5 On the Evolution of Large Size in Mammalian Herbivores of Cenozoic Faunas of Southern South America

Sergio F. Vizcaíno, Guillermo H. Cassini, Néstor Toledo, and M. Susana Bargo

Abstract

One of the major features of the continental Cenozoic faunas of South America is the presence of native lineages of herbivorous mammals, and among them the largest representatives of each fauna. They include a diversity of taxa within the Xenarthra, Pyrotheria, Astrapotheria, Notoungulata, Litopterna, Cetartiodactyla, Perissodactyla, Proboscidea and Rodentia. We analyze the evolution of the large body size of these mammals in relation to their taxonomic richness. As the South American mammalian fossil record is largely restricted to southern parts of the continent, with comparatively few Tertiary land mammal-bearing localities outside of Argentina, we limit our samples to faunas from that country. Faunal lists from 6 different ages were selected. Genera were classified in 4 body mass categories: (I) less than 100 kg, (II) 100 to 500 kg, (III) 500 to 1000 kg, and (IV) more than 1000 kg. The Pleistocene represents the spectacular climax in terms of body size. In general, but particularly for those faunas in which xenarthrans are dominant, the number of mega-mammals only distantly related to living counterparts raises problems in interpreting their paleobiology. Particularly for the Pleistocene, communities dominated by mega-mammals of very low metabolism (xenarthrans) have no counterpart in living faunas. Large size explains most of their vulnerability to extinction at the end of the Pleistocene in South America. Although the impact of the mega-mammal extinction on the post-Pleistocene evolution of plant communities has not been studied for South America, it is clear that it produced an enormous ecological gap in the herbivorous guild.

5.1 Introduction

The faunas of South America's Cenozoic (fig. 5.1) were dominated until the late Pliocene by endemic lineages of placental mammals (Marshall and Cifelli 1989; Simpson 1950, 1980; Webb 1991) in addition to the New World marsupials (Ameridelphia). Even the two placental groups (rodents and primates) that arrived from other continents in the late Eocene-Oligocene evolved as endemic

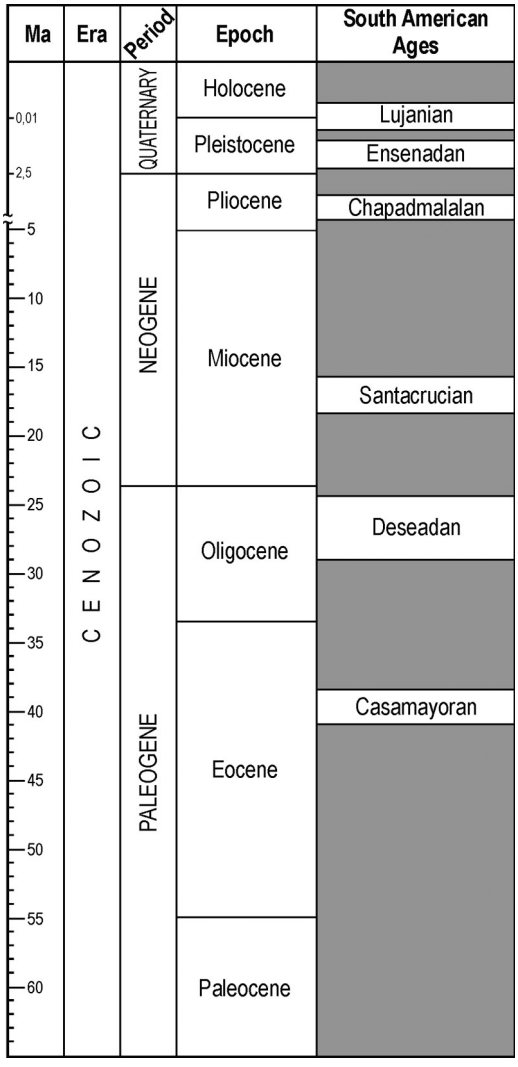

Figure 5.1 Chronologic chart of the Cenozoic.

lineages (caviomorphs and platyrrhines, respectively) in South America. Large marsupials occupied the mammalian predator guild in most faunas before placental carnivores arrived from the North during the Neogene, while the noncarnivorous forms were usually small sized. Most specialists recognize at least six major groups of predominately herbivorous placentals that have been mostly or entirely restricted to South America: the xenarthrans and five main groups of ungulates.

Xenarthrans include the Cingulata and the Pilosa. The Cingulata are exemplified by armadillos and glyptodonts, noted for the bony armor covering the head, body, and tail. The Pilosa are composed of two groups: the Vermilingua and the Folivora. The Vermilingua, or anteaters, are characterized by an elongate, tubular skull, the absence of teeth, and a prehensile tongue used in acquiring prey. Among xenarthrans, only the armadillos have been recognized as exploiting a dietary spectrum from omnivory to carnivory (see Vizcaíno 2009; Vizcaíno, Fariña, Bargo, et al. 2004, Vizcaíno, Bargo, and Fariña 2008 and references therein). The Folivora, or sloths, include many fossil forms and are also known as Tardigrada or Phyllophaga (Delsuc and Douzery 2008; Fariña and Vizcaíno 2003; Gardner 2005). Modern sloths are almost exclusively arboreal herbivores; however, many extinct forms were much larger, more terrestrial, and are generally considered to have been exclusively herbivorous, although some degree of carnivory has been proposed for certain species (see Fariña and Blanco 1996, and discussions in Bargo 2001; Bargo and Vizcaíno 2008; Prevosti and Vizcaíno 2006).

Over the past several decades, morphology-based studies of xenarthrans and their phylogenetic position have tended to place them in a remote position within Placentalia (Gaudin and McDonald 2008), for example, as the sister taxon to other placentals (Epitheria), although perhaps allied with pangolins (Order Pholidota) and the extinct Palaeanodonta (Novacek 1992; Novacek and Wyss 1986). Placement of the Xenarthra as the sister group to the other placentals was first advocated by early cladistic studies of morphology (McKenna 1975). The Xenarthra/Epitheria dichotomy has been criticized by other studies (Gaudin and McDonald 2008; Gaudin et al. 1996; Rose and Emry 1993), and both morphological and molecular work have failed to support the xenarthran/pholidotan clade (Delsuc et al. 2002; Rose and Emry 1993; Rose et al. 2005) or have supported a close relationship between Xenarthra and Afrotheria (Prasad et al. 2008; Wible et al. 2007).

