplogrupos A, B, C y D. Esto sugiriere, no sólo una continuidad de linajes en la región pampeana, sino también la ausencia de diferenciación genética en toda la macro región analizada, pero dicha ausencia de estructuración puede deberse a problemas de muestreo (Figueiro, 2011). A su vez, las investigaciones iniciadas por Figueiro (2013) han propuesto cierta homogeneidad genética desde principios del Holoceno. La misma se habría mantenido por eventos de flujo génico con diversas regiones, conservando una diversidad genética similar a poblaciones del centro-Norte de Argentina. Hacia el Holoceno tardío se verifican ciertos linajes diferenciales, producto de desarrollos *in situ* y otros posiblemente por flujo con otras regiones (Figueiro, 2013; Sans *et al.*, 2012, 2015).

Recientemente se han presentado los primeros resultados utilizando técnicas de secuenciación masiva, obteniendo 2 mitogenomas de alguno de los restos más tempranos del sitio Arroyo Seco 2 con edades cercanas a los 8.000 años AP (Llamas *et al.*, 2016). Se lograron definir los linajes A2ae y D1a gracias al análisis de las secuencias obtenidas, los cuales se encuentran presentes en baja frecuencia en poblaciones actuales y extintas de la región (Crespo, 2015).

En su conjunto, los datos aportados por las investigaciones mencionadas parecerían apoyar la propuesta de un escenario de rápida colonización de Sudamérica, posiblemente por una ruta pacífica, con posteriores migraciones transcordilleranas. Sin embargo, la reciente identificación del linaje D4h3a5 en la costa atlántica patagónica podría indicar la importancia de este litoral como posible corredor costero en el cono Sur de Sudamérica (Crespo *et al*., 2015; Motti *et al*., 2015). La baja demografía y la ocurrencia de deriva o cuellos de botella -o ambos- podrían haber modelado la estructura genética de las poblaciones iniciales de ambas regiones. Sin embargo, en sectores pampeanos pueden verse reflejados eventos de flujo con otras regiones en momentos más tardíos, demostrando mayor variabilidad genética y una dinámica poblacional posiblemente más compleja, con mayor demografía. Adicionalmente, ciertas poblaciones patagónicas actuales han demostrado poseer linajes mitocondriales presentes en las poblaciones antiguas, demostrando la continuidad y persistencia a nivel poblacional de los haplotipos de los primeros grupos que ocuparon la región.

Estudios tafonómicos

Desde la arqueología, la evidencia sobre la relación entre humanos y megafauna siempre fue un tema controvertido (Monjeau *et al*., 2015) debido a la escasez de evidencias que sustenten una predación importante sobre este tipo de animales (Borrero, 2009). Además, aun la presencia de la misma es discutible en relación al tipo de acceso que los humanos tuvieron sobre estos (Borrero, 1999, 2009; Cione *et al*., 2009; Gutiérrez y Martínez, 2008; Miotti y Salemme, 2003, entre otros).

En este caso, la revisión tafonómica de la Colección Rodrigo Botet depositada en el Museo de Ciencias Naturales de Valencia ha aportado algunos datos preliminares (Chichkoyan, 2011; Chichkoyan *et al*., 2015, entre otros). Recientemente se ha retomado esta investigación y se han sumado las colecciones depositadas en otros museos europeos. En este caso se incorpora el resultado de las colecciones depositadas en Italia. La mayoría del material comercializado proviene de excavaciones que se concentraban en lo que es actualmente el Noreste de la Provincia de Buenos Aires (Chichkoyan, 2016). Algunas localidades referenciadas son Río de la Plata, Río Salado, Mercedes, Lujan y Bahía de Samborombón.

En las distintas colecciones analizadas, se seleccionaron elementos óseos mayores a 2 cm, que tuviesen la cortical conservada y que tengan identificación taxónomica y anatómica. Se ha revisado el material en búsqueda de acciones de agentes biológicos –huellas antrópicas o marcas de carnívoro- que pudieran haber afectado su superficie. Las primeras se diferencian de marcas producidas en la extracción y/o manipulación en los museos, ya que presentan algunos de los atributos definidos para las huellas de corte, como escotadura en V, presencia de microestrías en sus paredes internas, que sean alargadas y con orientación transversal o longitudinal. En algunos casos se distribuyen en forma agrupadas -varias huellas cercanas- o se localizan en zonas del hueso relacionadas con diversas actividades de procesamiento de las carcasas (Binford, 1981; Galán y Domínguez- Rodrigo, 2013; Lyman, 1994; Pérez *et al.*, 2005; Redmond *et al.*, 2012; Saunders, 2007, Yravedra, 2013, entre otros). Además, tienen las mismas características de conservación que el resto del hueso, lo que implicaría que habrían sido afectadas por los mismos agentes posdepositacionales que el resto del elemento donde se presentan (Labarca, 2003; Redmond *et al.*, 2012; Saunders, 2007, Toledo, 2009). Dentro de los segundos, se consideraron improntas, surcos, perforaciones o vaciados, descriptos en diversos trabajos (Binford, 1981; Haynes, 1983; Lyman, 1994; Martin, 2008, Sala y Arsuaga, 2016; Yravedra, 2013; entre otros). Además, se han registrado los agentes postdeposicionales observados en su superficie, como la acción de pisoteo, meteorización, agentes químicos -manchas de manganeso y óxido-, raíces, erosión fluvial, presencia de sedimento, acción del fuego y tipo de fractura postdepositacional (Behresmeyer, 1978; Binford, 1981; Lyman, 1994; Yravedra, 2013; entre otros). Se revisó el material a ojo desnudo, con lupa de aumentos -5 X y 12 X-, con Microscopio Dinolite modelo 4113, y el caso del Museo de Ciencias Naturales de Valencia también con microscopio Wild Heerbrugg M3B.

Se volvió a examinar una parte de la colección de Valencia -NISP: 1478. Se han descartado los elementos indeterminados y las placas de Cingulata. Se detectó acción carnívora en la tibia derecha nº 64-492 de cf. Scelidotheriinae gen. -Mylodontidae. Las marcas se encuentran distribuidas entre el sector de la epífisis distal, cara medial y en menor cantidad en la epífisis proximal (Figura 1). En la epífisis distal es donde más cantidad de marcas se registraron. La cara articular presenta una impronta dental cercana al borde medial de al menos 4 dientes (Figura 1A). La misma es superficial y con base plana, donde una tiene forma rectangular y mide 0,9x0,6 cm. Esta marca se encuentra rodeada de surcos superficiales. Del otro lado de la cara articular, se han detectado 2 surcos más largos y profundos que cruzan en forma transversal esta cara. Sobre la epífisis distal, cara medial, a continuación de la impronta, se detectaron surcos paralelos entre sí que rodean un vaciado (Figura 1B). Esta acción significó una importante extracción de tejido óseo, que se extiende desde la cara posterior a la anterior. También se detectó otro vaciado en la epífisis y metadiáfisis proximal (Figura 1E). Ambos se encuentran rodeados en la cara posterior y anterior de improntas y tienen bordes crenulados (Figura 1C y E). Las que se encuentran sobre la cara posterior, que son las más distinguibles, son elongadas, paralelas entre sí, y tienen una orientación posterio-medial. En la metadiáfisis distal se han contabilizado 5 marcas de aproximadamente 1,5x0,4x0,1 cm, y 2 en la proximal de 1,5x0,5x0,1 cm. Además, sobre la diáfisis, cara medial, se han visto 3 gruesos surcos que corren en forma transversal (Figura 1D). La cantidad e intensidad de marcas registradas en este elemento podría estar relacionado a un evento de carroñeo. Esto implicaría que un primer grupo de carnívoros podría haber explotado los tejidos blandos mientras que un segundo grupo habría provocado los daños registrados y consumido también parte del hueso.

Por otro lado, se han analizado las colecciones depositadas en los siguientes museos italianos: Museo Geologico Giovanni Capellini di Bologna, Museo Civico di Storia Naturale di Milano, Museo Regionale di Scienze Naturali di Torino y Museo di Storia Naturale di Firenze. En esta última colección, compuesta por un NISP: 30, se encontró un atlas de *Megatherium americanum* - IGF 14826- con huellas antrópicas. Este elemento presenta un recrecimiento óseo en el foramen, lo que indica que es un individuo adulto. Las huellas se distribuyen en cuatro grupos: 2 sobre la cara dorsal y 2 sobre la ventral, hacia el límite con las facetas de articulación con el axis y con orientación transversal al plano sagital de la pieza. Cada grupo se compone de entre 3 a 6 huellas que miden alrededor de 0,2 y 0,3 cm a 3 cm y son paralelas entre sí. Se le ha adjudicado un número a cada grupo (Figura 2). Así los grupos 1 y 2 ubicados en la cara ventral se caracterizan por contener marcas más largas que los grupos 3 y 4, ubicados en la cara dorsal. En estos dos últimos grupos, las marcas miden 1 cm y se extienden entre el borde de la articulación y el foramen alar posterior. Sobre la cara dorsal hay 2 cortes más de alrededor 1 cm. En cambio, los cortes ubicados en la cara ventral tienen marcas más largas, de hasta 2 o 3 cm, rodeadas de marcas más pequeñas de 0,2 y 0,3 cm y hasta 0,5 y 1 cm. Además, los grupos 1 y 4 del lado derecho, son ligeramente más profundos que los grupos 2 y 3 del lado izquierdo. Según Binford (1981) este tipo de marcas puede relacionarse con la separación

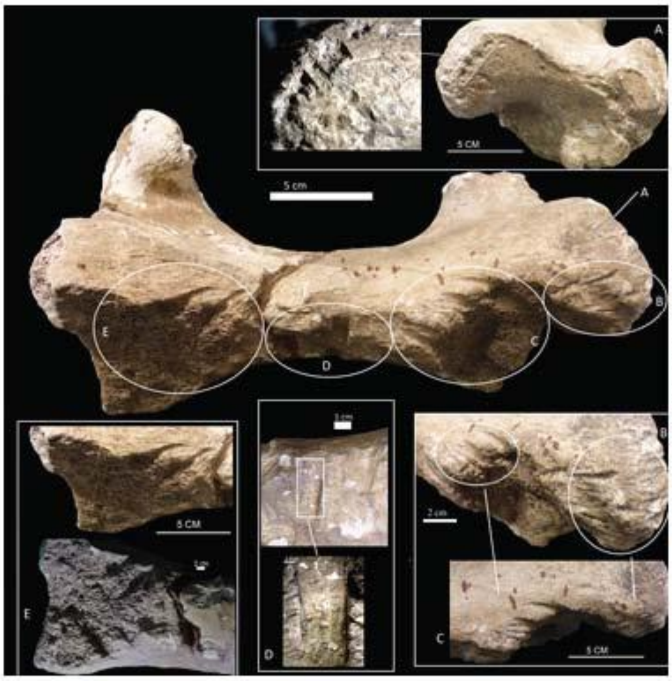

Figura 1. Tibia derecha cf. Scelidotherinae gen CRB 64-492, vista posterio- medial: A) Epífisis distal con indicación de la impronta dental en la cara articular. B) Epífisis distal con surcos paralelos que rodean el vaciado. C) Improntas elongadas con borde crenulado que también rodean el vaciado. D) Diáfisis, cara medial, con gruesos surcos. E) Vaciado e improntas elongadas de epífisis y metadiáfisis proximal

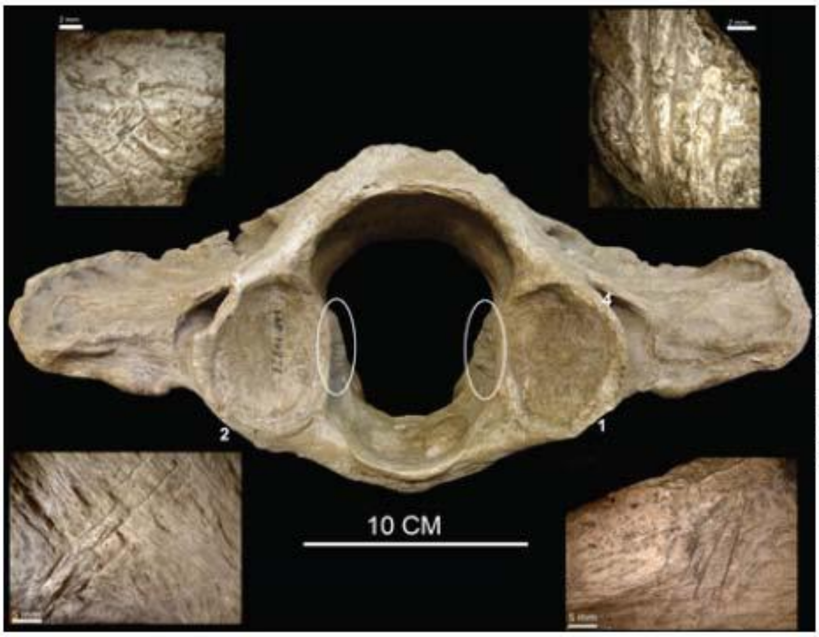

Figura 2. Atlas of *Megatherium americanum* MLP 14826 vista posterior con indicación de los recrecimientos óseos y de los grupos de cortes descriptos en el texto, junto con su amplificación.

del cráneo del esqueleto postcraneal en un primer acceso a la carcasa. Sin embargo, también esta evidencia puede relacionarse con la explotación de los contenidos del esqueleto craneal en un acceso secundario.

