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Loss of ancient diversity of xenarthrans and the value of protecting extant armadillos, sloths and anteaters

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Abstract Armadillos, sloths and anteaters represent a small fragment of a much more diverse fossil assemblage of xenarthrans that includes bizarre forms such as the armored glyptodonts and the giant ground sloths. We reconstruct extinct xenarthrans as living animals, describing their basic biology, behaviors and ecological roles. In this contribution we provide two examples of the ecological diversity of xenarthrans in the geological past that largely surpass the one we know today. One is the Santacrucian fauna that developed in southern Patagonia during the Middle Miocene Climatic Optimum (17 to 15 Ma). The richness of Santacrucian xenarthrans recorded in a single locality comprises 21 genera in seven families, exceeding the present total diversity in the continent as a whole (14 genera within five families). The other is the Lujanian fauna that inhabited the Pampean Region during the late Quaternary (0.130 to 0.07 Ma). The total large mammal (above 100 kg) and megamammal (above a ton) richness during Lujanian times may have been as high as 83 species distributed in 48 genera. Most megaherbivores were xenarthrans, which constituted about 80% of the mammals above 500 kg: at least four genera of glyptodonts (Glyptodontidae) and five genera of ground sloths (Mylodontidae and Megatheriidae). There was also a giant armadillo-like herbivore that must have reached 200 kg (Pampatheriidae). This ancient diversity is lost forever, and we therefore urge that autochthony and past taxonomic richness and ecologic diversity be recognized as values for establishing conservation priorities and policies.

***Keywords*:** conservation, ecological diversity, extinct xenarthrans, taxonomic richness

Pérdida de la diversidad pasada de xenartros y la importancia de proteger a los armadillos perezosos y osos hormigueros actuales

Resumen Armadillos, perezosos y osos hormigueros representan una pequeña fracción de los mucho más diversos xenartros extintos, que incluyen formas extrañas como gliptodontes acorazados y los perezosos terrestres gigantes. Nosotros reconstruimos los xenartros extintos como animales vivientes, describiendo su biología básica, comportamiento y rol ecológico. Aquí aportamos ejemplos de diversidad ecológica de xenartros en el pasado geológico que supera la que conocemos en la actualidad. Uno es la fauna Santacrucense de Patagonia Austral durante el Óptimo Climático del Mioceno Medio (17-15 Ma). La riqueza de xenartros santacrucenses en una localidad comprende 21 géneros en siete familias, superando en mucho la diversidad total actual en el continente (14 géneros dentro de cinco familias). El otro es la fauna Lujanense de la Región Pampeana durante el Cuaternario tardío (0,130-0,07 Ma). La riqueza total de mamíferos grandes (más de 100 kg) y megamamíferos (más de una tonelada) podría haber sido de hasta 83 especies distribuidas en 48 géneros. La mayoría de los megaherbívoros eran xenartros (cuatro géneros de gliptodontes –Glyptodontidae– y cinco de perezosos terrestres –Mylodontidae y Megatheriidae)– que constituía aproximadamente el 80% de los mamíferos por encima de 500 kg. También hubo un armadillo herbívoro gigante (Pampatheriidae) que habría llegado a los 200 kg. Esta antigua diversidad se perdió para siempre. Por lo tanto, reclamamos que se considere la autoctonía y la riqueza taxonómica y diversidad ecológica pasada como valores fundamentales para el establecimiento de prioridades y políticas de conservación.

***Palabras clave*:** conservación, diversidad ecológica, riqueza taxonómica, xenartros extinguidos

Introduction

Current molecular evidence indicates that the South American Xenarthra represent one of the four major clades of placental mammals, although a consensus on patterns of relationships has not been achieved (see Delsuc & Douzery, 2008; Asher & Helgen, 2010; Meredith *et al.*, 2011). Recently, O'Leary *et al.* (2013), based on a combined molecular and morphological study, found support for a sister group relationship of Xenarthra to all other placental mammals (**Fig. 1**). Molecular evidence suggests that the clade arose about 100 Ma (million years ago) (Delsuc *et al.*, 2004), which implies, given that xenarthrans are known with certainty only since the dawn of the Cenozoic (some 55 Ma during the Paleocene; **Fig. 2**), a "ghost" lineage that left no traces for nearly 50 million years. However, the most widely accepted scenario envisions the origin of the Xenarthra in South America following separation from Africa about 65–80 Ma. No doubt, together with the marsupials, xenarthrans are the mammals with the longest history in South America.

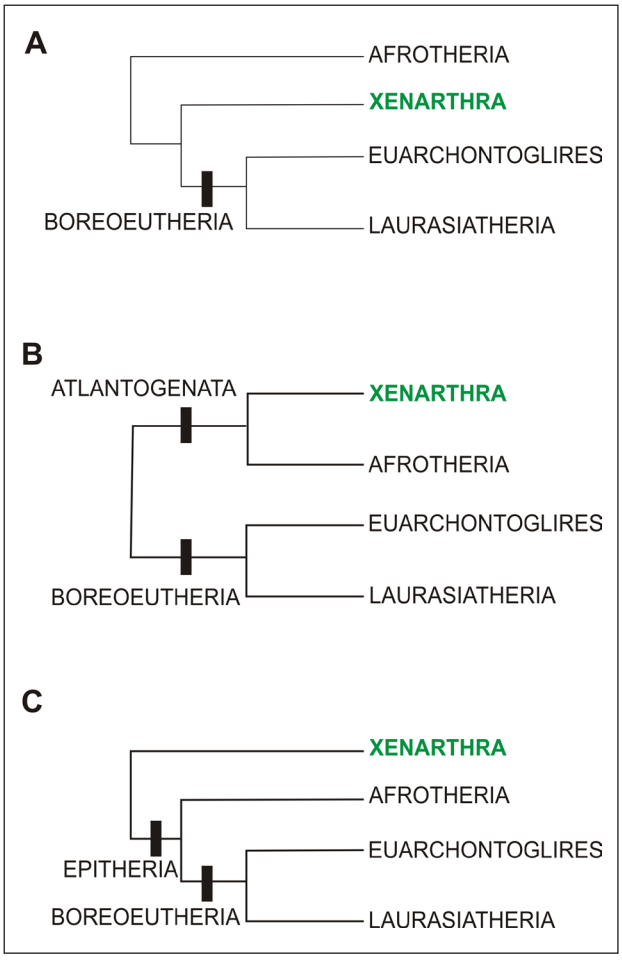

Figure 1. Summary of the phylogenetic relationships among the four major mammalian clades. A. Following Delsuc & Douzery (2008) and references therein, B. Following Asher & Helgen (2010). C. Following O'Leary *et al.* (2013).