South American ungulates have always been compared to living herbivorous analogues (see Croft 1999 for a summary). South America's native ungulates include five groups: the astrapotheres, pyrotheres, notoungulates, litopterns, and xenungulates (Marshall and de Muizon 1988; Simpson 1980). The phylogenetic relationships of these groups are unclear (Cifelli 1985, 1993). They were all once united in a single taxon, Meridiungulata, on the idea that all endemic South American ungulates were monophyletic (McKenna 1975). However, the term "ungulate" here does not imply that the ungulate groups endemic to South

America and modern Ungulata (Perissodactyla and Cetartiodactyla) share a most recent common ancestor or even form a single clade themselves.

Astrapotheres (including trigonostylopids) were rhinoceros-like mammals (Cifelli 1985) found in deposits Paleocene to Miocene in age. They attained maximum diversity during the early Miocene Colhuehuapian and Santacrucian ages (Johnson and Madden 1997; Marshall and Cifelli 1989).

Pyrotheres were elephant-like, with tusks and bilophodont cheek teeth, and were never as diverse nor did they cover as great a time span as the astrapotheres. They are known only from the middle Eocene (Casamayoran) through the late Oligocene (Deseadan).

Notoungulates are by far the most diverse and abundant lineage of South American ungulates (nearly 140 species in 13 families; Croft 1999). This group includes animals similar to rhinoceroses, hippopotamuses, rabbits, and rodents. Other notoungulates do not closely resemble any living mammal. Many had high-crowned cheek teeth.

Litopterns were the second most successful group of South American ungulates in terms of diversity and longevity, spanning from the late Paleocene (Itaboraían) to the late Pleistocene (Marshall and Cifelli 1989). They include forms similar to antelopes, horses, and camels, all with relatively low-crowned cheek teeth.

Xenungulates are primitive, poorly known, tapir-like mammals, restricted to Paleocene deposits of Brazil and Argentina (Gelfo, López, and Bond 2008).

Based on both the fossil record and molecular dates, primates and rodents appeared in South America by the late Eocene and early Oligocene. They probably arrived as a result of trans-Atlantic migrations (see Pascual 2006; Poux et al. 2006). Each of these lineages of herbivorous placentals had a different fate in South America. Fossil South American primates are rare, and the present-day taxa are the result of a relatively recent (early Miocene or later) diversification that resulted in arboreal forms no larger than 10 kg. By contrast, caviomorph rodents are among the most abundant taxa in every post-Eocene fauna. Caviomorphs radiated soon after their arrival into a series of lineages that persist to the present, and some families evolved forms that weighed in excess of 100 kg.

"About 2.5 Ma tectonic activities along the Pacific margin caused the American continents to be sutured, and thus began one of the great biogeographic experiments, known to paleobiologists as the Great American Biotic Interchanges" (Webb 1991, 266). The first North American forms to arrive

in South America included cricetid rodents, procyonid carnivorans, mustelid carnivorans, and tayassuid artiodactyls. The early Pleistocene marks the first appearance in South America of five major herbivore lineages: gomphotheriids among proboscideans, camelids and cervids among artiodactyls, and equids and tapirids among perissodactyls, in addition to several carnivoran lineages (felids, canids, and ursids).

One feature of these Cenozoic faunas is the tendency to increase maximum size in many lineages. Some remarkable gigantic forms are the mammalian Astrapotheria and Pyrotheria (Oligocene) and the avian phororhacoids or "terror birds" (Miocene). But the climax of body size evolution was reached during the Quaternary (the last 2 Ma). Among the more than 120 genera of mammals known, the estimated adult masses of about 40 genera exceeded 100 kg, of which about 20 were megaherbivores. Although a 2004 symposium on vertebrate giants revealed that no other fossil mammalian fauna is known to have contained such a diversity of megaherbivores (Bargo 2004), so far no analysis has considered the evolution of large body size in relation to taxonomic richness. The goal of this study is to provide a preliminary analysis of the evolution of large size in mammalian herbivores of the Cenozoic of South America. For this purpose, we followed a definition of "large mammal" that is commonly used in archaeology and paleontology (see Cione, Tonni, and Soibelzon 2003, 2009; Johnson 2002; Martin and Steadman 1999), considering only taxa $>$44 kg (100 pounds).

The South American mammalian fossil record is largely restricted to southern parts of the continent, with comparatively few Tertiary land mammal-bearing localities outside of Argentina (Ortiz-Jaureguizar and Cladera 2006, and references therein). Therefore, we limit our sample to faunas from Argentina. In this way, we are representing almost the same area that Ortiz- Jaureguizar and Cladera defined as Southern South America (i.e., the area south of 15° S) to reconstruct historic and ecologic relationships of the Patagonian biota with that of the rest of South America. Our goal is to identify new working hypotheses to test in a future long-term project on the paleobiology of the South American Cenozoic faunas. Our greatest interest is in the giants of the Pleistocene, which are dominated by ancient South American descendants: ground sloths and glyptodonts (Xenarthra), macrauchenians (Litopterna), toxodonts (Notoungulata), and mastodonts (Proboscidea). Some of these forms are characterized by peculiar adaptations of the masticatory and locomotory systems, which lack clear ecological equivalents among living mammals. Understanding the basis for their very large size is our research goal.

5.2 Evolution of the Paleofloras and Climates During the Cenozoic

The succession of environments in which the large herbivore mammals (and all the fauna) occurred can be envisioned through a summary of four major paleofloras described for the southern part of South America (Frenguelli 1953; Hinojosa and Villagrán 1997; Menéndez 1971; Romero 1978, 1986; Troncoso and Romero 1998). The spatial and temporal successions of these paleofloras appear to have been closely related to tectonic and climatic events that occurred during the Cenozoic (Hinojosa and Villagrán 1997). For extensive reviews on this topic, see recent articles by Hinojosa (2005) and Barreda et al. (2007).