Es así que los conjuntos fósiles históricos depositados en distintos museos cobran valor a partir de su estudio actual. Estos datos están sesgados; tanto por agentes postdepositacionales, al igual que otros yacimientos paleontológicos y/o arqueológicos, como por factores histórico-culturales, que influyeron a que se extrajeran ciertas especies y/o elementos sobre otros (Wolff, 1975). Sin embargo, su revisión, permite obtener información novedosa, como la que reseño brevemente en esta sección que puede ser integrada a nivel regional. En consecuencia, estos datos se suman a otras colecciones y sitios pampeanos que poseen evidencia de explotación de megafauna como Arroyo Seco 2, Paso Otero 5, La Moderna o Campo Laborde (Gutiérrez y Martínez, 2008; Miotti y Salemme, 1999; Martínez *et al.*, 2013; Prates *et al.*, 2013; Toledo, 2009), donde distintas especies de Xenarthros y Ungulados fueron utilizadas tanto para consumo como para materias primas.

Integrar líneas de evidencias

Ambas líneas de evidencia se están desarrollando dentro del marco presentado para profundizar en la singularidad del poblamiento americano en distintas regiones (Lanata *et al.*, 2008 a y b; Lanata, 2011). Focalizar en *Homo sapiens* como especie invasora permite integrarlas para comparar el tiempo y el modo de la dispersión humana en distintas regiones.

La evidencia genética estaría indicando una rápida dispersión, probablemente utilizando corredores costeros (Miotti y Salemme, 2003). El uso de estos permite el acceso a una amplia variedad de recursos, logrando complementariedad de ambientes. Esto podría influir en el crecimiento demográfico y, a su vez, acelerar el movimiento de las primeras poblaciones. Sin embargo, el progresivo estrechamiento del continente hacía latitudes altas y la mayor rigidez climática, podrían implicar una menor densidad poblacional y también, una menor variabilidad genética. Esta relación entre diversidad genética y latitud ha sido corroborada en modelos teóricos de correlación entre distancias geográficas y biológicas (Ramachandran y Rosenberg, 2011) y ha sido propuesta para explicar la característica craneal –robusticidad- y la diferenciación biológica presente en poblaciones de Patagonia (Bernal *et al*., 2006, 2010). Así, la evidencia mencionada anteriormente estaría indicando que la región pampeana presenta, al parecer, una dinámica poblacional más compleja en términos de eventos de flujo y cercanía biológica con otras regiones, evidenciado esto por los haplogrupos y haplotipos tipificados hasta el momento, sobre todo para el Holoceno tardío. Posiblemente dicho fenómeno fue persistente desde los primeros momentos del poblamiento de la región, pero se habría acrecentado hacia los últimos milenios. Por su parte, Patagonia parece conservar los mismos haplogrupos fundantes que posiblemente estuvieron presentes en la ocupación inicial y que pueden encontrarse en poblaciones actuales, según las investigaciones ya mencionadas. Seguramente esta variabilidad genética reducida estaría indicando procesos microevolutivos relacionados con la deriva y una demografía posiblemente baja en comparación con la región pampeana. Consecuentemente, a pesar de la simultaneidad en la ocupación de ambas regiones, genéticamente los registros indicarían una dispersión y tasa de ocupación diferencial.

Esto también tendría su correlato con la forma de explotación de las faunas nativas en estos sectores, ya que, si bien en ambos se ha registrado una amplia variabilidad en el aprovechamiento de los recursos, correlacionado con una estrategia generalista (Gutierréz y Martínez, 2008; Miotti y Salemme, 1999), al menos en lo que refiere a la explotación de grandes mamíferos y megafauna habrían diferencias (Borrero, 2009).

El mencionado uso de corredores costeros para la dispersión y el aprovechamiento de los ríos para la exploración interna (Miotti y Salemme, 2003) implicaría el acceso a sectores ricos en recursos faunísticos como la región pampeana, que podría considerarse como un *hot spot* (Lanata *et al*., 2008 a y b; Lanata, 2011). Esto podría haber permitido una explotación más variada de la fauna y a su vez, beneficiado el aumento de la demografía humana notado para la región. Esto también podría haber implicado una competencia con otros carnívoros que consumían estos grupos de animales (Chichkoyan *et al*., 2015). A nivel de la evidencia presentada, esto estaría representado por los Xenarthros, que presentan explotación biológica de ambos tipos -tanto carnívora como humana. Aunque en general destaca la escasa evidencia de acción carnívora en la región (Scanferla *et al*., 2013). Esto puede deberse a problemas de muestreo y sesgos de recolección de las colecciones revisadas. Sin embargo, también hay que tener en cuenta que el menor registro de marcas carnívoras en general, podría estar relacionado con un acceso más esporádico que tenían los carnívoros sobre estos herbívoros de gran tamaño. Este sería el caso de los Megatherios, por ejemplo, en especial los adultos, que no tendrían predadores naturales (Prevosti y Vizcaíno, 2006), pero que habrían sido explotados por humanos, según los resultados presentados aquí y en sitios como Campo Laborde, Arroyo Seco 2 o Paso Otero 5 (Gutiérrez y Martínez, 2008; Martínez *et al.*, 2013). Así, las relaciones de competencia con otros carnívoros habrían sido diferenciales, dependiendo de los taxones involucrados. En consecuencia, la presencia de *Homo sapiens* en la región implicaría relaciones paleoecológicas nuevas (Chichkoyan *et al.*, 2015) tanto a nivel de acceso primario como secundario. Esta presencia habría sido lo suficientemente importante para suponer un desequilibrio de la cadena trófica existente (Martínez *et al.*, 2013).

En Patagonia en cambio, la geografía de la región posee sectores de acceso diferenciado y en estas latitudes imperarían condiciones ambientales más extremas, lo que dificultaría la movilidad de los primeros grupos humanos. Destacan sitios arqueológicos con megafauna extinta como Piedra Museo en la región de la Cuenca del Deseado, y más al Sur sitios como Cueva Tunel, Casa del Minero o Los Toldos donde se aprovecharon camélidos y caballos extintos y/o asociación con fogones, y en el sitio El Trébol se habría explotado Mylodontidae (Borrero, 2009; Hajduk *et al.*, 2004; Miotti y Salemme 1999, 2003; Paunero 2003; Prates *et al.*, 2013). Además en esta región, el registro de acción carnívora en los distintos restos óseos provenientes de diversas especies de megafauna, fue interpretado como resultado de la acción de *Panthera onca mesembrina* como principal protagonista en la mayoría de los casos. La intervención humana fue escasa, relacionada al carroñeo (Martin, 2008). Es así que la región Sur del extremo continental presentaría una situación más desfavorable para la expansión, crecimiento y desarrollo de las poblaciones humanas, que, a su vez, pudiesen haber influido en la cadena trófica e impactar sobre la fauna nativa. Esto a su vez significaría que la modificación y/o generación de nichos habría sido menor o nula (Borrero, 1999; Borrero y Martin, 2012). Lo que también estaría reflejado en una escasa cantidad de sitios y especies que evidencien explotación antrópica de estos recursos (Borrero, 2009). Por ello, la situación en este caso difiere con lo propuesto para Pampa, porque no solamente las poblaciones habrían tenido un crecimiento demográfico hasta después de haber entrado en las condiciones más benignas del Holoceno (Borrero, 1999), sino que algunas extinciones de la megafauna habrían sucedido previo a la entrada *Homo sapiens* (Borrero, 1999).

Así, la introducción de los grupos humanos en el Cono Sur Sudamericano podría haber tenido características de especie invasora, con un comportamiento diferencial según los ambientes y recursos involucrados. La información presentada y su integración a estudios existentes, indicaría que el proceso de poblamiento humano habría sido relativamente rápido y su impacto en los ambientes, complejo.

Conclusiones

En este trabajo se repasó el modelo de invasiones ecológicas y se introdujo líneas de evidencias que están siendo desarrolladas dentro de este marco. El enfoque ecológico que trata a *Homo sapiens* como especie invasora, permite evaluar la singularidad de la dispersión en América. Según el modelo presentado, el ritmo de movimiento en los distintos espacios estaría correlacionado con las características ambientales y los recursos disponibles en cada espacio. No se puede subsumir toda la diversidad de situaciones bajo una sola visión debido a la variabilidad ambiental de las Américas.

La genética y la tafonómia se han tomado para analizar el *tempo* y modo de dispersión, y están aportando información novedosa. Su correlación e integración a otros estudios de ambas regiones permite caracterizar la dispersión bajo esta perspectiva. Este tipo de trabajo está siendo realizado en diversas colecciones de restos humanos y fauna, de Argentina, depositadas en instituciones del país y del exterior. La obtención de fechados se está realizando sobre distintas muestras, para delimitar temporalmente esta información. Los futuros trabajos aportarán mayor información en este sentido.

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EL PATRIMONIO ARQUEOLÓGICO Y PALEONTOLÓGICO DE LA CUENCA SUPERIOR DEL RÍO LUJÁN: INVESTIGACIÓN Y GESTIÓN

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Palabras clave: cuenca del Río Luján - arqueología - paleontología - patrimonio cultural

Key words: Lujan River basin - archaeology - palaeontology - cultural heritage

Introducción

La cuenca del río Luján es un lugar privilegiado para los estudios arqueológicos y paleontológicos. Desde fines del siglo XVIII y durante todo el siglo XIX el estudio de los fósiles procedentes de las barrancas del río Luján y sus afluentes sentó las bases del conocimiento a nivel mundial sobre la megafauna pleistocena extinguida (Tonni y Pascuali 2005), al tiempo que el estudio del "hombre fósil" y su cultura material contribuían al desarrollo inicial de la arqueología argentina de la mano de Florentino Ameghino. Este autor fue además quien vinculó por primera vez la arqueología con la paleontología de la región postulando la coexistencia del hombre con la megafauna, con un intenso debate que trascendió su muerte (Ameghino 1918[1880-81]; Orquera 1971; Politis *et al*. 2011; Lanzelotti y Acuña 2014, entre otros). Durante todo el siglo XX y lo que va del siglo XXI, continuaron apareciendo nuevos materiales arqueológicos y restos de fauna que abarcan el Pleistoceno y Holoceno (e.g. Bonaparte y Pisano 1950; Chiri 1973; Petrocelli 1975; Pascuali 2002; Loponte y Acosta 2003; Ramos *et al*. 2008; Zurita *et al*. 2008, 2010, Pérez *et al*. 2010; Viloria *et al*. 2011; Lanza 2011; Acosta *et al*. 2013; Arzani *et al*. 2014), aunque otra gran parte de los hallazgos permanecen inéditos.

El proyecto que presentamos aquí se focaliza en el sector correspondiente a la cuenca superior del río Luján, que abarca parte de los partidos de Suipacha, Carmen de Areco, San Andrés de Giles y Mercedes. Este proyecto tiene como objetivo general producir nueva información sobre la base de los bienes patrimoniales arqueológicos y paleontológicos de la cuenca superior del río Luján, así como trabajar en el análisis de los fenómenos de patrimonialización e identidad asociados. Interesa abordar la cultura material de las sociedades cazadoras-recolectoras que poblaron inicialmente la región en contacto con la megafauna pleistocena, así como también la historia posterior que incluye los cazadores recolectores del Holoceno temprano, medio y tardío, y los procesos resultantes del contacto con la sociedad europea y criolla, los orígenes de las principales localidades actuales y su relación con el período de organización nacional.

Metodología

La información patrimonial se obtuvo a partir de la sistematización del catálogo y archivo del Museo Municipal de Ciencias Naturales "Carlos Ameghino" (MCA) de la ciudad de Mercedes, institución que nuclea actualmente las investigaciones arqueológicas y paleontológicas de la región. La información de fue complementada con la realización de entrevistas no estructuradas a actores clave, relevamiento bibliográfico sobre la temática (tanto académica como no académica) y trabajo de campo para la validación de los datos previamente obtenidos y su georreferenciación (Lanzelotti *et al.* 2015). Se trabajó con Sistemas de Información Geográfica, entorno en el que se creó una capa de información patrimonial que se articuló con la base topográfica y geográfica de la cuenca superior del río Luján. La información se clasificó en: sitio arqueológico, yacimiento paleontológico, y sitios históricos (monumentos, edificios y lugares históricos), aunque estos últimos no serán abordados en esta ponencia. Se incluyeron variables tales como normativa de protección (municipal, provincial y nacional) y estado de preservación actual. También se consultaron catálogos y el acervo de otros museos nacionales y europeos donde habrían sido llevados materiales procedentes de la cuenca del río Luján.

