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Alberto Luis Cione
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The Great American Biotic Interchange

A South American Perspective

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Pleistocene continental beds cropping out in the coastal cliffs south of Miramar, Buenos Aires Province. Note the chimango, a terrestrial bird at the *left*, and a gull, a marine bird at the *right*. Photo by Esteban Soibelzon

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Alberto Luis Cione
División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo
UNLP
La Plata
Argentina

Germán Mariano Gasparini
División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo
UNLP
La Plata
Argentina

Esteban Soibelzon
División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo
UNLP
La Plata
Argentina

Leopoldo Héctor Soibelzon
División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo
UNLP
La Plata
Argentina

Eduardo Pedro Tonni
División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo
UNLP
La Plata
Argentina

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The most emblematic South American mammals are the guanaco, the tapir, and the spectacled bear. However, the closest ancestors of these animals did not originate in the continent: They were recent immigrants from North America.

Yes, we got a problem: The evidence is at the bottom of the bottle and we are not drunks

Preface

The Great American Biotic Interchange (GABI) between North and South America is one of the most important events in the history of land mammals. The first authors that considered the interchange between the Americas were Wallace, Ameghino, and few others as early as the second half of the nineteenth century. Notwithstanding that a huge effort was made by thousands of paleontologists, zoologists, botanists, geologists, and professionals of other disciplines, we are far from having a precise panorama about one of the most important events in the history of mammals.

However, we are confident that a more complete survey of mammal bearing units in southern South America as well as discovering others in the central and northern Andes and Central America will give us the factual evidence for proposing, confirming, or rejecting many hypotheses. Moreover, the expanding molecular studies will provide the minimum age for the origin of many endemic clades of North American families whose first appearance is not adequately explained.

In this book, we consider the extinction of megafauna in South America as a part of GABI. Several paleontologists (including the authors of this book) are commited to the study of the process that modified permanently the composition and distribution of land mammals in South America. The entrance of hunter-gatherers at the end of the Pleistocene occasioned the spectacular extinction of megafauna. However, this process is being completed by modern man. For this, research on recent distribution of vertebrates in South America has to be accelerated. During the last twentieth and twenty-first centuries, terrestrial and aquatic environments changed radically because modern human activities occasioned extinction, pseudoextinction, and alteration of distribution of many mammals. This disruption might make conventional and molecular studies of historical patterns and relationships between different lineages extremely difficult. However, fossils are still in the rocks. They are waiting for us to find them, unearth them, and make them drops of light for explaining the origin of a treasure in danger: the richest land mammal fauna of the world.

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Contents

Chapter 1
Introduction

Abstract The Great American Biotic Interchange (GABI) between North and South America is one of the most important events in the history of land mammals. The interchange occurred in several phases during more than nine million years. The oldest genera of North American origin in southern South America occur in beds of Late Miocene age. However, the major episodes of mammalian dispersal from North America appear to have occurred from the Marplatan (Latest Pliocene–Early Pleistocene) to the Lujanian (Late Pleistocene–Early Holocene). In this book, we focus on mammals of southern South America, where the most important and richest localities with fossil vertebrates of Late Miocene–Holocene age were reported.

Keywords Chronology · Mammal · Panama isthmus · Endemic · Immigrant · Biogeography · Macroevolution · Neogene · Quaternary

During most of the Cenozoic, South America was isolated from the other continents excepting for a non-permanent land connection with east Antarctica that probably lasted until the Late Paleocene (Reguero et al. 2014). Afterward, during the period of isolation, a very singular mammalian fauna evolved in South America and only primate and rodent waif immigrants reached South America from Africa (Ameghino 1889; Simpson 1980; Poux et al. 2006; Flynn et al. 2007).

The insularity of South America finished when the Panamá isthmus was permanently established in southern Central America by the end of Cenozoic (ca. 2.8 Ma; Woodburne 2010) or perhaps even earlier (Prothero et al. 2014). Every continental collision or terrestrial connection between two previously isolated great continents should generate an important biogeographic event. Certainly, the mixing of North American and South American continental faunas was one of the most important episodes in the history of mammals (Ameghino 1910; Scott 1937; Simpson 1950; Woodburne et al. 2006; Woodburne 2010). This faunal interchange was named the Great American Biotic Interchange (GABI, “Gran Intercambio Biótico Americano” in Spanish, GIBA) by Webb (1985).

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The mode and timing of the GABI is controversial (see Cione and Tonni 1995; Albert and Reis 2011; Prothero et al. 2014). For example, Webb (1985) suggested that during the "Uquian" (presently Marplatan), 8 mammal families of Holarctic origin suddently appeared in South American. However, this was demonstrated incorrect by Tonni et al. (1992) and Cione and Tonni (1995). More recently, Woodburne (2010) restricted the term GABI almost exclusively to the Pleistocene interchange (after 2.8 Ma; GABI 1 to 4) when a permanent dry land connection between South and Central America was established. Here, we prefer to name as GABI the whole interchange including Late Miocene to Holocene dispersals. The pre-Vorohuean dispersals are named ProtoGABI (see below).

During the GABI, South American land mammal faunas were subject to selective pressures related to the dramatic tectonic, climatic, and especially biogeographical changes in the region. The impact of northern mammals is shown by the fact that, taking into account the non-flying and non-marine groups, about 40 % of the South American mammal families and 50 % of the genera and species derive from this interchange (Marshall et al. 1982). The immigration of other animals than mammals and plants has been much less studied, and some of the results are debatable (e.g., fishes, Albert and Reis 2011). The most spectacular event of GABI in South America occurred at the very end of the Pleistocene and the beginning of Holocene, when humans entered and eliminated all the local large mammals (the megafauna) provoking a major ecological disruption that is presently being completed by modern man (Cione et al. 2003, 2009).

The mammal biostratigraphic record that constitutes the Late Cenozoic local standard chronostratigraphic scale for South America is mostly based on type sequences from Argentina (Figs. 1.1, 1.2, and 1.3). Bolivia, Brazil, Uruguay, and Chile also include some important paleontological localities. Consequently, the most significative fossils that constitute the silent testimonies of the dispersal of North American mammals into South America are found in the southern part, a comparatively marginal part of the continent.

Until the end of twentieth century, studies about the GABI in South America relied on the framework of "land mammal ages" conceptual frame as used in the continent (e.g., by Pascual et al. 1965; Marshall et al. 1983, 1984). This approach dismissed detailed biostratigraphic studies in South America and relied greatly on "biochronological" ordering (see discussion in Cione and Tonni 1995, 1996). In consequence, the ordering and importance of first occurrence of northern mammals in South America was very tenuously known. In addition, the systematics of most groups was far to be well known and many of the previously recognized taxa were artifacts. More recent field work and critical revision of previous evidence in light of the chronostratigraphic view showed that the pattern of first record of northerners (at least in southern South America) is very different (Tonni et al. 1992; Cione and Tonni 1995). On the basis of that good faunistic record, a zonation for the Upper Cenozoic in the Pampean region that was proved useful in other regions was proposed (Cione and Tonni 1995). It is calibrated in several parts by radiometric dating and magnetostratigraphic analyses.

Unfortunately, some of the classic paleontological and historical sites are being altered by human activities with important loss of putatively relevant sites. Part of this cultural heritage, which gives a sense of identity to our community, would be lost for ever (Cenizo et al. 2011).

In sum, although we acknowledge that the entire biota of South America suffered the influence of the GABI, this book deals only with land mammals. We summarize the history of the establishment of the land connection between continents as well as the land mammal biostratigraphy and chronostratigraphy, the climatic evolution, and the biogeographic patterns of southern South America from Late Miocene to recent times as a frame for dealing with the gradual process of dispersal of North American mammals into southern South America. Posteriorly, we analyze part of the present land mammal composition of South America as a result of the presumed interaction between the faunal substrate from the insular period and the new immigrants from North America. Finally, we discuss the deleterious action of the Late Pleistocene hunter/gatherers that entered from Asia as well as the extraordinary modifications caused by the modern men that came from Europe.

Fig. 1.1 A: general map of southern South America; B: location of the paleontological sites mentioned in text; C: southeastern coast of Buenos Aires Province. BUE: Buenos Aires city; LUJ: Luján city; LP: La Plata city; MDP: Mar del Plata city; BLL: Barranca los Lobos; CHA: Chapadmalal; PSA: Punta San Andrés; PV: Punta Vorohué; MI: Miramar; NE: Necochea; and MH: Monte Hermoso. Jujuy Province: UQ: Uquía. Bolivia: TAR: Tarija Valley. Argentina provinces: *1* Jujuy; *2* Salta; *3* Formosa; *4* Catamarca; *5* Tucumán; *6* Santiago del Estero; *7* Chaco; *8* Misiones; *9* Corrientes; *10* La Rioja; *11* Córdoba; *12* Santa Fe; *13* Entre Ríos; *14* San Juan; *15* San Luis; *16* Buenos Aires; *17* Mendoza; *18* La Pampa; *19* Neuquén; *20* Río Negro; *21* Chubut; *22* Santa Cruz; and *23* Tierra del Fuego

Fig. 1.2 Coastal cliffs at Punta Hermengo, Miramar (General Alvarado County, Buenos Aires Province). This paleontological site was described by Florentino Ameghino at the beginning of twentieth century. *Above* view at 2005. The lower half of the sequence at Punta Hermengo contains Ensenadan fossil remains. *Below* view at 2007. County authorities had the intention to protect the cliffs from marine erosion by locating large quartzite blocks at the base of ravines. However, they frustrated additional survey for new paleontological specimens (Cenizo et al. 2011). The *black arrows* show the same structures. Photographs by Esteban Soibelzon

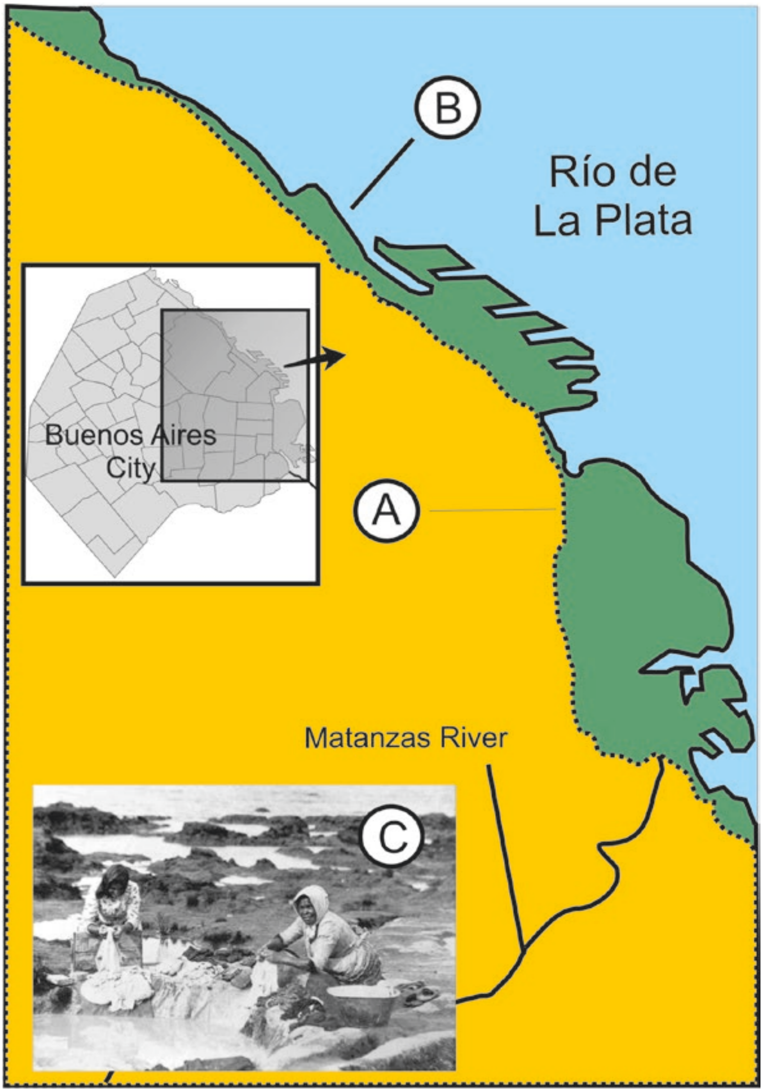

Fig. 1.3 Map of Buenos Aires Buenos Aires City. A: coastline in 1853; B: current coastline. Green area, land reclaimed to Río de La Plata by the growing city. C: Picture taken at the end of the nineteenth century (owned by E.P.T) showing women washing clothes. Modified from Soibelzon et al. (2008)

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Chapter 2
Continental Relationships, Chronostratigraphy, Climates, and Mammalian Biogeography of Southern South America Since Late Miocene

Abstract The biotic interchange between the Americas occurred in several phases during more than nine million years. In this book, we focus on mammals of southern South America, where the most important and richest localities with fossil vertebrates of Late Miocene–Holocene Age were reported. We here provide basic information about taxonomic composition, biostratigraphy, climate evolution, continental tectonics, and biogeography for better understanding the GABI. Furthermore, we analyze the chronology and dynamics of the GABI, the evolution of some South American mammalian groups through time, and the Quaternary mammalian extinctions. As the GABI was a complex process, we divide it into ProtoGABI and GABI 1 to 4.

Keywords Chronology · Mammal · Panama isthmus · Endemic · Immigrant · Biogeography · Macroevolution · Neogene · Quaternary

2.1 General Continental Relationships of South America

The GABI is closely related to the latest tectonic evolution of Central America, the Caribbean islands, and South America. This evolution resulted in the final connection between the Americas with the establishment of the Panamá Isthmus. The geology and paleogeography of Central America and northern South America have been intensively described (e.g., Coates et al. 2004; Iturralde-Vinent 2006; Coates and Stallard 2013; Figs. 2.1, 2.2 and 2.3).

In Pangean times, the South American continent occupied a central-western position (Iturralde-Vinent 2006; Ortiz Jaureguizar and Pascual 2011; Fig. 2.1). After different stages, Pangea split into the supercontinents of Gondwana and Laurasia (Rapela and Pankhurst 1992; Iturralde-Vinent 2006). Rifting processes since Jurassic times provoked the separation of Western and Eastern Gondwana. The first evidence of separation of Africa and North America is the magnetic anomaly of 160 Ma (earliest Middle Jurassic; Benedetto 2010). A marine gap was present between North and South America by the Callovian (Iturralde-Vinent and MacPhee 1999) and the last connection of South America with Africa occurred at about 110 Ma ago (the Aptian–Albian times; Parrish 1993).

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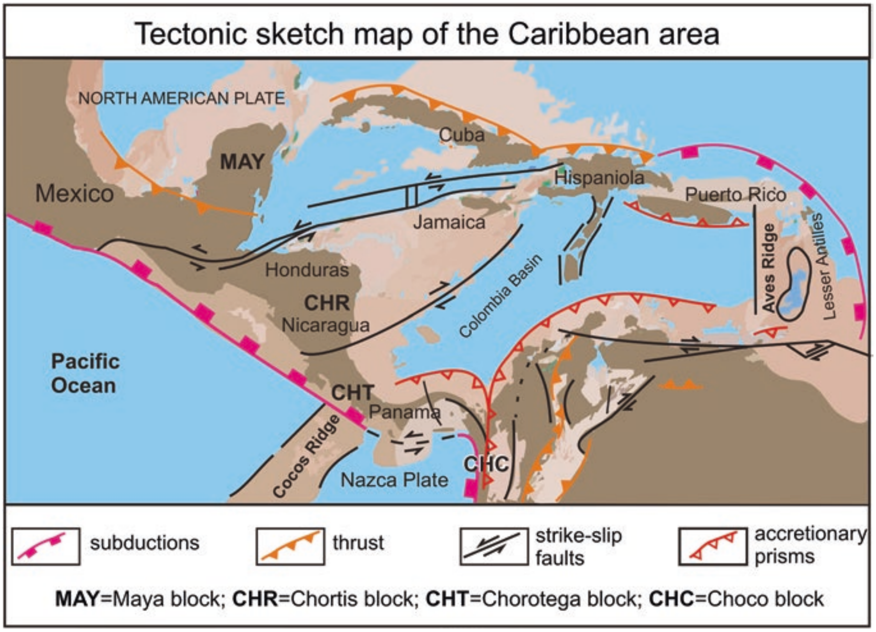

Fig. 2.1 Tectonic sketch map of the Caribbean region (modified from Giunta and Orioli 2011)

Between North and South America, the Proto-Antilles formed a volcanic island arc, which was interpreted as a transient putative sweepstake route since about 140–120 Ma (Brown and Lamolino 1998; Fig. 2.1). According to the fossil record, a biotic interchange of land vertebrates (e.g., boid snakes, dinosaurs, and mammals) occurred between the Americas during the Late Cretaceous (Campanian–Maastrichtian) and the Early Paleocene (Pascual et al. 1996; Ortiz Jaureguizar and Pascual 2011; Hastings et al. 2013; Woodburne et al. 2014).

In the Panamanian Isthmus region, Late Cretaceous to Early–Middle Miocene beds of the San Blas Complex (and the Clarita, Darien, and Porcona formations) were deposited in deep depths in an open ocean, low energy, essentially non-siliciclastic sedimentary environment distant from South America. Similar environments have been recorded for the Uva and Naipipi formations (Early to Middle Miocene) of the Atrato Basin of northwestern Colombia and the Early Miocene Punta Alegre Formation of western Panama (Coates et al. 2004) (Fig. 2.2a).

However, the oldest land bridge between West Indies and the main land dates to the latest Eocene–earliest Oligocene (according to the Gaarlandia hypothesis) and bridged the Greater Antilles with South America through the Aves Ridge (Jestrow et al. 2012).

In the austral part, South, South America was intermittently connected with Antarctica and Australia until the Late Paleocene (Reguero et al. 2014). After this, and until the latest Cenozoic, South America was practically an island continent.

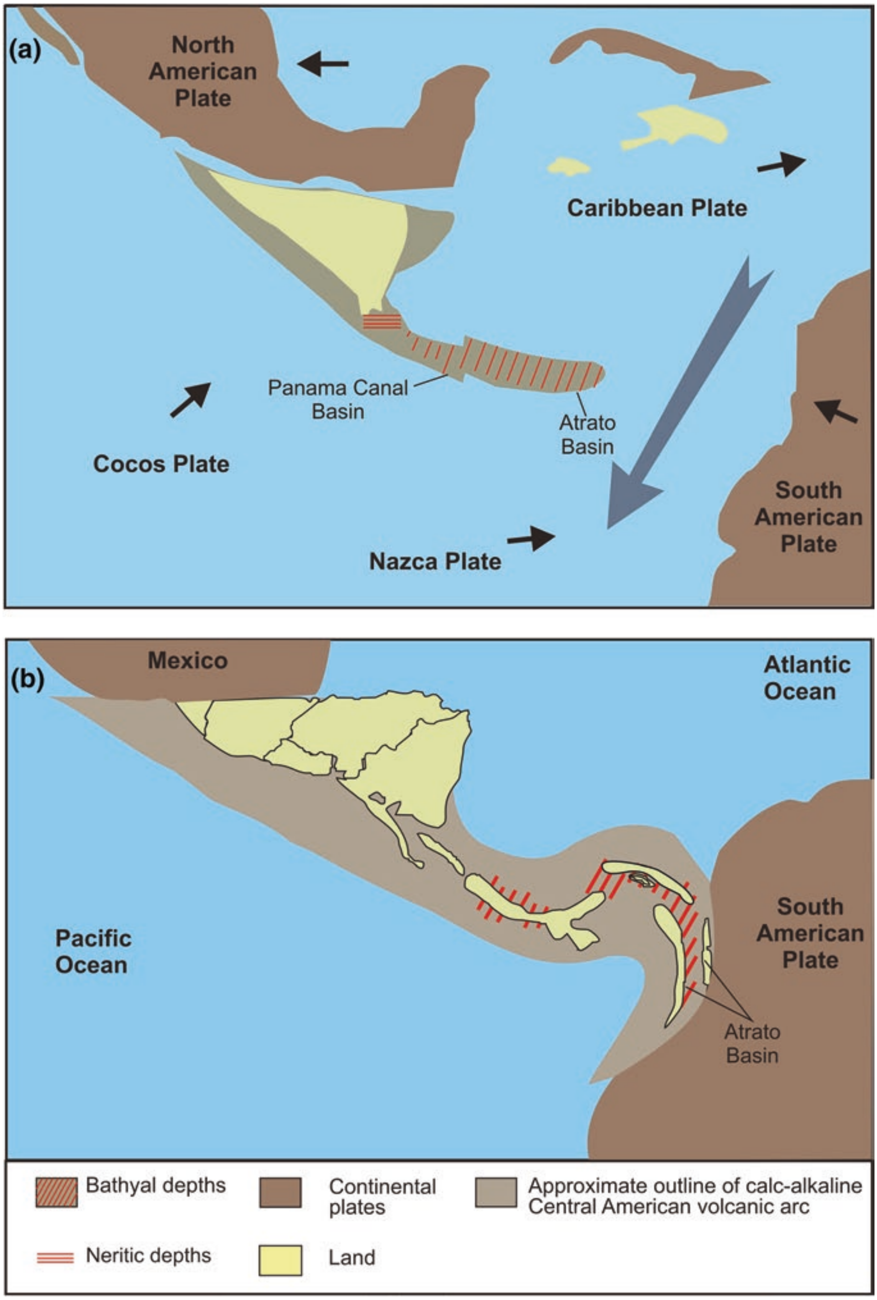

Fig. 2.2 **a** Geologic setting of the Central American volcanic arc in the Early Miocene (20 Ma, pre-collision). The *gray arrow* indicates complete interchange of Atlantic and Pacific waters. **b** Central American volcanic arc at the latest Miocene (6 Ma, post-collision). This is a post-collisional phase as the Panama microplate and the area become extensively emerged. Strongly modified from Coates et al. (2004)

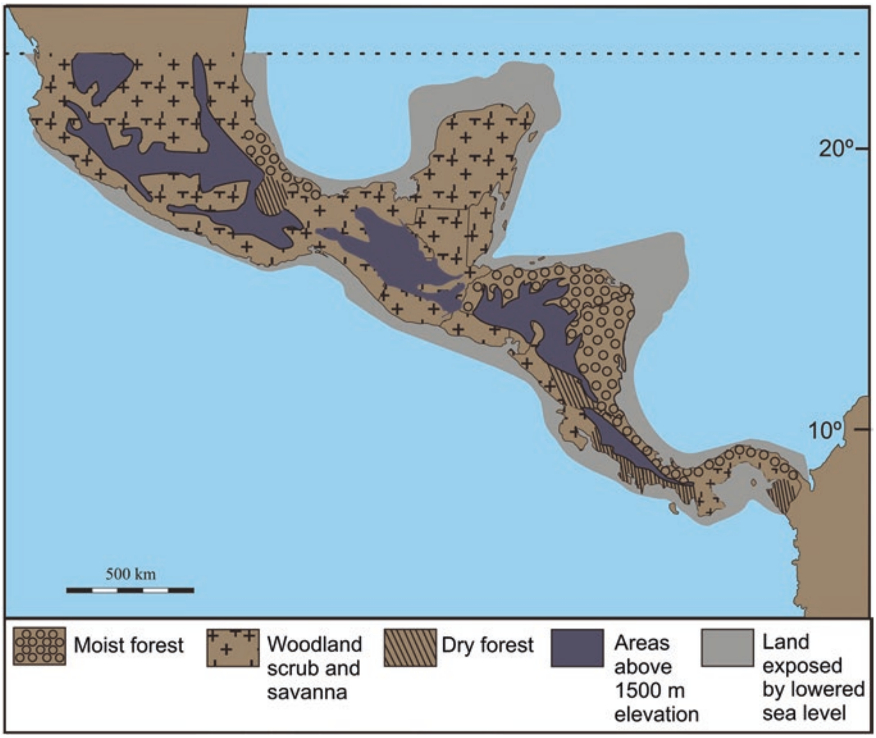

Fig. 2.3 Putative distribution of lowland Neotropical forest associations at the Last Glacial Maximum (18 ka BP). Land exposed by lower than today's positions of the Pleistocene sea level during maximum glacial advance is indicated. *Black areas* are elevations above 1500 m a.s.l. Modified from Woodburne (2010)

2.2 Evolution of the Physical Connection Between Central and South America

The geodynamic history of the Caribbean region is very complex because it involved not only the North and South American margins but also diverse continental fragments that rotated and showed transcurrent displacements (Benedetto 2010). The largest blocks are the Chortis and Yucatan plus Florida peninsula or Florida–Bahamas.