Due to the later impressive diversification of the group, their fossils are among the most prominent and abundant in South America. It has been noted often that extant species of armadillos, sloths, and anteaters represent but a small fragment of a much more diverse fossil assemblage of xenarthrans that includes such well-known oddities as the glyptodonts and pampatheres related to armadillos within the Cingulata, and giant ground sloths within the Pilosa (which also includes anteaters). In contrast to the 13 extant genera (nine armadillos, two sloths and three anteaters), according to the already dated compilation by McKenna & Bell (1997), fossil forms representing more than 180 genera have been identified, including about 80 sloths and over

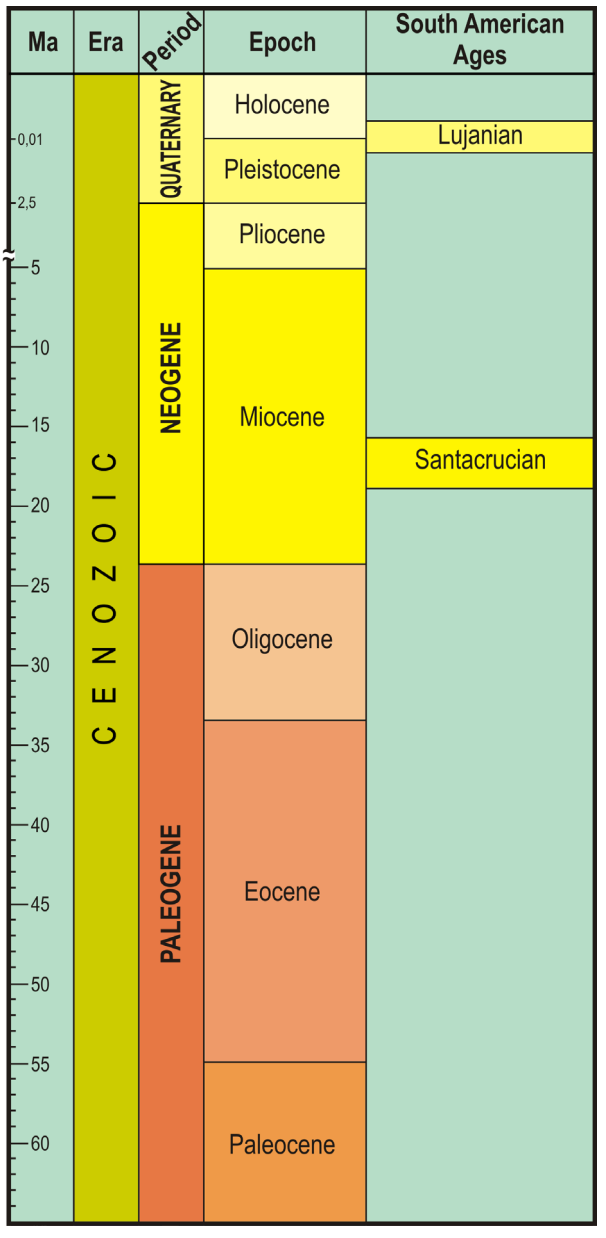

Figure 2. Chronologic chart of the Cenozoic including the Santacrucian and Lujanian ages treated in this article.

100 cingulates, 65 of which correspond to glyptodonts. Anteaters, on the other hand, have never been particularly abundant or diverse (McDonald *et al*., 2008). The number of xenarthran species would be, were they to be listed, even more astonishing, but we have refrained from counting them because they were based largely on typological methodology, which raises any minor morphological and metric difference to new species status, without attempting to evaluate that variation based on extant forms. This was particularly true in the last part of the 19th century, when most of them were named, but unfortunately this flawed methodology has begun to reappear in professional paleontological research over the past decade or two. For instance, a parataxonomy on the abundant and diverse carapace scutes of fossil cingulates has been generated that, so far, has been poorly checked against other features such as the cranial and postcranial skeleton (but see Fernicola *et al*., 2008; Fernicola & Porpino, 2012; De Iuliis *et al*., 2014). The phylogenetic analyses including extant and extinct xenarthrans that are followed in this contribution were performed by Gaudin (2004), Gaudin & Wible (2006), Fernicola (2008), and Porpino *et al*. (2010) (**Fig. 3**).

The closure of the Central American Seaway that separated South from North America, by means of the Central American landmass, allowed xenarthrans to extend to the north. Although few xenarthran species live there now, fossils are found during the late Neogene and the Pleistocene (from ~9 to 0.011 Ma) in Central and North America, and the Holocene in the Caribbean (till ~0.005,000 Ma). Xenarthrans began to disappear from Central and North America after the so-called Great American Biotic Interchange (Stehli & Webb, 1985). In contrast to this, xenarthrans remained very diverse in South America until the end of the Pleistocene (~0.011 Ma).

The remarkable diversity of fossil xenarthrans include many unique and, in some cases, bizarre anatomical features, such as, among others, a dentition with a strongly reduced tooth number in many forms, lack of enamel in adults and of deciduous teeth in almost all extant and extinct xenarthrans (see Castro *et al*., 2014; Ciancio *et al*., 2014), and absence of the tribosphenic cuspal pattern that characterizes other mammals. For these reasons, many past naturalists recognized xenarthrans, together with aardvarks (Tubulidentata) from Africa and pangolins (Pholidota) from Africa and Asia, as members of the group called Edentata (which has given its name to this newsletter). The name was coined by Vicq d'Azyr and Cuvier more than two centuries ago (Edentati Vicq d'Azyr, 1792) from the Latin for "toothless", a characteristic that really applies only to vermilinguans and pangolins, which achieved this state independently. We have noted before that the reduced dentition produced in most naturalists, including some Xenarthra specialists, a heightened but mistaken sense of simplification and lack of diversification in the masticatory apparatus of the group. A modern perspective suggests quite