Resultados y discusión

Se identificaron y georreferenciaron un total de 119 sitios de interés patrimonial para la cuenca superior del río Luján (Figura 1). De ellos, 31 corresponden a Sitios Arqueológicos, y 52 a Yacimientos Paleontológicos. Se observó que la mayoría de los lugares señalados como "patrimonio cultural" por la ciudadanía, no cuentan con declaración patrimonial formal ni reglamentación de protección (Lanzelotti *et al.* 2015).

Respecto al registro de los materiales del área de estudio que se encuentran alojados en diversos museos nacionales y europeos, observamos que su origen se remonta hacia fines del siglo XVIII y principios del XX, momento en el que los museos de Ciencias Naturales comenzaban a ser un núcleo importante para la generación de nuevos conocimientos científicos. En el contexto de los museos nacionales, hay material en el Museo de La Plata, donde se ubicamos parte de la colección descripta por Ameghino 1918 [1880-81], y en el Museo Etnográfico (Ameghino, en Torcelli 1936:621). En Europa se destacan la colección Krncsék en el Naturhistorisches Museum Wien (Vienna), parte de la colección Laussen, excavada por Larroque en el Natural History Museum of Denmark (Copenhagen), algunos óseos depositados en el Museo Civico di Storia Naturale di Milano (Milan) que sobrevivieron al bombardeo que sufrió esta institución hacia 1943 y moldes donados por Ameghino al Muséum Nationel d' Historie Naturelle (Paris).

Por otro lado la realización de prospecciones pedestres nos permitió evaluar el estado de preservación de los sitios registrados por Florentino Ameghino (Lanzelotti y Acuña 2014) y otros inéditos, tales como la "Estación García", El "Tiro Federal" y la Reserva Natural Arroyo Balta. Durante las prospecciones también se pudo recuperar material lítico aunque en muy baja densidad. Asimismo realizamos sondeos en el sitio histórico "La 24".

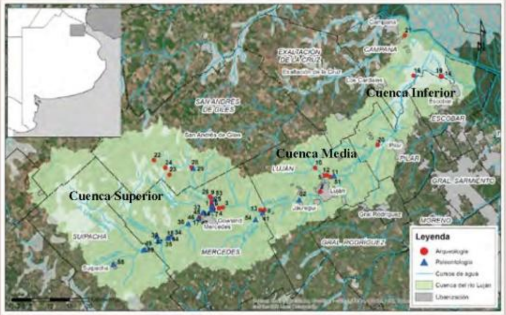

Figura 1. Cuenca del Río Luján con indicación de los principales sitios arqueológicos y paleontológicos. Tomado y modificado de Acuña et al. (2014).

Nuestro proyecto procedió al rescate de un ejemplar de *Glyptodon reticulatus* y otro asignable a *Smilodon* que se encontraban a una distancia de 300 metros uno de otro, sobre sedimentos "Lujanenses" (Mb Guerrero de la Fm Luján) sobre las márgenes del río Luján. La limpieza a los restos permitió registrar una importante fractura en el fémur izquierdo, reconstituida, y el notable fortalecimiento de las inserciones musculares de los miembros anteriores (Acuña *et al.* 2015). Además, en el Parque Municipal Independencia se

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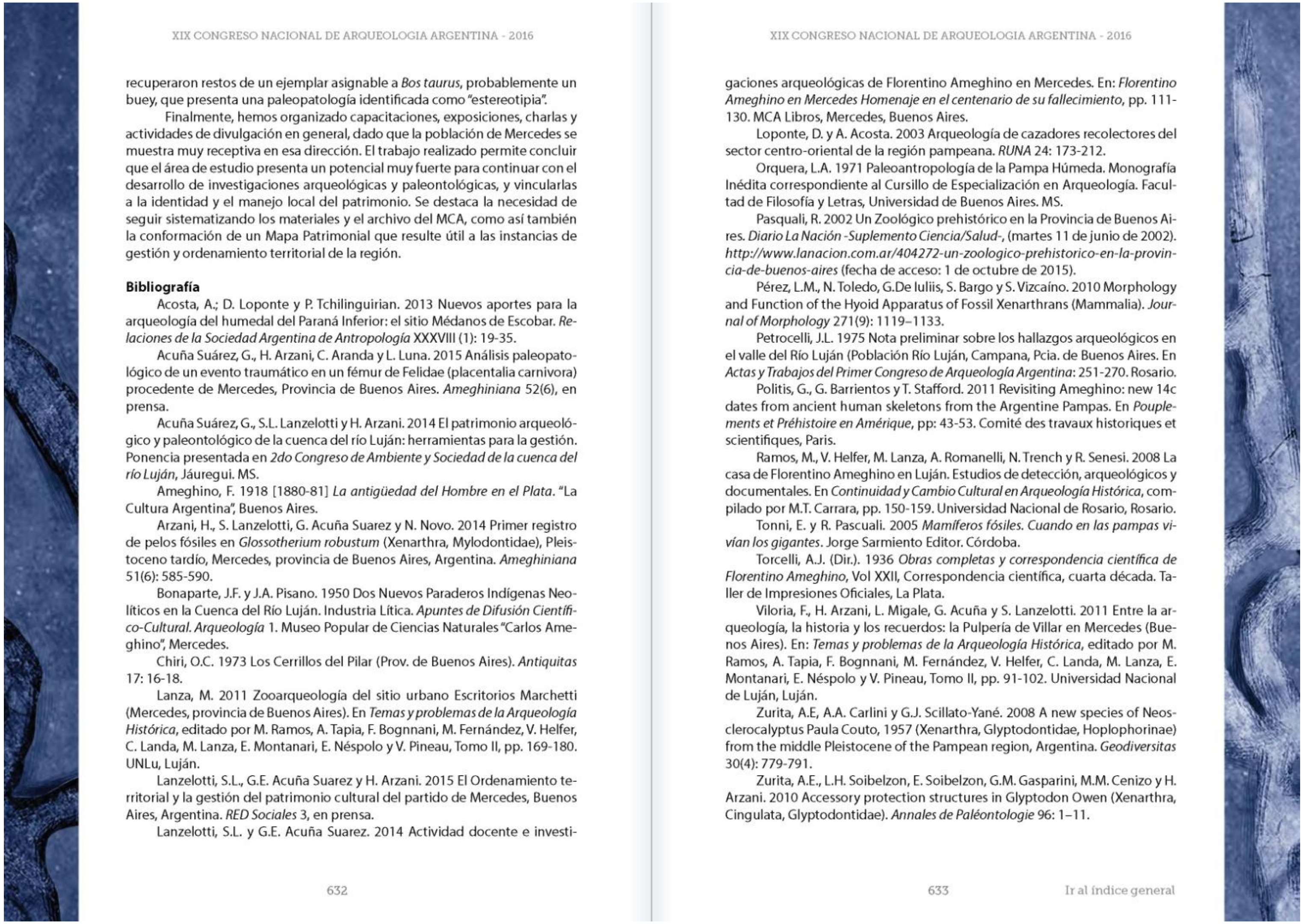

recuperaron restos de un ejemplar asignable a *Bos taurus*, probablemente un buey, que presenta una paleopatología identificada como "estereotipia".

Finalmente, hemos organizado capacitaciones, exposiciones, charlas y actividades de divulgación en general, dado que la población de Mercedes se muestra muy receptiva en esa dirección. El trabajo realizado permite concluir que el área de estudio presenta un potencial muy fuerte para continuar con el desarrollo de investigaciones arqueológicas y paleontológicas, y vincularlas a la identidad y el manejo local del patrimonio. Se destaca la necesidad de seguir sistematizando los materiales y el archivo del MCA, como así también la conformación de un Mapa Patrimonial que resulte útil a las instancias de gestión y ordenamiento territorial de la región.

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CONSERVACIÓN PREVENTIVA DE LA COLECCIÓN DE MEGAFAUNA EN EL MUSEO MUNICIPAL DE CIENCIAS NATURALES CARLOS AMEGHINO, MERCEDES, BUENOS AIRES

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Palabras clave: acervo museográfico - arqueología - paleontología - conservación preventiva

Key words: museum acquis - archaeology - palaeontology - preventive conservation

Introducción

Esta ponencia tiene como objetivo presentar el trabajo de reorganización que se está realizando sobre los fondos antiguos de megafauna procedente de la región pampeana que posee el Museo Municipal de Ciencias Naturales "Carlos Ameghino" (MCA) de Mercedes (Buenos Aires). Este tipo de trabajo nos permite reflexionar sobre la utilidad presente que poseen estos materiales en nuestra disciplina.

Las colecciones de materiales arqueológicos y/o paleontológicos depositados en los museos se han convertido en una herramienta de trabajo indispensable en los últimos años. Estos se han excavado en el pasado bajo distintos marcos teóricos y metodológicos, por lo que su revaluación e inclusión en debates actuales es necesaria. En este sentido una de las líneas de trabajo es la revisión zooarqueológica y tafonómica de estos materiales en relación a la temática del poblamiento temprano y su relación con la megafauna.

Breve historia del museo

El MCA se fundó en el año 1947a instancias de un grupo de vecinos que asumen la responsabilidad de crear una institución dedicada al estudio de las ciencias naturales y del hombre, sobre la base de un conjunto de fósiles recuperados en las márgenes del río Luján.
La institución recibió el nombre de Museo Popular de Ciencias Naturales Carlos Ameghino con la intensión explícita de reconocer la obra de Florentino Ameghino y su hermano Carlos en esta región. La misma ocupó originalmente, hasta 1953, una habitación de la planta alta de la Casa del Pueblo del Partido Socialista, y luego el hall de entrada de la Biblioteca Popular Domingo Faustino Sarmiento (Archivo MCA). En el año 1965 el MCA pasa a la órbita municipal y comienza a denominarse Museo Municipal de Ciencias Naturales y Tradicional de Mercedes. En ese mismo año se traslada definitivamente a su actual emplazamiento, ocupando una pequeña sala hasta que, con sucesivas ampliaciones edilicias, en 2015 alcanza su fisonomía actual.

Lamentablemente en cada traslado y remodelación se perdió o se dañaron elementos que integraban las colecciones fundacionales.

Aun así el MCA cuenta con importantes colecciones arqueológicas y paleontológicas, producto de las excavaciones propiciadas por este museo a lo largo de sus 68 años de historia, del intercambio con otras instituciones, y de donaciones de particulares. Por su ubicación geográfica, la mayor parte del acervo patrimonial procede del norte de la provincia de Buenos Aires, pero también incluye materiales del resto del país. En la presente contribución enfocaremos únicamente en las colecciones procedentes de la región pampeana.

Medidas de conservación en el nuevo siglo

A partir del año 2013 comenzamos a ordenar el acervo del Museo, con el objetivo de mejorar las condiciones en que se encontraban las colecciones. Estas estaban dispersas por diferentes salas y clasificadas sin un criterio estándar. Los materiales se encontraban en pésimo estado de conservación (hongos, humedad, restauraciones mal hechas, piezas barnizadas, materiales sin limpiar, huesos rotos). Ante esta situación y en primer lugar se destinó y se preparó un espacio específico como sala de bodegaje y conservación preventiva.

Se limpiaron los materiales con cepillos de cerda suave y se clasificaron los materiales por lugar de procedencia. Para el almacenaje se utilizaron materiales (cajas y bolsas) libres de ácido.

Paralelamente a este trabajo que todavía continúa, se creó una base de datos digital que incluye tanto información recuperada de los archivos (libretas de campo, fotos, informes inéditos, recortes de diarios, etc.) como su descripción actual con la información de los materiales y su ubicación georreferenciada. Esto permite rescatar no solamente la memoria histórica de estas colecciones, sino también, relocalizar antiguos yacimientos y contextualizar los materiales excavados (Acuña *et al.* 2014; Lanzelotti *et al.* 2015).

Discusión y consideraciones finales

Este tipo de trabajos de conservación del patrimonio nos conduce a pensar en la utilidad actual de estas antiguas colecciones de megafauna en nuestra disciplina. El gran trabajo de reorganización que se realiza actualmente de la colección de megafauna del MCA permite tener un rico fondo de fósiles que puede ser estudiado a partir de nuevas perspectivas e integrarlo en estudios actuales. Al incorporar estas colecciones bajo esta visión, este tipo de patrimonio se suma a la dinámica actual de estudio, que de otra manera quedaría guardado en depósitos estáticos. Esto les otorga un valor agregado,

que trasciende las fronteras de "objetos para exposición" y permite rescatar potencial información útil para nuevos trabajos.