The opening of the Caribbean was associated with large displacement faults such as the Volcanic Trans-Mexican Alignment. Along the Pacific Ocean, the subduction of the Farallon plate generated a volcanic arc that was the origin of the Greater Antilles (Benedetto 2010).

The Central American Seaway (CAS) that separated Central America from South America was largely interrupted by an evolving volcanic arc as early as 12 Ma ago, while the Caribbean plate collided with the South American Continent (Coates et al. 2004; Woodburne 2010). Neritic depths were predominant throughout the Darien region and the collision of the Central American arc with South America is suggested by a regional unconformity by Early–Late Miocene (Coates et al. 2004). Besides, extensive emergence and rapid uplift in the Central American Isthmus in the latest Miocene is suggested by the absence of Pliocene deposits from either the Darien or the Panama Canal Basin and of sediments younger than 5 Ma in the Atrato Basin of Colombia (Coates et al. 2004). Central American archipelago putatively served as a sweepstakes route during the Late Miocene when there was a limited biotic interchange among North and South America (Brown and Lamolino 1998).

Complete docking and widespread uplift of the Central American Isthmus (including Panama) is reflected by a widespread unconformity at about 8.6–7.1 Ma. This could have fostered the entry of the Procyonidae to South America (Woodburne 2010).

Shallow marine conditions adjacent to emergent lands between the latest Miocene and the Early Pliocene from Costa Rica to Colombia (and in Colombia and in Costa Rica in the Pliocene) are indicated by marine beds. Subsequent to this, the region was further strongly uplifted, including the final emergence of the Panamanian district (Woodburne 2010) (Fig. 2.2b). The CAS was increasingly shallowing with a short marine episode at about 6 Ma (Coates et al. 2004).

Woodburne (2010) has suggested that land mammals began to extend their ranges across Central America soon after the initial tectonic closure from about 12 Ma. The first sloths arrived in North America at about 9 Ma, that is only a minimum age regarding their actual crossing of the isthmian region, and whether they were present in Central America, prior to their occurrence in continental North America, remains to be determined. In fact, the degree to which Central America acted as a holding pen for any trans-isthmian dispersal is still an open question (Woodburne 2010).

The fossil evidence indicates that the main interchange began at about 2.6 Ma (GABI 1 of Woodburne 2010) with the first major dispersal of both North and South American taxa indicating that the isthmus was formed but, as discussed below, climate fluctuations and modifications of vegetation were fundamental for such strong interchange (Woodburne 2010; see also Leigh et al. 2014).

Iturralde-Vinent (2006) suggests that the isthmus suffered interruptions shown by interchange record known between the Pacific and Caribbean seas (e.g., gastropods). The interruption became definitive at about 0.7 Ma. Since then, the Caribbean geography is similar to the present one and new marine endemic species emerged. However, the Central American region increased its area during the sea lowstands during glaciations (Fig. 2.3).

More recently, a new model of formation of the Isthmus of Panama proposes that its establishment is much older (15 Ma; Coates and Stallard 2013). The new model uses cooling of magmas in the Cretaceous to Early Miocene Central American volcanic arc to propose Eocene emergence of the discrete structural blocks of the arc and then U/Pb dating, paleomagnetic pole rotations, and Atlantic seafloor anomalies to reconfigure the blocks for different time slices back to 25 Ma (Coates and Stallard 2013). The closure at 15 Ma was suggested because by this time the alignment of the blocks leaves no space for trans-isthmian marine passages. Besides, Prothero et al. (2014) suggest that a permanent land connection of unknown duration (the Baudo Pathway) existed probably no later than

10 Ma between the Serranías de San Blas-Darién and the Serranía de Baudo as the allochthonous Choco Terrane was being attached to the Istmina Hills region of southwestern Colombia. This connection would permit the first interchange (see below). Finally, Prothero et al. (2014) propose that a permanent connection existed at least since 5 Ma. However, considerable debate is currently in progress in the geological community (see also Leigh et al. 2014). Supporting the first scenario, molecular data from cross-isthmian divergence times of marine organisms reported on 34 trans-isthmian sister clades of fish, mollusks, and crustaceans suggest the absence of a marine dispersal barrier between the Atlantic and Pacific until the Late Neogene (Baker et al. 2014).

2.3 History and Conceptual Framework of Mammal Stratigraphy of the Southern Cone of South America Since the Miocene

2.3.1 The Stratigraphy of the Pampas

Alcide d'Orbigny (1802–1857) named "*terrains pampéens*" and "*argille pampéens*" the reddish brown sediments cover most of the Pampas (Tonni 2011). Later, Charles R. Darwin (1809–1882) called them the "*Pampean formation*" (Tonni 2011). The Spanish use of the "Pampean Formation" outlasted and gave rise to others such as "Pampiano Formation" or "Pampean sediments", the latter commonly used in geological and stratigraphic literature since the end of the nineteenth century (Fidalgo et al. 1975; Cione and Tonni 1995). Auguste Bravard (1803–1861) was the first researcher to give a brief mineralogical description of these deposits which he called indistinctly "Pampa Formation," "Pampa silt," or "Pampa terrain" (see Tonni 2011). He recognized their mainly eolian origin, in contrast to what was supported by d'Orbigny and Darwin (see Tonni and Pasquali 2006; Tonni et al. 2008) and emphasizing the volcaniclastic supply.

The German chemist, zoologist, and geologist Adolf Doering (1848–1925), who joined as a geologist in the Scientific Commission that accompanied the expeditionary army to the Río Negro led by General Julio Argentino Roca, conducted a detailed classification of the land they were exploring. This classification consisted of fourteen geological horizons or "stages" including, among others, the "Araucana," "Pampeana," "Tehuelche," "Querandina," and "Ariana" "formations" (Doering 1882).

The stratigraphic classification of Doering was the base for that one proposed by Florentino Ameghino (1854–1911). Thus, Ameghino (1881) divided these sediments into "terreno pampeano inferior," "terreno pampeano superior," and "terreno pampeano lacustre." Later, he named them together as "formación pampeana" (Ameghino 1889), with the "stages" "ensenadense" ("pampeano inferior"), "belgranense" ("pampeano medio"), "bonaerense" ("pampeano superior"), and "lujanense" ("pampeano lacustre"). In the same paper, he included the oldest "sedimentos pampeanos" in what he named "formación araucana," with two "stages" ("geological

Fig. 2.4 Chapadmalalan to Ensenadan continental beds cropping out in the coastal cliffs north of Miramar, Buenos Aires Province. Photograph by Esteban Soibelzon

horizons"): "hermósico" and "pehuelche," the latter in place of the name "piso puelche" used by Doering, and the youngest sediments in what he named "formación cuaternaria"—with the "stages" "querandino" or "post-pampeano marino" and "platense" or "post-pampeano lacustre"—and "formación reciente," which comprised the "stages" "aimará" and "ariano" (Cione and Tonni 1995).

In his publication on the stratigraphy and paleontology of the Atlantic Bonaerian coast (Fig. 2.4), Ameghino (1908) provided his last stratigraphic scale. He added a new unit to the "formación araucana," the "Chapalmalan Stage," placed between the "hermosense" ("hermósico" of Ameghino 1889) and the "puelchense" ("pehuelche" of Ameghino 1889). Additionally, he included the "stages" "preensenadense," "ensenadense basal," "interensenadense"—marine in origin—and "ensenadense cuspidal" in the "formación pampeana" (Ameghino 1908). The name "ensenadan" was created by Ameghino on the basis of the observations made in the town of Ensenada, Buenos Aires Province, during the construction of the harbor of La Plata (see Soibelzon et al. 2008a). The name "Lujanian" was also coined by Ameghino for sediments cropping out in the banks of the Río Luján near Luján, eastern Buenos Aires Province (see Fig. 1.1).

When Ameghino consolidated his stratigraphic framework, in the last decade of the nineteenth and early twentieth centuries, he used the terms "formation" and "stage"—"horizon" or "subformation"—which currently define units of the lithostratigraphic and chronostratigraphic classification. However, at the time of

Ameghino, the meaning of these terms was different. A "formation" was a unit defined from the fossil content, where the lithology was not the essential element or the only one in the definition. The "stage" (or "subformation" or "geological horizon") was merely a subdivision of the "formation" and did not differ largely from the current biostratigraphic units (see Cione and Tonni 1995; Tonni 2011).

In the mid-twentieth century, and based on previous observations, the Italian naturalist, Gioacchino Frenguelli (1883–1958), continued with the stratigraphic framework of Ameghino, but simplified—apparently—with another connotation, adjusted to the new stratigraphic classifications established since the 1940s (see Tonni 2011). Frenguelli's stratigraphic framework is crystallized in his contribution of 1950; he recognized "Series" and a set of "stages" subordinate to them, i.e., units that currently—and since 1941—belong to the chronostratigraphic classification. However, Frenguelli (1950, 1957) never explained that his stratigraphic framework responded to formal categories. He named the "formación pampeana" as Series Pampiano and post-pampiano. The three "pisos pampianos" of Frenguelli (1950) are the "Chapalmalan," (currently Chapadmalalan), the Ensenadan, and the Bonaerian. The "pisos post-pampianos" are the Lujanian, Platan, Querandinian ("estuarine"), and the Cordoban and Aymaran. From a chronological point of view, the three "Pampianos" are referred to the Pleistocene and the five "post-pampianos" to the Holocene (Frenguelli 1950, 1957). The only significant chronological changes to this scheme are currently the inclusion of the Chapadmalalan in the Pliocene and the Lujanian in the Late Pleistocene and the Early Holocene (Fig. 2.5).

In 1952, Jorge Lucas Kraglievich established a stratigraphic framework for southeastern Buenos Aires Province putatively based on the classification proposed by Ashley et al. (1933), for "*rock units*" (the modern lithostratigraphic units). This framework, which was extended in subsequent publications, involved the use of the nomenclature of Ameghino (1908), but with a different connotation. Thus, for example, the "piso chapalmalense" became the "Chapadmalal Formation." For the coastal area of the Buenos Aires Province, between the north of Mar del Plata and Miramar (Fig. 2.6), he recognized the following "formations," from earliest to latest: Chapadmalal, Barranca de los Lobos, Vorohué, San Andrés, Miramar, Arroyo Seco, Santa Isabel, Cobo, and Lobería (Kraglievich 1952, 1953).

In 1965, Rosendo Pascual and his students published a chronological framework for the Cenozoic of Argentina based on the biochronological concept of "Mammal Ages" (Pascual et al. 1965) which was originally proposed by Savage (1962). The biochronologic classification of Pascual et al. (1965) involves, for the Pliocene and Pleistocene, the "Mammal Ages" Montehermosan, Uquian, Ensenadan, and Lujanian. The "piso chapalmalense" of Ameghino (1908) and the Chapadmalal "Formation" of Kraglievich (1952) together with the fauna are included within the Montehermosan Mammal Age (Pliocene); the Uquian "Mammal Age" includes the "piso puelchense" of Ameghino and the Barranca de los Lobos, Vorohué, and San Andrés "formations" of Kraglievich and their respective faunas. The "piso bonaerense" of Ameghino (and the Arroyo Seco and Santa Isabel "formations" of Kraglievich) and its fauna are included in the Lujanian "Mammal Age." For each "Mammal Age," Pascual et al. (1965) gave a list of mammals putatively useful as guide fossils.

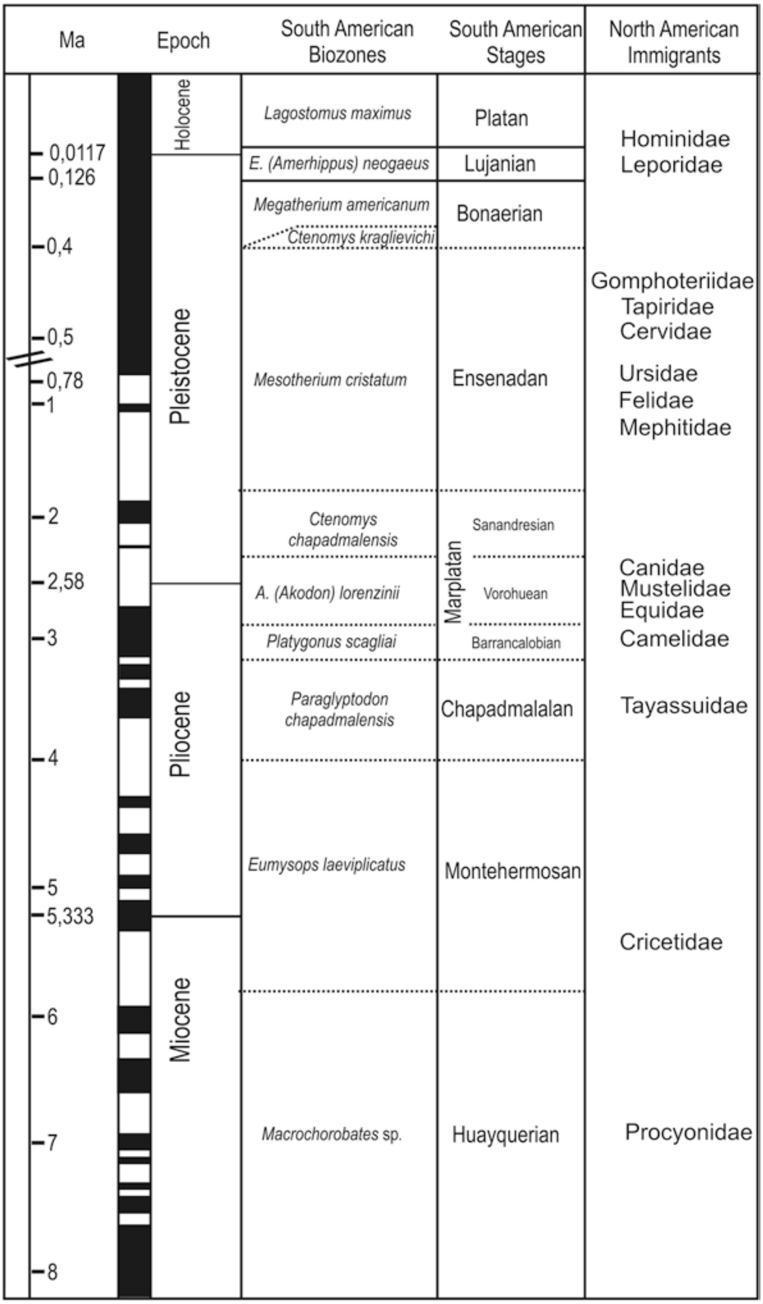

Fig. 2.5 Chronological scale of South America with first record of mammals families of North American origin. Age boundaries are approximate. The epoch boundaries are according to Cohen et al. (2013)

Fig. 2.6 Coastal cliffs at Miramar (General Alvarado County, Buenos Aires Province). Photograph by Esteban Soibelzon

The current chronostratigraphic framework for the continental Late Cenozoic of the Pampean region has been developed almost entirely in the southeastern region, namely the coastal cliffs between Mar del Plata and Miramar and cliffs in the Coronel Rosales County known in the literature as "Farola Monte Hermoso." This framework is based on the above background and began to be developed in the mid-1990s, when Cione and Tonni (1995), following the recommendations of the Argentine Code of Stratigraphy, proposed to hold to the chronostratigraphic/geochronologic classification, with a biostratigraphic basis (Fig. 2.5).

The theoretical aspects, under which the paradigm of the "Land Mammal Ages" was developed, were examined by Cione and Tonni in several publications (e.g., Cione and Tonni 1995, 1996, 1999). Although the "Land Mammal Ages" are not formal geochronologic units (based on stages), Cione and Tonni (1995) suggest that there is no essential distinction between those and formal ages. "Land Mammal Ages" would be formal ages defined on a less accurate way than the ages based on stages defined on marine sequences. South American "Land Mammal Ages" are in fact based on poorly defined stages according to the modern requirements in geosystematics (Cione and Tonni 1995) as Simpson (1971) had already recognized in an almost forgotten paper.

The level of abstraction is increased when considering the biostratigraphic, chronostratigraphic, and geochronologic units. All these are not "real" entities, i.e., they are not part of nature. However, biostratigraphic units have characters such as the spatial distribution of certain fossils, which can be observed in the field, although there is some level of abstraction in its recognition. Chronostratigraphic units are based on an unobservable character (deposition time) and that is why the recognition of this character is involved in the distinction of other units: biozones, magnetozones, or on datings obtained by radiometric methods. Currently, there are favorable opinions about establishing a single chronologic scale, discarding the difference between chronostratigraphic and geochronologic scales, using the stage category and rejecting the age category (see Tonni 2009). However, this has not been considered by the International Union of Geological Sciences.

New and intense paleontological surveys in different sections cropping out in the Pampean region, especially in the coastal area between Mar del Plata and Miramar, resulted in new collections with precise stratigraphic provenance. In addition, many specialists restudied the existing collections in different institutions. This work concluded in the refining of faunal lists and the establishment of the first and last records of the taxa involved. Based upon this knowledge, a biostratigraphic framework involving the continental sediments and faunas of the Pampean region, from the Late Miocene to the present, was developed. Cione and Tonni (2005) recognized 13 biozones (Association Zones or alternatively Interval Zones, see CAE 1992; Murphy and Salvador 1999) for this interval, which represent the biostratigraphic basis for the recognition of as many stages and substages which are the material basis (chronostratigraphic) supporting the corresponding ages and subages. Further investigation determined some modifications and/or additions to the scheme proposed by Cione and Tonni (2005) (e.g., Verzi et al. 2004; Soibelzon et al. 2008a, 2010).

2.3.2 *Comments on the Pampean Loess and Lithostratigraphic Units of the Pampean Region*

The loess deposits in South America cover a wide area between 23°S and 38°S (Zárate 2003), more than 1,000,000 km^2 of central and northern Argentina (Bidegain et al. 2007). González Bonorino (1965) suggested that the Pampean sediments derive mainly from the denudation of Cenozoic formations of peripheral areas of La Pampa Province (Norpatagonian Mesozoic vulcanites, Tertiary Patagonian basalts, and the crystalline basement of the Pampean Ranges) and from the activity of Pleistocene volcanoes of the cordillera. More recent studies indicate several areas of loess supply (besides the classical ones) to the north and west of the Chaco-Pampean plain, involving different stages (see Zárate 2003, and literature cited therein), where fluvial transport was more important than eolian. Rabassa et al. (2005) assigned the Pampean loess deposit to eolian activity generated by glacial climatic conditions, which influenced the marine anticyclone centers (both the Pacific and Atlantic), shifting northward (see Rabassa et al. 2005).

These sediments, which correspond to the continental Late Cenozoic, are represented by a sedimentary sequence relatively homogeneous in lithology (Zárate 2005). This sedimentary cycle began in the Late Miocene and continued even in the Holocene. Along the history of geologic and paleontological studies of this region, they have been referred to numerous lithostratigraphic or allostratigraphic units (e.g., Epecuén Formation, Arroyo Chasicó Formation, Arroyo Seco Formation, Playa Los Lobos Alloformation). According to Zárate (2005) and Folguera and Zárate (2009), the Late Miocene sediments were grouped into the Araucanian in Catamarca Province, the Cerro Azul Formation in La Pampa and Mendoza provinces, and Epecuén and Arroyo Chasicó formations in Buenos Aires Province. The Late Miocene–Middle/Late Pliocene interval includes in southeastern Buenos Aires the Río Negro, La Norma, Monte Hermoso, Chapadmalal formations and the Playa San Carlos and Playa Los Lobos alloformations. For the Late Pliocene–Early Pleistocene, Zárate (1989, 2005) assigns the Barranca Los Lobos, Vorohué, San Andrés, and Miramar "formations" of Kraglievich (1952) to the Punta Martínez de Hoz and Punta San Andrés alloformations (see details of the subsequent subdivision of this formation in Sect. 2.4) of the northeastern area, which was later named Ensenada and Buenos Aires formations. For the Late Pleistocene–Holocene, several stratigraphic proposals have been established for the fluvial sediments that include the Ameghino's "post-pampeano" with the Lujanian and Platan substages, afterward included in the Luján Formation as Guerrero and Río Salado members, respectively. Later works include the La Chumbiada Member underlying the Guerrero Member. Likewise, the Lobería "Formation" of Kraglievich (1952) and the Arroyo de Lobería Alloformation (see Zárate 2005) are included in this interval. The eolian facies of this interval belong to the La Postrera Formation (see Zárate 2005).

2.4 The Late Cenozoic Mammals of the Pampean Region. A Biostratigraphical Point of View

It has been evident for all mammal sequences in the world that there is an increasing interest in developing biostratigraphic schemes to properly identify stratigraphic sequences that can be dated radiometrically, analyzed magnetoestratigrafically, and correlated as certainly and broadly as possible (Cione et al. 2007). This is especially true for the Late Miocene to recent times in the eastern Pampean area of Argentina where an almost continuous biostratigraphic sequence constitutes the basis of the chronological scale of South America (see Fig. 2.5). In the last 20 years, the biostratigraphic resolution in the continental Cenozoic of South America has been doubled in relation to previous scales (Cione and Tonni 2005).