First, the Neotropical Paleoflora developed mainly during the Paleocene when South America, Antarctica, and Australia maintained geographic connections, and warm climatic conditions extended to at least 50°S. The mean annual temperatures and rainfall ranged between 2 and 25°C, and 1500 and 2000 mm respectively (Hinojosa 2005). This flora was replaced during the Eocene and early Oligocene by the Mixed Paleoflora, coincident with a decrease of temperature levels and annual mean precipitation. According to Hinojosa (2005), the mean annual temperature was 17–20°C, and the mean annual precipitation was ~570 mm. The Mixed Paleoflora was characterized by taxa distributed today in the tropics and the Austral-Antarctic territories, as well as forms now endemic to tropical and subtropical regions of the continent.

From the late Eocene/early Oligocene up to early Miocene, global temperatures fell as glaciations developed in eastern Antarctica after the separation of Australia from Antarctica-South America. Accordingly the Mixed Paleoflora was mostly replaced by an Antarctic Paleoflora, characterized by the dominance of taxa from temperate-cold environments. The notable increase of the annual thermal amplitude would have favored the development of taxa adapted to colder conditions (mean annual ~15°C) and extreme temperatures. Annual rainfall averages increased to 870 mm by the late Oligocene and to 1120 mm by the Early Miocene (Hinojosa 2005).

Finally, the Subtropical Flora appeared as a consequence of the global warming that characterized the middle Miocene. The mean annual temperatures ranged 21–26°C (Hinojosa 2005). According to Zachos et al. (2001), the Climatic Optimum occurred around 15–17 Ma. After the late early Miocene Climatic Optimum, temperature and rainfall decreased (430 mm), related to an increase of the thermal difference between extreme temperatures, producing conditions favoring the development of xeric subtropical floras.

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 the 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 and Villagrán 1997; Villagrán and Hinojosa 1997).

The periodic climatic alternation of glacial and interglacial epochs during the middle late Pleistocene dramatically modified the distribution, composition, and biomass of plant and animal communities in South America (Cione, Tonni, and Soibelzon 2003).

5.3 Methods

Faunal lists from six different ages were selected, based on the quality of the information available: the middle Eocene Casamayoran from Patagonia and northern Argentina (Pascual and Ortiz-Jaureguizar 2007), the late Oligocene Deseadan, from Cabeza Blanca (Chubut) and La Flecha (Santa Cruz) in Patagonia (Reguero 1999), the early Miocene Santacrucian at the Atlantic coast (Santa Cruz) in Patagonia (Tauber 1997; Vizcaíno and colleagues, unpublished data), the late Pliocene Chapadmalalan at the Atlantic coast (Buenos Aires Province), Pampean region (Vizcaíno, Fariña, Zárate, et al. 2004), the early Pleistocene Ensenadan, and the late Pleistocene-early Holocene Lujanian (Buenos Aires Province), Pampean region (Cione and Tonni 2005; fig. 5.1).

A database of body mass estimates was built using different methods: from previously published estimates, using regression equations generated from modern relatives, from geometric similarity with a phylogenetically close relative (of known mass for living ones or with an appropriate estimation for fossil ones), or using gross anatomical similarity with living analogues (see table 5.1). Orders and genera were chosen as the working taxonomic levels. We chose to use genera rather than species because they are discrete taxonomic units accepted by most paleontologists, and they are less affected by the problems of evaluating intraspecific variation in fossils. Species of the same genus were considered only in those cases in which they attained body masses that fell into different categories, as described later.

Table 5.1 List of taxa represented for each age with their body mass estimates.

Order	Family	Genus	BM (Kg)	Source
CASAMAYORAN				
Astrapotheria	Astrapotheriidae	*Albertogaudrya*	60.28	Croft 2000
		Scaglia	200	CLA-*Tapirus terrestris*
	Trigonostylopidae	*Tetragonostylops*	200	CLA-*Tapirus terrestris*
		Trigonostylops	200	CLA-*Tapirus terrestris*
Litopterna	Sparnotheriodontidae	*Sparnotheriodon*	400	Vizcaíno et al. 1998
		Victorlemoinea	400	Vizcaíno et al. 1998
Notoungulata	Henricosborniidae	*Othnielmarshia*	50	CLA-*Ovis aries*
		Peripantostylops	50	CLA-*Ovis aries*
	Isotemnidae	*Anisotemnus*	48.68	Croft 2000
		Pampatemnus	50	CLA-*Ovis aries*
		Thomashuxleya	113.04	Croft 2000
	Notohippidae	*Pampahippus*	50	CLA-*Ovis aries*
		Plexotemnus	50	CLA-*Ovis aries*
	Notostylopidae	*Boreastylops*	50	CLA-*Ovis aries*
		Edvardotrouessartia	50	CLA-*Ovis aries*
		Homalostylops	50	CLA-*Ovis aries*
		Notostylops	50	CLA-*Ovis aries*
	Oldfieldthomasiidae	*Oldfieldthomasia*	50	CLA-*Ovis aries*
		Paginula	50	CLA-*Ovis aries*
Pyrotheria	Pyrotheriidae	*Carolozittelia*	200	CLA-*Tapirus terrestris*
DESEADAN				
Astrapotheria	Astrapotheriidae	*Parastrapotherium*	1900	GS-*Astrapotherium* (Kramarz and Bond 2008)
Notoungulata	Homalodotheriidae	*Asmodeus*	330	GS- *Homalodotherium*
	Leontiniidae	*Ancylocoelus*	288	GS-*Leontinia*
		Leontinia	288	RE
	Mesotheriidae	*Trachytherus*	45	Croft and Weinstein 2008
	Notohippidae	*Argyrohippus*	60	CLA-*Ovis aries*
		Eurygenium	60	CLA-*Ovis aries*
		Morphippus	60	CLA-*Ovis aries*
		Rhynchippus	120	CLA-*Ovis aries*
	Toxodontidae	*Proadinotherium*	90	GS-*Adinotherium*
Pyrotheria	Pyrotheriidae	*Pyrotherium*	3500	Shockey and Anaya 2004
Cingulata	Paleopelthidae	*Paleopeltis*	600	GS-*Neosclerocalyptus*
	Peltephilidae	*Peltephilus*	50	GS-*Priodontes*
Folivora	Orophodontidae	*Octodontotherium*	700	GS-*Glossotherium*

(continues)

Table 5.1 (*continued*)