Una línea de investigación que está siendo desarrollada es la de reevaluar las antiguas colecciones de megafauna aquí alojadas desde un punto de vista zooarqueológico y tafonómico, para detectar posibles intervenciones antrópicas como marcas de corte. Los antecedentes arqueológicos en la zona hacen necesario este trabajo, en especial porque la cuenca del río Lujan fue pionera en el estudio de la coexistencia del hombre y la megafauna (Lanzelotti y Acuña 2014). La datación por AMS de dos falanges de un *Homo sapiens* descubierto por Ameghino en 1870-74 a orillas del Arroyo Frías arrojó un fechado de *ca*. 12.750 y 11.200 años cal. AP siendo el más temprano en la región pampeana y uno de los más antiguos de la Argentina (Politis 2014).

Metodologías y técnicas relacionadas con la zooarqueología y la tafonomía, disciplinas que han tenido un avance importante en las últimas décadas, son útiles para revisar materiales excavados sin el control estratigráfico tal como se hace actualmente. Este tipo de trabajo permite también registrar marcas de carnívoros o paleopatologías, útiles para comprender la interacción entre las especies, que pueden dar cuenta de enfermedades y/o calidad de vida que pudieron haber tenido estas especies. (Zurita *et al.* 2008,2010; Acuña *et al.* 2015; Arzani *et al.* 2014).

De esta manera, la reorganización y puesta a punto de las colecciones de megafauna depositadas en el MCA permite rescatar una de las colecciones más importantes de megafauna de la región pampeana. La misma se fue conformando casi desde el inicio del siglo pasado producto de excavaciones de numerosos naturalistas y aficionados. Estos trabajos permiten revalorizar estas colecciones paleontológicas desde el punto de vista arqueológico y contribuir a la conservación del patrimonio excavado en el pasado.

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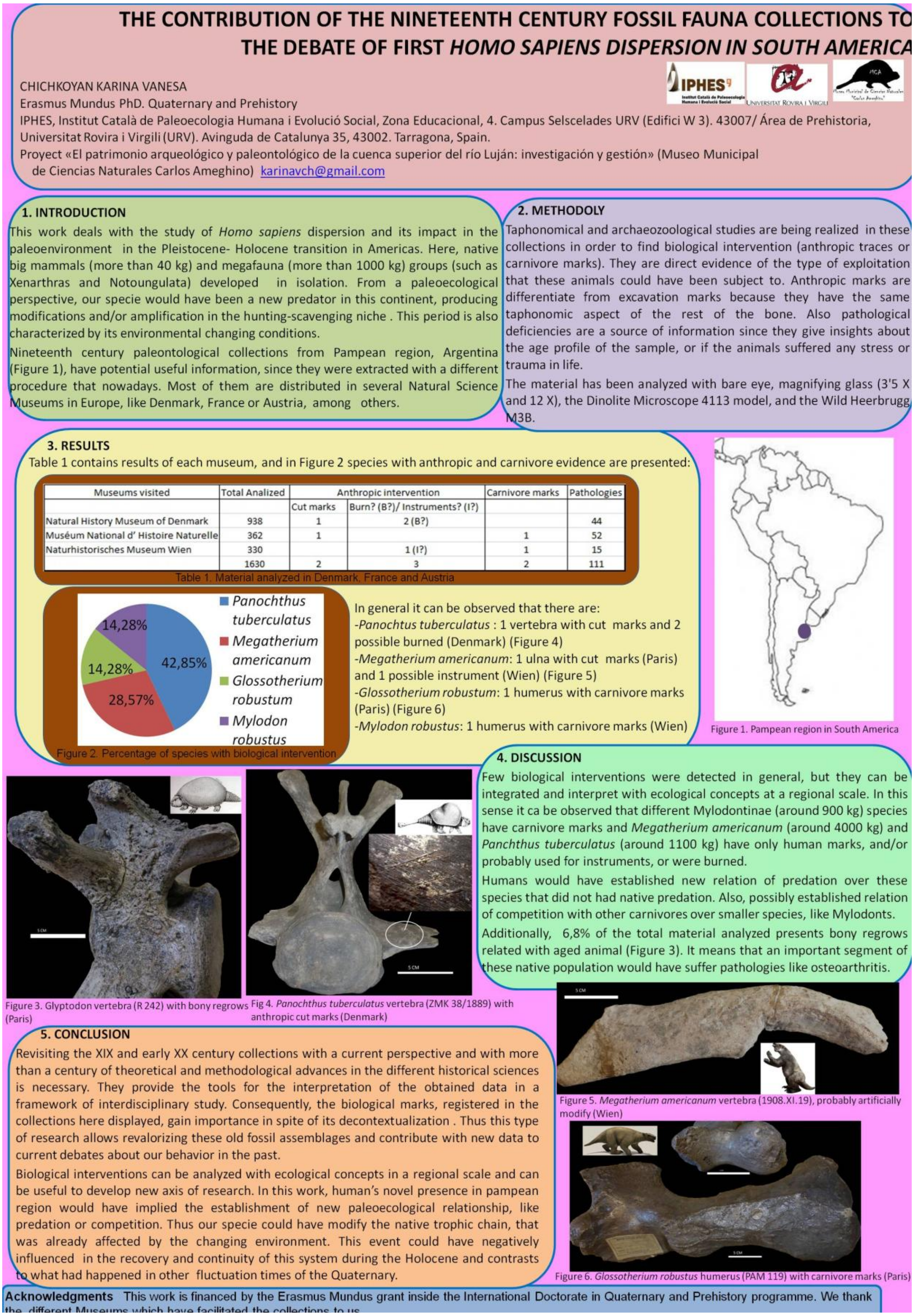

THE CONTRIBUTION OF THE NINETEENTH CENTURY FOSSIL FAUNA COLLECTIONS TO THE DEBATE OF FIRST *HOMO SAPIENS* DISPERSION IN SOUTH AMERICA

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1. INTRODUCTION

This work deals with the study of *Homo sapiens* dispersion and its impact in the paleoenvironment in the Pleistocene- Holocene transition in Americas. Here, native big mammals (more than 40 kg) and megafauna (more than 1000 kg) groups (such as Xenarthras and Notoungulata) developed in isolation. From a paleoecological perspective, our specie would have been a new predator in this continent, producing modifications and/or amplification in the hunting-scavenging niche . This period is also characterized by its environmental changing conditions.

Nineteenth century paleontological collections from Pampean region, Argentina (Figure 1), have potential useful information, since they were extracted with a different procedure that nowadays. Most of them are distributed in several Natural Science Museums in Europe, like Denmark, France or Austria, among others.

2. METHODOLY

Taphonomical and archaeozoological studies are being realized in these collections in order to find biological intervention (anthropic traces or carnivore marks). They are direct evidence of the type of exploitation that these animals could have been subject to. Anthropic marks are differentiate from excavation marks because they have the same taphonomic aspect of the rest of the bone. Also pathological deficiencies are a source of information since they give insights about the age profile of the sample, or if the animals suffered any stress or trauma in life.

The material has been analyzed with bare eye, magnifying glass (3'5 X and 12 X), the Dinolite Microscope 4113 model, and the Wild Heerbrugg M3B.

3. RESULTS

Table 1 contains results of each museum, and in Figure 2 species with anthropic and carnivore evidence are presented:

Museums visited	Total Analized	Anthropic intervention		Carnivore marks	Pathologies
		Cut marks	Burn? (B?)/ Instruments? (I?)		
Natural History Museum of Denmark	938	1	2 (B?)		44
Muséum National d' Histoire Naturelle	362	1		1	52
Naturhistorisches Museum Wien	330		1 (I?)	1	15
	1630	2	3	2	111

Table 1. Material analyzed in Denmark, France and Austria

42,85% ■ *Panochthus tuberculatus*
28,57% ■ *Megatherium americanum*
14,28% ■ *Glossotherium robustum*
14,28% ■ *Mylodon robustus*

Figure 2. Percentage of species with biological intervention

In general it can be observed that there are:
-*Panochtus tuberculatus* : 1 vertebra with cut marks and 2 possible burned (Denmark) (Figure 4)
-*Megatherium americanum*: 1 ulna with cut marks (Paris) and 1 possible instrument (Wien) (Figure 5)
-*Glossotherium robustum*: 1 humerus with carnivore marks (Paris) (Figure 6)
-*Mylodon robustus*: 1 humerus with carnivore marks (Wien)

Figure 1. Pampean region in South America

4. DISCUSSION

Few biological interventions were detected in general, but they can be integrated and interpret with ecological concepts at a regional scale. In this sense it ca be observed that different Mylodontinae (around 900 kg) species have carnivore marks and *Megatherium americanum* (around 4000 kg) and *Panchthus tuberculatus* (around 1100 kg) have only human marks, and/or probably used for instruments, or were burned.

Humans would have established new relation of predation over these species that did not had native predation. Also, possibly established relation of competition with other carnivores over smaller species, like Mylodonts.

Additionally, 6,8% of the total material analyzed presents bony regrows related with aged animal (Figure 3). It means that an important segment of these native population would have suffer pathologies like osteoarthritis.

Figure 3. Glyptodon vertebra (R 242) with bony regrows (Paris)

Fig 4. *Panochthus tuberculatus* vertebra (ZMK 38/1889) with anthropic cut marks (Denmark)

5. CONCLUSION

Revisiting the XIX and early XX century collections with a current perspective and with more than a century of theoretical and methodological advances in the different historical sciences is necessary. They provide the tools for the interpretation of the obtained data in a framework of interdisciplinary study. Consequently, the biological marks, registered in the collections here displayed, gain importance in spite of its decontextualization . Thus this type of research allows revalorizing these old fossil assemblages and contribute with new data to current debates about our behavior in the past.

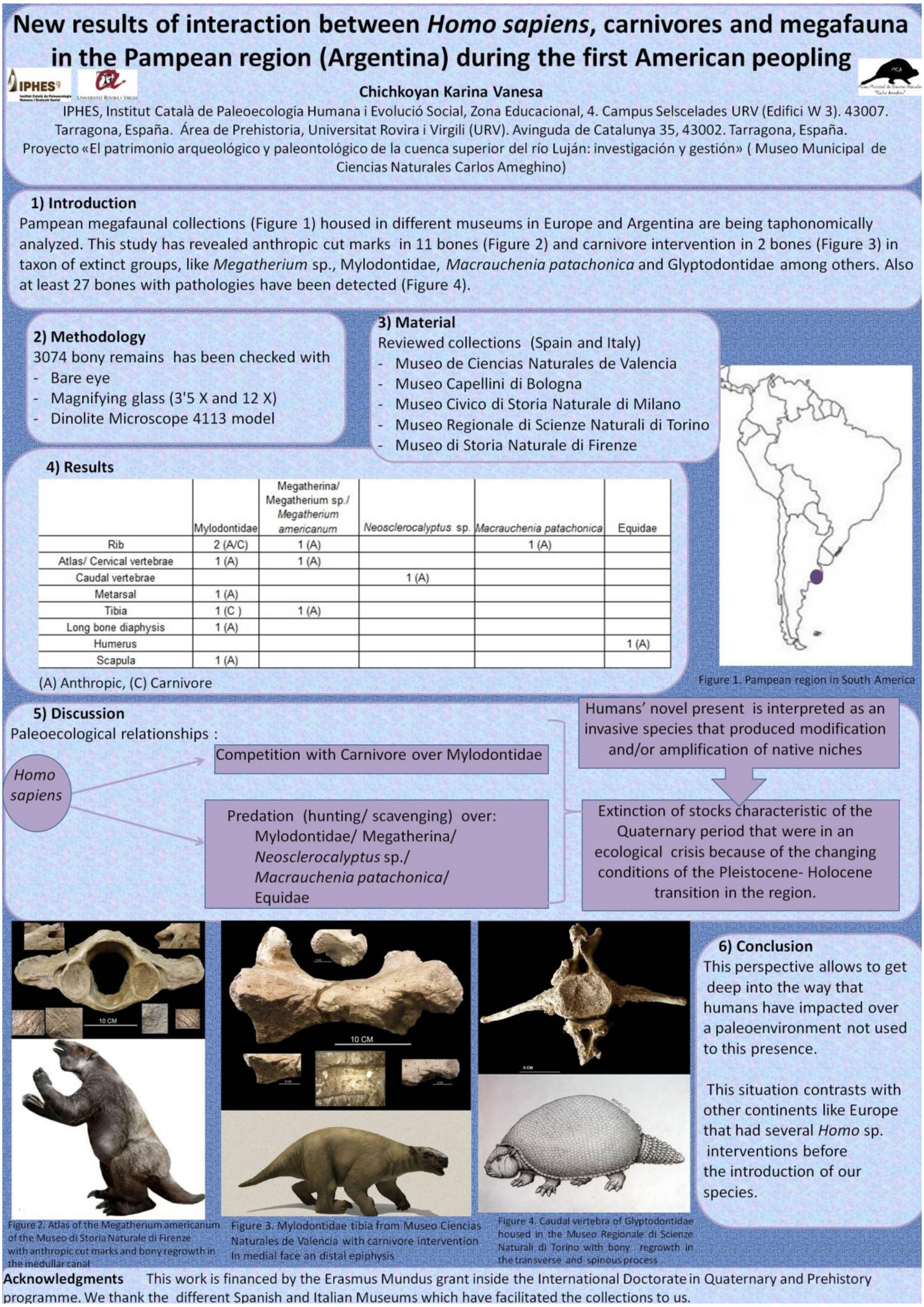
Biological interventions can be analyzed with ecological concepts in a regional scale and can be useful to develop new axis of research. In this work, human's novel presence in pampean region would have implied the establishment of new paleoecological relationship, like predation or competition. Thus our specie could have modify the native trophic chain, that was already affected by the changing environment. This event could have negatively influenced in the recovery and continuity of this system during the Holocene and contrasts to what had happened in other fluctuation times of the Quaternary.