The refining of the biostratigraphic-type sequence of the Pampean region has shown the ordering of first appearance of mammals of North American origin. In the continent have allowed discussions on the correlation of type sections in the Pampean area with other regions (e.g., northwestern Argentina: Reguero and Candela 2011; Bolivia: Cione and Tonni 1996; Tonni et al. 2009; Corrientes, Argentina: Scillato-Yané et al. 1998; Gasparini and Zurita 2005; Uruguay:

Ubilla and Perea 1999; La Rioja: Tauber 2005) (Fig. 1.1). Besides, other regional biostratigraphic sequences have also been proposed (e.g., Deschamps 2005). A putative biostratigraphical but actually biochronological scale for the Late Miocene of central Argentina, and supported by rodents, try to refine the correlations and temporal assignments of some Late Cenozoic units (Verzi et al. 2003, 2008; see comments in Sect. 2.4.11).

In this chapter, we follow the chronostratigraphic scheme of Cione and Tonni (2005) with additional refinements proposed by other authors (Alberdi and Prado 1992, 1993, 2004; Alcaraz 2010; Alcaraz and Francia 2013; Alcaraz and Ferrero 2013; Alcaraz and Zurita 2004; Avilla et al. 2013; Berman 1994; Bond 1999; Bond et al. 2001; Brandoni et al. 2008; Carlini and Scillato-Yané 1999; Carlini and Vizcaíno 1987; Carlini et al. 2004, 2005; Cruz 2013; Cruz et al. 2011; Deschamps et al. 2012, 2013; Esteban 1996; Ferrero 2009; Gasparini 2004, 2007, 2013; Gasparini et al. 2006, 2011, 2014; Gasparini and Ferrero 2010; Gasparini and Zurita 2005; Goin 1991; Goin and Pardiñas 1996; Krmpotic et al. 2004, 2009; Menegaz 2000; Miño-Boilini et al. 2006, 2014; Miño-Boilini and Carlini 2007, 2009; Miño-Boilini 2012; Montalvo and Casadío 1988; Montalvo and Verzi 2002; Montalvo et al. 1995, 1998; Olivares et al. 2012; Olivares and Verzi 2014; Pardiñas 1995, 1999; Pardiñas and Tonni 1998; Prado and Alberdi 1996, 2010; Prado et al. 1998, 2000; Prevosti 2006, 2010; Prevosti et al. 2004, 2005, 2006; Prevosti and Soibelzon 2012; Quintana 1994, 1996, 1998; Reig 1978, 1987, 1994; Reig and Quintana 1992; Scillato-Yané 1982; Scillato-Yané et al. 1995, 2010; Soibelzon 2004, 2008; Soibelzon et al. 2005, 2006b, 2008b, 2009a, b, 2010, 2012; Soibelzon and Prevosti 2008; Soibelzon and Schubert 2011; Sostillo et al. 2014; Tauber 1997, 2000; Tomassini 2012; Tomassini et al. 2013; Urrutia et al. 2008; Verzi 2002; Verzi and Montalvo 2008; Verzi et al. 2002, 2008; Verzi and Olivares 2006; Vizcaíno et al. 2009; Voglino and Pardiñas 2005; Vucetich et al. 1997, 2014; Vucetich and Verzi 1995, 2002; Wang et al. 2004a, b; Zamorano and Brandoni 2013; Zamorano 2013; Zamorano and Scillato 2011; Zamorano et al. 2011, 2012, 2013, 2014; Zurita 2002, 2007; Zurita et al. 2004, 2006, 2008, 2009a, b, 2010, 2011a, b, c, 2013).

2.4.1 *Biozone of Macrochorobates scalabrinii (See Fig. 2.7)*

This is the local representation of the Lower Huayquerian (Late Miocene). It is defined at the lower valley of the Chasicó Creek (Tonni et al. 1998). The base is the lower part of an innominated lithostratigraphic unit formed by coarse sands to conglomerates resting unconformably on the Las Barrancas Member of the Arroyo Chasicó Formation.

Other four "biozones" are based on micromammals; they were proposed by Verzi et al. (2008) for the Upper Huayquerian cropping out especially at the eastern part of La Pampa Province and southwestern Buenos Aires Province (see below).

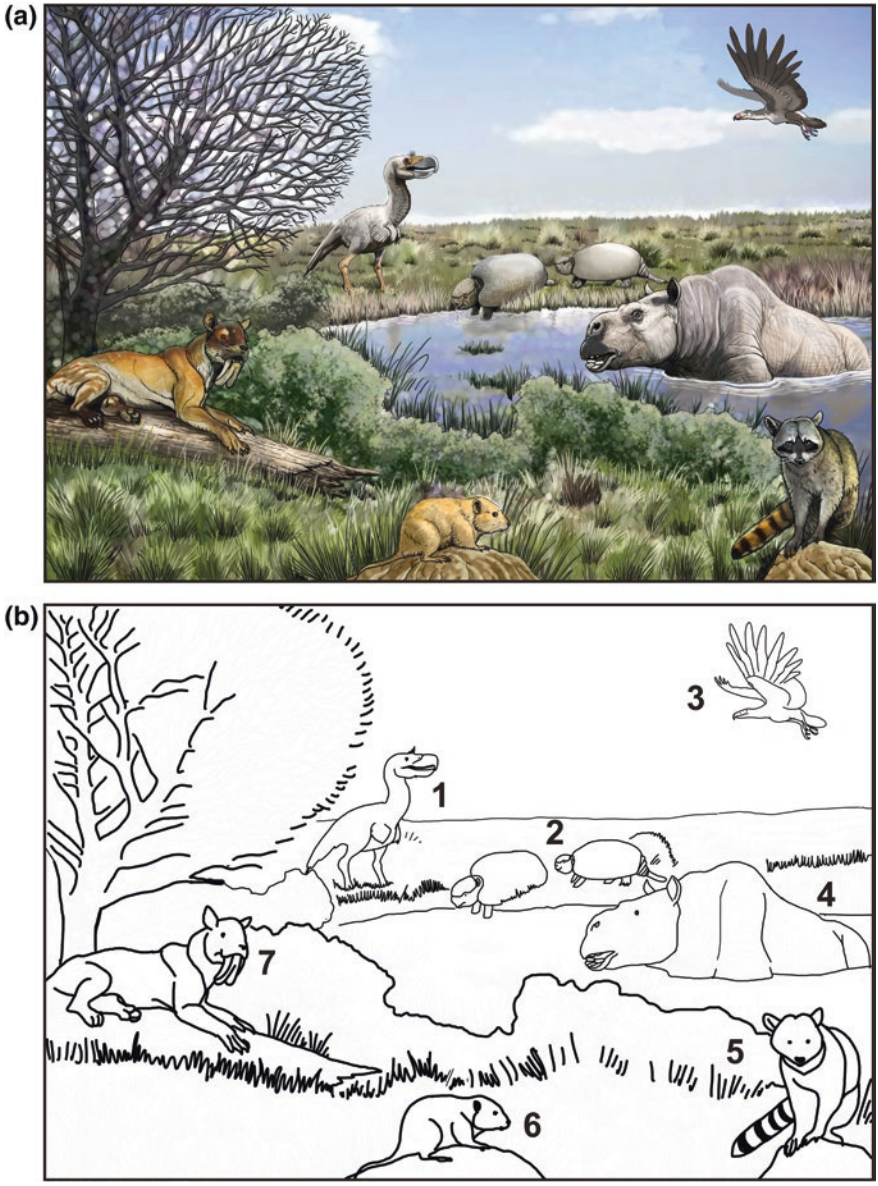

Fig. 2.7 Representation of the environmental characteristics and the mastofauna of Pampean region of Argentina during the Huayquerian Stage (Late Miocene). *Numbers* indicate taxa: *1* fororracid (*Onactornis*); *2* glyptodontid; *3* teratornitid (*Argentavis*); *4* native ungulate (*Toxodon*); *5* procyonid (*Cyonassua*); *6* echimyid; *7* marsupials (*Thylascomylus*). Drawings by Jorge González

2.4.2 Biozone of Eumysops Laeviplicatus (Tomassini 2012; Tomassini et al. 2013 = Trigodon gaudryi and Neocavia depressidens Biozones of Cione and Tonni 2005)

Cione and Tonni (2005) proposed two biozones for the marine cliffs of Farola Monte Hermoso, the *T. gaudryi* and *Neocavia depressidens* biozones, which supported the Montehermosan and Lower Chapadmalalan stages, respectively. Tomassini (2012) proposed that the Monte Hermoso Formation, in its type locality (Farola Monte Hermoso), is represented by a single biostratigraphic unit. Such unit is the Range Zone of *Eumysops laeviplicatus* and represents the biostratigraphic base of the Montehermosan Stage/Age, which is assigned to the Late Miocene–Early Pliocene. Besides *E. laeviplicatus*, the exclusive taxa of this biozone are as follows: *Hyperdidelphys inexpectata*, *Sparassocynus bahiai*, *Eumysops formosus*, *Pithanotomys columnaris*, *Pithanotomys macer*, *Phugatherium cataclisticum*, and probably *Argyrolagus palmeri* (see Deschamps et al. 2012; Olivares et al. 2012; Vucetich et al. 2014). However, *T. gaudryi*, the typical mammal taxon of the *T. gaudryi* Biozone, has not been recorded in the upper levels (the upper part of the *E. laeviplicatus* Biozone of Tomassini 2012; Tomassini et al. 2013).

This biozone should be the biostratigraphic basis of the Montehermosan Stage. There are some different opinions about the age of the base of this stage, however. Tomassini (2013) consider that dating of escorias provides an age of 5.28 Ma for the age. On the contrary, Reguero and Candela (2011) proposed to date the base at 7.1 Ma. In this second case, the first record of North American taxa would correspond to the Montehermosan. We do not follow this latter view here.

The first sigmodontine rodents (field mice) are first recorded in this biozone.

2.4.3 Biozone of Paraglyptodon chapadmalensis (See Fig. 2.8)

It is the biostratigraphic base for the Chapadmalalan (Late Pliocene). It was defined, as well as the three following units, in the area of Barranca de los Lobos (General Pueyrredón County)—Cañadón Chapar (General Alvarado County) in southeastern Buenos Aires Province. It is partially coincident with the Chapadmalal "Formation" of Kraglievich (1952, 1953, 1959).

The Holarctic family Tayassuidae is recorded for the first time in South America in this biozone. The remains are assigned to the North American genus *Platygonus* (Gasparini 2007, 2013).

The caviomorph genus *Microcavia*, also recorded in this biozone, has its first record in the area of Farola Monte Hermoso cliffs but with unknown stratigraphic provenance (Quintana 1996).

The Chapadmalalan fauna is very diverse indicating different environments. The presence of arid and semiarid indicators is noteworthy (argyrolagid marsupials,

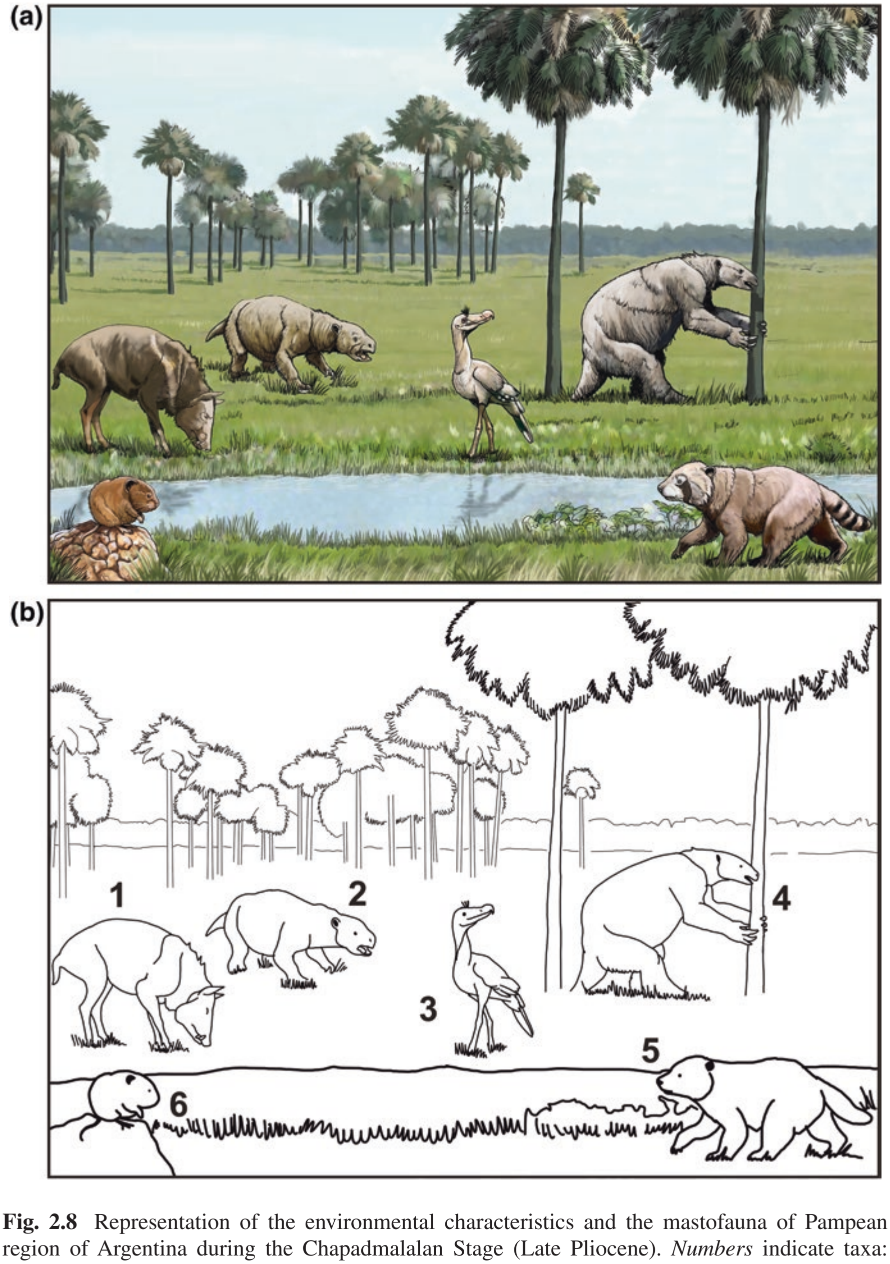

Fig. 2.8 Representation of the environmental characteristics and the mastofauna of Pampean region of Argentina during the Chapadmalalan Stage (Late Pliocene). *Numbers* indicate taxa: *1* tayassuid (*Platygonus*); *2* xenarthran (*Glossotheridium*); *3* forusrhacid (*Psilopterus*); *4* xenarthran (*Scelidotheridium*); *5* procyonid (*Chapadmalania*); *6* cricetid (*Dankomys*). Drawings by Jorge González

see Simpson (1970); abundance of fossorial rodents) as well as others related to conditions similar to the modern ones but more rainy and with presence of gallery forests or forest patches (certain didelphid marsupials, see Simpson 1972). Small mammals are dominant, such as the rodentiform notoungulate *Paedotherium* and the caviomorph rodent *Actenomys*, being the megamammal remains very scarce. By the end of the Chapadmalalan, around 3 Ma (Schultz et al. 1998), a strong process of extinction involved numerous authochtonous species, genera, and even families (Thylacosmilidae, Argyrolagidae).

Zamorano et al. (2014) cited the oldest record of the genus *Panochthus* from this unit. Remarkably, it is unknown in the overlying Marplatan and, as a Lazarus taxon, appears again in the Ensenadan.

2.4.4 Biozone of Platygonus scagliai (See Fig. 2.9)

It is the biostratigraphic base of the lower part of the Marplatan Stage (Barrancalobian Subage). It spatially coincides with the Barranca de los Lobos "Formation" of Kraglievich (1952, 1953, 1959).

The guide species in this biozone is the tayassuid *Platygonus scagliai*. However, Gasparini (2007) found one specimen from the coastal cliffs between Lobería Creek and Punta Vorohué (General Pueyrredón County, Buenos Aires Province) in the overlying Sanandresian. Thus, this taxon is no more exclusive of the Barrancalobian.

Members of the Holarctic family Camelidae (vicuñas, guanacos) are first recorded, as well as the first *Dolichotis* (rodent genus that includes the modern mara or Patagonian hare) and *Lagostomus* (modern vizcacha).

2.4.5 Biozone of Akodon (Akodon) lorenzinii (See Fig. 2.9)

It is the biostratigraphic base of the Middle Marplatan (Vorohuean Subage). It roughly corresponds to the Vorohué "Formation" of Kraglievich (1952, 1953, 1959).

Both the Barrancalobian and Vorohuean faunas are much less diverse than the Chapadmalan. However, the Biozone of *Akodon* (*Akodon*) *lorenzinii* includes the first appearance of several families of Holarctic origin indicating the beginning of the GABI (sensu Woodburne 2010). These families are the Equidae (extinct horses of the genus *Hippidion*), Canidae (foxes of the genus *Dusicyon*), and Mustelidae (ferrets of the genus *Galictis*).

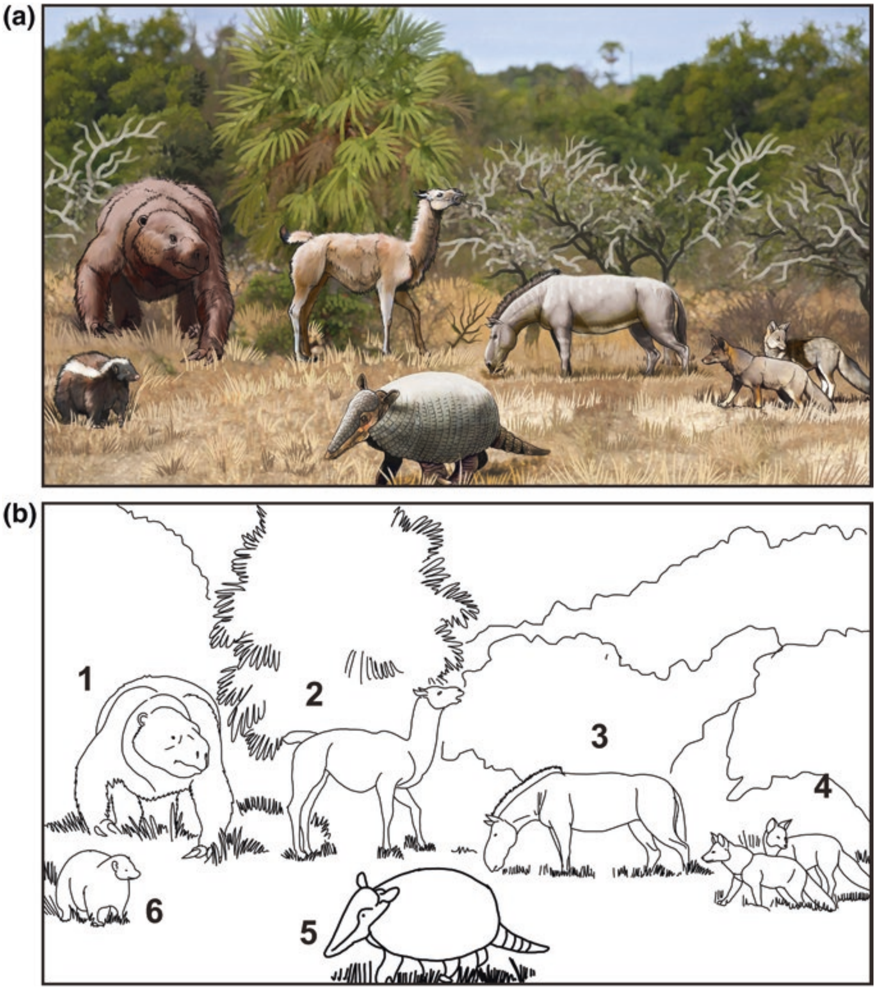

Fig. 2.9 Representation of the environmental characteristics and the mastofauna of Pampean region of Argentina during the Marplatan Stage (Late Pliocene). *Numbers* indicate taxa: *1* giant ground sloth (*Glossotherium*); *2* camelid (*Lama*); *3* equid (*Hippidion*); *4* foxes (*Dusicyon*); *5* giant armadillo (*Eutatus*); *6* skunk (Mephitinae). Drawings by Jorge González

2.4.6 Biozone of Ctenomys chapalmalensis (=Zone of Paractenomys chapadmalensis of Cione and Tonni 1995; See Verzi and Lezcano 1996) (See Fig. 2.9)

This is the biostratigraphic base of the Upper Marplatan (Sanandresian Subage), which coincides spatially with the San Andrés “Formation” (Fig. 2.10) of Kraglievich (1952, 1953) and Teruggi et al. (1974).

The Sanandresian includes an important faunal turnover in relation to the Vorohuean that putatively corresponds to the beginning of the Quaternary. During the Sanandresian, several species adapted to cold and arid or semiarid conditions are firstly recorded in the Pampean region, such as the marsupial *Lestodelphys* and the large tardigrades (xenarthrans or edentates) that will characterize the Pampean Pleistocene. Coincidentally, this is the moment of the last record of the Echimyidae rodents of the genus *Eumysops*, whose species were very frequent during the Pampean Pliocene and earliest Pleistocene (Olivares et al. 2012). These rodents currently inhabit intertropical and subtropical areas; they persisted with some sporadical occurrences in the Pampean area during the Ensenadan represented by a still-living genus. The deposition of the Sanandresian sediments and its fauna is coeval with glacial advances in southern Argentina (Rabassa et al. 2005) related to MIS 82–78 (see Tonni 2009). A vertebra possibly referable to Gomphotheriidae was reported from Sanandresian beds in northwestern Argentina (López et al. 2001). A Miocene record of Gomphotheriidae from Peru (Campbell et al. 2000, 2010) has been questioned systematically as well as stratigraphically (see Prado et al. 2005).

Fig. 2.10 Vorohuean and Sanandresian beds cropping out in the coastal cliffs at Punta San Andrés, Mar del Plata (General Pueyrredón County, Buenos Aires Province). Photograph by Esteban Soibelzon

2.4.7 *Biozone of Mesotherium cristatum (See Verzi et al. 2004; Soibelzon 2008; Soibelzon et al. 2008a, b, 2009b, 2010. Biozone of Tolypeutes Pampaeus—Daedicuroides, Cione and Tonni 1995; Biozone of Tolypeutes Pampaeus, Cione and Tonni 2005) (See Fig. 2.11)*

This is the biostratigraphic base of the Ensenadan (Early to Middle Pleistocene). It coincides spatially with the Ensenada Formation in southeastern Buenos Aires Province (see Tonni et al. 1999; Soibelzon et al. 2008c) and also with the Miramar "Formation" (Kraglievich 1952, 1953; Soibelzon et al. 2009b).