Order	Family	Genus	BM (Kg)	Source
SANTACRUCIAN				
Astrapotheria	Astrapotheriidae	*Astrapotherium*	1021.63	RE
Litopterna	Macraucheniidae	*Theosodon*	95.61	RE
	Proterotheriidae	*Diadiaphorus*	70.25	RE
Notoungulata	Homalodotheriidae	*Homalodotherium*	340	RE
	Toxodontidae	*Adinotherium*	121.26	RE
	Toxodontidae	*Nesodon*	554.61	RE
Cingulata	Glyptodontidae	*Cochlops*	80	GS - *Propalaehoplophorus*
		Eucinepeltus	115	Croft 2001
		Propalaehoplophorus	73.40	Vizcaíno, Bargo, and Cassini 2006
Folivora	Megalonychidae	*Eucholaeops*	80	Bargo, Vizcaíno, and Kay 2009
	Megatherioidea	*Analcimorphus*	160	GS-*Hapalops*
		Hapalops	70	Bargo, Vizcaíno, and Kay 2009
		Planops	300	GS-*Hapalops*
		Prepotherium	525	GS-*Scelidotherium*
	Mylodontidae	*Nematherium*	423.98	GS-*Scelidotherium leptocephalum*
CHAPADMALALAN				
Cetartiodactyla	Tayassuidae	*Argyrohyus*	50	CLA-*Catagonus wagneri*
Litopterna	Macraucheniidae	*Promacrauchenia*	400	GS-*Macrauchenia patachonica*
Notoungulata	Toxodontidae	*Toxodon*	1642	Fariña, Vizcaíno, and Bargo 1998
		Xotodon	300	GS-*Toxodon platensis*
Rodentia	Dinomyidae	*Telicomys*	600	GS-*Hydrochoerus*
	Hydrochoeridae	*Chapalmatherium*	200	GS-*Hydrochaerus*
Cingulata	Glyptodontidae	*Paraglyptodon*	800	CF-*Glyptodon reticulatus*
		Plesiomegatherium	3000	GS-*Pyramiodontherium scillatoyanei* (De Iuliis et al. 2004)
		Plohophoroides	263	CF-*Plohophorus*
		Plohophorus	263	Vizcaíno, Bargo, and Cassini 2006
		Trachycalyptus	600	CF-*Neosclerocalyptus*
		Urotherium	600	CF-*Neosclerocalyptus*

Table 5.1 (*continued*)

Order	Family	Genus	BM (Kg)	Source
	Pampatheriidae	*Pampatherium*	200	GS-*Holmesina* (Vizcaíno, Bargo, and Cassini 2006).
Folivora	Mylodontidae	*Glossotheridium*	580	GS-*Glossotherium robustum*
		Proscelidodon	430	GS-*Scelidotherium leptocephalum*
		Scelidotheridium	430	GS-*Scelidotherium leptocephalum*
ENSENADAN				
Cetartiodactyla	Camelidae	*Hemiauchenia*	400	GS-*Lama guanicoe*
		Lama	120	CLA- *Lama guanicoe*
	Cervidae	*Antifer*	120	CLA- *Blastoceros dichotomus*
		Epieuricerus	120	CLA-*Blastoceros dichotomus*
	Tayassuidae	*Catagonus*	50	CLA-*Catagonus wagneri*
		Platygonus	50	CLA-*Catagonus wagneri*
Litopterna	Macrauchenidae	*Macraucheniopsis*	1200	GS-*Macrauchenia patachonica*
Notoungulata	Mesotheriidae	*Mesotherium*	60	GS-*Pseudotypotherium*
	Toxodontidae	*Toxodon*	1642	Fariña, Vizcaíno, and Bargo 1998
Perissodactyla	Equidae	*Equus*	379	Alberdi and Prado 2004
		Hippidion	460	Alberdi and Prado 2004
Proboscidea	Gomphotheriidae	*Stegomastodon*	7580	Fariña, Vizcaíno, and Bargo 1998
Rodentia	Caviidae	*Neochoerus*	110	GS-*Hydrochoerus hydrochaeris*
Cingulata	Dasypodidae	*Propraopus*	50	Fariña and Vizcaíno 1997
	Glyptodontidae	*Daedicuroides*	1100	CF- *Doedicurus clavicaudatus*
		Doedicurus	1468	Fariña, Vizcaíno, and Bargo 1998
		Glyptodon clavipes	2000	Fariña 1995

(continues)

Table 5.1 (*continued*)

Order	Family	Genus	BM (Kg)	Source
		Glyptodon reticulatus	862	Fariña, Vizcaíno, and Bargo 1998
		Lomaphorus	600	CF-*Neosclerocalyptus ornatus*
		Neosclerocalyptus	598	Vizcaíno, Bargo, and Cassini 2006
		Neothoracophorus	600	CF-*Neosclerocalyptus ornatus*
		Neuryurus	311	Vizcaíno, Bargo, and Cassini 2006
		Panochthus	1061	Fariña, Vizcaíno, and Bargo 1998
		Plaxhaplous	1100	CF- *Doedicurus clavicaudatus*
	Pampatheriidae	*Pampatherium*	200	GS-*Holmesina* (Vizcaíno, Bargo, and Cassini 2006)
Folivora	Megatheriidae	*Megatherium*	3950	Fariña, Vizcaíno, and Bargo 1998
	Mylodontidae	*Glossotherium*	1344	Fariña, Vizcaíno, and Bargo 1998; Christiansen and Fariña 2003
		Mylodon	1986	Christiansen and Fariña 2003
		Scelidotherium	1057	Fariña, Vizcaíno, and Bargo 1998
LUJANIAN				
Cetartiodactyla	Camelidae	*Eulamaops*	150	Prevosti and Vizcaíno 2006
		Hemiauchenia	400	GS-*Lama guanicoe*
		Lama	120	CLA-*Lama guanicoe*
	Tayassuidae	*Catagonus*	50	CLA-*Catagonus wagneri*
		Tayassus	50	CLA-*Tayassus tajacu*
Litopterna	Macraucheniidae	*Macrauchenia*	988	Fariña, Vizcaíno, and Bargo 1998
Notoungulata	Toxodontidae	*Toxodon*	1642	Fariña, Vizcaíno, and Bargo 1998
Perissodactyla	Equidae	*Equus (Amerhippus)*	379	Alberdi and Prado 2004