Figure 5. *Megatherium americanum* vertebra (1908.XI.19), probably artificially modify (Wien)

Figure 6. *Glossotherium robustus* humerus (PAM 119) with carnivore marks (Paris)

Acknowledgments This work is financed by the Erasmus Mundus grant inside the International Doctorate in Quaternary and Prehistory programme. We thank the different Museums which have facilitated the collections to us

Poster presented in Postgraduate Zooarchaeology Forum (PZAF). IPHES, Institut Català de Paleoecologia Humana i Evolució Social in 2015



New results of interaction between *Homo sapiens*, carnivores and megafauna in the Pampean region (Argentina) during the first American peopling

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Proyecto «El patrimonio arqueológico y paleontológico de la cuenca superior del río Luján: investigación y gestión» (Museo Municipal de Ciencias Naturales Carlos Ameghino)

1) Introduction

Pampean megafaunal collections (Figure 1) housed in different museums in Europe and Argentina are being taphonomically analyzed. This study has revealed anthropic cut marks in 11 bones (Figure 2) and carnivore intervention in 2 bones (Figure 3) in taxon of extinct groups, like *Megatherium* sp., Mylodontidae, *Macrauchenia patachonica* and Glyptodontidae among others. Also at least 27 bones with pathologies have been detected (Figure 4).

2) Methodology

3074 bony remains has been checked with
- Bare eye
- Magnifying glass (3'5 X and 12 X)
- Dinolite Microscope 4113 model

3) Material

Reviewed collections (Spain and Italy)
- Museo de Ciencias Naturales de Valencia
- Museo Capellini di Bologna
- Museo Civico di Storia Naturale di Milano
- Museo Regionale di Scienze Naturali di Torino
- Museo di Storia Naturale di Firenze

Figure 1. Pampean region in South America

4) Results

	Mylodontidae	Megatherina/ Megatherium sp./ *Megatherium americanum*	*Neosclerocalyptus* sp.	*Macrauchenia patachonica*	Equidae
Rib	2 (A/C)	1 (A)		1 (A)	
Atlas/ Cervical vertebrae	1 (A)	1 (A)			
Caudal vertebrae			1 (A)		
Metarsal	1 (A)				
Tibia	1 (C)	1 (A)			
Long bone diaphysis	1 (A)				
Humerus					1 (A)
Scapula	1 (A)				

(A) Anthropic, (C) Carnivore

5) Discussion

Paleoecological relationships :

Homo sapiens

Competition with Carnivore over Mylodontidae

Predation (hunting/ scavenging) over:
Mylodontidae/ Megatherina/
Neosclerocalyptus sp./
Macrauchenia patachonica/
Equidae

Humans' novel present is interpreted as an invasive species that produced modification and/or amplification of native niches

Extinction of stocks characteristic of the Quaternary period that were in an ecological crisis because of the changing conditions of the Pleistocene- Holocene transition in the region.

6) Conclusion

This perspective allows to get deep into the way that humans have impacted over a paleoenvironment not used to this presence.

This situation contrasts with other continents like Europe that had several *Homo* sp. interventions before the introduction of our species.

Figure 2. Atlas of the Megatherium americanum of the Museo di Storia Naturale di Firenze with anthropic cut marks and bony regrowth in the medullar canal

Figure 3. Mylodontidae tibia from Museo Ciencias Naturales de Valencia with carnivore intervention In medial face an distal epiphysis

Figure 4. Caudal vertebra of Glyptodontidae housed in the Museo Regionale di Scienze Naturali di Torino with bony regrowth in the transverse and spinous process

Acknowledgments This work is financed by the Erasmus Mundus grant inside the International Doctorate in Quaternary and Prehistory programme. We thank the different Spanish and Italian Museums which have facilitated the collections to us.

Poster presented in VII Congress of Archaeology of the Argentinean Pampean Region. Centro Cultural Roberto Fontanarrosa in 2014

Investigación Arqueológica En Museos: Un Nuevo Enfoque.

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Introducción

En este trabajo se presenta el estudio tafonómico realizado en la Colección Rodrigo Botet depositada en el Museo de Ciencias Naturales de Valencia, España. Esta es producto de excavaciones no sistemáticas del Noreste de la región Pampeana. Aquí se reconocieron distintas marcas antrópicas sobre especies de Mylodontidae, Megatherium sp., Macrauchenia patachonica y Cingulata.

El análisis tafonómico de colecciones paleontológicas de fauna nativa depositadas en diversos museos es un novedoso enfoque que permite abordar la temática del impacto y desarrollo de relaciones paleoecológicas de la primera dispersión humana en el Cono Sur Sudamericano desde una perspectiva regional.

Figura 2: Material de la colección Rodrigo Botet con marcas antrópicas

3) Discusión y Conclusiones

Las marcas de corte reconocidas en esta colección pertenecen a especies que se extinguieron luego de la transición Pleistoceno- Holoceno y después de la entrada de Homo sapiens a la región. Esta habría sido una especie invasora con la capacidad de generar nuevos nichos ecológicos en un momento de importantes cambios ambientales. La región Pampeana se habría conformado como un refugio para la fauna y los humanos, lo que habría facilitado relaciones de competencia y depredación (Figura 3). Este tipo de enfoque se está desarrollando en éste y otros museos para brindar mayor información y desarrollar nuevos ejes de estudios interdisciplinarios.

1) Marco teórico

El estudio de colecciones decimonónicas paleontológicas no es una línea de investigación regularmente utilizada dentro de la investigación arqueológica. La falta de control en las excavaciones, su descontextualización y la referencia general de la localidad de hallazgo implican su exclusión en trabajos actuales. Especialmente durante fines del siglo XIX se formó con Europa una red de comercialización de material de megafauna provenientes de la región Pampeana que se destaca por la abundancia y variedad de especies. Estas colecciones poseen no solamente un valor histórico, sino también patrimonial y de investigación. Por ello se considera fundamental examinar estas colecciones arqueológicamente ya que pueden proveer información novedosa. A pesar de las condiciones de su hallazgo, los distintos avances teóricos, metodológicos y técnicos, permiten contextualizar los datos obtenidos. En este caso, estas colecciones de megafauna pueden ser estudiadas desde una perspectiva tafonómica y con una visión interdisciplinar.

2) Análisis de los datos

Se observó la superficie cortical de 11.466 huesos con lupa binocular Olympus SZ-PT y microscopio Wild Heerbrugg M3B. Se recuperaron 10 elementos con distintos tipos de intervenciones antrópicas de distintas especies (Figuras 1 y 2).

Figura 1: Porcentaje por especies de óseos con intervención antrópica de la Colección Rodrigo Botet

1) DEPREDACIÓN: A CONSUME/ EXPLOTA A B COMO RECURSO
2) COMPETENCIA: A COMPITE CON C POR LOS MISMOS RECURSOS

A) ESPECIE INVASORA (Homo sapiens)

B) HERVÍVOROS (Mylodon sp., Megatherium sp., Macrauchenia patachonica, Cingulata)

C) CARNÍVOROS (Smilodon populator)

Figura 3: Relaciones paleoecológicas entre humanos y fauna nativa

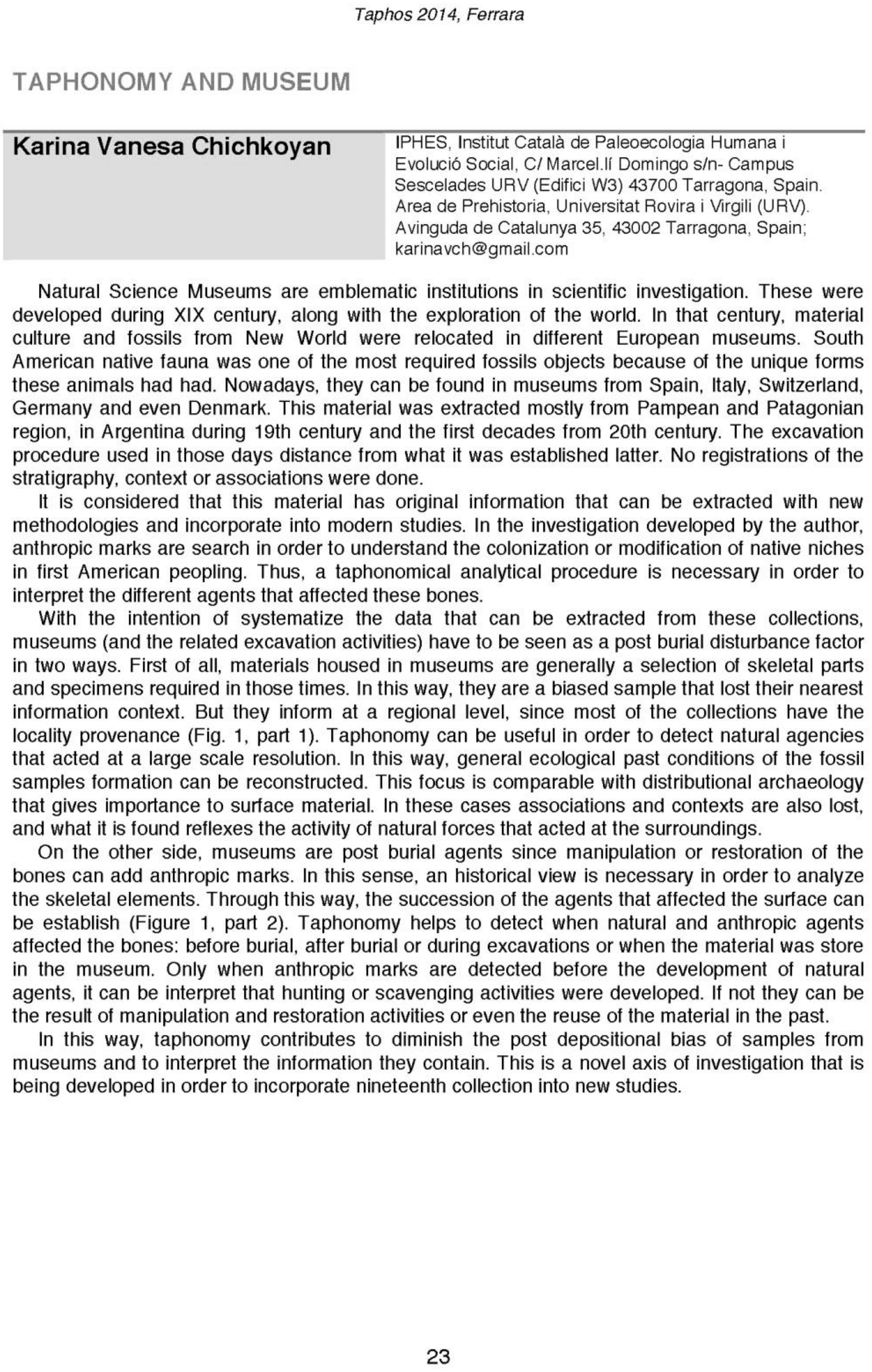
Agradecimientos

Este trabajo fue financiado por la beca Erasmus Mundus (Master in Quaternary and Prehistory and International Doctorate in Quaternary and Prehistory). Muchas gracias al Museo de Ciencias Naturales de Valencia por permitirme analizar la Colección Botet. A mis directores Bienvenido Martínez- Navarro, Margarita Belinchón y José Luis Lanata por el apoyo y confianza. A la Università degli studi di Ferrara, Italia, URV, IPHES, España e IIDyPCA- Conicet, Argentina por la colaboración en el proyecto "Dispersión humana y megafauna en el Cono Sur Sudamericano -UNRN". Mi gratitud especial a Jorge Sebastián Szigety por la ayuda con el programa para realizar este poster.

CARPA VII
Congreso de Arqueología de la Región Pampeana Argentina

GSF Gobierno de Santa Fe

Abstracts presented in 7th International Meeting on Taphonomy and Fossilization Taphos. Università degli Studi di Ferrara Congress in 2014



Taphos 2014, Ferrara

TAPHONOMY AND MUSEUM

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Natural Science Museums are emblematic institutions in scientific investigation. These were developed during XIX century, along with the exploration of the world. In that century, material culture and fossils from New World were relocated in different European museums. South American native fauna was one of the most required fossils objects because of the unique forms these animals had had. Nowadays, they can be found in museums from Spain, Italy, Switzerland, Germany and even Denmark. This material was extracted mostly from Pampean and Patagonian region, in Argentina during 19th century and the first decades from 20th century. The excavation procedure used in those days distance from what it was established latter. No registrations of the stratigraphy, context or associations were done.