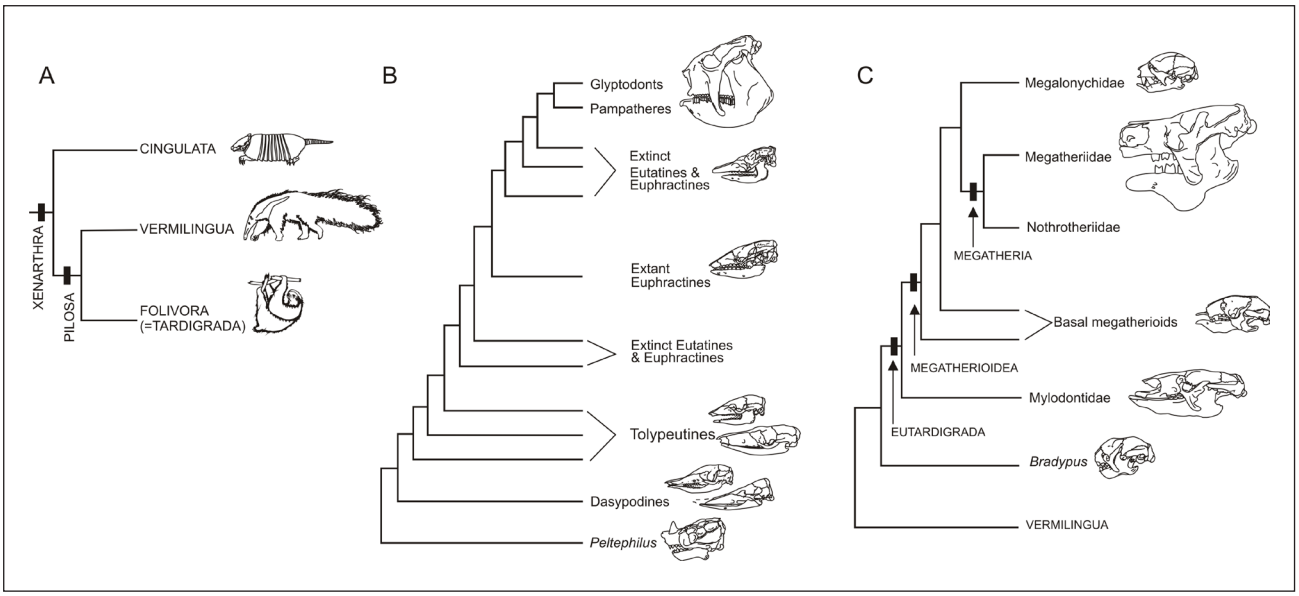

Figure 3. A. Cladogram summarizing relationships among major clades of xenarthrans. B. Cladogram summarizing relationships within cingulates, following Gaudin & Wible (2006), Fernicola (2008), and Porpino *et al*. (2010). Sketches of skulls in lateral view from top to bottom: *Glyptodon* sp. (Pleistocene glyptodontid); *Proeutatus* sp. (Miocene eutatine); *Euphractus sexcinctus* (extant euphractine); *Tolypeutes matacus* and *Priodontes maximus* (extant tolypeutines); *Dasypus novemcinctus* (extant dasypodine); *Stegotherium* sp. (Miocene dasypodine); *Peltephilus* sp. (Miocene peltephiline). C. Cladogram summarizing relationships within sloths, as proposed by Gaudin (2004). Sketches of skulls in lateral view from top to bottom: *Choloepus* sp. (extant megalonychid); *Megatherium* sp. (Pleistocene megatheriid); *Hapalops* sp. (Miocene megatherioid); *Scelidotherium* sp. (Pleistocene mylodontid); *Bradypus* sp. (extant bradypodid).

the opposite: the combination of dental features that characterize xenarthrans might be seen as the key innovation for the ecological diversity subsequently developed among xenarthrans, breaking the mold of the tribosphenic condition that constrained the evolution of the other major clades of mammals (Vizcaíno, 2009). In some cases xenarthrans represent less extreme versions of patterns developed in other major clades of mammals (marsupials, afrotheres, euarchontoglires, and laurasiatheres) clearly predetermined by a tribosphenic dental morphology, whereas in others they represent unique novelties indicative of particular biological roles.

As paleobiologists, our group is interested in reconstructing extinct xenarthrans as living animals, describing their habitats, ecological roles, behaviors, and basic biology, and considering diversity in ecological terms rather than as taxonomic richness. In the following sections we will briefly provide two examples of the ecological diversity of xenarthrans in the geological past that largely surpass the one we know today.

Reconstructing past ecological diversity in xenarthrans

One important tool for inferring the habits of extinct forms is the principle of actualism, according to which past events are reconstructed by analogy with currently observable processes. Mammals are very diverse in present times and most of them have fossil representatives. Reciprocally, most fossil mammals can be assigned to extant orders. For these reasons paleomammalogists apply actualism with a rather restrictive criterion, assuming that extinct species had similar habits to their current relatives. However, the dramatically reduced diversity of extant xenarthrans relative to their fossil kin means that few living analogs are available for comparison with extinct forms. This has severely constrained, and in some cases even misled, the interpretation of the natural history of fossil xenarthrans (Vizcaíno *et al*., 2008). Also, as we mentioned above, xenarthrans evolved in relative isolation in South America during a good part of the Cenozoic and developed important dental, skeletal, and muscular peculiarities that markedly distinguish them from other mammals. Consequently, in many cases the latter are not reliable analogues either (Vizcaíno & De Iuliis, 2003 and references therein).

For xenarthrans, as well as in all vertebrate paleontology, the main sources of information are fossilized bones and teeth; the majority of our paleobiological information is derived from these data and a "form-function correlation approach" (Radinsky, 1987) applies. According to this principle, function can be inferred from form. If appropriate homologies are lacking, biological analogues must be used; if biological ones are not available, then mechanical analogues can be helpful. Functional morphology, biomechanics, and ecomorphology can be applied to interpret form-function relationships: functional morphology analyzes how form causes, allows, or restricts the functions an organism can perform; biomechanics studies the relationships between form and function using the principles of physics and engineering; and ecomorphology investigates form and function with regard to environment (Plotnick & Baumiller, 2000). Although, as mentioned before, actualism is problematic in studies of extinct xenarthrans, relationships between form and function in living species are still needed.

A basic protocol in paleobiological studies implies the definition of three biological attributes that are essential for each taxon: size, diet, and usage of substrate, including type of locomotion (Vizcaíno *et al*., 2008 and references therein). These allow the development of novel interpretations of xenarthran modes of life that, coupled with paleoenvironmental data (geology, paleoclimatology, and reconstruction of paleovegetation), provide insightful information on the paleoecological context in which these animals existed.

Xenarthrans in Patagonia during the Middle Miocene Climatic Optimum

The Middle Miocene Climatic Optimum (MMCO, approximately between 17 to 15 Ma) was a period of global warmth (perhaps as much as 4–5 °C warmer than today) punctuating the overall cooling trend that has characterized the last 50 million years. During this period, which coincides with the late Early Miocene, warm surface water transported southward by the Brazil Current extended subtropical conditions southward from Amazonia (Barron *et al*., 1985; Hodell & Kennett, 1985). Much of the Andean uplift had not yet occurred (Blisniuk *et al*., 2005; Ramos & Ghiglione, 2008), so Andean rain-shadow effects over Patagonia had not yet been established. The Patagonian climate must have been very dissimilar to that of today, unusual and without modern equivalents, given that seasonality in energy availability at ~50°S latitude must have had an effect upon biotic productivity (Kaufman, 1995). By this time South American mammals had undergone diversification and ecological specialization in isolation from other continents (Simpson, 1980, Fariña *et al*., 2013). In southern Patagonia a fauna referred to by paleontologists as the Santacrucian developed. This fauna marked the peak of diversification achieved by mammals after the arrival of African primates and rodents, but before the arrival of most North American immigrants. Xenarthrans were a quintessential component of this fauna, and their diversity was surprising, particularly considering the limited geographic range.