Table 5.1 (*continued*)

Order	Family	Genus	BM (Kg)	Source
		Hippidion	460	Alberdi and Prado 2004
Proboscidea	Gomphotheriidae	*Stegomastodon*	7580	Fariña, Vizcaíno, and Bargo 1998
Rodentia	Caviidae	*Neochoerus*	110	GS-*Hydrochoerus hydrochaeris*
Cingulata	Dasypodidae	*Eutatus*	50	Vizcaíno, Milne, and Bargo 2003
		Propraopus	50	Fariña and Vizcaíno 1997
	Glyptodontidae	*Doedicurus*	1468	Fariña, Vizcaíno, and Bargo 1998
		Glyptodon clavipes	2000	Fariña, 1995
		Glyptodon reticulatus	862	Fariña, Vizcaíno, and Bargo 1998
		Lomaphorus	600	CF-*Neosclerocalyptus ornatus*
		Neosclerocalyptus	598	Vizcaíno, Bargo, and Cassini 2006
		Neothoracophorus	600	CF-*Neosclerocalyptus ornatus*
		Panochthus	1061	Fariña, Vizcaíno, and Bargo 1998
		Plaxhaplous	1100	CF- *Doedicurus clavicaudatus*
	Pampatheriidae	*Pampatherium*	200	GS-*Holmesina* (Vizcaíno, Bargo, and Cassini 2006)
Folivora	Megatheriidae	*Megatherium*	3950	Fariña, Vizcaíno, and Bargo 1998
	Mylodontidae	*Glossotherium*	1344	Fariña, Vizcaíno, and Bargo 1998; Christiansen and Fariña 2003
		Lestodon	3397	Fariña, Vizcaíno, and Bargo 1998
		Mylodon	1986	Christiansen and Fariña 2003
		Scelidotherium	1057	Fariña, Vizcaíno, and Bargo 1998

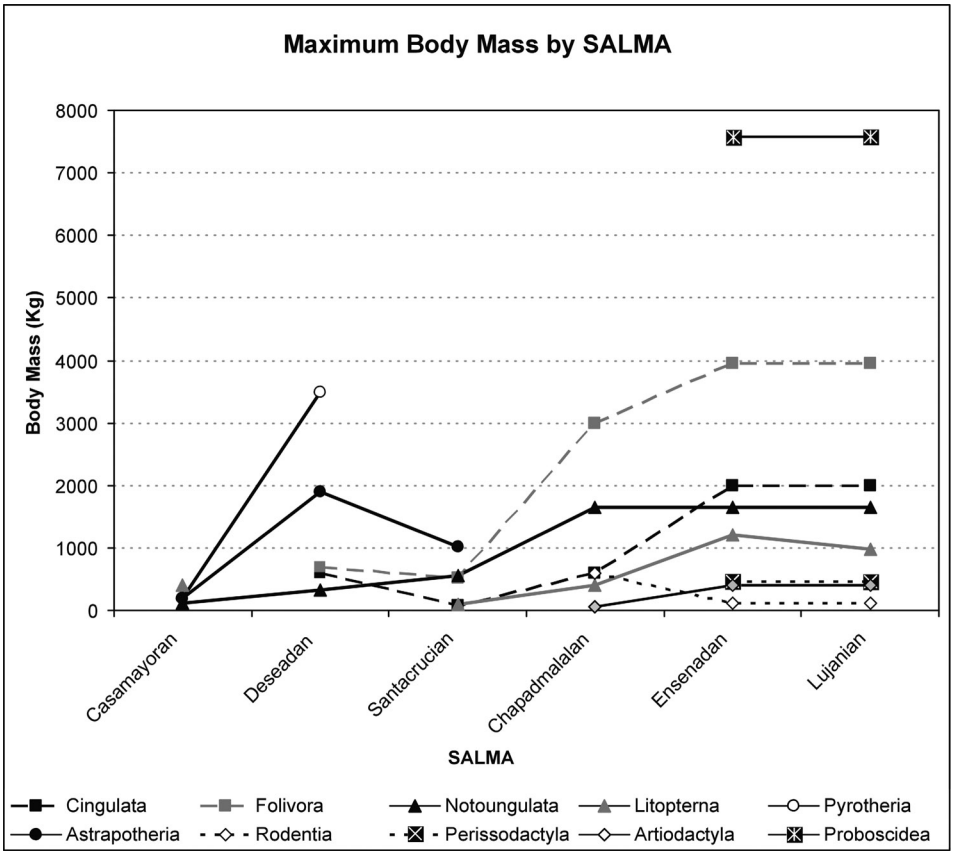

Figure 5.2 Maximum body mass of herbivorous mammals throughout the Cenozoic.

For each genus, the body mass estimate of the largest species was selected. As mentioned earlier, we considered large mammals as only those taxa >44 kg (100 pounds).

Two analyses were performed. First, in each age the genus with the maximum body mass (MBM) was selected to represent each order. The results were plotted on an XY graph, where the X-axis represents time (in geologic ages) and the Y-axis represents the body mass estimate in kg (fig. 5.2). For the second analysis, genera were classified in four body mass categories: (I) <100 kg; (II) 100–500 kg; (III) 500–1000 kg; and (IV) >1000 kg. The number of genera per order in each category and age was plotted in histograms (fig. 5.3).

5.4 Results

Maximum body mass of herbivorous mammals throughout the Cenozoic are depicted in table 5.1 and fig. 5.2. In general, maximum body mass (MBM) for most of the native orders of Cenozoic South American herbivorous mammals (notoungulates, litopterns, cingulates, and sloths) increases over time, especially after the Chapadmalalan (Pliocene). Pyrotheres and astrapotheres reach their largest sizes in the Deseadan (Oligocene). While pyrotheres are not recorded in the Santacrucian (Miocene) and following ages, astrapotheres, cingulates, and sloths attain smaller MBM during that age than in the previous Deseadan, and astrapotheres disappear after the Miocene. Among rodents, cow-sized forms are recorded during the Chapadmalalan (although maximal sizes were attained earlier; see Discussion section) and MBM decreases by the Ensenadan and Lujanian (Pleistocene-early Holocene).

