

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 America 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

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 America. 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 connexion 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 through the historical biogeography of the bee genus *Diadasia*; Pinto-Sánchez 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 equid *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 be 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 later to become 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 Marplatian 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 *Chapadmalania* 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 muniti*, *Macrauchenia ensenadensis*, *Megatherium gallardoi*, and *Panochthus intermedius*, see Soibelzon et al. 2010). This unique situation involved also autochthonous herbivores, whose tendency to gigantism 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 et 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 significantly 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).

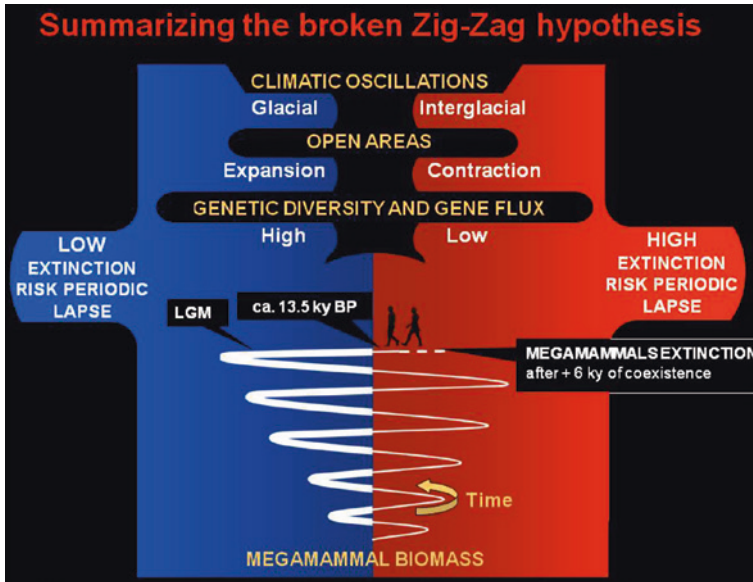


Fig. 3.3 Graphic representation of the Zig-Zag Hypothesis (modified from Soibelzon 2008)

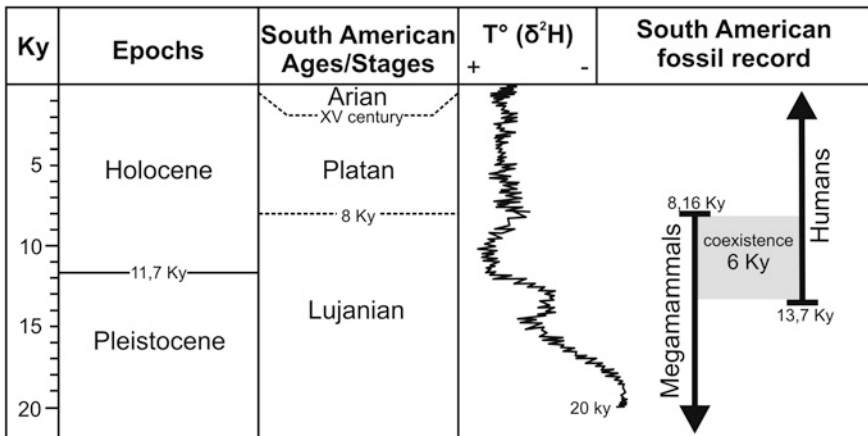


Fig. 3.4 Chronological chart of the latest Pleistocene–Recent in southern South America and climatic oscillations represented by Antarctica δ²H (Jouzel et al. 2007) and the fossil record of megamammals and humans in South America

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 megamammals 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 than 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 epitharians 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 epitharians and, therefore, for a specific type of food, require lower intakes than epitharians 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.