Florentino Ameghino (1887) provided the first descriptions of Santacrucian xenarthrans. Among cingulates, he named 11 species of armadillos that are currently assigned to two families, and include the genera *Peltephilus* (Peltephilidae; **Fig. 4A**), *Stegotherium* (Dasypodidae, Dasypodinae), *Prozaedyus*, *Vetelia*, *Proeutatus*, and *Stenotatus* (Dasypodidae, Euphractinae). He also named two species of glyptodonts of the genus *Propalaehoplophorus* (Glyptodontidae, Propalaehoplophorinae). In subsequent years, he added three new genera of armadillos, the peltephilids *Anantiosodon* and *Peltecoelus* and the dasypodid *Eodasypus*, and four propalaehoplophorine glyptodonts, *Asterostemma*, *Cochlops*, *Eucinepeltus* (**Fig. 4B**), and *Metopotoxus*. This taxonomic arrangement has changed little since then. In our recent efforts to reconstruct the paleoecology of Santacrucian cingulates we confirmed that at least five genera of armadillos and four genera of glyptodonts were sympatric (Vizcaíno *et al*., 2012b) in the rocks that contain this fauna in the Atlantic coast of Patagonia.

Among Pilosa, several taxa from the Santacrucian coastal localities were originally referred to Vermilingua by Ameghino (1893, 1894, 1904), including nine species in the genera *Adiastaltus*, *Plagiocoelus* (Adiastaltidae), *Anathitus* (Anathitidae), *Protamandua*, *Promyrmephagus* (Myrmecophagidae), *Argyromanis*, and *Orthoarthrus* (Manidae Ameghino 1904: Mammalia *incertae sedis* following Mones 1986). According to the most recent overview, *Protamandua rothi* is the only species from the Santa Cruz Formation that can be confidently referred to

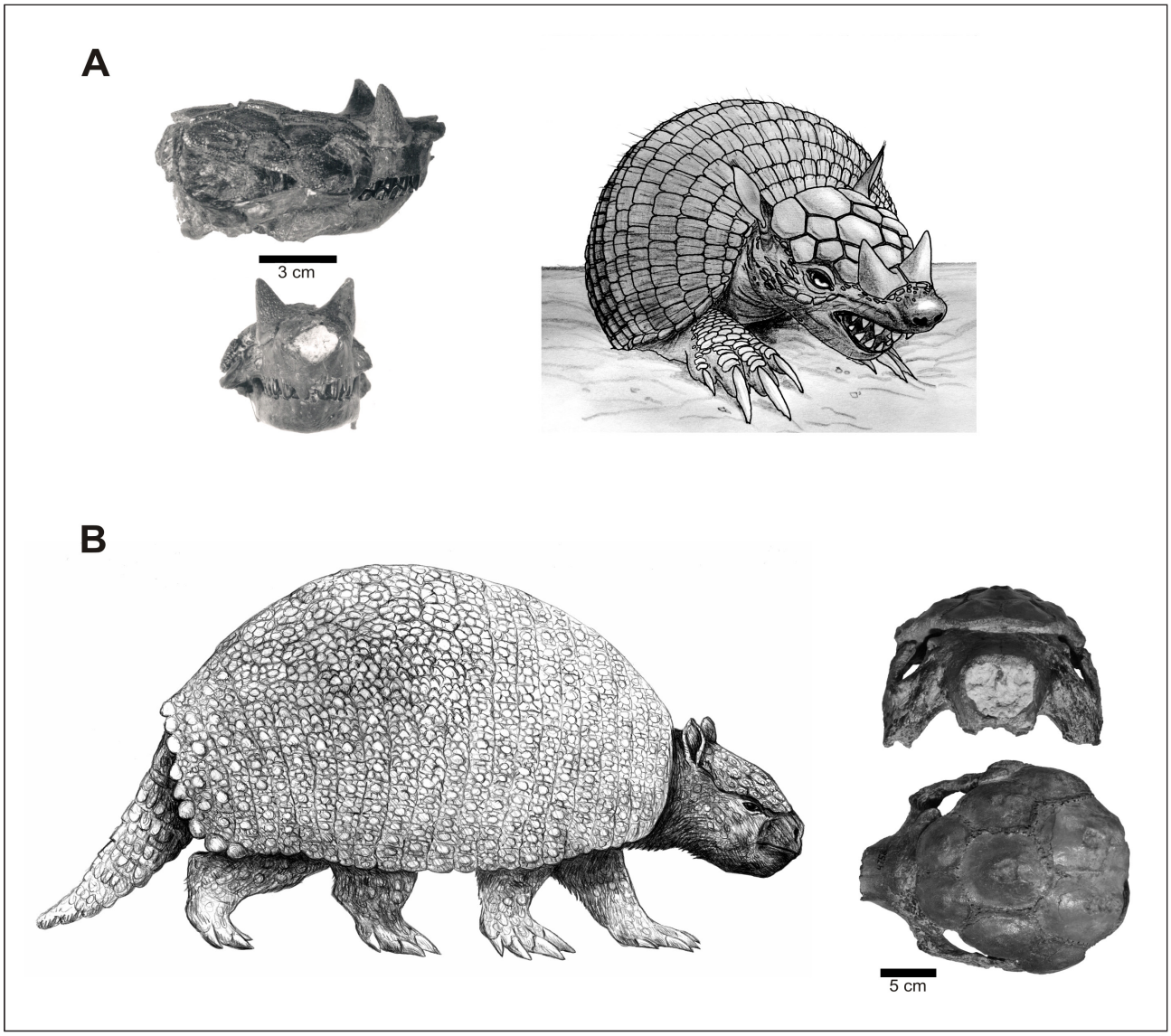

Figure 4. Cingulates from Santa Cruz Formation (Santacrucian, Early Miocene, Patagonia). A. Lateral and frontal view of the skull of the armadillo *Peltephilus pumilus* (MACN-A 7784) housed in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina and life reconstruction of a peltephilid by Néstor Toledo. B. Skull of the propalaehoplophorine glyptodont *Eucinepeltus petesatus* (MACN-A 4758) housed in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina, and life reconstruction of the propalaehoplophorine *Cochlops muricatus* by Marcelo Canevari.

Vermilingua and as a Myrmecophagidae, although other poorly known remains could belong to vermilinguans (McDonald *et al*., 2008).