It is considered that this material has original information that can be extracted with new methodologies and incorporate into modern studies. In the investigation developed by the author, anthropic marks are search in order to understand the colonization or modification of native niches in first American peopling. Thus, a taphonomical analytical procedure is necessary in order to interpret the different agents that affected these bones.

With the intention of systematize the data that can be extracted from these collections, museums (and the related excavation activities) have to be seen as a post burial disturbance factor in two ways. First of all, materials housed in museums are generally a selection of skeletal parts and specimens required in those times. In this way, they are a biased sample that lost their nearest information context. But they inform at a regional level, since most of the collections have the locality provenance (Fig. 1, part 1). Taphonomy can be useful in order to detect natural agencies that acted at a large scale resolution. In this way, general ecological past conditions of the fossil samples formation can be reconstructed. This focus is comparable with distributional archaeology that gives importance to surface material. In these cases associations and contexts are also lost, and what it is found reflexes the activity of natural forces that acted at the surroundings.

On the other side, museums are post burial agents since manipulation or restoration of the bones can add anthropic marks. In this sense, an historical view is necessary in order to analyze the skeletal elements. Through this way, the succession of the agents that affected the surface can be establish (Figure 1, part 2). Taphonomy helps to detect when natural and anthropic agents affected the bones: before burial, after burial or during excavations or when the material was store in the museum. Only when anthropic marks are detected before the development of natural agents, it can be interpret that hunting or scavenging activities were developed. If not they can be the result of manipulation and restoration activities or even the reuse of the material in the past.

In this way, taphonomy contributes to diminish the post depositional bias of samples from museums and to interpret the information they contain. This is a novel axis of investigation that is being developed in order to incorporate nineteenth collection into new studies.

23

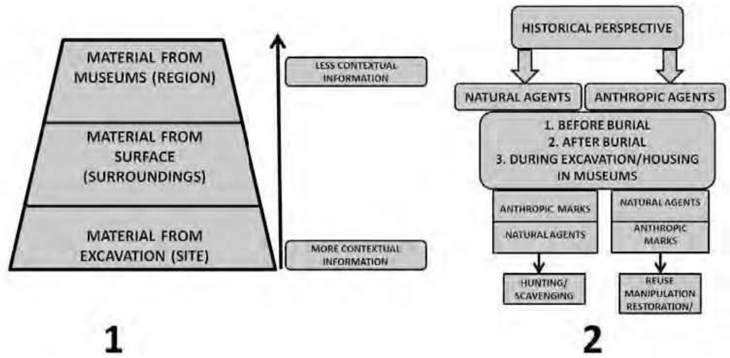

Fig. 1. Museums as post burial agent. (1) Consideration of the context within museums samples. (2) Historical perspective in order to detect cut marks related with hunting or scavenging activities

Abstracts presented in XVII UISPP, Union Internationale des Sciences Préhistoriques et Protohistoriques. Universidad de Burgos, in 2014

ORAL

18. EARLY HOMO SAPIENS, AND THE NATIVE FAUNA EXTINCTION IN THE SOUTH AMERICA SOUTHERN CONE

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Dispersion is a survival *Homo sapiens* adaptive strategy to confront variable environmental stresses in different spaces. To compare how it developed in diverse paleoecological settings is useful in order to understand how this adaptive capacity was used in niche construction or modification. Resources to be exploit, competency with other species and passing through different climatic or geological barriers, are keys items in this question.

America is an excellent opportunity to understand how dispersion was, in a landscape free from previous Hominini intervention. Focus emphases over the Pampean Region, Argentina, located at 36º S and 64 W. *Homo sapiens* would have created new niches of predation which would have allowed a fast dispersion timing.

Taphonomical analysis was done in Rodrigo Botet Collection housed in the Museo de Ciencias Naturales de Valencia, Spain. This is the result of non-systematic excavations done at the north-eastern sector of the Pampas Region at the end of XIX century. Taphonomical history of these bones, species and squeletal parts can give information about agents involved in its burial, ecology of the native fauna and its habitat. This evidence can be related with human's movements into the region at a coarse-grain level and thus understand how ecological relationship were constructed.

11,466 elements were analysed, from which 10 elements, coming from different species, were detected showing different kinds of anthropic traces: four Mylodontidae bones, one *Megatherium* sp. rib and other two from *Macrauchenia patachonica*, three osteoderms with pentagonal and hexagonal shape, one from Glyptodontidae and two from *Eutatus*.

These native fauna developed during Pleistocene times and extinct just after humans colonized the region –except *Eutatus*, which survived until recent times. Because its size, they have low carnivore predation and consequently few avoidance behaviours. Also slow sexual maturity and low reproduction structure. In these populations, stressed by paleoenvironmental changes, sporadic human predation could have influenced its extinction.
Dispersion into empty Hominini continents constituted a new ecological situation into human's evolution. Therefore different dispersion dynamics can be compared and evaluated between first entries of humans in South America and Iberic Peninsula. While in Europe early *Homo sapiens* dispersions could have taken at least 10.000 years, in America, the dispersion would have been fastest, between 3.000 or 2.000 years.

This contrast with the general idea that fast dispersion is favored with previous knowledge. This should have happened in Europe, were previous hominid incursions happened since early Pleistocene. America, in return, was an uninhabited. Recognition of resources and geophorms should have taken longer time. Thus in contrast

ORAL

1. FROM FAR AWAY: MUSEUMS, COLLECTIONS AND SCIENTIFIC RESEARCH

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Nineteen century was of movements and immigration of large contingents of people. But this also included the extrapolation and storage of fossil materials in different museums, like happened with South American paleontological collections that were translocate to Europe. In an era where crossing frontiers was easier, objects moved along with peoples, and control over the exit of national territory and entrance into a new one was generally celebrated. This contrast with nowadays situation, were patrimonies are reclaimed and increasing controls are done in order to stop the illegal contraband of archaeological and paleontological pieces.

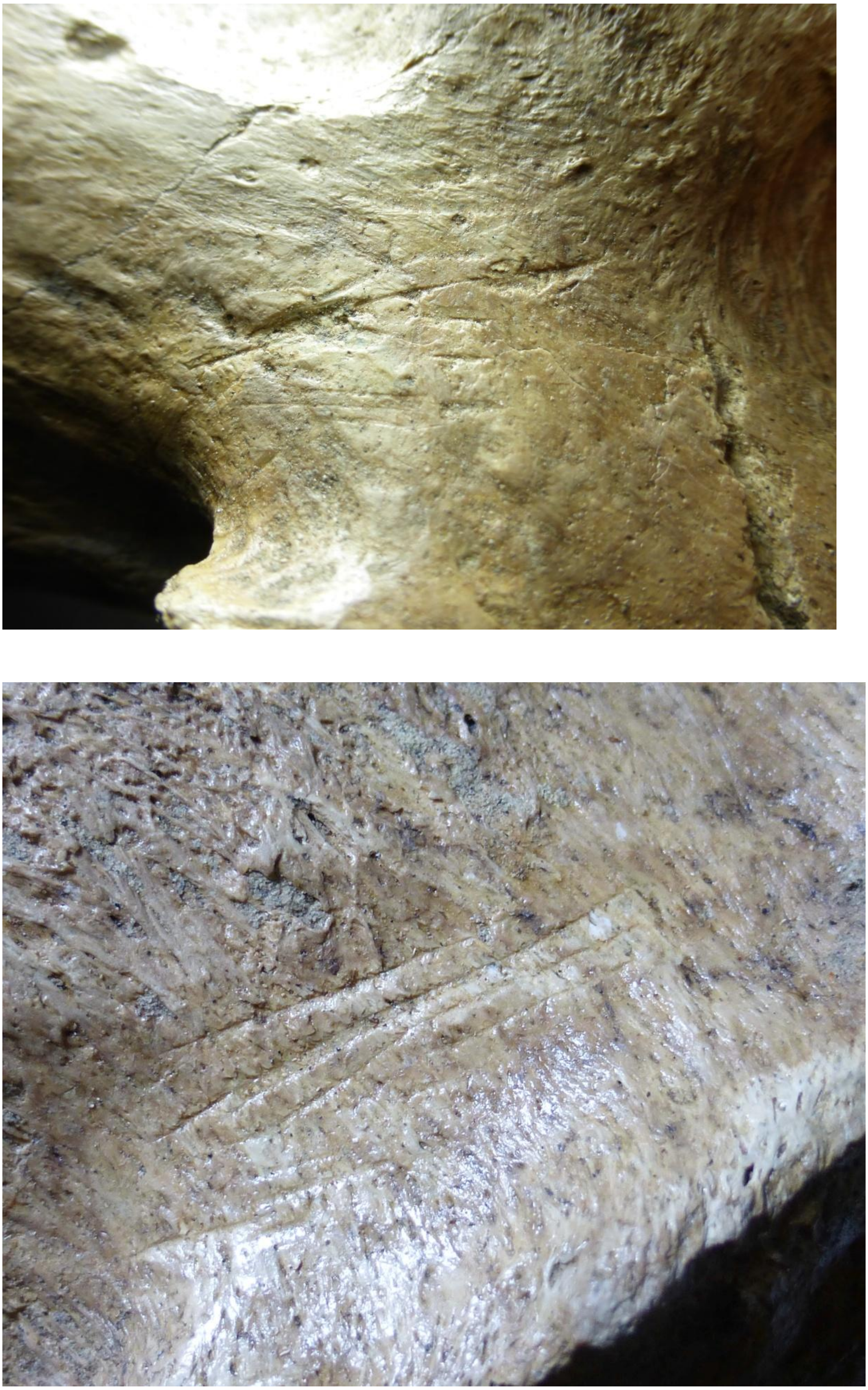
Today we found these collections distribute in several museums and institutions, miles away from its original point. A reflection about this situation is useful after one hundred years of this event: shall they return to their home countries or shall they stay away. Although the importance in housing material in its original places, a different point of view is taken here: material housed outside allows the diffusion of the own patrimony to citizens that perhaps will never travel to those countries, and encourages intercultural knowledge, but also they provide useful material to realize new studies in internationals programs which imply an extension of the institutional ties. This material can be focus with the application of methodologies that are not used in the original country, so in an indirect way, this patrimony provides to the research developed there. These conditions also allow integrating and contrasting different theoretical frameworks and data that improve interregional/intercontinental comparisons.

The experience realized in the Natural Science of Valencia, Spain where the Rodrigo Botet collection is housed, is an interesting example case. This is the most important collection of South American fossil megafauna in Europe and was studied by Boscá Casanoves, first curator of the museum. It was part of the first Paleontological Museum in Europe and it is characterized by the diversity and the large amount of material. The same was donated by Rodrigo Botet at the end of the XIX Century and it is the result of non-systematic excavations done by Enrique de Carles at the north-eastern sector of the Pampas Region in Argentina. It also has important human remains, as the "Samborombon skeleton", that unleashed in Spain the polemic about the antiquity of the first American peopling, as was postulated by Ameghino at that time. This collection was studied under the Erasmus Mundus Master in Quaternary and Prehistory program and currently is part of a PhD. thesis that will include material from this country housed in different museums in Europe and were translocate to this continent in the Nineteen century.

This kind of experiences can only developed because of the political situation the world was passing thought more than one hundred years ago. Thanks to that flow of goods, today, investigation outside the country can be realized and this allows the application of different methodologies, provides new data, and, contrary to what it is supposed, it broaden scientific research from far away.