In this biozone, several families of Holarctic origin (Cervidae, Ursidae, Tapiridae, Felidae, and Gomphotheriidae) as well as many genera and species of autochthonous clades are first recorded: *Neolicaphrium*, *Propraopus*, *Dasypus*, *Glyptodon*, *Panochthus*, *Neuryurus*, *Doedicurus*, *Lomaphorus*, *Scelidotherium*, *Mylodon*, *Megatherium*, *Pampatherium typum*, *Myocastor*, and *Neochoerus*. Several taxa of North American origin are also first recorded in the Ensenadan: *Akodon azarae*, *Lundomys*, *Scapteromys*, *Necromys*, *Calomys* (*Calomys cf. C. laucha*–*C. musculinus*; see Pardiñas 1999, 2004) *Hippidium principale*, *Hemiauchenia*, and *Catagonus*. The species *Megatherium tarijensis* would not be a valid species, and its stratigraphic provenance is dubious (Soibelzon 2007). The cervid *Antifer ensenadensis* is cited as exclusive taxon by Cione and Tonni (2005) in the Pampean region; however, Labarca and Alcaraz (2011) mention that this species is also present in the Lujanian Toropí Formation (Corrientes Province).

Concerning "*Megatherium*" *istilarti* from the "Irenense" of the Quequén Salado River (Lower Chapadmalalan; after Cione and Tonni 1995), its inclusion in *Megatherium* is likely incorrect (Brandoni 2006) since some characters of this species are more related to *Pyramiodontherium*.

The type locality of the Ensenadan of Ameghino (1889) (La Plata harbor, Ensenada) is no longer available for study. However, a profile in a quarry was proposed a new type section as a new type locality (Hernández, La Plata County, 34° 54′ 35″S and 58° 00′ 15″W). The characteristic fossils of the Biozone of *Mesotherium cristatum* here occur (Bidegain 1991; Tonni et al. 1999).

In northeastern Buenos Aires Province, the characteristic fossils of the Biozone of *Mesotherium cristatum* are found in sediments deposited from more than 0.98 Ma (C1r1n subcron) up to the lower part of the Brunhes Chron (less than 0.78 Ma) (Soibelzon et al. 2008a). Consequently, this biozone could extend up to the unconformity that separates the Ensenada Formation from the Buenos Aires Formation, which, in some cases, decapitates a paleosol (El Tala Geosol, Tonni et al. 1999) (see comments in Soibelzon et al. 2008a). This partly coincides with the proposal of Verzi et al. (2004) who tentatively place the border between the Bonaerian and Ensenadan stages in the beginning of the isotopic stage 11 (ca. 0.40 Ma). Recent findings in another quarry in La Plata (Buenos Aires Province) suggest that the lower border may extend up to the Olduvai event (C2n chron, between 1.95 and 1.77 Ma; see Soibelzon et al. 2008a).

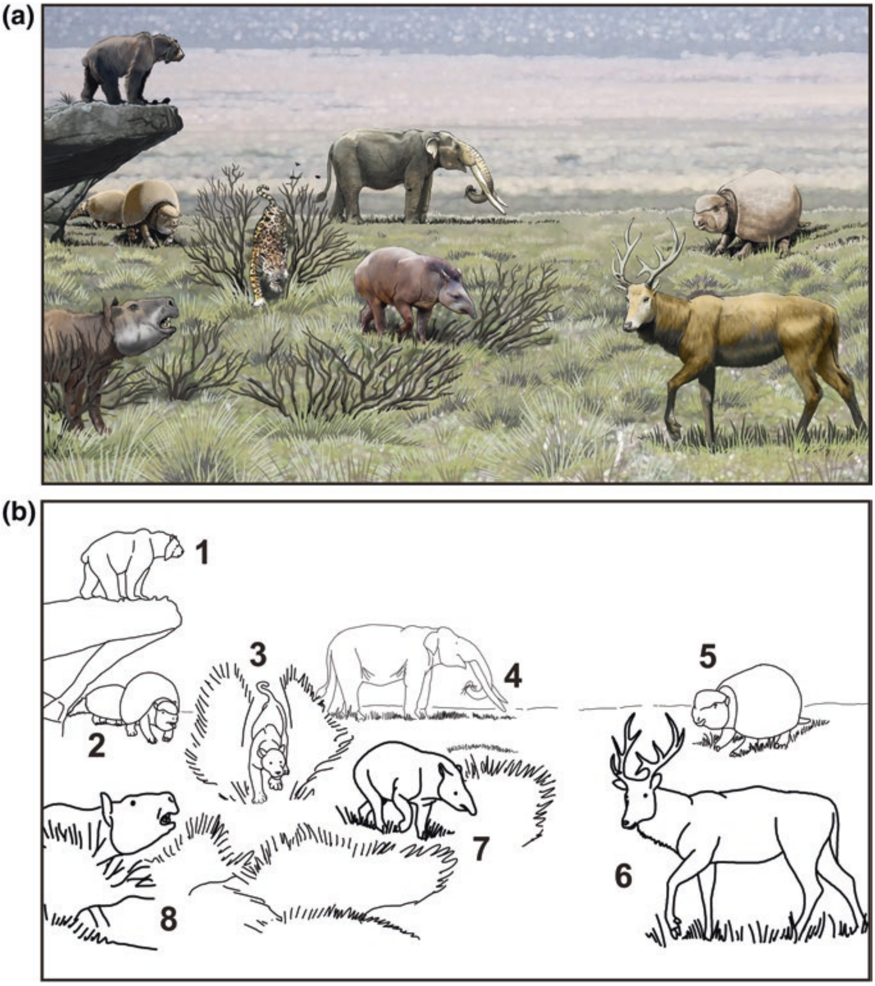

Fig. 2.11 Representation of the environmental characteristics and the mastofauna of Pampean region of Argentina during the Ensenadan Stage (Early to Middle Pleistocene). *Numbers* indicate taxa: *1* bear (*Arctotherium*); *2* xenarthran (*Glyptodon*); *3* felid (*Panthera*); *4* gomphotherid (*Stegomastodon*); *5* xenarthran (*Neosclerocalyptus*); *6* cervid (*Antifer*); *7* tapir (*Tapirus*); *8* native ungulate (*Toxodon*). Drawings by Jorge González

2.4.8 Biozone of Megatherium americanum (Cione and Tonni 1999)

This is the biostratigraphic base of the Bonaerean (Middle Pleistocene). Its lower boundary coincides with the base of the Buenos Aires Formation in northeastern Buenos Aires Province (Tonni et al. 1999; Nabel et al. 2000) and probably with the base of the Arroyo Seco “Formation” (Kraglievich 1952, 1953) in the southeast.

The cervid *Antifer ultra* Ameghino, cited as an exclusive taxon by Cione and Tonni (2005), has been recorded in southern Argentine Mesopotamia (Entre Ríos Province) in sediments referable to the Lujanian Stage (Arroyo Feliciano Formation, see Alcaraz et al. 2005). *Antifer* sp. is also recorded in the Toropí Formation, in Corrientes Province (Alcaraz and Zurita 2004), with OSL datings that refer temporally this unit to the Lujanian Stage (Tonni et al. 2005). The genus *Antifer* is recorded as well in the Late Pleistocene of Uruguay (Kraglievich 1932), Chile (Casamiquela 1968, 1984; Tavera 1978; Labarca and López 2006) and southern Brazil (Souza Cunha and Magalhaes 1981). *Epieuryceros* cf. *proximus* has been recorded in sediments probably Lujanian in age in the Formosa Province (Alcaraz and Zurita 2004).

One biozone based on micromammals, the Biozone of *Ctenomys kraglievichi* (Rusconi), has been described for southern Buenos Aires Province (Verzi et al. 2004; Deschamps 2005). This biozone is correlated to the base of the Biozone of *Megatherium americanum* and bears micromammals related to a warm climatic pulse. The records include caviomorph rodents such as the ctenomyid *Ctenomys kraglievichi*, an echimyid related to the living *Clyomys*, the dasyproctid *Plesiaguti totoi*, and the chiropteran *Noctilio* (Vucetich and Verzi 2002; Merino et al. 2007). *Plesiaguti totoi* is the single dasyproctid recorded in the Argentine Pleistocene. *Clyomys* and *Plesiaguti* of Brazilian affinities (sensu Hershkovitz 1958) suggest their relation to a strong warm pulse, probably seasonally dry (see Vucetich et al. 1997; Vucetich and Verzi 1999, 2002).

2.4.9 Biozone of Equus (Amerhippus) neogaeus (Cione and Tonni 1999) (See Fig. 2.12)

This is the biostratigraphic base of the Lujanian Stage (Late Pleistocene–Early Holocene), as was defined by Cione and Tonni (1999, 2001). The Lujanian of Cione and Tonni 1999, 2005) does not correspond to the Lujanian of Pascual et al. (1965) and Marshall et al. (1984). These latter include in their Lujanian the beds with Bonaerean fossils. The guide fossil *E. (A.) neogaeus* is represented from the base of the unit that corresponds to the interglacial represented by the MIS 5e (130 ka BP, base of the Late Pleistocene, see Pardiñas et al. 1996; Cione and Tonni 2005). The marine coastal levels of the Pascua Formation (Fidalgo et al. 1973) are likely to represent this interglacial. However, recent radiocarbon datings suggest that at least part of the deposits referred to the "Belgranense" and the Pascua Formation may be correlated with part of MIS 3 (Tonni et al. 2010). Previously, Cortelezzi (1977), Weiler et al. (1987), González and Ravizza (1987), and Weiler and González (1988) described coastal marine sediments in Buenos Aires Province attributed to the last interstadial between 25,000 and 38,000 ^{14}C years BP. Rabassa (1983) described beach marine sediments from the Antarctic Peninsula considered to be isostatically raised and attributed them

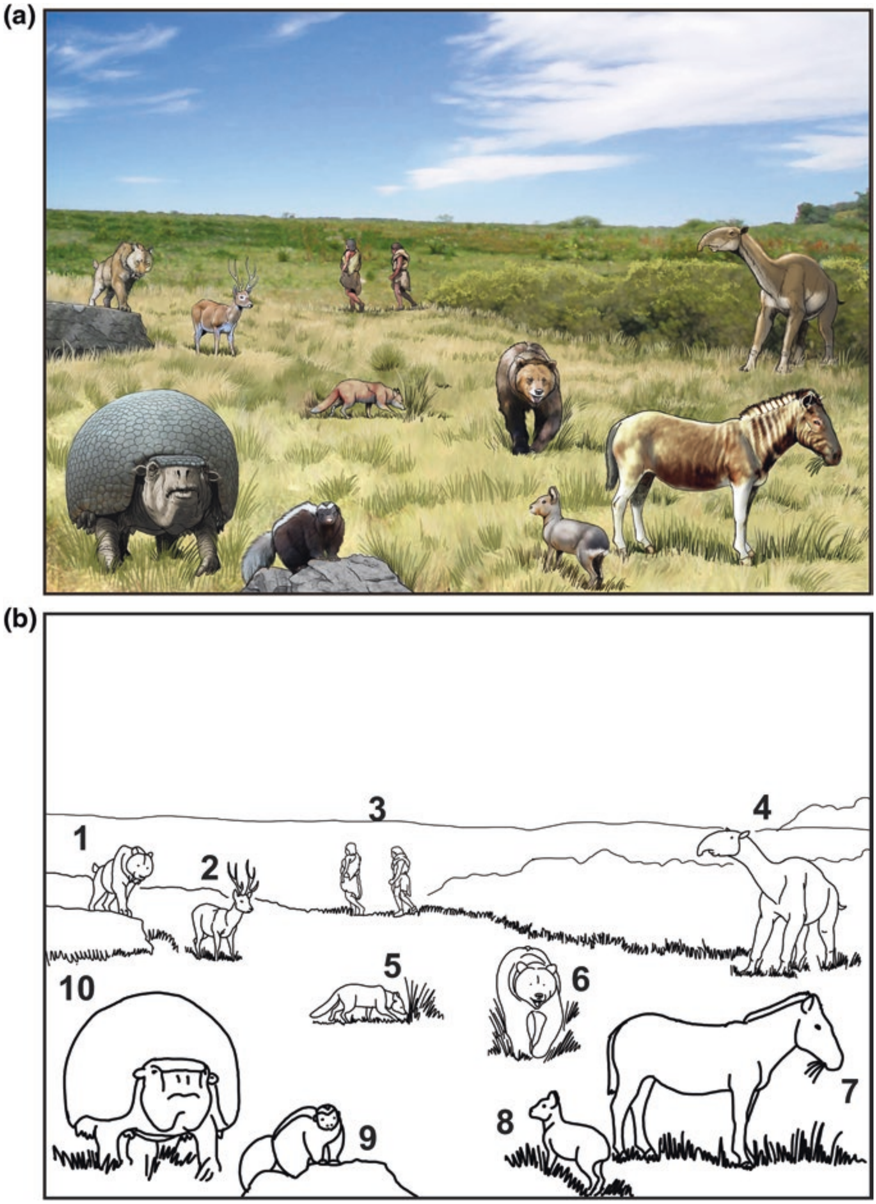

Fig. 2.12 Representation of the environmental characteristics and the mastofauna of Pampean region of Argentina during the Lujanian Stage (Late Pleistocene–Early Holocene). *Numbers* indicate taxa: *1* felid (*Smilodon*); *2* cervid (*Morenelaphus*); *3* man (*Homo sapiens*); *4* native ungulate (*Macrauchenia*); *5* fox (*Lycalopex*); *6* bear (*Arctotherium*); *7* equid (*Equus* (*Amerhippus*)); *8* mara (*Dolichotis*); *9* skunk (*Conepatus*); *10* xenarthran (*Glyptodon*). Drawings by Jorge González

to a partial glacier recession. Shells of the mollusk *Laternula elliptica* (King and Boderip) found in life position gave an age of 34,115 ± 1110 ^{14}C years BP (Hv-11002), which also corresponds to the end of MIS 3.

The earliest records of *Homo sapiens* in the Pampean region occur in this biozone (Flegenheimer and Zárate 1997; Politis and Gutiérrez 1998). Many typical South American megafaunal taxa became extinct at the end of this age. However, in the Pampean area, there also were pseudoextinctions (Tapiridae, Tayassuidae). The typical bears that inhabited the area became extinct, but a new North American bear genus has its first appearance in the Holocene: the spectacle bear with the local species *Tremarctos ornatus*.

Most Lujanian vertebrates of the Buenos Aires Province were found in flood plain sediments of the Guerrero Member of the Luján Formation. This unit was deposited during the interval between ca. 21,000 ^{14}C years BP and ca. 10,000 ^{14}C years BP (Tonni et al. 2003), during which several climatic events took part (LGM, Younger Dryas, among others; see Tonni et al. 2003 and literature therein) that were reflected in the faunal distribution.

Martínez et al. (2013) described two archaeological sites in the middle basin of the Quequén Grande River (38° 12′S–59° 07′W), with datings between 10,440 ± 100 and 7314 ± 73 radiocarbon years BP. These sites include abundant faunistic remains both of extinct megafauna and living species.

2.4.10 *Biozone of Lagostomus maximus (Cione and Tonni 1999) (See Fig. 2.13)*

This is the biostratigraphic base of the Platan (Early Holocene–sixteenth century), as it was originally defined by Tonni (1990). Its base coincides with that of the Río Salado Member of the Luján Formation and includes in the water divides eolian sediments of the La Postrera Formation. The base is dated around 7000 ^{14}C years BP and the top in the 16th, when the fauna introduced by Spaniards in the Pampean region was firstly recorded.

In this biozone, only living species of autochthonous fauna are recorded, with the exception of *Dusicyon avus* which became extinct near 1600 ^{14}C years BP (Tonni and Politis 1982; Politis et al. 1995).

In the southern Buenos Aires Province, Deschamps (2005) recognized and described the Biozone of *Ozotoceros bezoarticus*, referable to the Platan Stage. The type area is the valley of the Arroyo Napostá Grande (Chacra Santo Domingo). The stratotype is the upper section of the Agua Blanca Sequence. The characteristic assemblage is *O. bezoarticus*, *Lama guanicoe*, *Lagostomus maximus*, *Cavia aperea*, and *Ctenomys* (Fig. 2.14).

The Early Holocene (10–8 ^{14}C ka BP) witnessed arid conditions with probable lower than present temperatures in different parts of the Buenos Aires Province (see Pardiñas 2001 and literature therein). Around 7 ^{14}C ka BP began a warm and

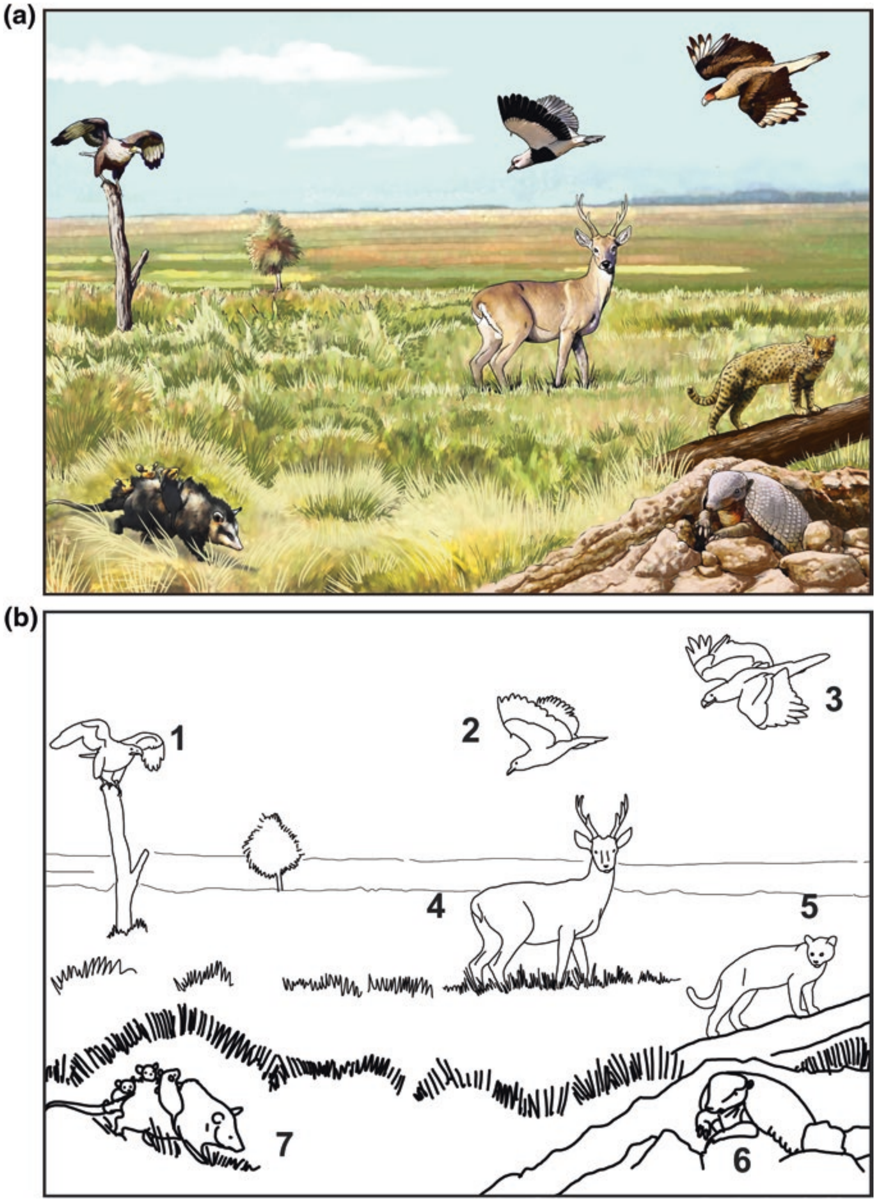

Fig. 2.13 Representation of the environmental characteristics and the mastofauna of Pampean region of Argentina during Recent times. *Numbers* indicate taxa: *1*, *3* falconid (*Caracara*); *2* charadrid (*Vanellus*); *4* cervid (*Ozotoceros*); *5* felid (*Leopoardus*); *6* xenarthran (*Chaetophractus*); *7* opossum (*Didelphis*). Drawings by Jorge González

Fig. 2.14 Rodents. *Upper left* Cricetidae *Akodon* sp.; *right* Caviidae *Dolichotis patagonum*; *lower left* Chinchillidae *Lagostomus maximus*; *right* Hidrochoeridae *Hidrochoeris hidrochoerus*. Photograph by Esteban Soibelzon

humid event represented by pedogenesis and expansion of the subtropical fauna. This event gave place to a marine ingression that produced important beach deposits (the Las Escobas Formation, Fidalgo et al. 1973) with abundant pelecypod and gastropod remains mainly along the coast of the Río de La Plata. Semiarid to arid conditions prevail again near 5 ^{14}C ka BP. Between the years 900 and 1300 AD, another pedogenetic event coincides with the southern displacement of subtropical species, especially micromammals. *Dasypus hybridus* is a subtropical dasypodid found at La Toma, an archaeological site of the piedmont area of the Sierra de la Ventana system (Buenos Aires Province, 38° 17′S), in sediments that have a radiocarbon dating of 995 ± 64 years BP. The record of *D. hybridus* at La Toma represents a new southern expansion of Brazilian elements during the Holocene, being the first of these expansions, that of the presence of *Scapteromys* in La Moderna (37°S) between 7000 and 7500 radiocarbon years BP (Politis et al. 2003). These southward advances of Brazilian (subtropical) elements are isolated events along the Holocene, in which mainly arid and semiarid conditions prevailed. Such conditions occurred up to the second half of the nineteenth century, after which the conditions became similar to the present ones, more humid and warmer, that favored the return of Brazilian fauna (Tonni 2006).

In the site Tala Huasi (Córdoba Province), Soibelzon et al. (2013) records *D. hybridus* dated at 274 ± 29 radiocarbon years BP in association with *O. bezoarticus* and *Hevea brasiliensis*. In the site Lobería 1, Lobería County, Buenos Aires Province, with a radiocarbon dating of 440 ± 60 years BP, *D. hybridus* is associated with *O. bezoarticus*, *Dolichotis patagonum* and *L. guanicoe*. *O. bezoarticus* and *D. patagonum* are locally extinct between the end of the nineteenth century and beginning of the twentieth century, whereas *L. guanicoe* became extinct locally just before the contact of Spaniards and aboriginals (Tonni 1990). From the end of the eighteenth century and up to the second half of the nineteenth century, the faunal records suggest semiarid to arid conditions with lower temperatures than modern ones.