Several other early workers erected a plethora of sloth genera and species. Despite the fact that many of these taxa are based on fragmentary remains and are thus poorly known, most Santacrucian genera are clearly identifiable taxonomic units. According to McKenna & Bell (1997) the following genera (all but one named by Ameghino), belonging to three families and four subfamilies, are recorded in the Santacrucian fauna of Patagonia: *Eucholoeops* and *Megalonychotherium* Scott (Megalonychidae), *Hapalops* (**Fig. 5**), *Hyperleptus*, *Pelecyodon*, *Analcimorphus*, and *Schismotherium* (Megatheriidae, Schismotheriinae); *Planops* and *Prepotherium* (Megatheriidae, Megatheriinae), and *Nematherium* and *Analcitherium* (Scelidotheriidae, Scelidotheriinae). Recent field work in the coastal exposures of the Santa Cruz Formation has yielded several nicely preserved specimens of *Eucholoeops*, *Hapalops*, *Pelecyodon*, *Hyperleptus*, and *Nematherium* (Bargo *et al*., 2012) that permit the undertaking of comprehensive systematic reviews (e.g., De Iuliis *et al*., 2014).

In summary, the taxonomic richness of Santacrucian xenarthrans in a single locality, on which a comprehensive paleoecological study was performed (Kay *et al*., 2012), comprises at least nine genera of cingulates in three families, one genus and family of anteater, and 11 genera in three families of sloths, for a total of 21 genera in seven families. This far surpasses the present total diversity in the continent as a whole (14 genera within five families).

Figure 5. Sloth from the Early Miocene Santa Cruz Formation (Santacrucian, Patagonia). Skull of the basal megatherioid *Hapalops longiceps* (YPM-VPPU 15523) housed in Yale Peabody Museum, New Haven, USA, and life reconstruction by Néstor Toledo.

As indicated above, paleobiological studies performed on these xenarthrans (Bargo *et al*., 2012; Vizcaíno *et al*., 2012b) include estimation of body mass, analysis of the limbs so as to infer substrate use, and studies of the masticatory apparatus to infer probable feeding habits. Body masses were calculated based on a variety of scaling models, allometric equations, multiple regressions, and geometric similarity. Substrate use was determined through morphometric and qualitative-comparative morphofunctional analyses, indices previously modeled in living dasypodids using morphogeometric analyses, and application of a strength indicator. Feeding habits were inferred from jaw biomechanics, the anatomy of the masticatory apparatus as a whole, the shape, arrangement, and wear patterns on teeth, and from ecomorphological analyses. The results of these studies can be summarized as follows.

Among cingulates (Vizcaíno *et al*., 2012b), all armadillos were in the range of medium-sized living armadillos, and all glyptodonts were larger than any living armadillo, slightly greater than 100 kg. Despite some variation in limb proportions, all armadillos were good diggers but none reached the degree of fossoriality found in the specialized living *Chlamyphorus*; all glyptodonts were non-fossorial. In contrast, the variation in the masticatory apparatus of the armadillos exceeds that in living species, denoting a broader range of specializations and strong niche partitioning among the fossil species. Inferred diets of fossil forms range from herbivory to strict myrmecophagy. *Proeutatus* species were omnivorous, showing the most specialized morphology known for a cingulate herbivore with an armadillo-like skull pattern. *Stenotatus* species may have been omnivorous; they are morphologically and ecologically intermediate between living euphractines and dasypodines, with some specialization towards insectivory. *Prozaedyus* species were perhaps omnivorous, with a preference for rotting flesh and larvae as well as cocoons of ants and/or termites – a diet comparable to that of small living euphractines. *Stegotherium* was clearly more specialized for a myrmecophagous diet than any living armadillo. *Peltephilus* may have specialized on roots or tubers, although scavenging habits cannot be ruled out. The degree of variation in the masticatory apparatus of glyptodonts does not show the range of morphological diversity present in contemporaneous armadillos; some morphological traits allowed us to identify some ecological partitioning within the category of selective feeding in relatively closed to closed habitats.

Among Pilosa (Bargo *et al*., 2012), the Santacrucian anteater *Protamandua* was a relatively small animal, about 6 kg, well suited for climbing

and for scratch-digging the substrate in search for its preferred food, social insects. Various sloths were moderately large-sized forms, the largest reaching about 100 kg, with a locomotor pattern distinct from that of living sloths, instead resembling more that of vermilinguans and pangolins. The results suggest well-developed digging capabilities, but semi-arboreal habits cannot be ruled out. Megatherioid sloths were most likely leaf eaters. Mylodontids may have fed on more compact, three-dimensional, and fibrous food items such as the underground storage organs of plants. The semiarboreal habits suggested for anteaters and, probably, sloths indicate they lived in forests or that forested areas were present nearby.

Xenarthrans in the Pampean Region at the End of the Pleistocene

From the middle Miocene/Pliocene, with the culmination of the separation process between Antarctica and South America, the establishment of the Circumpolar and Humboldt oceanic currents in their present trajectories produced higher temperatures and increased aridity in the subtropics. The final elevation of the Andes produced a rain shadow effect that, by the Plio/Pleistocene, caused fragmentation of the subtropical paleoflora and the spread of taxa of arid environments along the so-called "arid diagonal" that extends from the southeastern tip of the continent, across the Andes in central Chile, and continuing along the Pacific coast to near the Equator (Hinojosa & Villagrán, 1997; Villagrán & Hinojosa, 1997). The periodic climatic alternation of glacial and interglacial epochs during the middle and late Pleistocene dramatically modified the distribution, composition, and biomass of plant and animal communities in South America; dry and cold climate caused open areas to predominate in South America (Cione *et al*., 2003). As mentioned above, the volcanic Isthmus of Panama rose up during the last part of the Pliocene, bridging North and South America and allowing a bidirectional migration of fauna and flora between the continents. Xenarthrans crossed the bridge to the north and became abundant in North America. In South America, the success of herbivorous xenarthrans subsequent to the Interchange has been explained by their ability to avoid competition with northern placental lineages by evolving increased size (Vizcaíno *et al*., 2012a).

During the Quaternary (the last 2.58 Ma; **Fig. 2**) several lineages of South American mammals evolved gigantic body sizes. Among the more than 120 genera of mammals known, the estimated adult masses of about 40 exceeded 100 kg, about 20 of which were megaherbivores (Vizcaíno *et al*., 2012a). Certainly, no other fossil mammalian fauna is known to have contained such a diversity of megaherbivores (i.e., above one ton of body mass). But even more interesting for this contribution is that most of them were xenarthrans.