Taxonomic representation of body mass categories during the Cenozoic is shown in table 5.2, which summarizes the number of taxa (and percentages) of each body mass category (I to IV) represented in each age. Figure 5.3 shows the representation of groups in each category through the different ages.

During the Eocene Casamayoran, category I is represented by mostly notoungulates, with only one astrapothere. Category II includes mainly astrapotheres and litopterns, with minor representation of pyrotheres and notoungulates. There are no representatives of categories III and IV.

During the Oligocene Deseadan, category I includes mostly notoungulates and one cingulate. Category II is represented only by notoungulates. Category III is equally represented by cingulates and sloths. Category IV is equally represented by astrapotheres and pyrotheres.

During the Miocene Santacrucian, category I is represented by similar proportions of litopterns, cingulates, and sloths. Category II includes mainly sloths and a minor proportion of notoungulates, while category III is represented by equal proportion of these orders. Category IV is made up of one astrapothere, with a mass estimation slightly above 1000 kg.

During the Pliocene Chapadmalalan, category I is represented by a single artiodactyl, although one mesotheriid notoungulate has mass estimates close to the lower limit. Category II includes 3 cingulates, 2 sloths, 1 notoungulate, 1 litoptern, and 1 rodent. Category III is represented by 3 cingulates, 1 tradigrade, and 1 rodent, while category IV is represented by only 1 sloth and 1 notoungulate.

During the early Pleistocene Ensenadan, category I is represented mainly by 2 artiodactyls, 1 cingulate, and 1 notoungulate. In Category II, artiodactyls are dominant while perissodactyls, cingulates, and rodents are represented in lower proportions. Category III is entirely composed of cingulates. Cingulates and sloths largely dominate category IV, which also includes 1 notoungulate, 1 litoptern, and 1 proboscidean.

During the late Pleistocene-early Holocene Lujanian, artiodactyls dominate

Table 5.2 Number (and percentages) of taxa in body mass categories I to IV represented in each age.

BMC	TAXA	CAS	DES	SAN	CHA	ENS	LU
Category I (44 **to** 100 **kg**)	Cingulata		**1** (17%)	**2** (34%)		**1** (25%)	**2** (33%)
	Folivora			**2** (34%)			
	Notoungulata	**12** (92%)	**5** (83%)			**1** (25%)	
	Litopterna			**2** (34%)			
	Astrapotheria	**1** (8%)					
	Artiodactyla				**1** (100%)	**2** (50%)	**4** (67%)
Cat. II (100 **to** 500 **kg**)	Cingulata				**3** (37.5%)	**2** (22%)	**1** (17%)
	Folivora			**4** (67%)	**2** (25%)		
	Notoungulata	**1** (14%)	**4** (100%)	**2** (33%)	**1** (12.5%)		
	Litopterna	**2** (29%)			**1** (12.5%)		
	Pyrotheria	**1** (14%)					
	Astrapotheria	**3** (43%)					
	Rodentia				**1** (12.5%)	**1** (11%)	**1** (17%)
	Perissodactyla					**2** (22%)	**2** (33%)
	Cetartiodactyla					**4** (45%)	**2** (33%)
Cat. III (500 **to** 1000 **kg**)	Cingulata		**1** (50%)		**2** (40%)	**4** (100%)	**3** (75%)
	Folivora		**1** (50%)	**1** (50%)	**2** (40%)		
	Notoungulata			**1** (50%)			
	Litopterna						**1** (25%)
	Rodentia				**1** (20%)		
Cat. IV (more than 1000 **kg)**	Cingulata					**5** (43%)	**4** (36%)
	Folivora				**1** (50%)	**4** (33%)	**5** (46%)
	Notoungulata				**1** (50%)	**1** (8%)	**1** (9%)
	Litopterna					**1** (8%)	
	Pyrotheria		**1** (50%)				
	Astrapotheria		**1** (50%)	**1** (100%)			
	Proboscidea					**1** (8%)	**1** (9%)