According to Deschamps (2003) and Cione and Tonni (2005), it is useful to define a Biozone of *Bos taurus*/*Ovis aries* for those sediments in which there is fauna introduced by Spaniards.

2.4.11 An Alternative Scheme for the Late Miocene Based on Biochronology

Verzi et al. (2008) proposed four "biozones" for the Late Miocene. We note that these "biozones" are not stacked and the ordering is according to the "*stage of evolution*" of several taxa.

Biozone of *Chasichimys scagliai* or *Chasichimys* "morphotype a"

Reference section: The type area and section is Bajo Giuliani (36° 43′S–64° 18′W, La Pampa Province). The stratotype is recognized at the levels of the Cerro Azul Formation cropping out at this locality. It includes other octodontoid rodents such as *Reigechimys simplex*, *Neophanomys pristinus*, *Palaeoctodon* aff. *simplicidens*, and *Pampamys emmonsae* and other taxa such as *Pliolestes venetus*, *Zygolestes tatei*, *Thylamys pinei*, and *Microtragulus rusconi* (see Montalvo and Casadío 1988; Verzi et al. 1994, 1999; Goin et al. 2000; Sostillo et al. 2014).

Biozone of *Xenodontomys simpsoni*

Reference section: the type area and section is Barrancas Coloradas (36° 41′S–64° 11′W, La Pampa Province). The stratotype is recognized at the lower levels of the Cerro Azul Formation in this locality.

Other taxa present in the association are *Phtoramys hidalguense*, aff. *Clyomys*, *Chasicotautus ameghinoi*, and *Microtragulus rusconi* (see Montalvo et al. 1998).

Biozone of *Xenodontomys ellipticus*

Reference section: The type area and section is Cantera Seminario (38° 45′S–62° 11′W, Buenos Aires Province); the stratotype is recognized at Level 2 of the Saldungaray Formation (Deschamps et al. 1998). Other taxa recorded are *Phtoramys* cf. *hidalguense*, *Borhyaenidium*, *Aspidocalyptus*, and *Berthawyleria* (see Verzi et al. 2008).

Biozone of *Xenodontomys elongatus*

Reference section: The type area and section is Caleufú (35° 41′S–64° 40′W, Rancul Department, La Pampa Province). The stratotype is recognized at the lower levels of the Cerro Azul Formation in this locality. Other taxa recorded are *Neophanomys recens*, *Phtoramys homogenidens*, *Ringueletia simpsoni*, and *Chasicotatus ameghinoi* (Montalvo and Verzi 2002; Urrutia 2004). Verzi et al. (2008) and Verzi and Montalvo (2008) proposed that this biozone contains the first representatives of Muridae (Cricetidae) and Mustelidae in South America, but Prevosti and Pardiñas (2009) contend that the "*stage of evolution*" used by Verzi and Montalvo (2008) to justify the assignment of the association of the Caleufú locality (Biozone of *Xenodontomys elongatus*) to the Upper Huayquerian (Late Miocene) is not a biostratigraphic tool and its reference to the Montehermosan (Early Pliocene) cannot be discarded. Likewise, they stated that several characters of the specimen referred to Mustelidae seem to match better with those of a didelphimorph marsupial.

2.5 Paleoclimatology of the Southern Cone of South America Since the Miocene

Plant and animal organisms recovered from different units provide valuable information for reconstructing past environments and the climatic conditions. In recent decades, geochemical techniques gave rise to new proxies. In this way, the marine records of stable isotopes, especially ^{18}O, provide an important basis for understanding past climates. Oxygen isotope records primarily reflect changes in temperature and volume of the ice sheets, associated with glacial–interglacial cycles. The demonstration of the synchronicity of climatic events and the establishment of a chronology turned these records in the most useful tool to establish stratigraphic correlations in the Pliocene and Quaternary (Lisecki and Raymo 2005, and literature cited therein). Another source of information about past climates results from stable isotope analysis in ice cores from Greenland, Antarctica, and mid-latitude and even intertropical glaciers (Petit et al. 1999; see also literature cited in Tonni 2006). These analyses show that the climate of the Late Pleistocene and Holocene is characterized by relatively synchronous rapid changes in different areas. For instance, glaciations in the southern Argentine territory could be correlated with the chronostratigraphic of the Pampean region (see Rabassa et al. 2005; Rabassa 2008; Coronato and Rabassa 2011).

2.5.1 Climates in Patagonia Since the Miocene

The rising of the Patagonian Cordillera since Middle Miocene times has been recognized as the main cause of the desertification of Patagonia (Pascual and Odreman Rivas 1973). Quattrocchio et al. (1988), on the basis of palynomorphs and vertebrate remains, stated that a marked climatic deterioration occurred by the end of the Miocene in the Colorado Basin of northern Patagonia. Scillato-Yané et al. (1993) analyzed the variation of the xenarthran diversity during the Middle Miocene interval and determined that the shift toward colder and drier conditions was a gradual process, resulting in the conditions that prevailed since the Chasicoan (Early–Late Miocene). This change of climatic conditions influenced the xenarthran diversity selectively and progressively, being the tardigrades the first group showing a relevant taxonomical change, followed by the cingulates. The new environmental conditions are compatible with open areas of grasslands developed during dry seasons. Montalvo and Verzi (2004) arrived to similar conclusions based on octodontoid rodents for the following interval, the Huayquerian–Montehermosan ages (Late Miocene–Early Pliocene), reinforcing the idea that the trend of the climatic environmental change had a defined directionality since the Middle Miocene.

From the Early Pleistocene (ca. 2.6 Ma), frequent glaciations occurred in southern Patagonia, with a remarkable increase of the continental ice sheet between 1.5 and 1.2 Ma (Singer et al. 2005). In the latest Pleistocene (ca. 13–11 ^{14}C ka BP), a new glacial advance in southern Patagonia under humid conditions (McCulloch et al. 2000; see also Strelin and Denton 2005) generated favorable environments for herbivores, including megaherbivores and their predators (Tonni et al. 2003). These conditions seem to have favored also the southern expansion of the running bird *Rhea americana* (see Tambussi and Tonni 1984). From the Santacrucian to the Late Lujanian ages, within the territory of the present Patagonian region, the different faunal associations correspond to a variety of climatic changes. These changes may be summarized in successive climatic scenarios (Tonni and Carlini 2008; Madden et al. 2010).

1. During the Early Miocene (Colhuehuapian), previously to the GABI, central Patagonia presented heterogeneous vegetation that included wet forest, palm-tree associations, restricted grassy environments, and flooded or paludal areas on variable topography. Most climate indicators accord with the view that Patagonian climates at this time were warm and humid during all or most of the year at a time when the Patagonian Andes did not act as a continuous orographic barrier to the moisture-laden winds coming from the southern Pacific Ocean (Madden et al. 2010, p. 434).
2. During the Middle Miocene (Colloncuran and Mayoan ages), still previously to GABI, more open environments became predominant, allowing the occurrence of more cursorial and larger mammals. The forested areas would have been restricted to the valleys of the rising cordillera, hosting a few tree-dwelling species (e.g., the last record in Patagonia of Primates and Erethizontidae). This change occurred progressively along the "Friasian" Age and affected selectively different mammalian lineages; for example, among the Xenarthra, the Pansantacrucian Tardigrada were more sensitive than cingulates and were replaced by the beginning of the Friasian sensu stricto, for the lineages that became dominant during the Panaraucanian period.

3. Partially in coincidence with the Late Miocene tectonic Quechua phase, neatly open environments with at least one dry season developed, including extensive savannas with *Attini* (Formicidae) mounds (see Laza 1982). In several mammalian lines, there was a tendency toward increasing size, and the first representatives of typical Pampean lineages were recorded. During this time, Holarctic taxa (Procyonidae) occur for the first time in southern South America.
4. During the last glacial advance in Late Glacial times (13–11 ^{14}C ka BP), higher moisture was recorded in southern Patagonia what permits a high diversity of large mammals corresponding to Pampean lineages inhabiting the South (e.g., Mylodontidae, Glyptodontidae, Tremarctidae bears, Macraucheniidae, smilodons).

2.5.2 Climates in the Pampean Region from the Late Miocene to the Pliocene

Pascual and Bondesio (1982) named as the "Edad de las Planicies Australes" ("Age of the Southern Plains") the period estimated between 11 and 3 million years before present, i.e., from the Chasicoan to the Chapadmalalan (Pascual and Bondesio 1985). The environmental conditions during the "Edad de las Planicies Australes" were characterized by aridization, comparatively colder climates, and more varied environmental fragmentation (see also Ortiz Jaureguizar 1998).

Campbell and Tonni (1980) suggested that the presence of some mammalian taxa in the Huayquerian (Late Miocene) outcrops at Salinas Grandes de Hidalgo, western Pampean area (Argentina) indicates subtropical climate with a dry season, though data are insufficient to determine whether that seasonality included a cold winter (see Pascual 1986).

Several vertebrates from the Monte Hermoso Formation (Late Miocene–Early Pliocene) (Tomassini 2012; Tomassini et al. 2013) indicate that prevailing open environments with xerophitic vegetation and seasonal variation in precipitation were similar to those of the present Chacoan Domain of northern Argentina (Cabrera and Willink 1980). Among these taxa are Echimyidae and Dinomyidae rodents, a Myrmecophagidae xenarthran, Cariamidae birds, Boidae and Teiidae reptiles, and Bufonidae and Ceratophryidae anurans (Tonni 1974; Gasparini and Báez 1974; Chani 1976).

Erra et al. (2010) reported preliminary and exploratory results on silicophytoliths in paleosoils related to the so-called escorias and/or tierras cocidas in the upper section of the Chapadmalalan (Late Pliocene), cropping out between the cities of Mar del Plata and Miramar along the coast of Buenos Aires Province, Argentina. These authors detected paleocommunities dominated by palms (Arecaceae), as well as Gramineae of C4 metabolic route, and Ulmaceae, Celtidaceae, and Moraceae. These plants would indicate bushy savannas with a dry season and over 10 °C in the cold season.

In the same unit and geographical area, Genise (1989) described paleocaves attributed mainly to the activity of rodents. He determined that 75 % of these caves were occupied by the ctenomyine rodent *Actenomys*. Following other authors, he suggested that digging habits appear as a response to xeric climatic conditions and to predation pressure in open areas. Later, Genise (1997) described signs of termite activity (*Tacuruithnus farinai*) for the Barrancalobian (Early Marplatan, Late Pliocene) in the Terrazas del Marquesado (southeastern Buenos Aires Province). The environment in which these termites currently inhabit is a forest with over 1500 mm of annual precipitation and a mean annual temperature of over 21 °C. Considering the strong dependence of termites on specific climatic conditions, he postulated that similar values of precipitation and temperature must have prevailed during the deposition of the Barrancalobian (Early Marplatan; Late Pliocene) along the coast of southeastern Buenos Aires Province. Similar conditions (subtropical climate with marked seasonality) were inferred on the basis of the presence of termite mounds of *Barberichnus bonaerensis* for the Late Marplatan (Sanandresian; Late Pliocene–Early Pleistocene) at Punta Negra, Necochea (south of Buenos Aires Province) (Laza 2006).

2.5.3 Climates in the Pampean Region During the Quaternary

The Pleistocene

Away from the Andean Cordillera, the Pleistocene ice covering only affected the southern tip of Argentina (Tierra del Fuego and southern Santa Cruz provinces, mainly; for a summary, see Rabassa 2008) and westwards—mainly to the center of the territory—just the immediate piedmont sector.

The Pampean region was never directly affected by the action of the ice, but during the successive glaciations, there were cold and arid climatic conditions in the lowlands, in some cases similar to those currently prevailing in northern Patagonia (Tonni et al. 1999; see also the literature cited in Cione et al. 2009).

The faunal turnover that began during the Sanandresian Age (earliest Pleistocene) was intensified during the Ensenadan Age. However, the last tapirids and medium-sized procyonids in the Pampean region indicate that warm and humid conditions occurred in the Bonarian coast at least in some moments during the Ensenadan (Tonni 2009). Presently, more benign environmental conditions still occur in the Río de la Plata western coast. In southeastern Buenos Aires Province, cold and arid conditions are recorded in Ensenadan levels (Soibelzon and Tonni 2009) which were probably coeval with the C1r1r paleomagnetic Chron (<0.98 to >0.78 Ma) and are characterized by different taxa, e.g., some Dasypodidae (*Tolypeutes matacus* and *Zaedyus pichiy*) (Fig. 2.15) and micromammals (Verzi et al. 2002; Soibelzon et al. 2008b, 2010). During the Bonaerian Age (upper part of the Middle Pleistocene Stage), according to the faunal evidence, begins with a warm event, dominated by pedogenesis and the record of Brazilian indicators. Considering these characteristics and the stratigraphic position, Verzi et al. (2004) suggested that the Bonaerian Stage starts during the Marine Oxygen Isotopic Stage (MIS) 11 interglacial, around 0.4 Ma. This interglacial epoch was the warmest and longest recorded in the last 0.5 Ma, which led to a significant sea

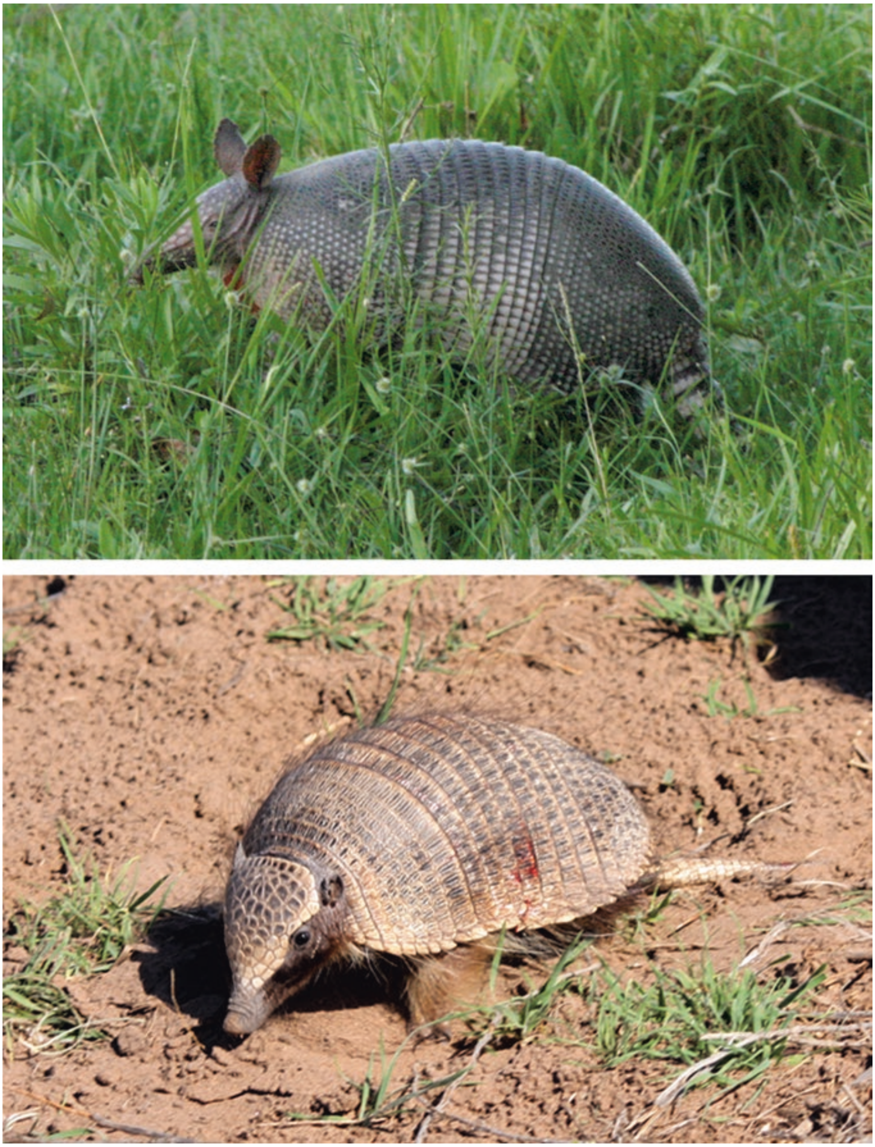

Fig. 2.15 Xenarthran Dasypodidae. *Upper Dasypus novemcinctus*; *Lower Zaedyus pichiy*. Photograph by Esteban Soibelzon

level rise (Hearty 2007). Beach sediments in southeastern Buenos Aires Province have been related to this impressive sea level rise since Ameghino (1908; see also Cione et al. 2002). However, other authors such as Isla et al. (2000, and references cited therein) have considered them only as old as the last interglacial or even the Holocene Hypsithermal.

The Late Pleistocene (Lujanian Age) began with a warm event, probably linked to the MIS 5e or alternatively to MIS 3 (see below).

During the Last Glaciation Maximum (LGM; between 26,500 and 19,000 cal year BP; see Clark et al. 2009), the eastern sector of southern South America was greatly increased due to a sea level fall of about 120 m. This happened several times, with each glaciation. In some sectors, the coastline was displaced eastward for about 300 km or more away from the present Argentine coast (Tonni and Cione 1997; Guilderson et al. 2000; Cione et al. 2005). However, the dry climatic conditions that developed in the Pampas during the LGM were not exclusively the product of more continentality; the changes in ocean currents during that period should also be considered (Ab'Saber 2000), since they influence the climatic characteristics of the southeastern South American coast. A singular modern example is the event that takes place in Brazil around 23°S, consisting on the upwelling waters of the central South Atlantic seasonally controlled by the intensity of the trade winds from the NE. This situation causes local semiarid conditions in the area, dominated by a dry forest (locally known as *caatinga*).

Accordingly, the Pampean region was inhabited by a typical fauna of open habitats, arid to semiarid, which had a large latitudinal distribution during the LGM. Most of the region was covered by steppe vegetation developed on dunes and loess fields (see Tonni et al. 1999; Vivo and Carmignotto 2004).

Faunistic elements' indicators of arid to semiarid and cold conditions are frequent in outcrops of the Guerrero Member of the Luján Formation, found in the Pampean region, which was deposited between more than 21,000 and about 10,000 radiocarbon years before present (Tonni 2009), i.e., between 25,000 and 11,600 years BP. They include species that today characterize the Patagonian Zoogeographic Domain, such as the marsupial *Lestodelphys halli*, the cricetid rodent *Eligmodontia typus*, the mustelid *Lyncodon patagonicus*, the canid *Lycalopex griseus*, and the caviid rodent *Microcavia australis*. The geographical distribution of the latter currently comprises arid areas of the south and center areas of Argentina, whereas in the Province of Buenos Aires, this species is only sympatric with *C. aperea* (the cavy that currently characterizes the Pampean Zoogeographic Domain of Ringuelet 1961) in the southwest portion of the province. The typical cold indicators are accompanied by extinct megamammals (species with body mass greater than or equal to one ton) that give unique associations in the Late Pleistocene fauna of the Pampas.

Around 15,500 radiocarbon years BP, there was a rapid increase in temperature shown by the occurrence of some subtropical faunal elements. Between 13,000 and 11,000 radiocarbon years BP, temperature and precipitation decreased, coincidently with a temporary readvance of the Andean glaciers. During this interval, the mammal fauna was similar to that of the LGM, even including several megamammal species. The earliest records of man in the Pampean region also belong to this interval.

Mammalian extinctions throughout the Neogene at specific, generic, and even familial level were putatively related to climate and environmental changes affecting different members of the biota. However, toward the end of the Pleistocene and the beginning of the Holocene (boundary at 11,700 years BP), there was a unique extinction event. During this interval, all megamammals and much of the large mammals (over 44 kg) disappeared in South America. This extinction was attributed to climate change, epidemics, or human action. More recently, Cione et al. (2003, 2009) proposed an alternative explanation, which they called the “Broken Zig Zag” (see below).

The Holocene

In the last decade, the climatic conditions that prevailed at the beginning of the current interglacial were better understood greatly from the study of ice cores from Antarctica and Greenland. According to this evidence, the Holocene climate was characterized by rapid and relatively synchronous changes between the Northern and Southern hemispheres. The high-latitude ice cores’ evidence was supplemented by others such as ice cores in intertropical areas, ocean temperatures, growth rings of trees, speleothems, and historical climatology for the Late Holocene (see references in Tonni 2006).

The Holocene thermal maximum in the Pampas

During part of the Holocene Thermal Maximum (HTM, ca. 7500–4500 radiocarbon years BP), global temperatures were higher than today what resulted in a significant, worldwide sea level rise. There is not a full consensus about the elevation reached by sea level along the Atlantic Bonaerian coast; however, some studies estimated it at +6.5 m for the Río de la Plata (Cavallotto et al. 2004), but +3.5 m (Isla 1998) for the southeastern coast of Buenos Aires Province.

Temperatures during the last 1000 years

The results obtained through different proxies support the hypothesis of Lamb—which was suggested in the 1970s—according to which two significant climatic events were recorded during the last millennium in the Northern Hemisphere: the Medieval Thermal Maximum (MTM, also called Medieval Climatic Optimum or Medieval Climatic Anomaly) and the Little Ice Age (LIA). Subsequent investigations determined the global extent of both events (see references in Tonni 2006).

The Medieval Thermal Maximum (MTM)

In the Northern Hemisphere, the MTM took place between 800 and 1200 AD. One of the best known historical consequences arising from it are the colonization of Greenland by the Vikings or the lesser known abandonment of the Anasazi villages—caused by persistent droughts—in the southern portion of the Colorado plateau (see Tonni 2006).

In the Pampas, around 1300 AD, the micromammal record indicates higher temperatures than today at least in two localities (see Tonni 2006). These conditions led to the southward displacement of micromammals, including a subtropical hematophagous chiropteran of the genus *Desmodus*. In some cases (e.g., the cricetids *Pseudorizomys wavrini* and *Bibimys chacoensis*), their displacements involved more than 10° latitude with respect to modern records.

The record of the armadillo *D. hybridus* in the Pampean region (38°S–61°W), ca. 1000 AD in a paleosol which corresponds to an edaphic process under humid and temperate conditions (see Tonni 2006) and in an archaeological sites at Cordoba Province (Soibelzon et al. 2013), is probably related to this warm event.

Also in northern Buenos Aires Province (34° 22′S–58° 35′W) there are faunal indicators of warmer and wetter conditions than today around 680 ± 80 radiocarbon years BP, i.e. ca. 1290 AD (see Tonni 2006).