In central Argentina, in the Pampean Region in particular, the basis of the so-called Lujanian Age (~0.130 to 0.07 Ma) was established. The total mammalian richness during Lujanian times may have been as high as 286 genera. According to Cione *et al*. (2009), the total large mammal (and megamammal) diversity present during Lujanian times could have been as high as 83 species distributed in 48 genera. At least four genera of glyptodonts within the family Glyptodontidae (*Glyptodon*, *Plaxhaplous*, *Doedicurus* and *Panochthus*; **Fig. 6**) reached body masses varying between one and two tons. Among ground sloths, five genera in two families weighed more than one ton: *Glossotherium*, *Mylodon* (**Fig. 7**), *Scelidotherium*, *Lestodon* (Mylodontidae), and *Megatherium* (Megatheriidae); the last two reaching up to three or four tons. There were also two armadillos (*Eutatus* and *Propraopus*, Dasypodidae: Eutatinae and Dasypodinae, respectively) of about 50 kg and one pampathere (*Pampatherium*, Pampatheriidae), a giant armadillo-like herbivore that must have reached 200 kg. Xenarthrans alone constitute about 80% of the mammals above 500 kg (the other putative Lujanian xenarthrans are armadillos of the extant genera *Dasypus*, *Chaetophractus*, *Zaedyus*, *Euphractus*, *Tolypeutes*, and *Chlamyphorus*). The other mammals above 500 kg were two native ungulates (Notoungulata and Litopterna) and one gomphothere (Proboscidea). Immigrant ungulates, artiodactyls and perissodactyls, were all smaller than one ton, mostly less than 500 kg (Vizcaíno *et al*., 2012a).

The total number of mammalian herbivore species larger than a ton in the Lujanian is even more impressive than in present-day African faunas; as many as 19 such species occur in a single locality (Fariña & Vizcaíno, 1999). This seems to be too much for the flora that had to support them (Fariña, 1996). However, as mentioned before, megaherbivores were dominated by xenarthrans, which are characterized by their low metabolism and, consequently, lower energetic requirements than other placentals. Therefore, for a specific type of food they required lower intake than other placental mammals of similar body masses (Vizcaíno *et al*., 2006). Certainly, this ecological scenario has no counterpart in living faunas.

Nonetheless, xenarthran diversity was ultimately reduced as all of these giant forms suffered the widespread extinction event at the very end of the Pleistocene and the beginning of the Holocene, although they were the only megamammals that seem to have survived it very briefly (Gutierrez *et al*., 2010). All megamammals (37 species) and most large mammals (46 species) present during the Lujanian became extinct in South America (Cione *et al*., 2003, 2009). As most megamammals in South

Figure 6. Glyptodont from the Late Pleistocene-Early Holocene Luján Formation (Lujanian, Pampean Region). Skull of *Panochthus tuberculatus* (MLP 1) mounted at the exhibition hall of the Museo de La Plata, La Plata, Argentina in frontal and lateral view, and life reconstruction by Néstor Toledo.

America were xenarthrans, most megamamals affected by extinction in this continent were xenarthrans (albeit litopterns and notoungulates also became extinct).

Although the impact of the extinction of the giant xenarthrans (and other megamammals) on the evolution of present plant communities has not been studied for South America, it clearly produced an enormous ecological gap in the herbivorous guild that may have affected plant communities (Galliari & Goin, 1993). As in other continents (Johnson, 2002, 2009), the ecological aftershocks of those extinctions persist today.

Concluding remarks

We have addressed two moments during the Cenozoic in southern South America (one in Patagonia and the other in the Pampean Region) in

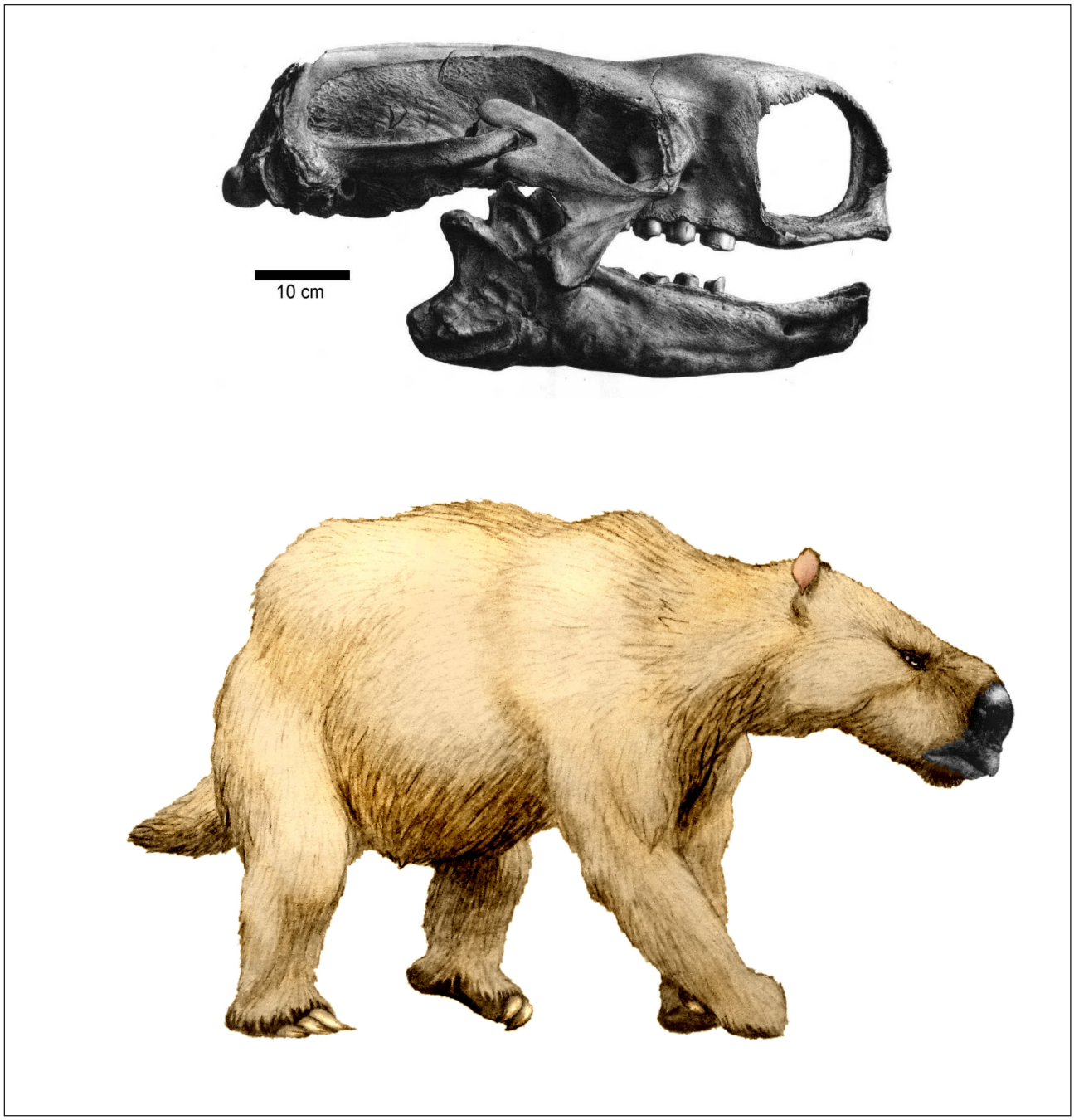

FIGURE 7. Ground sloth from the Late Pleistocene-Early Holocene Luján Formation (Lujanian, Pampean Region). A. Skull of *Mylodon darwini* (CN 43) housed in the Zoologisk Museum in Copenhagen, Denmark, and life reconstruction by Néstor Toledo.

which xenarthran taxonomic richness and ecological diversity was much higher than today; even north to the Tropic of Capricorn, where most of the present richness and diversity accumulates.