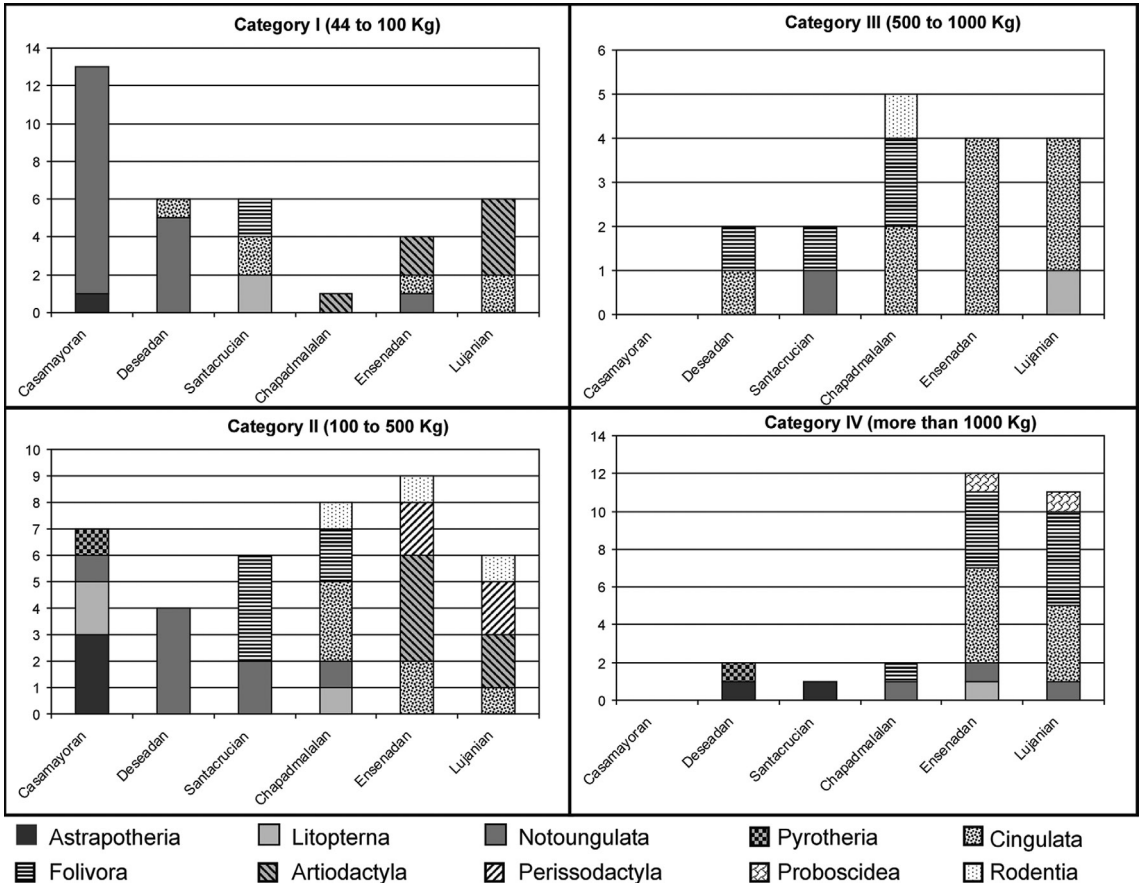

Figure 5.3 Body mass categories and their representation through time.

category I, the remaining members being cingulates. Category II is dominated by artiodactyls and perissodactyls in equal proportions, and also includes 1 rodent and 1 cingulate. Category III is mostly represented by cingulates and 1 litoptern. Sloths and cingulates largely dominate category IV, which also includes 1 notoungulate and 1 proboscidean.

5.5 Discussion

The evolution of large size in Cenozoic mammals in South America can be divided into two main periods. The first one unites what Pascual et al. (1985, 230–234) distinguished as the "most autochthonous part of the history," and the subsequent "first major change toward a modernization." During this lapse, the basic diversification of the South American mammals occurred, as did a faunal turnover that appears to be regionally connected to climatic and environmental changes related to various geotectonic events, like the Andean diastrophic phases and the opening of the Drake Passage that separated South America from Antarctica (see Pascual 2006).

During this period, the only mega-mammals sensu stricto (i.e., those >1000 kg) were pyrotheres and astrapotheres, archaic lineages of brachydont ungulates that peaked in size in the Oligocene Deseadan Age. Two exceptionally large genera were the astrapothere *Parastrapotherium*, at an estimated 1900 kg, and the pyrothere *Pyrotherium*, at 3500 kg.

By the Miocene Santacrucian Age, pyrotheres were extinct, and astrapotheres remained the only mega-mammals of the fauna (*Astrapotherium magnum*, ~1000 kg). By this time, the archaic lineages of brachydont ungulates (including litopterns and notoungulates) had gradually changed from protohypsodont to almost euhypsodont types (Pascual 2006). Eventually, these were replaced by euhypsodont native ungulates (notoungulates, and to a lesser extent litopterns), which characterized most of the native ungulates of all subsequent Cenozoic faunas. While large litopterns reached only category I (i.e., >44 kg but <100 kg, e.g., *Diadiaphorus*, 70 kg; *Theosodon*, 95 kg), large notoungulates rose to categories II and III (i.e., 100–1000 kg: *Adinotherium*, 121 kg; *Homalodotherium*, 340 kg; *Nesodon*, 554 kg). At the same time, large xenarthrans are more diverse but smaller than in the previous age, although sloths rivaled notoungulates in size.

Culminating in the Pliocene, the volcanic Isthmus of Panama rose up from the sea floor and bridged the formerly separated continents of North and South America. This geologic event had an extraordinary impact on South American faunas, including the evolution of large size. It allowed a bidirectional migra-

tion of fauna and flora between the continents, with its most dramatic effects on the mammals. This is the start of the second period considered here.

During the Pliocene-Pleistocene, and probably during the early Holocene, large native ungulates, now represented only by notoungulates and litopterns, increased in MBM, attaining only a modest representation in the categories >500 kg. By contrast, immigrant ungulates clearly dominated the categories <500 kg.

Interestingly, the xenarthrans did not suffer apparent decrease in diversity or abundance, at least not until the widespread extinction event at the very end of the Pleistocene. Furthermore, several xenarthrans crossed the bridge and became abundant in North America, and xenarthrans are the only mega-mammals that seem to have survived (albeit only briefly) the aforementioned extinction (Gutierrez et al., in press). The persistent success of herbivorous xenarthrans subsequent to the Interchange might be explained by their ability to avoid competition with northern placental lineages by evolving increased size. Beginning in the Pliocene, sloths, pampatheres, and glyptodonts in particular, evolved a large diversity of gigantic forms unparalleled by analogous eutherian taxa in South America. The evolutionary success of xenarthrans has been considered in terms of the taxonomic diversity of the clade through the Cenozoic and related to the unusual set of features that characterize their dentitions. These features made them particularly well suited to dealing with an increase in the abundance of dentally abrasive particles in their environment (Vizcaíno 2009). Pascual (2006) and Ortiz-Jaureguizar and Cladera (2006) reviewed environmental and ecological changes in South America during the Cenozoic.

In the Pliocene Chapadmalalan, rodents attained unusually large size with *Chapalmatherium* (~200 kg) and *Telicomys* (~600 kg). *Chapalmatherium* is a hydrochoerid, related to extant amphibious capybaras (~60 kg), whereas *Telicomys* is a dinomyid related to the living pacaranas (10–15 kg). Other rodents not included in our analysis reached even larger sizes. During the late Miocene and early Pliocene of Argentina, Brazil, and Venezuela, the neoepiblemid (a chinchilloid) *Phoberomys* reached 700 kg (Horowitz et al. 2006; Sánchez-Villagra, Aguilera, and Horovitz 2003). The Pliocene-early Pleistocene dinomyid *Josephoartigasia monesi* (Uruguay) was proposed as the largest known rodent, with a body mass ~1000 kg (Rinderknecht and Blanco 2008). Since then, MBM of rodents has decreased. By the end of the Pleistocene, only hydrochoerids maintained large sizes (*Neochoerus*, ~100 kg), but even this exceeds the size of living rodents.