The Little Ice Age (LIA)

According to De Menocal (2001), the LIA developed in the interval 1550–1900 AD. This cold event was recognized in northern Europe through the study of the advancing glaciers in historical times, especially since the sixteenth century. For Argentine Patagonia, researchers from IANIGLA (a research institute at the city of Mendoza, western Argentina) compiled extensive data on climatic variations during and immediately after the LIA (Masiokas et al. 2008, 2010).

The LIA is known in Argentina almost exclusively through faunal observations in the eastern Pampas. The faunal records point to semiarid to arid conditions with temperatures lower than today. They are more frequent and significant from the late eighteenth until the second half of the nineteenth centuries.

Reports of qualified travelers (see Deschamps et al. 2003, and the literature cited therein) referred to environmental conditions during this time. In this regard, the watercolors and descriptions of Emeric Essex Vidal, correspondent of the Royal British Navy in Buenos Aires between 1816 and 1818, are quite illustrative. In his reference to the market of Buenos Aires, he commented that the armadillos were brought for sale by the Indians from "forty leagues inland" (see Deschamps et al. 2003). In the description of this armadillo, he noted that when chased "*…escapa de sus perseguidores rodando como si fuera una pelota pendiente abajo…*" ("…it escapes from its pursuers rolling like a ball downhill…;" see Deschamps et al. 2003: 10). This feature, unique among armadillos, is typical of the mataco or quirquincho bola (*T. matacus*), a dasypodid that currently inhabits the arid and semiarid portion of the Argentine territory from the north through the center to the north of San Luis.

Along the coast of the Río de la Plata estuary, which is the northern edge of the "Pampa Deprimida," there is a relictual population of the armadillo *Chaetophractus vellerosus* that currently lives in the center of the Argentine territory under arid to semiarid conditions (Soibelzon et al. 2006a). Its presence in the area was explained as a consequence of population disjunctions caused by climatic change after the LIA (Deschamps et al. 2003) and the edaphic characteristics of the soils (Soibelzon et al. 2007).

Deschamps et al. (2003) conducted a study of the evolution of precipitation in Buenos Aires from the eighteenth to the twentieth centuries, using semiquantitative data derived from historical climatology and faunal data. These authors concluded that (1) seasons in which major precipitation occurs varied from a Fall–Summer–Spring–Winter sequence to Summer–Fall–Spring–Winter; consequently, the water availability that supports the Pampas grasslands changed with time; (2) until 1842, over 268 years, there were 98 years of drought (36 %) and 15 years of flooding (5 %) of the total "normal" years, i.e., those for which there are no special references concerning any of both events; (3) from 1842 onwards, over 155 years, there were 16 drought years (10 %) and 39 years of flooding (25 %) of the total "normal" years; consequently, since 1842, a major change in vegetation occurred, reflected in the increase of grasslands.

This increase in precipitation is documented since there is continuous instrumental record. Although during the second half of the nineteenth century and in the twentieth century, periods of decreased precipitation were recorded, being the increasing trend relatively constant (see Hoffmann 1988).

In this way, this period began to take shape what we now know as humid pampas, which in the 1900s helped Argentina to become the "breadbasket of the world" due to a combination of fertile loess soils and abundant and well-distributed rainfall.

2.6 Biogeography of the Recent Mammals of South America

The present mammal fauna composition and distribution of South America is the result of many million years of evolution. This history involves taxic origination, colonization, dispersion, radiation, and extinction (see Simpson 1950; Reig 1981). However, a first step to study the history of a fauna is to establish the present patterns of distribution.

The recent biogeography of South America began to be studied in the nineteenth century. Sclater (1858) recognized only one major biogeographical unit in South America, Central America, and the southernmost part of North America that named Neotropical region (see also Wallace 1876). Numerous proposals have been developed on the biogeographic configuration of the continent and its characteristic mammals afterward (see Morrone 2001, 2006, 2011a, b, 2014a, b, and literature cited therein).

The Neotropical region was originally proposed on the basis of the global geographic distribution of Passeriformes birds. Sclater (1858: 143) argues that "*There can be no question I think that South America is the most peculiar of all the primary regions in the globe as to its ornithology*." Later, Wallace (1876), in a seminal paper, stated that in the Neotropical region, "richness combined with isolation is the predominant feature" (Fig. 2.16).

Fig. 2.16 Map of the Neotropical region and subregions according to Wallace (1876)

Another author that addressed the biogeographic relationships in the Neotropical region was Von Ihering (1900) who, based on the distributions of the unionidmolluscan, divided this region into two subregions: Archiplata including Chile, Argentina, Uruguay, and southern Brazil; and Archamazonia including the rest of South America. According to his observations, these sectors respond to an ancient separation generated by a marine ingression during the Tertiary. In this paper, the author also discussed the relationships among mammal faunas of South America, North America, Africa, and Asia and their peopling routes, which is the second mention of interchanges of terrestrial fauna between continents currently distant, after Wallace proposal (1876). Besides, the recognition of two large biogeographic units for South America, based on different taxa, has been proposed repeatedly afterward by different authors.

More recently, the important contribution of Cabrera and Yepes (1940) recognized the Guayanan-Brazilian and Patagonian subregions. The first one includes the tropical part of South America, extending southward and following a line between Peru, east of Bolivia, and north of Argentina (including the delta of the Paraná River). The other subregion encompasses the rest of South America and partially coincides with the Chilian Subregion of Sclater (1858) and Wallace (1876). The Guayanan-Brazilian Subregion has typical representatives of marsupials (*Chironectes* and *Philander*), xenarthrans (*Priodontes*, *Cabassous*), chiropterans (*Desmodus* and *Noctilio*), and all the platyrrhine primates and tapirs (*Tapirus*), whereas the Patagónica Subregion distinguishes by the presence of certain cervids (*Hippocamelus*, *Pudu*), guanacos (*L. guanicoe*), and rodents (*Lagidium*, *Dolichotis*, and *Lagostomus*) (Fig. 2.17).

Later, Cabrera and Willink (1980) proposed two regions for South America, the Neotropical and the Antarctic, both formed by numerous districts. They based both on plant and animal distribution. In this proposal, the Neotropical region includes almost all the Argentine continental territory, except for the Sub-Antarctic Province (included in the Antarctic region) which is characterized by the Andean–Patagonian forests, several invertebrate, and vertebrate species (among mammals, *Hippocamelus bisulcus*, *Pudu pudu* and *Dromiciops*). According to these authors, the Neotropical region is distinguished by mammals such as the Cebidae, Callitrichidae, Chinchillidae, Ctenomyidae, Abrocomidae, Camelidae *Lama*, Didelphidae, Myrmecophagidae, Bradypodidae, and numerous Dasypodidae. Perhaps the main difference with other proposals is the exclusion of the Patagonia steppe from the Antarctic region.

Recent studies by Morrone (2001, 2006, 2014a, b), compiling numerous sources of information, confirm the Neotropical and Andean regions, separated by the Andean Cordillera which divides the continent into two different areas: western and eastern (Fig. 2.18). Taxa inhabiting the western portion of South America are related to Australia and New Zealand, whereas those of the eastern portion have affinities with the tropics of the Old World. From the point of view of the mammal composition, the Neotropical region of Morrone is characterized by the *Mazama americana*, *M. gouazoubira*, *Tayassu pecari*, *Leopardus pardalis*, *Herpailurus yaguarondi*, *Eira barbara*, *Lontra longicaudis*, *Procyon cancrivorus*, *Caluromys*, *Tapirus*, *Cebuella*, *Alouatta*, *Ateles*, *Cebus apella*, *Myoprocta*, *Proechimys*, *Coendou*, *Hydrochoerus hydrochaeris*, *Nectomys*, *Oecomys*, *Oryzomys*, *Sciurus aestuans*, *S. spadiceus*, *Priodontes maximus*, *Dasypus novemcinctus*, *Myrmecophaga tridactyla*, and *Tamandua tetradactyla*, whereas the Andean region only has two characteristic mammals, *Lycalopex*

Fig. 2.17 Artiodactyls. *Upper* Camelidae *Lama guanicoe*. *Lower left* Tayassuidae *Tayassu tajacu*. *Right* Cervidae: *Blastocerus dichotomus*. Photograph by Esteban Soibelzon

culpaeus and *Lontra feline*. However, the subregions and provinces included in the Andean region have other characteristics species such as *Vicugna*, *Hippocamelus*, *Chinchilla*, *Pudu*, *Dromiciops gliroides* and *Abrothrix*.

Two relatively recent contributions, notwithstanding that do not include biogeographic studies, give relevant information about mammal distributions (Redford and Eisenberg 1992; Gardner et al. 2005).

Most of the biogeographic studies, based both on phyto- and zoogeographic data, show that South America is composed of two regions (or subregions depending on the source) with a different evolutionary history and showing relationships with different continents in the past. This pattern is evident in the recent distributions but also comes clear in the fossil record. The Andean–Patagonian area (=Andean region sensu Morrone), which shows Gondwanic affinities, is characterized by the presence of at least one marsupial basal to the Australian radiation (*D. gliroides*, Microbiotheria, Microbiotheriidae) and other organisms (e.g., plants:

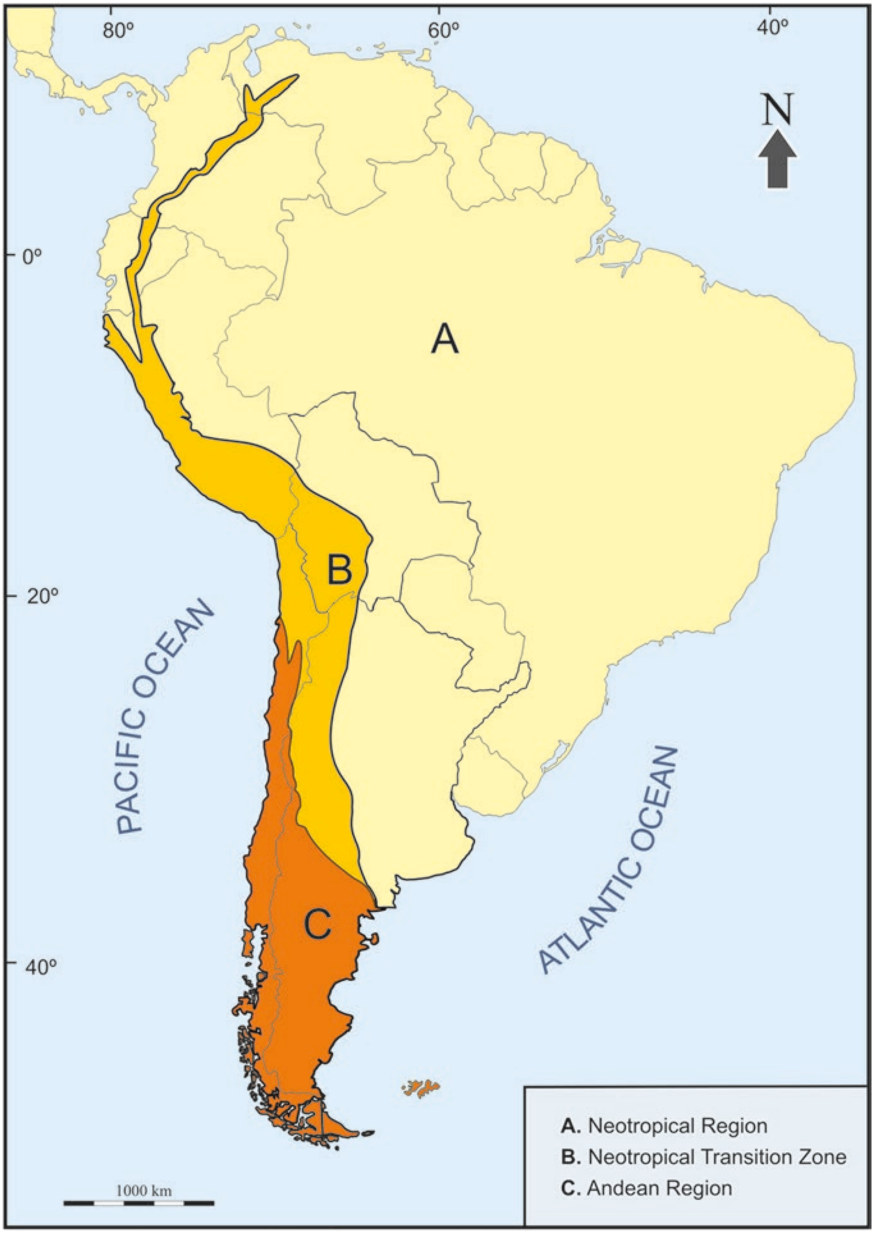

Fig. 2.18 Biogeographic map of Morrone (2014a). Neotropical region (*light yellow*), Neotropical Transition Zone (*dark yellow*) and Andean region (*orange*)

Nothofagus, Fagales, and Nothofagaceae; birds: *Rhea pennata*, Rheiformes, and Rheidae; scorpions, Bothriuridae). The rest of South America is included in the Neotropical region and includes the tropics. The Neotropical region constitutes a monophyletic unit (sensu Morrone 2014a), characterized by the presence of numerous endemic species of plants and animals (see Morrone 2001). Concerning mammals, there are taxa with a long history in the area (e.g., Xenarthra, didelphimorphid marsupials, platyrrhine primates, and caviomorph rodents) and other whose ancestors arrived during the GABI (e.g., *T. pecari*, Tayassuidae; *Lama*, *Vicugna*, Camelidae; *Tapirus terrestris*, *T. pinchaque*, *T. bairdii*, Tapiridae). Consequently, their inclusion as characteristic taxa of one region/subregion or another should be taken with precaution.

2.6.1 Biogeography of Argentina

We here stress that the best record of the GABI is in the southernmost part of South America, more precisely in the Pampean region of Argentina. The biogeography of Argentina was explored since the late nineteenth century, both by animal geographers (including vertebrates and invertebrates; Lahille 1899; Delétang 1920; Yepes 1938, 1941; Ringuelet 1956, 1961) and plant geographers (Cabrera 1953). In the following paragraphs, we describe the contributions of some of the authors that devised biogeographic schemes of relevance for the study of Argentine mammalian fauna.

The first important contribution was done by Lahille (1899), based on the scheme of Sclater (1858). He made a division of Argentina into three subregions (each of them subdivided in turn into provinces) with their characteristic mammalian fauna: (1) Andean subregion characterized by *Lagidium*, *Chinchilla*, *Dolichotis*, "*Furcifer*" (=*Hippocamelus*), "*Lama*" *vicugna* (=*Vicugna vicugna*), *Tremarctos*, "*Chlamydophorus*" (=*Chlamyphorus*), "*Burmeisteria*" (=*Calyptophractus*), *Tolypeutes*, "*Dasypus*" *vellerosus* (=*C. vellerosus*; concerning this species, it is noteworthy that a relict population was reported for the area of Bahía Samborombón, Buenos Aires Province; see Carlini and Vizcaíno 1987; Soibelzon et al. 2007), "*Eligmodon*" *morenoi* (=*Eligmodontia morenoi*), *Abrocoma*, *Aconaemys* and *Octodon*; (2) Central subregion characterized mainly by *Lagostomus*; and the Brazilian subregion characterized by Brazilian fauna with many species in common with the central subregion.

After the paper by Lahille (1899), the first significative contributions were those by Yepes (1938) and Cabrera and Yepes (1940). Yepes (1938) includes the distribution of taxa, phytogeographic features, and main climatic conditions, as well as an important photographic appendix depicting the environments. This is the first paper with a characterization of the environments along with the mammalian fauna. The most representative environments cited by the author are as follows: environments of "*médanos*" (dunes), characterized by *Chlamyphorus truncatus* and *Ctenomys talarum*, *Ctenomys mendocinus*, and *Ctenomys pundti*; environments of "*inundaciones frecuentes*" (frequently flooded; the lands over the Paraná-de la Plata fluvial basin), characterized by several species of cricetid rodents (*Holochilus*, *Scapteromys*, *Deltamys*, *Neotomys*, and *Thomasomys*); "*ambiente de monte*" (monte environment), characterized by *Euphractus sexcinctus*, *C. vellerosus*, *Graomys*, *Phyllotis*, and "*Marmosa*" (=*Thylamis*) *pallidior* (Fig. 2.19); "*ambientes con bosque chaqueño*" (environment with Chacoan forest),

Fig. 2.19 *Upper* Didelphidae *Thylamis pallidior*. *Lower* Felidae *Oncifelis geofroyii*. Photograph by Esteban Soibelzon

characterized by *T. tetradactyla*, *M. tridactyla*, *Cabassous unicinctus*; “ambientes con carácter de páramo” (moor-like environments), characterized by *Chinchilla brevicaudata*, *Lagidium*, and *Abrocoma*. In a later paper, Cabrera and Yepes (1940) gave a map of zoogeographic distribution for South America based essentially on mammals.

A distinguish zoologist, Ringuelet (1956, 1961), suggested that the Argentine fauna cannot be studied without its paleogeographic history. He proposed that the regional fauna is composed of two units the Guayanan-Brazilian Subregion including taxa of Gondwanan lineages together with modern ones and the Chilean Patagonian or Andean Patagonian with affinities with the faunas of Australia, Tasmania, and New Zealand). Ringuelet recognized the fauna that entered from North America during the GABI. This author pointed out that there is an undoubted biogeographic unit along the Andes, from Neuquén to Tierra del Fuego, which is different from the one from the extra-Andean Patagonia (Ringuelet 1961). This idea led him to separate both areas into the Andino-Patagónica Subregion and Araucana Subregion (Ringuelet 1961). In this paper, the author established six types of distribution of the Argentine fauna, according to their relationships with faunas from other continents. As well, he stated that there are numerous faunistic evidences that extend the subtropical domain along the margins of the Paraná River and its delta, up to the relicts of gallery forest of the Buenos Aires Province.

Subsequently to these contributions, there are no comprehensive studies on mammal biogeography of Argentina although there are many studies limited to a specific area (e.g., provinces or reserves) or a particular taxon (see for example, Massoia et al. 2000; Pautasso 2008). In this context, the publications of Parera (2002), Canevari and Fernández Balboa (2003), and Bárquez et al. (2006) provide a taxonomic and literature review on the mammals of Argentina, being an usual reference. However, they lack of updated or specific data of species distribution, especially considering the large environmental changes undergone by the Argentine territory since the mid-twentieth century with the development of intensive agriculture and livestock.

2.6.2 The Pampa Ecoregion

The Pampean region mentioned along this volume corresponds to the eastern sector of Argentina, covered by sandy, clayey sediments, and loess, deposited mainly since the Miocene. Presently, the meaning of the term “Formación Pampeana” (“Pampean Formation”) or “sedimentos pampeanos” (“Pampean sediments”) is more restricted than in the past and involves mainly two lithostratigraphic units, the Ensenada and Buenos Aires formations, which together represent approximately the last two million years (Late Pliocene to Late Pleistocene) of the geological and biological history of the Pampean region (see Tonni and Pasquali 2006, and bibliography cited therein). Thus, the Pampa ecoregion coincides partially with the

Fig. 2.20 Grassland and xeric forest (Espinal) at the Pampean region (La Pampa Province). Photograph by Esteban Soibelzon

Pampean region previously defined. It has a temperate and humid climate and is the most important grassland ecosystem of Argentina (Viglizzo et al. 2005) (Fig. 2.20), but is currently fragmented by farming and ranching, generating a mosaic with varying degrees of alteration (see details in Bilenca and Miñarro 2004).

This ecoregion is bounded by xeric forest or Espinal, which is the local representation of an arid diagonal extending NW to SE in the Argentine territory and constitutes a major barrier to the dispersal of taxa northeast–southwest (Bruniard 1982). Hence, the Espinal is an ecotone between the ecoregion of the Monte and Pampa and shares numerous species with the Pampa. General classifications of mammal distributions in the world state that the Pampean region has a specific richness between 45 and 66 mammal species (whereas the Espinal is 67–88) and a low number of endemisms (0–3, whereas the rest of the Argentine territory is between 4 and 6) (Olson et al. 2001).

According to the mammal composition, this ecoregion includes typical taxa of the subtropical, central, and Patagonian domains (sensu Ringuelet 1961) as a consequence of the expansion–retraction areas of distribution during glacials–interglacials cycles. A good example of this is the record of relict populations of the Dasypodidae *C. vellerosus* in the area of Bahía Samborombón (Carlini and Vizcaíno 1987; Soibelzon et al. 2006a, 2007; Carlini et al. in press). Remarkably, this ecoregion suffered recent changes in the composition of mammals due to both hunting pressure (e.g., *Puma concolor*, *Panthera onca*, *O. bezoarticus*) and the development of agro-ecosystems and recent migrations from other ecoregions (e.g., some rodents as *Bibimys*, *Scapteromys*, *Oxymicterus* and *Hydrochoerus* and bats).

2.6.3 Mammals Introduced by Man

Since the beginning of the twentieth century, a great variety of domestic and wild mammals have been introduced in Argentina for hunting (e.g., *Sus scrofa*, *Cervus elaphus*, *Axis axis*, *Dama dama*, *Elaphurus davidianus*, *Antilope cervicapra*, *Lepus europaeus*), fur (*Neovison vison*, *Castor canadensis*, *Oryctolagus cuniculus*), for their ornamental value or as pets (*Callosciurus erythraeus*, *Felis silvestris catus*), breeding for food (*Bubalus bubalis*, *Capra hircus*, *O. aries*, *B. taurus*), and transport (*Equus* spp.) (see details in Chébez 1994; Parera 2002; Canevari and Fernández Balboa 2003; Guichón et al. 2005), whereas others have been introduced from other ports as stowaways on ships (*Mus musculus*, *Rattus rattus*, *Rattus norvegicus*).

Noteworthy, several of these species were introduced in the early twentieth century (Novillo and Ojeda 2008) and are included among the 100 world's most invasive species (*C. elaphus*, *S. scrofa*, *O. cuniculus*, *F. catus*, *S. scrofa*, *R. rattus*, *M. musculus*), because of their strong capacity for adapting to different situations, climates, and environmental conditions (see details in Novillo and Ojeda 2008; Flueck 2010).

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Chapter 3
The GABI in Southern South America

Abstract The Great American Biotic Interchange (GABI) between North and South America is one of the most important events in the history of land mammals. The interchange occurred in several phases during more than nine million years. We here analyze the chronology and dynamics of the GABI, the evolution of some South American mammalian groups through time, and the Quaternary mammalian extinctions. As the GABI was a complex process, we divide it into ProtoGABI and GABI 1 to 4. In our concept, the extinction of the megafauna by the gatherer/hunters that entered South American during the latest Pleistocene is a part of the GABI. The putative scarce frequency of extinct mammals in archeological sites is discussed. The evolutive relevance of the GABI is reflected in that half of the species living in South America had a North American ancestry. A final process, not included in the GABI, is the remarkable alteration of ecosystems by modern man. Presently, the composition and distribution of almost all autochthonous land mammal faunas are changing dramatically. Moreover, frequently they are replaced with domesticated and/or wild exotic species.