Irremediably, those that are gone will never come back, unless molecular technology is able to clone them in some distant future. But even so, we (or, most probably, our descendants) would face the ethical conundrum of inserting them in modern ecosystems or keeping them as lab animals, zoo beasts or circus freaks.

In conservation terms, xenarthrans have been effectively invisible for a variety of reasons (Aguiar & Fonseca, 2008). This may change if a historical perspective with a geological time scale is applied. In a volume proposing environmental policies for Argentina, Galliari & Goin (1993) produced a largely ignored approach to the assessment of methodologies for conservation priorities of mammals that they called a "historical method." For the purposes of their analysis, they considered a measure of the age of the different lineages of mammals in South America as an "index of South American autochthony" or "index of time endemism", to recognize the intrinsic value (the uniqueness or oneness) of *in situ* evolution of the South American mammalian fauna. Because of its great antiquity and differentiation in

South America, Galliari & Goin (1993) found that armadillos reach a very high "rate of time endemism", which should translate into high priority in terms of conservation value.

Hence, by protecting armadillos, sloths and anteaters we are protecting the most representative lineage of mammals of South America on more than just its present faunal record. Consequently, we urge that autochthony and past taxonomic richness and ecologic diversity be recognized as values for establishing conservation priorities and policies at a continental scale.

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References

Aguiar J. M. & G. A. B. Da Fonseca. 2008. Conservation status of the Xenarthra. Pp. 215–231 in: The biology of the Xenarthra (S. F. Vizcaíno & W. J. Loughry, eds.). University Press of Florida, Gainesville.

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia. Boletín del Museo de La Plata 1: 1–26.

Ameghino, F. 1893. Nouvelles découvertes paléontologiques dans la Patagonie australe. Revue Scientifique 51: 1–731.

Ameghino, F. 1894. Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. Boletín de la Academia Nacional de Ciencias de Córdoba 13: 259–455.

Ameghino, F. 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. Anales de la Sociedad Científica Argentina 57: 162–175; 327–341.

Asher, R. J. & K. M. Helgen. 2010. Nomenclature and placental mammal phylogeny. BMC Evolutionary Biology 10: 1–9.

Bargo, M. S., N. Toledo & S. F. Vizcaíno. 2012. Paleobiology of the Santacrucian sloths and anteaters (Xenarthra, Pilosa). Pp. 216–242 in: Early miocene paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz formation (S. F. Vizcaíno, R. F. Kay & M. S. Bargo, eds.). Cambridge University Press, Cambridge.

Barron, J. A., G. Keller & D. A. Dunn. 1985. A multiple microfossil biochronology for the Miocene. Pp. 21-36 in: The Miocene ocean: paleoceanography and biogeography (J. P. Kennett, ed.) Geological Society of America Memoir 163, Ann Arbor, Michigan.

Blisniuk, P. M., L. A. Stern, C. P. Chamberlain, B. Idleman & P. K. Zeitler. 2005. Climatic and ecologic changes during Miocene surface uplift in the Southern Patagonian Andes. Earth and Planetary Science Letters 230: 125–142.

Castro, M. C., M. R. Ciancio, E. C. Vieytes & A. A. Carlini. 2014. Enamel in *Dasypus* (Xenarthra, Cingulata): phylogenetic relevance. P. 676 in IV International Palaeontological Congress, Mendoza.

Ciancio, M. R., E. C. Vieytes & A. A. Carlini. 2014. When xenarthrans had enamel: insights on the evolution of their hypsodonty and paleontological support for independent evolution in armadillos. Naturwissenschaften 101: 715–725.

Cione, A. L., E. P. Tonni & L. H. Soibelzon. 2003. The broken zig-zag: Late Cenozoic large mammal and tortoise extinction in South America. Revista del Museo Argentino de Ciencias Naturales 5: 1–19.

Cione, A. L., E. P. Tonni & L. H. Soibelzon. 2009. Did humans cause the Late Pleistocene-Early Holocene mammalian extinctions in South America in a context of shrinking open areas? Pp. 125-144 in: American megafaunal extinctions at the end of the Pleistocene (G. Haynes, ed.). Vertebrate Paleobiology and Paleoanthropology Series. Springer, New York.

De Iuliis G., F. Pujos, N. Toledo, M. S. Bargo & S. F. Vizcaíno. 2014. *Eucholoeops* Ameghino, 1887 (Xenarthra, Tardigrada, Megalonychidae) from the Santa Cruz Formation, Argentine Patagonia: implications for the systematics of Santacrucian sloths. Geodiversitas 36: 209–255.

Delsuc, F. & E. J. P. Douzery. 2008. Recent advances and future prospects in xenarthran molecular phylogenetics. Pp. 11–23 in: The biology of the Xenarthra (S. F. Vizcaíno & W. J. Loughry, eds.). University Press of Florida, Gainesville.

Delsuc F., S. F. Vizcaíno & E. J. P. Douzery. 2004. Influence of Tertiary paleoenvironmental changes on the diversification of South American mammals: a relaxed molecular clock study within xenarthrans. BMC Evolutionary Biology 4: 11.

Fariña, R. A. 1996. Trophic relationships among Lujanian mammals. Evolutionary Theory 11: 125–134.

Fariña, R. A. & S. F. Vizcaíno. 1999. A century after Ameghino: the palaeoecology of the large Quaternary land mammal fauna of South America revisited. Pp. 255–278 in: Quaternary vertebrate paleontology in South America (E. P. Tonni & L. A. Cione, eds.). Quaternary of South America and Antarctic Peninsula, Special Volume 12. A.A. Balkema, Rotterdam.

Fariña, R. A., S. F. Vizcaíno & G. De Iuliis. 2013. Megafauna. Giant beasts of Pleistocene South America. Indiana University Press, Bloomington. 448 pp.

Fernicola, J. C. & K. O. Porpino. 2012. Exoskeleton and systematics: a historical problem in the classification of glyptodonts. Journal of Mammalian Evolution 19: 171–183.