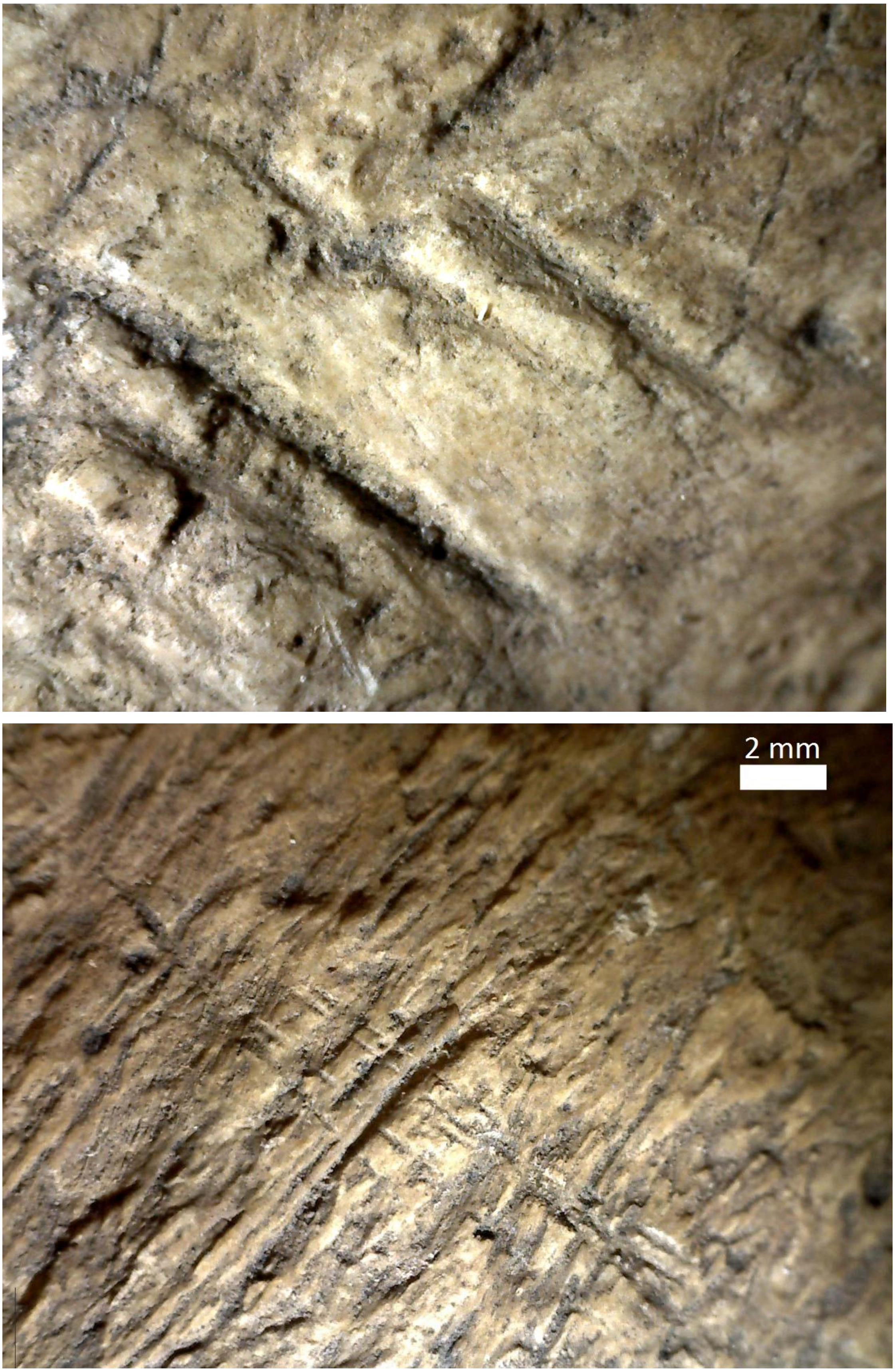
9.2. ADDITIONAL FIGURES AND TABLES

Appendix Figure 1. Detail of cut marks over ZMK 38/1889 vertebrae of Panochthus tuberculatus.

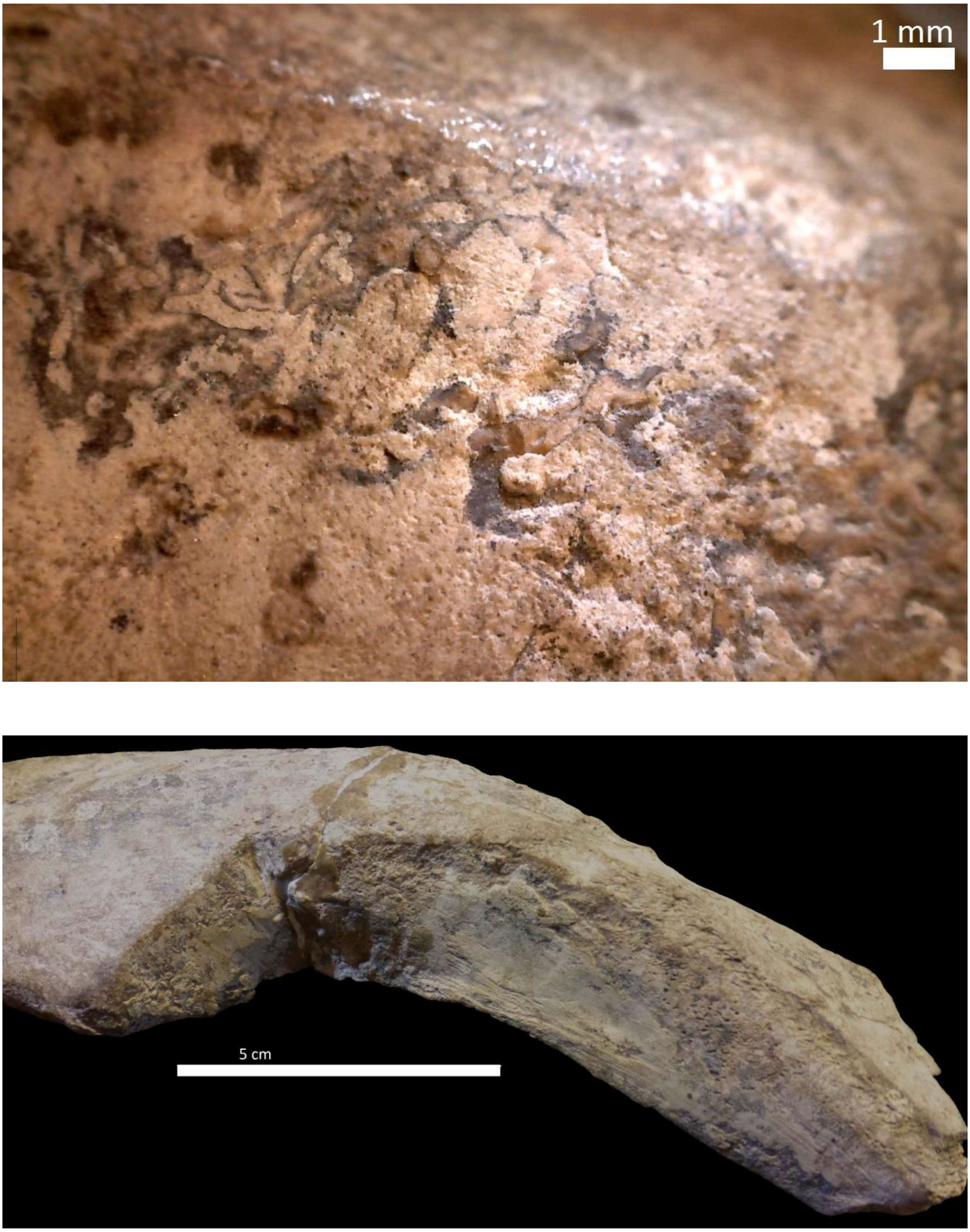


Appendix Figure 2. Detail of cut marks over MACN PV 6071 humerus of Doedicucus sp.

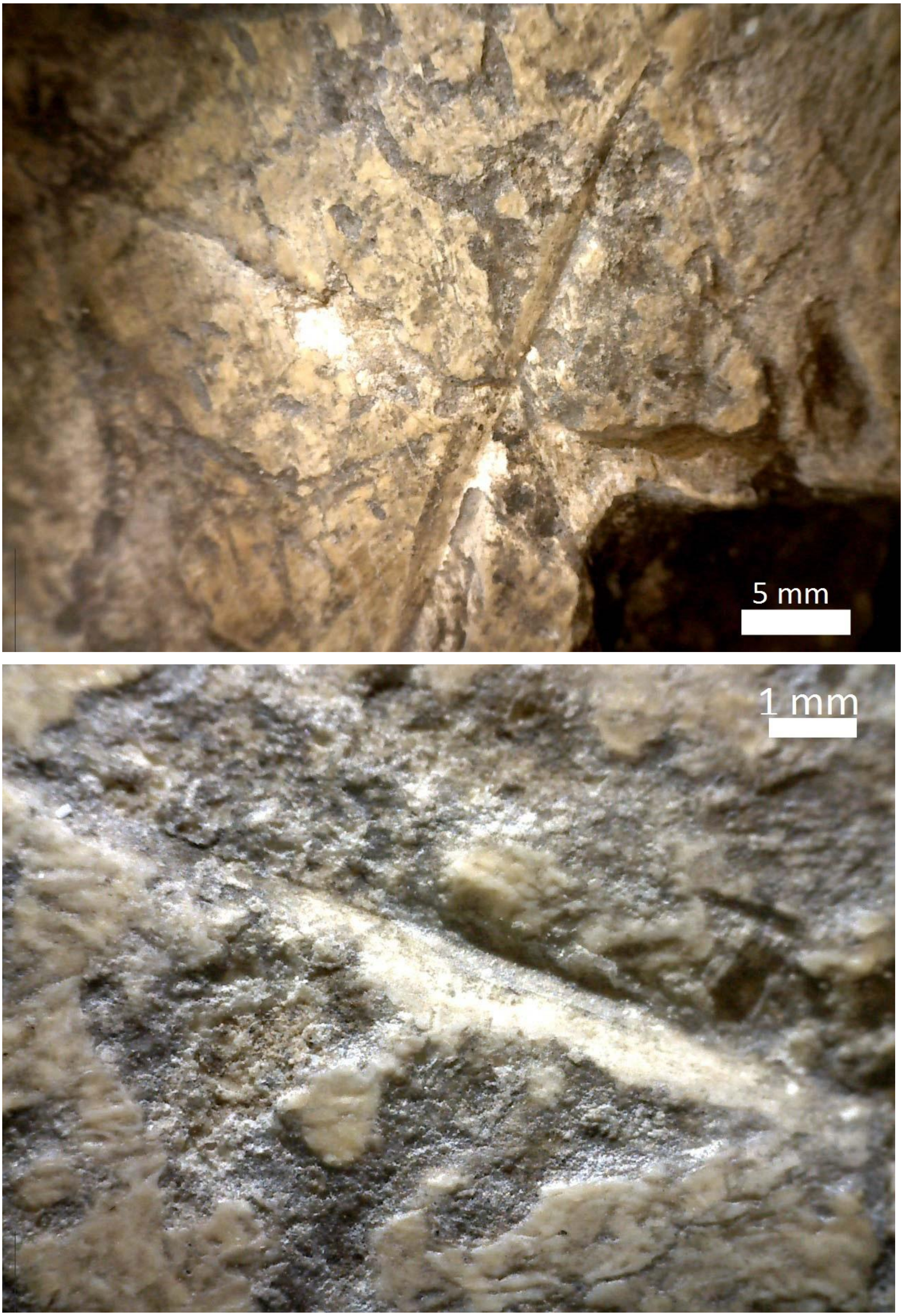
Appendix Figure 3. Detail of cut marks over IGF 14826 atlas of Megatherium americanum (groups 1 and 2).



Appendix Figure 4. Detail of cut marks over MNHN.F.PAM.751ulna of Megatherium americanum (groups A and D).



Appendix Figure 5. Detail of rib 1908.XL.19 of Megatherium americanum.

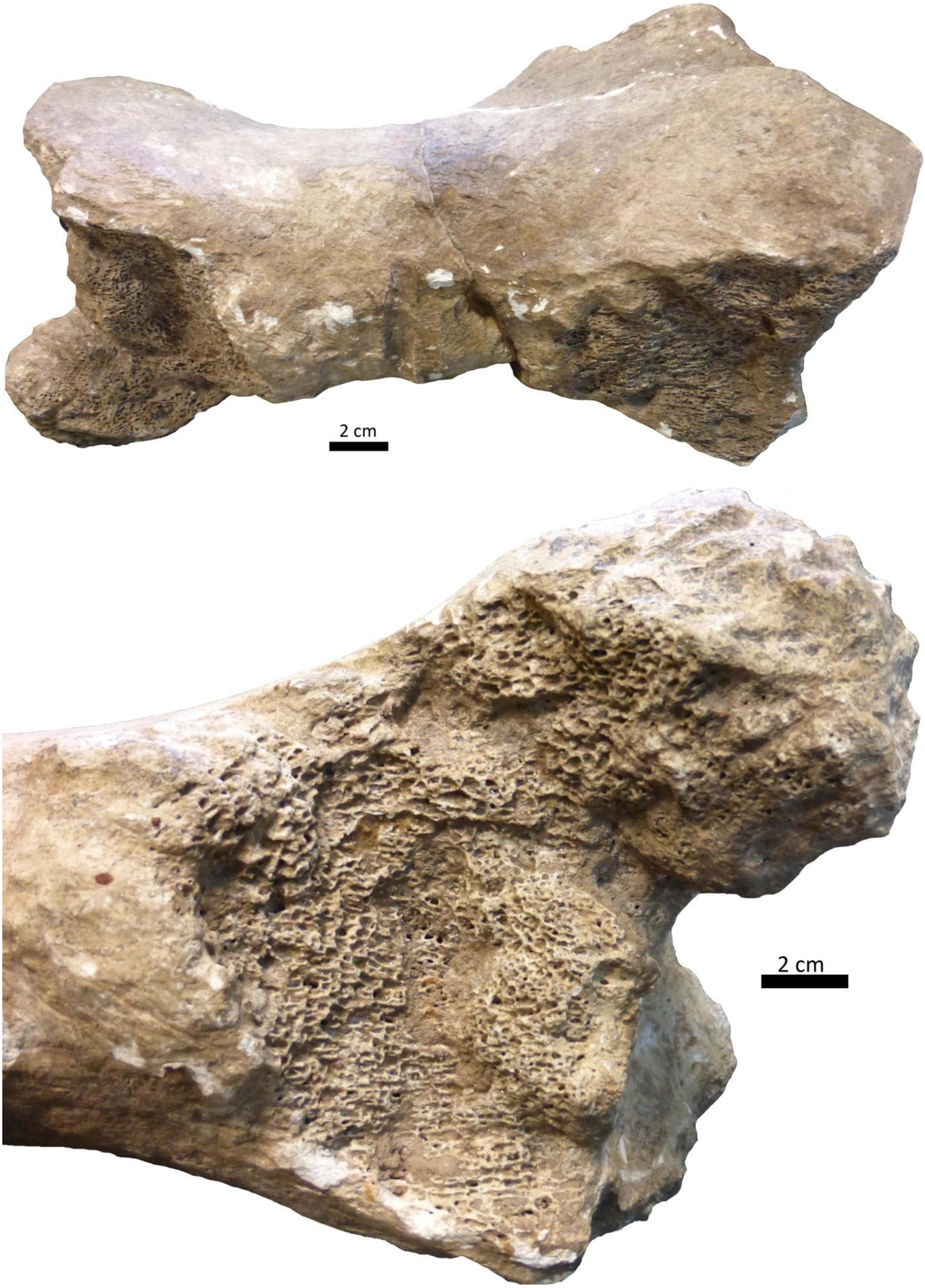


Appendix Figure 6. Detail of cut marks over MPCB 64-11/12BW scapula of Mylodontidae.