Keywords Chronology · Mammal · Panama Isthmus · Endemic · Immigrant · Biogeography · Macroevolution · Neogene · Quaternary

3.1 Short History of the Interchange and the Great American Biotic Interchange (GABI) Concept

The first authors to acknowledge the interchange of land vertebrates between the Americas and the resulting "mixed faunas" were Wallace (1876), Von Ihering (1900), and Ameghino (1907). Ameghino suggested that mammals originated in Patagonia and later dispersed to the rest of the planet. Later Matthew (1915), Scott (1937), and Simpson (1950) discussed the ideas of Ameghino from the "New York School of Zoogeography" point of view. They postulated that South America was

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originally devoid of mammals and was populated from North America, followed by in situ differentiation that was facilitated by its isolation during the “tertiary” (Morrone 2011).

Patterson and Pascual (1972) carried out a deep analysis of the South American fossil mammalian faunas throughout the Cenozoic. These authors suggested that competition and extinction occurred during the interchange. Pascual and Fidalgo (1972) and Webb (1976), among others, proposed a similar scenario. Since this suggestion, there was considerable debate as to whether placental carnivores arriving from North America actually caused the extinction of South American marsupial carnivores by competitive displacement (see Prevosti et al. 2013).

The expression “Great American Biotic Interchange” (GABI) or “Gran Intercambio Biótico Americano” (GIBA) was proposed by Webb (1985a). The denomination referred to a biogeographic process that lasted a relatively short time. Actually, Webb (1985b) suggested that during the “Uquian” (presently Marplatan), 8 mammal families of Holarctic origin suddenly appeared in South American. This was demonstrated incorrect by Tonni et al. (1992) and Cione and Tonni (1995). Moreover, Woodburne (2010) restricts the GABI almost exclusively to the Pleistocene interchange (after 2.8 Ma) as a consequence of the establishment of a permanent dry land conexion between South and Central America.

During the 1980 decade, intense paleontological study helped to clarify the evolution and integration of the mammalian communities in South America (see Simpson 1980; Reig 1981; Hoffstetter 1981; Marshall et al. 1979, 1982, 1983; Webb and Marshall 1982; Webb 1985a, b).

More recently, many articles appeared reviewing different aspects and actors of the GABI: Tonni et al. (1992) and Cione and Tonni (1995) reviewed the stratigraphic ordering of the North American taxa in South America and proposed that the interchange was episodic and not concentrated in the “Uquian” (presently the Marplatan); Cody et al. (2010) reviewed the plant migration and the historical assembly of tropical biomes; Woodburne et al. (2006) introduced the concept of holding pen; Woodburne (2010) proposed a division of the whole GABI into 4 episodes, linked with climate and landscape changes, that he named GABI 1 to 4; Wilson et al. (2014) investigated how the GABI shaped the distribution of arid-adapted species trough the historical biogeography of the bee genus *Diadasia*; Pinto-Sáncheza et al. (2012) and Castroviejo-Fisher et al. (2013) discussed the GABI in frogs; Morales-Castilla et al. (2012) focused their study on how the GABI affected the current geographic body size patterns of mammals in the Americas; Patterson and Costa (2012) edited a large volume on the history and geography of recent Neotropical mammals where many authors contributed from their respective fields of expertise; Ornelas et al. (2013) identified vicariance scenarios, reconstructed ancestral biogeographical areas, and investigated the role of geological events in generating genetic divergence through vicariance events in hummingbirds of Mesoamerica; Prevosti et al. (2013) discussed the incidence of North American placental carnivores on the extinction of local marsupial carnivores.

3.2 The GABI Chronology and Dynamics

3.2.1 First Record of Taxa of North American Origin in Southern South America Gives the General Pattern but does not Explain the Details

South America was an island continent during most of the Cenozoic (Pascual et al. 1965). During this time of isolation, rodents and primates arrived by rafting from Africa. The Panama Isthmus area appears to have been permanent dry land since ca. 2.8 Ma (Bartoli et al. 2005; see Leigh et al. 2014). However, the GABI (Fig. 3.1) was a biogeographic phenomenon that began several million years before the Pleistocene, during the Late Miocene and Pliocene, when relatively sparse faunal interchanges took place. The Miocene precursors were named "New Island Hoppers" (Simpson 1950) or "Heralds" (Webb 1985a). Presently, we know that before the final establishment of the Panama Isthmus, at least eight genera of four North American families appeared for the first time in southern South America. These interchanges are called here the ProtoGABI meaning that corresponds to the first stage of the GABI.

The GABI has been studied before and better in the southern part of South America. Certainly, the best representation of the continental Late Cenozoic is the sedimentary rocks that crop out in the Pampean region and neighboring areas (Cione and Tonni 1995, 1996; Cione et al. 2007). These beds are fossiliferous and frequently show several local biozones stacked in one single stratigraphic section (e.g., sedimentary rocks cropping out in the marine cliffs between Punta Mogotes, near the city of Mar del Plata, and Miramar, Buenos Aires Province; Cione and Tonni 1995). In many of these profiles, there are magnetostratigraphic analyses and many beds were radiometrically dated (see above). Although dispersal pattern is represented today by the biostratigraphic pattern of southern South America, new findings in other parts of South America would give relevant information in the future.

The first mammals of Holarctic origin in southern South America are the Huayquerian (Late Miocene, ca. 7 Ma) procyonids of the endemic genera *Cyonasua* and *Chapalmalania* (Prevosti and Soibelzon 2012; Prevosti et al. 2013). However, the occurrence of an endemic genus suggests that the migration was previous to the age of the record. Moreover, four taxa of North American origin were reported from the Amazon Basin from beds putatively older than those of the Miocene of Argentina (proboscideans, tapirids, peccaries, and dromomerycins; Prothero et al. 2014). The presence of an indeterminate mustelid in the Huayquerian (see Verzi and Montalvo 2008) was refuted by Prevosti and Pardiñas (2009). The next immigrants are endemic genera of sigmodontine rodents and the procyonid genus *Parahyaenodon* present in Montehermosan beds (latest Miocene–Early Pliocene; Pardiñas and Tonni 1998; Forasiepi et al. 2007). In Chapadmalalan rocks, south of the city of Mar del Plata (Buenos Aires Province), a North American genus, the peccary *Platygonus* (Tayassuidae), appears for the

Fig. 3.1 Artistic representation of the GABI (watercolor by Mariana Soibelzon taken from Soibelzon et al. 2013)

first time (Prevosti et al. 2006; Gasparini 2013). *Platygonus* is known from Early–Late Hemphillian faunas in North America at about 7 Ma (Woodburne 2010). The record of a mustelid in the Chapadmalalan (see Webb 1985a) was considered unsupported by Cione and Tonni (1995).

The first camelids in South America (represented by the endemic genus *Lama*) are recorded in the Barrancalobian substage (Early Marplatan, Late Pliocene) (Cione et al. 2007). The appearance of this savanna-adapted genus occurs within the early development of prominent Northern Hemisphere glaciation (Woodburne 2010). A larger number of taxa of North American origin are found in the Vorohuean: canids Caninae, mustelids Mustelinae, and equids (Equidae) (Cione and Tonni 1995). From that time onwards, the rate of new records of immigrant taxa increased.

Woodburne (2010) divided the mainstream of interchange into four units (GABI 1 to 4). The base of the Barrancalobian is younger than 3.3 Ma according to radiometric dating of "escorias" near the top of Chapadmalalan beds (Vizcaíno et al. 2004). The relatively large occurrence of mammals of North American origin in the Vorohuean (Middle Marplatan) represents the beginning of the GABI 1 at 2.8–2.6 Ma and putatively the evidence of dry land in the Panama Isthmus (Bartoli et al. 2005). Certainly, the final closure of the isthmus is the main cause for the dispersal, but climate change was also a key factor without which such a strong interchange would not have taken place (Woodburne 2010). A possible gomphotheriid vertebra was found in Sanandresian beds in northwestern Argentina (López et al. 2001).

Another strong dispersal pulse from the North American continent occurred during the next younger age, the Ensenadan (Early to Middle Pleistocene). Woodburne (2010) called it GABI 2. The carnivore guild peaked in diversity, when Ursidae, Felidae, Mephitidae, Lutrinae (Mustelidae), and large canids were firstly recorded in southern South America, as well as the tayassuid *Catagonus*, the camelid *Hemiauchenia*, the cervids *Epiuryceros* and *Antifer*, the tapir *Tapirus,* and the gomphotheriid "*Stegomastodon*" (Tonni et al. 1992; Cione and Tonni 2005; Soibelzon et al. 2005; Cione et al. 2007; Prevosti and Soibelzon 2012; Gasparini 2013). The occurrence of *Stegomastodon* in South America was questioned by Mothé et al. (2011, 2012). These authors suggested that the two species previously referred to *Stegomastodon* should be assigned to the endemic South American genus *Notiomastodon*. However, we believe that more studies had to be done for sustaining this taxonomic decision.

The GABI 3 is represented in Bonaerian beds (Middle Pleistocene) by new taxa such as the felid *Hepailurus*, the cervid *Paraceros,* and the tayassuid *Tayassu* (Cione and Tonni 2005; Prevosti 2006; Cione et al. 2007; Gasparini 2013).

The GABI 4 transpired during the Lujanian and Platan, although it is actually in progress today. Many new mammals dispersed to southern South America as evidenced by the glyptodontid *Glyptotherium*, the procyonid *Nasua*, the mustelid *Lontra*, the canid *Canis*, the felid *Leopardus* (*Oncifelis*), the leporid *Sylvilagus*, the equiid *Equus*, and the hominid *Homo sapiens* (Tonni et al. 1985; Cione and Tonni 2005; Prevosti 2006; Carlini et al. 2008).

As mentioned above, the establishment of dry land joining Central and South America is not the only cause of the dispersal. Many estenoic taxa such as tapirs and camelids passed the isthmus, but some eurioic taxa such as bovids and ursin bears did not. The dispersal of tapirs and camelids could be related with climatic modifications, vegetation, and topography. However, the absence of bovids and ursin bears in South American is not clearly explained. Woodburne (2010) noted that most newcomers to North American were xenarthrans and only a few taxa of endemic ungulates, marsupials, platyrrhine monkeys, and caviomorph rodents crossed the isthmus in a northward direction. Yet, this is not unexpected taking into account that the mammal South American fauna was mostly composed of xenarthrans before the extinction of the megafauna (about 160 genera with 400 species; see Carlini and Zurita 2010).

A remarkable fact is the dispersal of mammals of South American ancestry that occur first in North America than in South America. For example, the extinct hydrochoerid *Neochoerus* is recorded in beds dated about 3.1–3.9 Ma (Pliocene) in Guanajato, Mexico (Woodburne 2010), while is only known in Ensenadan (Early Pleistocene) beds in the Pampean area. However, it is not excluded that it could have been also in other areas in South America out of the Pampean area.

As we explained above, most of the knowledge about the continental Late Cenozoic mammals in South America comes from the Pampean area and nearby areas of Argentina and Uruguay. There are mammal-bearing Late Miocene (Huayquerian) beds in Venezuela and Brazil and Chapadmalalan and Ensenadan beds in Bolivia (Fig. 3.2), but mammal remains are poorly represented in comparison with those of the Pampean area. The dearth of fertile localities in other region causes that the GABI 1 to 3 record has been almost exclusively studied in Argentina. On the contrary, GABI 4 is widely represented by fossil occurrences in many countries where Lujanian (Late Pleistocene–Early Holocene) beds are widespread.

The genus *Equus* is considered to be part of the GABI 4. However, the species *Equus insulatus* is reported from putative beds of Ensenadan Age of Bolivia (MacFadden 2013). This is the sole location in South America where *Equus* appears to occur in the GABI 2. No *Equus* remain was found in the well-known and widely distributed Ensenadan beds of the Pampean area.

Both the Proto GABI and GABI 1 to 4 pattern of first appearances are clearly episodic. The first North American carnivores in South America could be compatible with the dynamic tectonic activity that affected the region from at least 9 Ma (Woodburne 2010) or with the important sea level fall near the Serravallian and Tortonian boundary (Zachos et al. 2001). The first appearance of peccaries and camelids during the Chapadmalalan and Barrancalobian could have been occasioned by the sea level drop of the Northern Hemisphere glaciation, which began at about 3.6 Ma, but exhibited its first glacial event at about 3.3 Ma (Mudelsee and Raymo 2005; Woodburne 2010).

Climate should have had an important role in the dispersal. However, different climates would be relevant form displacement of different taxa. When climate was warmer and more humid and forest areas were developed, there were adequate conditions for the dispersal of some mammals such as hydrochoerid rodents.

Fig. 3.2 Continental outcrops of putative Ensenadan and Lujanian in the Tarija valley (Bolivia) (photo by Esteban Soibelzon)

Otherwise, when climate was colder and dryer, nominally savanna-adapted taxa would have dispersed such as camelids and tayassuids.

Woodburne (2010) suggest that the first significant episode of faunal exchange (GABI 1; 2.6–2.4 Ma) is concurrent with the initiation of major Northern Hemisphere glaciation. Then, as well as earlier and later, most northward-moving taxa were xenarthrans, with hydrochoerid and porcupine rodents being another conspicuous contingent. Later, during GABI 2, more taxa dispersed southward than the reverse, but up to about 1.8 Ma, the average count for either direction was about equal (Woodburne 2010). The southward contingent tended to include taxa of clear savanna-like ecologies. On the other hand, the northward dispersants typically included xenarthrans, porcupines, and, in GABI 3, opossums, taxa that exhibited a wide range of ecological diversity. Remarkably, the last immigrants to South American were diverse (Woodburne et al. 2006). The dispersal episodes might correspond to glacial times with low sea level with expanded regions in the isthmian area.

During the last twentieth and twenty-first centuries, terrestrial and aquatic environments changed radically because modern human activities occasioned extinctions, pseudoextinctions, and alterations of distribution of many mammals. Besides, many were subject to hunting pressure. These processes obscure the original distributions and occasion that biogeographical patterns were difficult to study sometimes.

3.2.1.1 Biogeography and Immigration

The tropics of the Americas are well known for their remarkable biodiversity, which is due to habitat heterogeneity and a complex geological history, both being responsible for the patterns of geographical distribution of species and clades. Forests are among the most common Neotropical biomes, particularly the Amazon forest, but there are also extensive open biomes, e.g., the diagonal of South America comprising the Pampa, Chaco, Cerrado, and Caatinga (Morrone 2014).

Since the first appearance, the majority of the North American immigrant families are represented by endemic genera (e.g., *Cyonasua*, *Chapadmalania*, *Lama*, *Hippidion*, etc.). These genera have to have differentiated in some place that appears not to be southern South America. Buenos Aires Province coast is more than 5000 km from the Panama Isthmus. The tropical area located near the Amazon basin presently shows the largest species richness. This could the case during the GABI as well.

3.2.2 Integration of South American Mammalian Faunas: The Coexistence of Native and Immigrant Taxa

As we mentioned in the introduction, Patterson and Pascual (1972), Webb (1976), and Pascual and Fidalgo (1972), among others, proposed a scenario of competition between the Holarctic immigrants and the native South American mammals during the GABI, which in many cases latter to became extinct. After this proposal, there was considerable debate especially as to whether placental carnivores arriving from North America caused the extinction of South American marsupial carnivores by competitive displacement (e.g., Simpson 1950, and subsequent papers; Patterson and Pascual 1968, 1972; Werdelin 1987, 2009) or had not such responsibility (e.g., Forasiepi et al. 2007; Prevosti et al. 2009, 2013; Soibelzon 2011). The fossil record indicates that Sparassodonta (marsupial carnivores) only coexisted with procyonids, as they become extinct before the first record of canids in the Marplatan Stage. Moreover, when procyonids appeared, sparassodonts were already in severe decline (Marshall 1977; Forasiepi et al. 2007; Soibelzon 2011). On the other hand, most sparassodonts were hypercarnivores; therefore, they occupied a different ecological niche from that filled by procyonids. So, although the fossil record indicates that these taxa became extinct after a coexistence with procyonids (during the Huayquerian, Late Miocene; see Forasiepi et al. 2007), they were larger than *Cyonasua* (Procyonidae) and presumably occupied a different ecological niche. Noticeably, it was during this time span that *Cyonasua* experienced its greatest diversity (seven species recorded, out of ten described; Soibelzon 2011). During a relatively short time span (Middle to Late Pliocene), large procyonids (body mass ~25 kg in contrast to the ~6–7 kg of *Cyonasua*) belonging to the genus *Chapalmalania* Ameghino (closely related to *Cyonasua*;

Kraglievich and Olazábal 1959) were recorded in South America, but they quickly became extinct and their fossil record is unfortunately very poor. Noteworthy, *Chapalmalania* extinction appears to have been approximately synchronous with the last record of Sparassodonta (family Thylacosmilidae).

Therefore, large carnivores in South America were represented only by crocodiles, large snakes (Madtsoiidae), and terror birds (Phorusrhacidae) during most of the Late Cenozoic until the Early Pleistocene. After the Pliocene–Pleistocene boundary (subsequent to the GABI), the top predator guild in the South America Ensenadan ecosystems was composed of seven species: *Theriodictis platensis*, *Protocyon scagliarum*, *P. troglodytes, Canis* (?) *gezi* (Canidae: Prevosti 2006), and *Smilodon populator*, *Panthera onca* and *Puma* (Felidae: Soibelzon and Prevosti 2008), and *Arctotherium angustidens* (the largest and most powerful mammalian predator of South American terrestrial ecosystems that ever existed; Soibelzon et al. 2009; Soibelzon and Schubert 2011).

The Ensenadan ecosystems were characterized by the high frequency of herbivorous megamammals (e.g., *Glyptodon munizi, Macraucheniopsis ensenadensis*, *Megatherium gallardoi,* and *Panochthus intermedius*, see Soibelzon et al. 2010). This unique situation involved also autochthonous herbivores, whose tendency to giantism reached its maximal expression at that time (see Alberdi and Prado 1993), and only one megacarnivoran: the giant short-faced bear *A. angustidens*.

The biological consequences and behavioural reactions that could have been triggered by the introduction of a megacarnivoran such as the giant short-faced bear among the endemic Pampean megafauna, not only as a recently arrived predator but also as a powerful competitor for dens, were explored recently (Soibelzon et al. 2009). Herbivores appear to adjust quickly their behaviour in order to decrease predation risk after a recolonization of large carnivores in recent ecosystems. Changes in behaviour of prey related with increasing predation risk may cause, i.e., modifications in diet, temporal changes in feeding patterns, spatial changes in habitat use, or changes in patch selection (Lima and Dill 1990). Zurita et al. (2010) suggested that some glyptodonts developed a series of highly modified "spine"-like osteoderms (located at the anterolateral region and over the cephalic notch of the dorsal carapace) as a protection structures for the neck and abdomen. These are the most vulnerable body regions of these large armored animals, since they are not covered by the cephalic shield or carapace. The fossil record shows that these structures were not present in glyptodonts before the GABI, so Zurita el al. (2010) proposed that they could represent a reaction to the arrival of *Smilodon* and *Arctotherium,* the largest and most powerful terrestrial carnivores that ever lived in the Cenozoic of South America.

Studying the past behaviour of xenarthrans, Vizcaíno et al. (2001) suggested that giant sloths have depended on burrows to escape predation but also that these animals used burrows to avoid alternatively excessively cold or warm climatic conditions to conserve energy and water, to breed, and even to survive during the colder seasons due to the particular physiology of xenarthrans (see also McNab 1985, Vizcaíno and Loughry 2008). It is noteworthy that until Ensenadan times, there are scarce records of large burrows in the Pampean region although putative burrow excavators (see above) were present. Only small caves drilled by rodents or small notoungulates were found (e.g., Chapadmalalan; Genise 1989). We suggest that this behaviour would have been acquired or generalized after the arrival of large carnivores. Therefore, the arrival of the large carnivores appears to have affected the autochthonous megafauna not only by the addition of the top predator node in the ecological net, but also as direct competitors for dens (Soibelzon et al. 2009).

The carnivore guild began to be relevant in ecosystems since the Ensenadan Age when six families (Procyonidae, Ursidae, Canidae, Felidae, Mustelidae, and Mephitidae) occurred in South America. During this time, the two most omnivore carnivores (Ursidae and Procyonidae) changed their body size and diet in one case (Ursidae) and were pushed to extinction on the other (the procyonid *Cyonasua*, became extinct during the Ensenadan Age).

Soibelzon and Schubert (2011), Soibelzon (2011) suggested that the South American carnivore guild diversification during the Pleistocene (from the few precursory taxa that crossed the Panama Isthmus during the GABI) provoked the Tremarctinae bears (genus *Arctotherium*) to adjust their size and modify their diet in order to survive in the more competitive ecosystems of the Late Pleistocene. The huge and mostly carnivorous *A. angustidens* become extinct during the Middle Pleistocene (Soibelzon et al. 2005; Soibelzon and Schubert 2011) when other species of *Arctotherium* began to be recorded. Remarkably, Figueirido and Soibelzon (2010) proposed that these later species become more and more omnivore through time, with the youngest and smallest species (*A. wingei*) which has been inferred to be mostly herbivorous.

Regarding the herbivores intraguild competition, Tonni et al. (1992) and Cione and Tonni (1995) demonstrated that the arrival of Holarctic herbivore mammals into the Pampean region was more gradual than previously envisioned. Contrary to the opinion of Webb (1985a), Marshall et al. (1983), and several other authors, eight Holarctic families do not occur for the first time in the Marplatan Age. Actually, only four new families occur in the different levels of the Marplatan: Camelidae, Canidae, Equidae, and Mustelidae. The occurrence of Gomphotheriidae is not fully supported. The Holarctic families Tapiridae, Cervidae, and Gomphotheriidae range certainly only from the Ensenadan Age. The biomass and diversity of Holarctic immigrants were insignificant in the Pampean region during Chapadmalalan and Marplatan times. In consequence, the faunal turnover there observed would be due to other causes. The influence of northern herbivore mammals was surely much more important since the Ensenadan and especially from the Lujanian times.

Finally, a remarkable event took place at the end of the Pleistocene and beginning of the Holocene: the extinction of the megafauna, the last important step of the GABI for us. After this demise, half of the mammal species of South America was of Holarctic ancestry.