Mammals reached their most spectacular sizes in the Pleistocene. For instance, since the description of the first specimen ever collected from the Lujanian fauna — the ground sloth *Megatherium americanum* — the large body size of

its members has been remarkable (see Simpson, 1980). This fauna compares very favorably to that of present-day savannas of Africa, where four or five species have adult body masses exceeding a ton. The number of Lujanian mammal species larger than a ton is even more impressive than in present-day African faunas; as many as 19 such species occur in a single locality (Fariña and Vizcaíno 1999). This presents interesting intellectual challenges to a paleobiologist. The question of the trophic relationships of the Lujanian megafauna has been addressed by Fariña (1996), following the general ecological relationships between population density and body size, and between basal metabolic rate and body size. Fariña considered that there are 30 species of herbivorous mammals greater than 10 kg found in the Luján local fauna, more than half of them (16) are xenarthrans: 9 glyptodonts, 1 pampathere, and 6 ground sloths. The list is completed by 1 giant rodent, 4 notoungulates, 1 litoptern, 1 perissodactyl, 6 artiodactyls, and a gomphothere. The energy requirements for each species were obtained by multiplying its standing biomass by its basal metabolic rate. Introducing some assumptions, Fariña estimated their consumption of the habitat's primary productivity, and concluded that there was an excess of herbivores in relation to the plant resources available and in relation to estimates of carnivore biomass. By the process of elimination, Fariña reached the surprising conclusion that ground sloths may have had scavenging habits, which may have helped to redress this ecological imbalance.

During the last decade, new research has promoted alternative interpretations. For instance, Vizcaíno, Bargo, and Cassini (2006) emphasized that the Pleistocene communities were dominated by mega-mammals of very low metabolism (xenarthrans), which have no counterpart in living faunas. These authors found that xenarthrans have less dental occlusal surface area available for triturating food than other placental mammals of similar sizes, and related this to the low basal metabolic rates characteristic of living xenarthrans (between 40% and 60% of the rates expected from mass via Kleiber's relation for placental mammals; McNab 1985). This implies that xenarthrans have lower energetic requirements than epitherians and, therefore, for a specific type of food, required lower intake than other placental mammals of similar body masses. Other research has proposed that if high herbivore biomass occurred during the Lujanian, then a higher density of carnivores could be supported than was inferred from the power function of body size and population density (Prevosti and Vizcaíno 2006).

New evidence indicates that the large mammal and mega-mammal faunas were very well diversified at the end of the Pleistocene and not suffering from

any kind of declining trend in prior time intervals (Cione, Tonni, and Soibelzon 2009). Large size explains most of their vulnerability to extinction at the end of the Pleistocene in South America over other factors such as the geographic origin of the lineages (South American vs. North American) and dietary habits (herbivory vs. carnivory; Lessa and Fariña 1996). All mega-mammals (37 species) and most large mammals (46 species) present during the late Lujanian became extinct in South America (Cione, Tonni, and Soibelzon 2003, 2009). However, an analysis of the causes of large mammal extinctions in Australia, Eurasia, the Americas, and Madagascar during the late Quaternary concluded that large size was not directly related to risk of extinction. Rather, species with slow reproductive rates were at high risk regardless of their body size (Johnson 2002). This provides a biological framework for analyzing the extinction of large South American mammals. Cione, Tonni, and Soibelzon (2003, 2009) suggested that females probably reached sexual maturity late, had a very long gestation period and prolonged parental care, implying only one offspring in two or three years, and had a low lifetime reproductive yield. This reinforces the idea that large size influences extinction risk through several biological traits.

Humans arrived in South America ca. 13,000–11,000 BP. Some mega-mammals became extinct in South America during the early Holocene, perhaps as late as 7000 BP (but see Steele and Politis 2009). This extinction event lasted several thousand years: there is little support for the blitzkrieg extinction model for South America. However, a relatively small number of human foragers with specialized weapons could have been indirectly responsible for these extinctions if they focused their hunting efforts on key individuals (females, juveniles, or infants). This could have provoked a cascade of extinctions in herbivores as well as in large carnivores that preyed on the herbivores (Cione, Tonni, and Soibelzon 2003, 2009).

Johnson (2009) summarized the possible ecological consequences of late Quaternary megafaunal extinctions. Johnson maintained that there were significant changes in plant communities following megafaunal extinctions, and that the ecological aftershocks of those extinctions persist today (Johnson 2009). According to this author, large herbivores maintained biodiverse and complex habitats in dry, lowland, wooded landscapes. Some of these habitats became impoverished as a result of herbivore extinctions, while others contain anachronistic plants that may be in long-term decline.

Although the impact of the megafaunal extinctions on the evolution of Holocene plant communities has not been studied for South America, it clearly produced an enormous ecological gap in the herbivorous guild. As Darwin

stated at the very beginning of his career: "It is impossible to reflect without the deepest astonishment, on the changed state of this continent. Formerly it must have swarmed with great monsters, like the southern parts of Africa, but now we find only the tapir, guanaco, armadillo, capybara; mere pigmies compared to antecedent races" (Darwin, 1839, 210).

The conditions that allowed the establishment of the ecosystem of the Pampean Region, as it was known by the Spanish conquerors, appeared very recently (Cione, Tonni, and Soibelzon 2009), probably ca. 1000 years BP (Tonni and Cione 1997). At least in this region, the herbivorous gap mentioned earlier persisted for about 6000 years, until it was filled by herds of feral cattle whose ancestors were introduced by the Spanish in the second half of the sixteenth century. By the end of that century, cattle had become so numerous that the trade in cow hides became one of the main economic colonial activities for the next two centuries. As happened with bison in North America in the second half of the nineteenth century, cattle were hunted for their hides, with the carcass left behind to decay on the ground. It also affected the economy of the native people, who shifted from hunting camelids (*Lama guanicoe*), deer (*Ozotoceros bezoarticus*), and rheas (*Rhea americana*), each of which produce less than 60 kg of meat, to hunting cattle, which weighed 400–800 kg (Ramos et al. 2008).

In conclusion, we emphasize Johnson's (2009) view that to understand living plant communities, we need to imagine them with the full complement of Pleistocene megafauna that shaped their evolutionary histories. To do so, more paleobiological studies are needed. The great phylogenetic distance between some mega-mammals and their living counterparts raises serious problems in understanding their paleobiology. This is especially true for those faunas in which xenarthrans dominated. Particularly for the Pleistocene, communities dominated by hypometabolic mega-mammals (xenarthrans) have no counterpart in living faunas. Hence, paleoecological reconstructions lack strict analogues; therefore, alternatives to purely comparative actualistic approaches must be used.

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