Fernicola J. C., S. F. Vizcaíno & R. A. Fariña. 2008. The evolution of armored xenarthrans and a phylogeny of the glyptodonts. Pp. 79–85 in: The biology of the Xenarthra (S. F. Vizcaíno & W. J. Loughry, eds.). University Press of Florida, Gainesville.

Galliari, C. A. & F. J. Goin. 1993. Conservación de la biodiversidad en la Argentina: el caso de los mamíferos. Pp. 367–399 in: Elementos de política ambiental (F. J. Goin & R. G. Goñi, eds.). H. Cámara de Diputados, Provincia de Buenos Aires, La Plata.

Gaudin, T. J. & R. W. Wible. 2006. The phylogeny of living and extinct armadillos (Mammalia, Xenarthra, Cingulata): a craniodental analysis. Pp. 153–198 in: Amniote paleobiology: perspectives on the evolution of mammals, birds and reptiles (M. T. Carrano, T. J. Gaudin, R. W. Blob & J. R. Wible, eds.). University of Chicago Press, Chicago.

Gutierrez, M. A., G. A. Martinez, M. S. Bargo & S. F. Vizcaíno. 2010. Supervivencia diferencial de mamíferos de gran tamaño en la región pampeana en el Holoceno temprano y su relación con aspectos paleobiológicos. Pp. 231–241 in: Zooarqueología a principios del siglo XXI: aportes teóricos, metodológicos y casos de estudio (M. A. Gutiérrez, M. De Nigris, P. M. Fernández, M. Giardina, A. F. Gil, A. Izeta, G. Neme & H. D. Yacobaccio, eds.). Ediciones El Espinillo, Buenos Aires.

Hinojosa, L. F. 2005. Cambios climáticos y vegetacionales inferidos a partir de paleofloras cenozoicas del sur de Sudamérica. Revista Geológica de Chile 32: 95–11.

Hinojosa, L. F. & C. Villagrán. 1997. Historia de los bosques del sur de Sudamérica, I: antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. Revista Chilena de Historia Natural 70: 225–239.

Hodell, D. A. & J. P. Kennett. 1985. Miocene paleoceanography of the South Atlantic Ocean. Pp. 317–337 in: The Miocene ocean: paleoceanography and biogeography (J. P. Kennett, ed.). Geological Society of America Memoir 163. Ann Arbor, Michigan.

Johnson, C. N. 2002. Determinants of loss of mammal species during the Late Quaternary 'Megafauna' extinctions: life history and ecology, but not body size. Proceedings of the Royal Society of London, B, Biological Sciences 269: 2221–2227.

Johnson, C. N. 2009. Ecological consequences of Late Quaternary extinctions of megafauna. Proceedings of the Royal Society of London, B, Biological Sciences 276: 2509–2519.

Kaufman, D. M. 1995. Diversity of New World mammals – universality of the latitudinal gradients of species and bauplans. Journal of Mammalogy 76: 322–334.

Kay, R. F., S. F. Vizcaíno & M. S. Bargo. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. Pp. 331–365 in: Early Miocene paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz formation (S. F. Vizcaíno, R. F. Kay & M. S. Bargo, eds.). Cambridge University Press, Cambridge.

McDonald, G. H., S. F. Vizcaíno & M. S. Bargo. 2008. Skeletal anatomy and the fossil history of the Vermilingua. Pp 64–78 in: The biology of the Xenarthra (S. F. Vizcaíno & W. J. Loughry, eds.). University Press of Florida, Gainesville.

McKenna, M. C. & S. K. Bell. 1997. Classification of mammals above the species level. Columbia University Press, New York. 631 pp.

Meredith, R. W., *et al*. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334: 521–524.

O'Leary, M. A., *et al*. 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. Science 339: 662–667.

Plotnick, R. & T. Baumiller. 2000. Invention by evolution: functional analysis in paleobiology. Pp. 305–323 in: Deep time: paleobiology's perspective (D. H. Erwin & S. L. Wing, eds.). Supplement to vol. 26 of Paleobiology. The Paleontological Society, Boulder.

Porpino, K. O., J. C. Fernicola & L. P. Bergqvist. 2010. Revisiting the intertropical Brazilian species *Hoplophorus euphractus* (Cingulata, Glyptodontoidea) and the phylogenetic affinities of *Hoplophorus*. Journal of Vertebrate Paleontology 30: 911–927.

Radinsky, L. B. 1987. The evolution of vertebrate design. The University of Chicago Press, Chicago and London. 197 pp.

Ramos, V. A. & M. C. Ghiglione. 2008. Tectonic evolution of the patagonian Andes in the Late Cenozoic of Patagonia and Tierra del Fuego. Developments in Quaternary Sciences 11: 57–72.

Simpson, G. G. 1980. Splendid isolation: the curious history of South American mammals. Yale University Press, New Haven. 266 pp.

Stehli, F. G. & S. D. Webb. 1985. The great American biotic interchange. Plenum Press, New York and London. 532 pp.

Vicq d'Azyr, M. F. 1792. Système anatomique des Quadrupèdes. Encyclopédie méthodique. 2. Paris. 632 pp.

Villagrán, C. & L. F. Hinojosa. 1997. Historia de los bosques del sur de Sudamérica, II: análisis fitogeográfico. Revista Chilena de Historia Natural 70: 241–67.

Vizcaíno, S. F. 2009. The teeth of the 'toothless': novelties and key innovations in the evolution of xenarthrans (Mammalia, Xenarthra). Paleobiology 35: 343–366.

Vizcaíno, S. F. & G. De Iuliis. 2003. Evidence for advanced carnivory in fossil armadillos. Paleobiology 29: 123–138.

Vizcaíno, S. F., M. S. Bargo & G. H. Cassini. 2006. Dental occlusal surface area in relation to body mass, food habits and other biological features in fossil xenarthrans. Ameghiniana 43: 11–26.

Vizcaíno, S. F., M. S. Bargo & R. A. Fariña. 2008. Form, function and paleobiology in xenarthrans. Pp. 86–99 in: The biology of the Xenarthra (S. F. Vizcaíno & W. J. Loughry, eds.). University Press of Florida, Gainesville.

Vizcaíno S. F., G. H. Cassini, N. Toledo & M. S. Bargo. 2012a. On the evolution of large size in mammalian herbivores of Cenozoic faunas of southern South America. Pp. 76–101 in: Bones, clones and biomes: an 80-million year history of Recent Neotropical mammals (B. Patterson & L. Costa, eds.). University of Chicago Press, Chicago.

Vizcaíno, S. F., J. C. Fernicola & M. S. Bargo. 2012b. Paleobiology of Santacrucian glyptodonts and armadillos (Xenarthra, Cingulata). Pp. 194–215 in: Early Miocene paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation (S. F. Vizcaíno, R. F. Kay & M. S. Bargo, eds.). Cambridge University Press, Cambridge.

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