3.2.2.1 The Last Mammalian Extinction in South America

The present South American biota is remarkable because its singularity and richness (Simpson 1980; see details in "Composition of the recent mammalian fauna of South America"). However, even more striking is the fact that the largest diversity of megamammals (animals weighing more than 1 ton) and large mammals (more than 44 kg) in the world took place in this continent until their extinction a few thousand years ago (Ameghino 1889; Pascual et al. 1965; Cione and Tonni 2005; Cione et al. 2003, 2009). All the megamammals and 80 % of the large mammals became extinct. The last megamammal probably died about 8000 calibrated years BP or even later (Politis and Gutiérrez 1998; Politis 2007; Soibelzon et al. 2012). Besides, it is presumed that most of the extant mammals were present in the Early Holocene (the latest Lujanian according to the local chronology). Due to these reasons, the mammal diversity was significatively higher at this moment than during the Middle Holocene and the Recent (see Cione et al. 2009).

In the following chapter, the Broken Zig-Zag hypothesis (proposed by Cione et al. 2003, 2009, in order to explain the last mammalian extinction in South America) is summarized and some of its topics are discussed, such as: (1) the kind of extinction, (2) the predominance of xenarthrans in the megafauna, and (3) the scarce representation of the total diversity of the extinct megamammals and large mammals in the archaeological sites. We consider that the extinction of the megafauna is part of the GABI in South America. No doubt, humans participated in the GABI.

3.2.2.2 The Broken Zig-Zag: A Synthesis

Studies based on geochemical proxies in glacial ice cores from Greenland, Antarctica, and South America show that temperatures strongly fluctuated during at least the last 800,000 years (Lüthi et al. 2008) and that the present interglacial is not substantially different from the earlier ones (over 10 major events during the Middle–Late Pleistocene; Fig. 3.3; McCulloch et al. 2000; Blunier and Brook 2001; Steig 2006). The periodic changes in Pleistocene climate provoked dramatic modifications in the distribution and biomass of the biota in South America and other continents. We use the expression "Zig-Zag" to stress the periodicity of these biotic trends.

Cione et al. (2003) pointed that in modern South America, 18 % of the land is characterized as open areas, whereas medium vegetated areas make up 15 % and closed areas 67 % (based on maps of Cabrera and Willink 1980). In contrast, by using the reconstruction of South America during the LGM (Clapperton 1993), they calculated that open areas would have encompassed 31 % of the territory, medium areas 54 %, and closed areas 15 % of the total surface. Similar results were obtained by Vivo and Carmignotto (2004) based on the distribution of plant formations (Fig. 3.4; see also Johnson 2002).

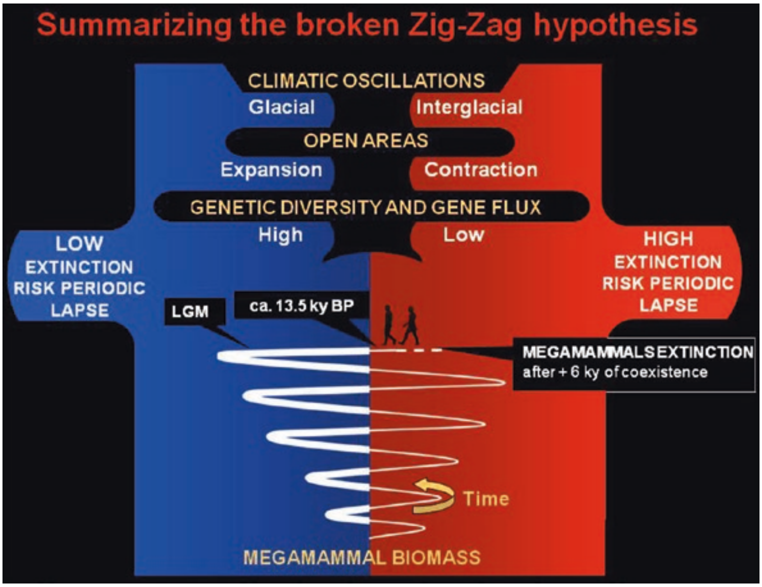

Fig. 3.3 Graphic representation of the Zig-Zag Hypothesis (modified from Soibelzon 2008)

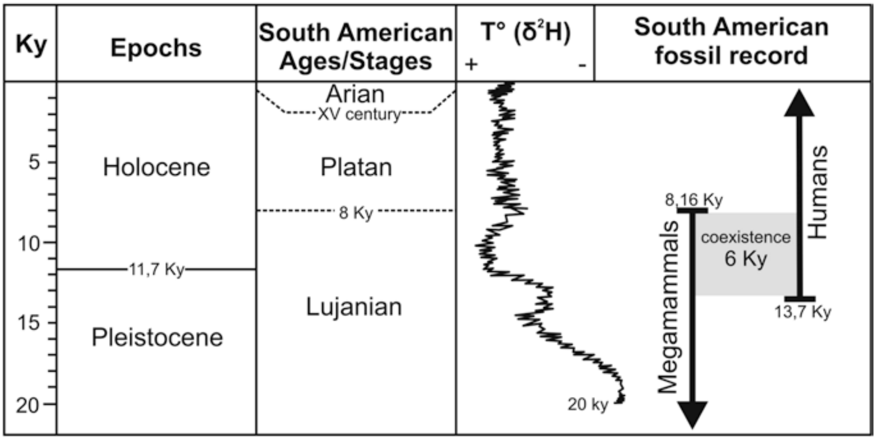

Fig. 3.4 Chronological chart of the latest Pleistocene–Recent in southern South America and climatic oscillations represented by Antarctica δ^2H (Jouzel et al. 2007) and the fossil record of megammamals and humans in South America

It is well known that the Late Pleistocene South American mammal diversity was higher than the present especially because many different species of large and megammamals were thriving in the Pampean area and the rest of the continent. However, although the taxonomic diversity was elevated, the number of individuals per species and the total biomass in each location probably were not high because most of the South American glacial ecosystems should not have been very productive. During glacial times, while climate was colder and drier at the extraglacial areas, open areas expanded and animals and plants adapted to these environments augmented their distribution and biomass (see discussion in Cione et al. 2009). During the shorter interglacial periods, when temperature was as high or even higher than present (see Lisiecki and Raymo 2005, and the bibliography cited herein), an expansion of the forested areas may be expected (Vivo and Carmignotto 2004) and with this an increase of the biomass of forest dwelling animals.

Remarkably, the fossil record does not suggest that these cyclic environmental changes either produced depletion of niches or caused massive extinction of mammals (Tonni et al. 1992; Cione et al. 2009). In the short interglacial periods, open areas adapted mammals were surely remarkably reduced in number of individuals and under ecological stress for obvious reasons. Some populations possibly were close to the minimal viable number and many surely became isolated and genetic flux greatly diminished among them, reducing the genetic variability. We proposed that during the present interglacial, when open-environment adapted huge mammals were in crisis, humans entered South America and provoked their extinction (Fig. 3.3).

In synthesis, the hypothesis (see Cione et al. 2003, 2009, and citations therein) is supported by (1) the global and local climatic evolution, (2) the vegetational history, (3) the positive biostratigraphic evidence, (4) the chronology of extinctions, (5) the paleobiogeography of mammals, (6) the adaptation to open environments of those mammals that became extinct which also were probably k-adapted (e.g., females probably attained sexual maturity late, with a very long gestation period [one year or more] and prolonged parental care, and a total low number of offsprings during life), (7) the selective disappearance of all continental megamammals and most large mammals, (8) the almost nil extinction of middle sized and small mammals, and of other vertebrates, animals or plants at the extinction event, (9) the protected environments where the few surviving large mammals live today, (10) the inferred variation in numerosity but not in diversity of megamammals during the cyclic shifts of vegetations, (11) the fact that the fauna was not declining by the time of the event; moreover, no significant extinction was detected during the Middle–Late Pleistocene before the extinction event, (12) the fact that both immigrants (of the GABI) and endemic mammals became extinct, (13) the fact that American mammals did not coevolve with humans, (14) the entrance of humans to the continent at the time of the extinction event, and (15) the fact that humans actually hunted the megamammals and greatly modified the original environments.

The theory is testable by analyzing the relationship between mammal extinction and climatic change throughout the lapse Middle Pleistocene–earliest Holocene.

The South American extinction appears to be different to the North American one because it lasted several thousands of years: Certainly, its demise was not caused by a blitzkrieg (Fig. 3.4).

3.2.2.3 Mass Extinction?

The extinction event was certainly spectacular. Some authors refer to it as a mass extinction (e.g., Marshall et al. 1984; Dayton 2001; La Violette 2011). However, was it a mass extinction? Mass extinctions share some common features (Benton and Harper 2009): (1) The extinct organisms span a broad range of ecological environments, including plants and animals, marine and non-marine forms, and large and small organisms; (2) Many species become extinct, usually more than 30 %; (3) The extinction event is worldwide, in continents and oceans; (4) The extinctions happened within a relatively short time and hence relate to a single cause or cluster of interlinked causes; (5) The level of extinction stands out as considerably higher than the background extinction level. This latter concept refers to the normal extinctions that happens without any broad-scale causes (see also Jablonski 2005; Erwin 2006).

Obviously, the Late Pleistocene–Holocene extinction did not encompass different kinds of organisms everywhere, including South America. Only terrestrial megamammals, large mammals, and very few small mammals disappeared. Neither plant nor marine organism extinctions are known.

Many species of mammals became extinct, but they were very far from the 30 % that has been suggested. The extinction was not worldwide. Several terrestrial mammals disappeared in the Americas, Eurasia, Australia, and many islands. Neither freshwater nor marine animals and both terrestrial and aquatic plants were affected.

The extinctions happened within a relatively short time but not simultaneously occurring at different times in different places (e.g., North and South America, Europe, Australia, different islands). The levels of extinction stand out considerably higher only in some mammals than the background extinction level.

3.2.2.4 In the Last Extinction, Most Were Xenarthran

South American megafauna was unique in being integrated by a majority of xenarthrans percentage (more that 50 %; Vizcaíno et al. 2009), peculiar mammals that greatly diversified in the continent (Fariña 1996; Cione et al. 2003, 2009; Gutiérrez et al. 2010) (Fig. 3.5). Some migrated during the GABI to North America (Woodburne et al. 2006; Woodburne 2010). We discuss if the peculiar biology of xenarthrans could be relevant to explain its demise.

Fig. 3.5 Glyptodonts and ground sloths: They dominated open environments during million years and became extinct just yesterday. Diorama in the Museo de La Plata. Photographs by Esteban Soibelzon

Metabolic rate of xenarthrans falls between 40 and 60 % of the rates expected from mass in the relation for placental mammals (Kleiber 1932; McNab 1985). According to Vizcaíno et al. (2006), low metabolism would have permit xenarthrans to attain large size in comparison with the low income of food. "Xenarthrans have less occlusal surface area available for triturating food than epitherians of similar sizes. This fact may be related to the low basal metabolic rates characteristic of living xenarthrans, which fall between 40 and 60 % of the rates expected from mass in Kleiber's (1932) relation for placental mammals (McNab 1985). This implies that xenarthrans have less energetic requirements than epitherians and, therefore, for a specific type of food, require lower intakes than epitherians of similar body masses" (Vizcaíno et al. 2006: 18).

Giant sloths would have depended on burrows to avoid excessive cold or warm climatic conditions in order to conserve energy and water, and to breed, and even to survive during the colder seasons because of the particular physiology of xenarthrans (see McNab 1985; Vizcaíno and Loughry 2008).

Gutiérrez et al. (2010) suggested that xenarthrans, especially glyptodonts and ground sloths, consumed a wide variety of plant resources and exploited different habitats. Therefore, the coexistence of various herbivore species of xenarthrans could be supported by differential consumption of a wide range of food resources.

The combination of factors such as diet, habitat preference, body mass, physiology, and ethology, among others, could have been played an important role in giant xenarthrans survival and extinction (Gutiérrez et al. 2010; see discussion in Cione et al. 2009).

3.2.2.5 Extinct Mammals in Archaeological Sites

The megamammal and large mammal fauna was remarkably rich in South America before the arrival of humans. During the latest Pleistocene, 32 species of megamammals and 45 of large mammals that later became extinct were present in the continent (a total of 77 extinct taxa). Most of them have not been recorded in archeological sites. This fact could be a strong objection raised to reject the hypothesis that humans had been a fundamental factor in the demise of the megafauna. However, little has been studied about the different number of mammal species and their biogeography.

We know that more than 70 megamammal and large mammal species existed in South America during the latest Pleistocene. However, almost the 60 % of them are only known by its holotype or just very few specimens. Consequently, only 40 % were relatively frequent species. Moreover, ecosystems should not admit many specimens of each species of such large mammals.

Besides, there were quite different areas of endemism. Many were restricted to northern or southern areas and others to highlands or lowlands (Fig. 3.6). Few of them reached southern South America. Consequently, although the total number of megamammals was outstanding, they were not present altogether in all areas.

Fig. 3.6 Distribution of some extinct large and megamammals in South America during the Late Pleistocene. **a** "*Stegomastodon*" *waringi*, "*S.*" *platensis,* and *Cuvieronius hyodon* (modified from Cione et al. 2009); **b** *Arctotherium tarijense* and *A. wingei* (Soibelzon et al. 2005); **c** *Eremotherium* and *Megatherium* (Cartelle 1994; Pujos and Salas 2004); **d** *Mixotoxodon* and *Toxodon* (Paula-Couto 1979; Carlini and Tonni 2000); **e** *Holmesina majus*, *H. occidentalis,* and *H. paulacoutoi* (modified from Scillato-Yané et al. 2005); **f** *Pampatherium typum* and *P. humboldti* (modified from Scillato-Yané et al. 2005); **g** *Xenorhinotherium bahiense* and *Macrauchenia patachonica* (de Melo et al. 2005; Carlini and Tonni 2000); **h** *Glyptodon* and *Glyptotherium* (Carlini and Tonni 2000; Carlini et al. 2008); **i** *Equus (Amerhippus) lasallei, E. (A.) insulatus, E. (A.) andium, E. (A.) neogaeus* (Alberdi and Prado 2004); **j** *Mylodonopsis* and *Mylodon* (Cartelle 1991; Brandoni et al. 2010); **k** *Hoplophorus* and *Neosclerocalyptus*; **l** *Galictis vittata* and *Galictis cuja*

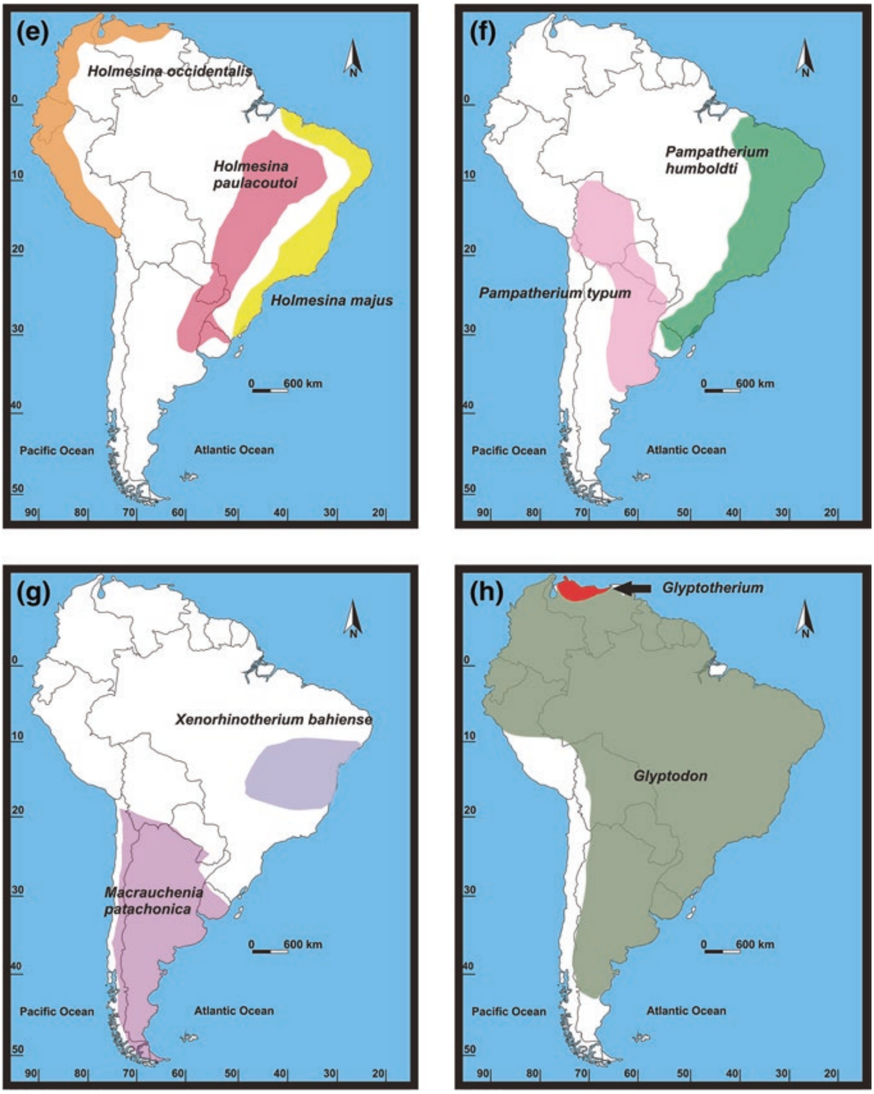

Fig. 3.6 (continued)

We consider here the particular case of the Pampean area, where a good paleontological and archeological record is known. Megamammal species present in the Pampean area during the Lujanian Stage were ***Doedicurus clavicaudatus****, ***Glossotherium robustum****, *Glyptodon clavipes*, ***Glyptodon reticulatus*** (*Glyptodon* sp. is present in archeological sites), *Hemiauchenia paradoxa**, *Lestodon armatus**, ***Macrauchenia patachonica****, ***Megatherium americanum****, *Mylodon darwinii* (*Mylodon* sp. is present in an archeological site), ***Panochthus tuberculatus*,**

Fig. 3.6 (continued)

“Stegomastodon” platensis, ***Toxodon platensis****. Large mammals species were the following: *Antifer ultra*, *Arctotherium bonariense*, ***Equus (A.) neogaeus****, ***Eutatus seguini****, ***Hippidion principale****, *Holmesina paulacoutoi*, ***Lama gracilis***, *Morenelaphus lujanensis*, *Pampatherium typum*, *Paraceros fragilis*, *Propraopus grandis*, ***Scelidotherium leptocephalum*** (*Scelidotherium* sp. is present in one archeological site), *S. populator*. Asterisk indicates that those taxa were found in archeological sites. Bold types indicate that it is a relatively common taxon in paleontological sites. Some of the species that are not recorded in Pampean archeological sites are present in archeological sites of other regions (e.g., *Lama gracilis*).

We find that only 54 % of the megamammals and large mammals were relatively common in the Pampean area. From these taxa, 77 % were present in archeological sites. Consequently, only 23 % of the recorded species in archeological sites were rare. As it can be expected, paleoindians appear to have particularly hunted the most common taxa. For this, the absence of several mammals in the archaeological sites would not indicate that they were depreciated for humans (see also Kay 2002). They could be just extremely rare. On this sense, horses are relatively infrequent in the archaeological sites but were not much difficult to hunt than a guanaco or a deer; hence, a possible explanation is the occurrence of a reduced population. Fariña (1996) estimated the population density of each herbivorous species on the Lujanian ecosystems of the Pampean region using the general equation described in Damuth (1981). These estimations showed that megaherbivores were less abundant than was thought before, for example, the estimated density for *M. americanum* (body mass ~4 tons) is ~0.2 individuals/km^2; for *D. clavicaudatus* (body mass ~1.3 tons) is ~0.4 individuals/km^2; for *G. clavipes* (body mass ~2 tons) is ~0.3 individuals/km^2; for *L. trigonidens* (body mass ~3 tons) is ~0.2 individuals/km^2; for *T. platensis* (body mass ~1.1 tons) is ~0.5 individuals/km^2; for *M. patachonica* (body mass ~1.1 tons) is ~0.5 individuals/km^2. Therefore, the absence or low record of megamammals in archeological sites could be reflecting their low abundance in the Late Pleistocene–Early Holocene ecosystems.

Another explanation is provided by the observations of Gary Haynes (in Fiedel and Haynes 2004) on modern kill sites (both cultural and non-cultural) in Africa. Haynes observed that modern death sites are rarely preserved (less than 0.01 % or less of total number being killed or dying naturally). Indirect evidence of hunting of some large mammals not recorded in archaeological contexts was obtained from blood present in lithic points (Kooyman et al. 2001) and micropolishes of bone and soft tissues on lithic instruments (Cueto and Castro 2012).

Remarkably, in one archaeological site (the Paso Otero 5 Site; see Martínez and Gutiérrez 2011), the mammal record previous to the extinction showed a large exploitation of extinct mammals and a more reduced one of guanacos (*Lama guanicoe*, one of the extant South American camelids). After the extinction of the larger mammals, hunting was concentrated on guanacos and other relatively small and medium size mammals (e.g., armadillos). This could be the representation of an opportunistic behaviour that resulted after the almost total extermination of the spectacular fauna of huge mammals that inhabited South America before the entrance of humans.

Epilogue

The first authors that considered the interchange between the Americas were Wallace, Ameghino, and few others as early as the second half of 19th. Notwithstanding the remarkable work done by thousands of paleontologists, zoologists, botanists, geologists, and professionals of other disciplines, we are far from having a precise panorama about one of the most important event in the history of mammals.

However, we are confident that more complete survey of mammal-bearing units in southern South America as well as the discovering others in the central and northern Andes and Central America will give us the factual evidence for proposing, confirming, or rejecting many hypotheses. Moreover, the expanding molecular studies will provide minimum age for the origin of many endemic clades of North American families whose first appearance is not adequately explained.

In this book, we consider the extinction of megafauna in South America as a part of GABI. Several paleontologists (including the authors of this book) are commited with the study of the processes that modified for ever the composition and distribution of land mammals in South America. The appearance of hunter–gatherers at the end of the Pleistocene occasioned the spectacular extinction of megafauna. However, this process is being completed by modern man. For this, research about recent distribution of vertebrates in South America has to be accelerated. During the last part of twentieth century and the beginning of the twenty-first century, terrestrial and aquatic environments changed radically because modern human activities occasioned extinction, pseudoextinction, and alteration of distribution of many mammals. This disruption might make conventional and molecular studies about historical patterns and relationships between different lineages extremely difficult. However, fossils are still in the rocks. They are waiting for us to find them, unearth them, and make them drops of light for explaining the origin of a treasure in danger: the richest land mammal fauna of the world.

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