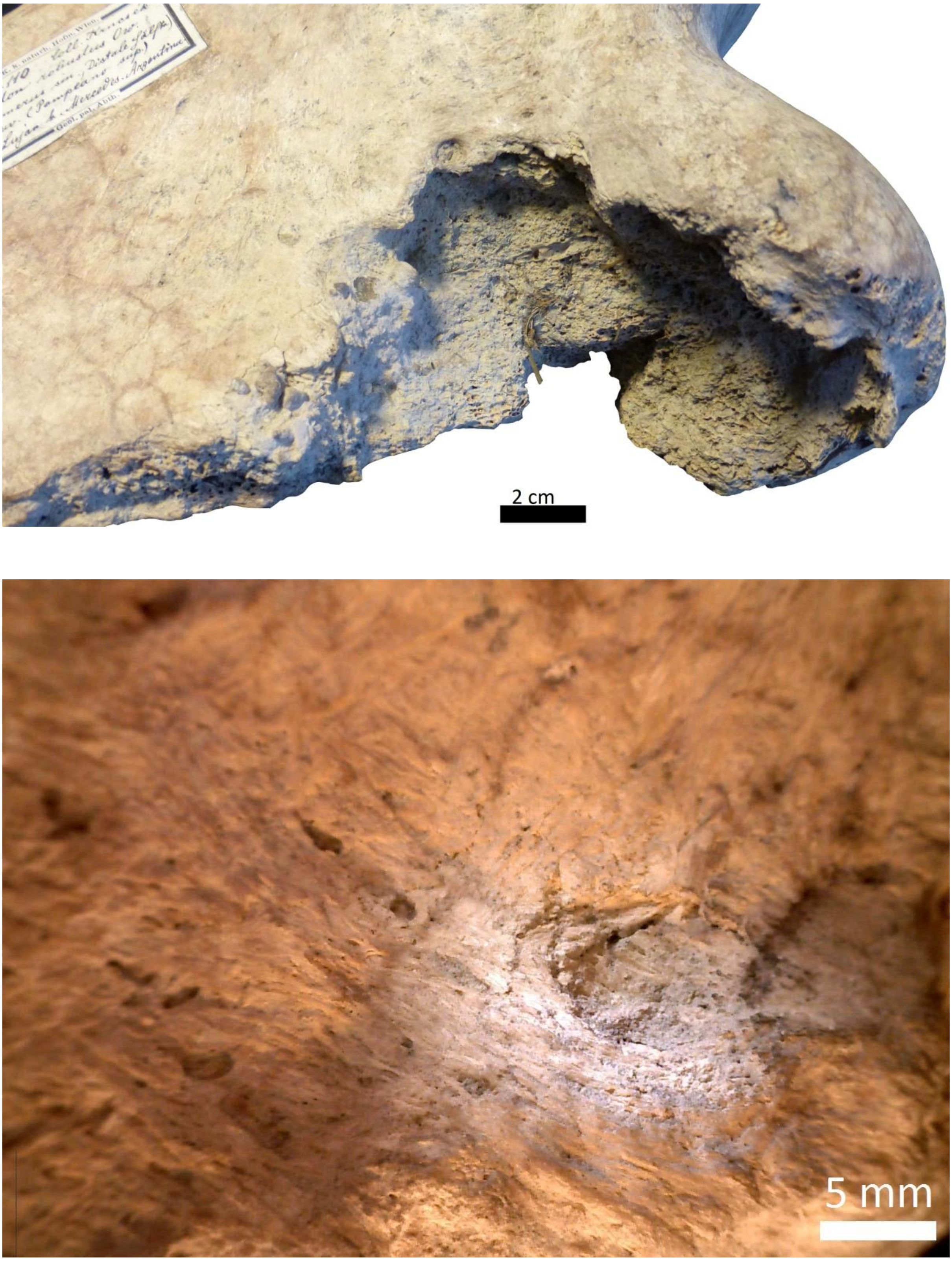
Appendix Figure 6. Detail of cut marks over 10/86 rib of Mylodontidae.

Appendix Figure 7. Detail of cut marks over 580 rib of Pseudolestodon.

Appendix Figure 8. Detail of carnivore marks over MNHN.F.PAM 119 humerus of Glossotherium robustus.

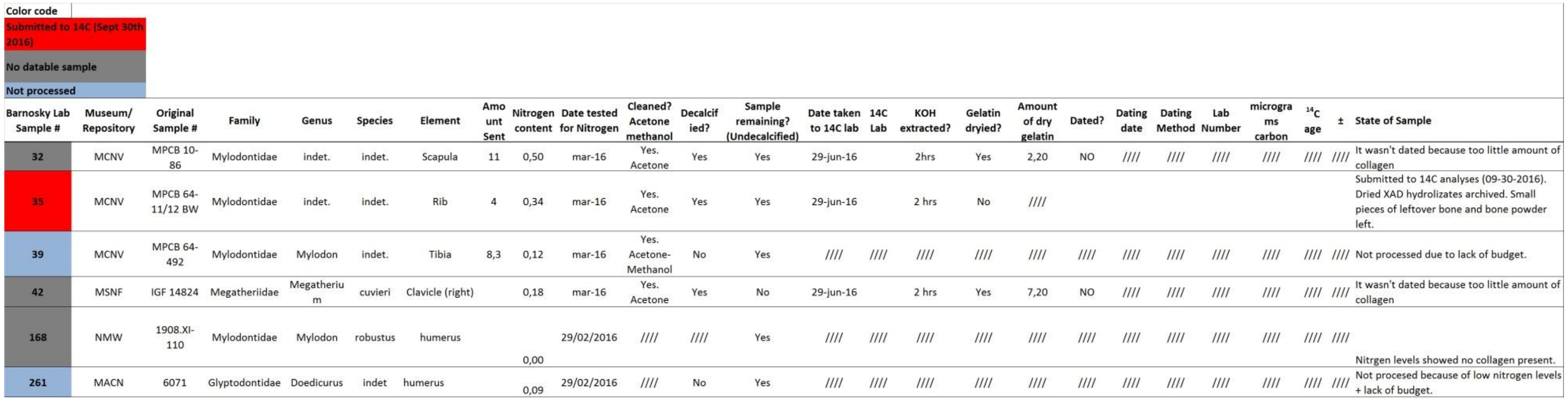


Appendix Figure 9. Detail of carnivore marks over 64-492tibia of cf. Scelidotheriinae gen.



Appendix Figure 10. Detail of carnivore marks over 1908.XI.110 humerus of Glossotherium robustum.

Appendix Figure 10. Detail of carnivore marks over MLP 15-I-20-32femur of Toxodontidae.



Color code
Submitted to 14C (Sept 30th 2016)
No datable sample
Not processed

Barnosky Lab Sample #	Museum/ Repository	Original Sample #	Family	Genus	Species	Element	Amount Sent	Nitrogen content	Date tested for Nitrogen	Cleaned? Acetone methanol	Decalcified?	Sample remaining? (Undecalcified)	Date taken to 14C lab	14C Lab	KOH extracted?	Gelatin dryied?	Amount of dry gelatin	Dated?	Dating date	Dating Method	Lab Number	micrograms carbon	^{14}C age	±	State of Sample
32	MCNV	MPCB 10-86	Mylodontidae	indet.	indet.	Scapula	11	0,50	mar-16	Yes. Acetone	Yes	Yes	29-jun-16		2hrs	Yes	2,20	NO	////	////	////	////	////	////	It wasn't dated because too little amount of collagen
35	MCNV	MPCB 64-11/12 BW	Mylodontidae	indet.	indet.	Rib	4	0,34	mar-16	Yes. Acetone	Yes	Yes	29-jun-16		2 hrs	No	////								Submitted to 14C analyses (09-30-2016). Dried XAD hydrolizates archived. Small pieces of leftover bone and bone powder left.
39	MCNV	MPCB 64-492	Mylodontidae	Mylodon	indet.	Tibia	8,3	0,12	mar-16	Yes. Acetone-Methanol	No	Yes	////	////	////	////	////	////	////	////	////	////	////	////	Not processed due to lack of budget.
42	MSNF	IGF 14824	Megatheriidae	Megatherium	cuvieri	Clavicle (right)		0,18	mar-16	Yes. Acetone	Yes	No	29-jun-16		2 hrs	Yes	7,20	NO	////	////	////	////	////	////	It wasn't dated because too little amount of collagen
168	NMW	1908.XI-110	Mylodontidae	Mylodon	robustus	humerus		0,00	29/02/2016	////	////	Yes	////	////	////	////	////	////	////	////	////	////	////	////	Nitrgen levels showed no collagen present.
261	MACN	6071	Glyptodontidae	Doedicurus	indet	humerus		0,09	29/02/2016	////	No	Yes	////	////	////	////	////	////	////	////	////	////	////	////	Not procesed because of low nitrogen levels + lack of budget.

Appendix Table 1. Results of the material send to University of California.

NUMBER	TAXON	ELEMENT	MEASUREMENTS (In mm)			COMPLETE	FRAGMENTED	SEDIMENT	WEATHERING*	ROOTS	MANGANESE	NON HUMAN BIOLOGICAL INTERVENTION (CARNIVORES)	HUMAN BIOLOGICAL INTERVENTION										RECENT MARKS	RESTAURATION
			HEIGHT	LENGTH	WIDTH								CUT MARKS	INSTRUMENT?	LOCATION				POSITION			ORIENTACION		
															ANTERIOR	POSTERIOR	MEDIAL	LATERAL	PROXIMAL	DISTAL	DIAPHYSIS	OBLIQUE/ PERPEND		
MPCB 64-11/12BW	Mylodontidae	Rib	105	10	35		X		1				X								X	X		
10/86	Mylodontidae	Scapula	180	70	40		X		1	X	X		X									X		
580	*Pseudolestodon*	Rib	115	40	15		X		1		X		X								X	X		
64-492	cf. Scelidotheriinae gen	Tibia	250	140	110	X		X	1			X												X
MNHN.F.PAM 119	*Glossotherium robustum*	Humerus	400	120	50	X			1			X												X
1908. XI.110	*Glossotherium robustum*	Humerus	280	160	50		X	X	1	X	X	X												
IGF14826	*Megatherium americanum*	Atlas	305	130	110	X			1		X		X			X						X	X	X
MNHN.F.PAM 751	*Megatherium americanum*	Ulna	580	180	170	X		X	1				X			X	X		X			X		
1908.XI.19	*Megatherium americanum*	Rib	310	60	25		X	X	1		X			X										
ZMK 38/1889	*Panotchus tuberculatus*	Caudal vertebra	200	190	65		X	X	1	X	X		X					X				X		X
MACN PV 6071	*Doedicurus* sp.	Humerus	290	90	80		X	X	1	X	X		X		X	X	X			X		X		X
MLP 15-I-20-32	Toxodontidae	Femur	110	80	70		X		1		X	X												

Appendix Table 2. Detail of megamammal bones with biological intervention. Colum Weathering (*) level according to Weathering Stages of Behrensmeyer (1978).

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