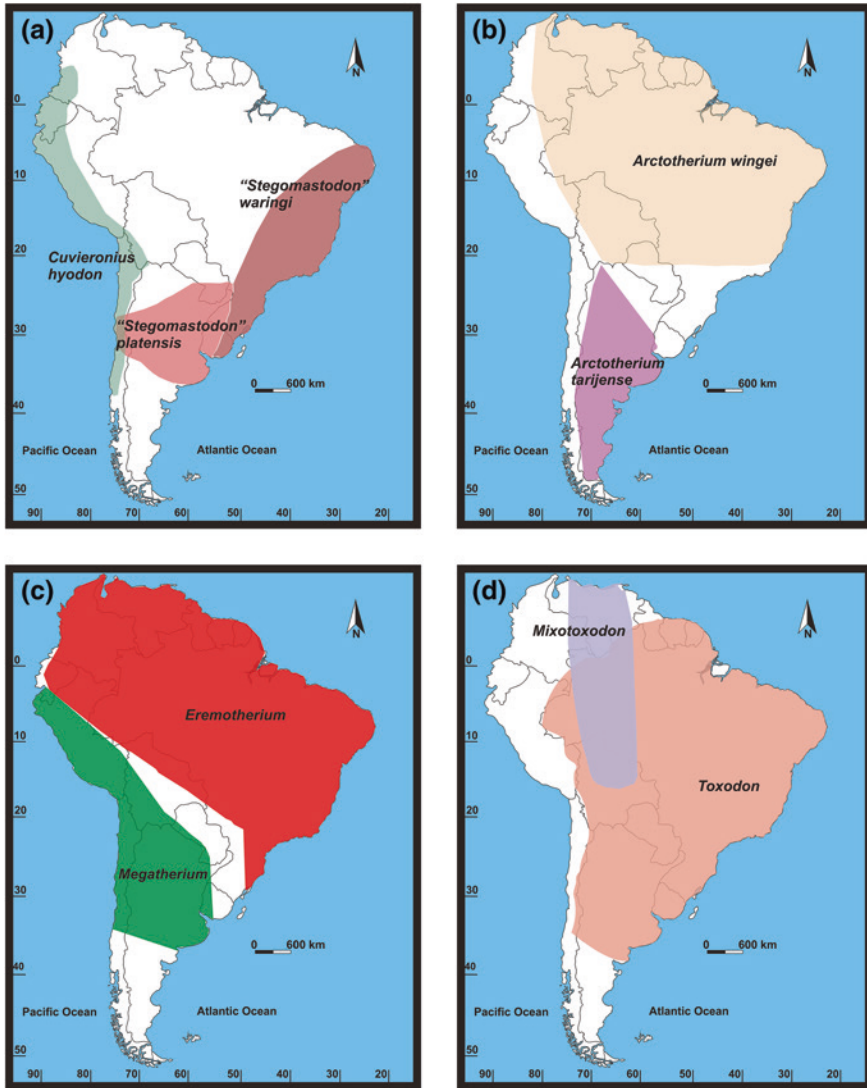


Fig. 3.6 Distribution of some extinct large and megamammals in South America during the Late Pleistocene. **a** “*Stegomastodon*” *waringi*, “*S.*” *platensis*, and *Cuvieronius hyodon* (modified from Cione et al. 2009); **b** *Arctotherium tarijense* and *A. wingei* (Soibelzon et al. 2005); **c** *Eremotherium* 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** *Myloodonopsis* and *Myloodon* (Cartelle 1991; Brandoni et al. 2010); **k** *Hoplophorus* and *Neosclerocalyptus*; **l** *Galictis vittata* and *Galictis cuja*

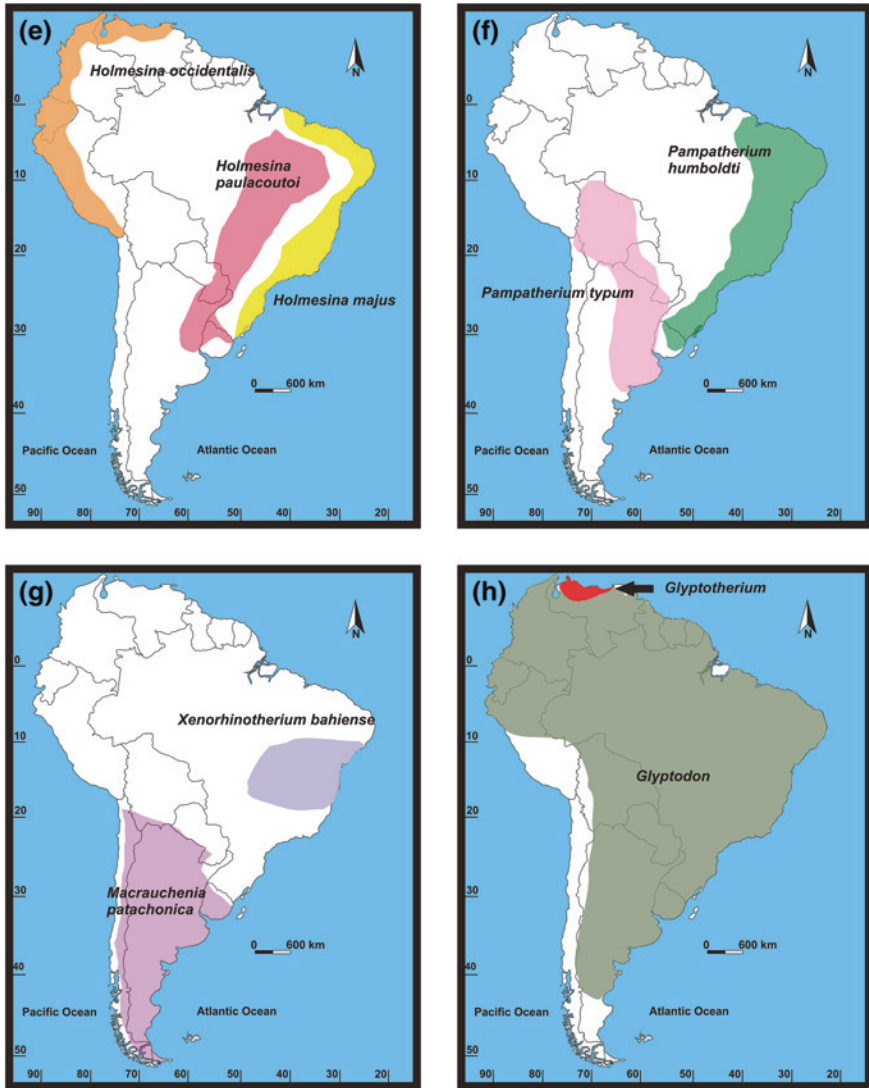


Fig. 3.6 (continued)

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**, *Myloodon darwini* (*Myloodon* 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 leptcephalum* (*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 archeological 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 archeological 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/km²; for *D. clavicaudatus* (body mass ~1.3 tons) is ~0.4 individuals/km²; for *G. clavipes* (body mass ~2 tons) is ~0.3 individuals/km²; for *L. trigonidens* (body mass ~3 tons) is ~0.2 individuals/km²; for *T. platensis* (body mass ~1.1 tons) is ~0.5 individuals/km²; for *M. patachonica* (body mass ~1.1 tons) is ~0.5 individuals/km². 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 archeological 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 archeological 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 committed 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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