

Chapter 4

Evolutionary Contexts

Abstract In order to understand the timing of metatherian radiations, adaptations, and extinctions, it is important to review the variety of strongly interrelated contexts that defined them. (1) During the Cenozoic Era, global climates shifted from Greenhouse to Icehouse conditions; this major change was quite obvious by the Eocene–Oligocene boundary (ca. 33 Ma). Other large-scale changes also occurred prior and subsequent to this shift: hyperthermal events, as the Paleocene–Eocene Thermal Maximum, or cooling phases, such as that triggered by the late Miocene closing of the Panama isthmus. (2) Many elements precursor to the Cenozoic South American ecosystems were already in place by the late Mesozoic Era. By the Paleocene–early Eocene, several of the most important types (e.g., Neotropical forest, broad-leaved forest types) had developed their modern versions, as is the case of the Grasslands seem to have been established, at least in southern South America, by the late Oligocene. (3) A recent biogeographical review supports the proposal that the southernmost tip of South America (the Andean Region) belongs to a distinct biogeographical unit, the Austral Kingdom. In turn, most of the remaining areas of South America, as well as southernmost North America and the Caribbean, comprise the Neotropical Region of the Holotropical Kingdom. South America’s Arid Diagonal is the great biogeographic divide between the Neotropical Region and the Andean Region. The distribution of this arid-semiarid belt, originally placed in much of southwestern Gondwana, closely matches the distribution of the Subtropical Seasonal Dry climatic belt since early Mesozoic times. (4) Reinforcing this climatic divide of the continent, paleogeographic reconstructions of South America suggest that the continent was split into northern and southern portions by means of epeiric seas due to marine transgressions. In southernmost South America, the paleogeography resulting from marine transgressions led to a very complex, almost archipelagic continental configuration. (5) At least six successive phases can be recognized in the evolution of Mesozoic–Cenozoic South American mammals: Early Gondwanian, Late Gondwanian, Early South American, Late South American, Interamerican, and Hypoamerican.

Keywords Metatheria • South America • Evolutionary contexts • Paleoclimates • Ecosystems • Biogeography • Paleogeography • Evolutionary phases

Taking in account that the inferred arrival of metatherians in South America probably dates back to the Late Cretaceous (see Chaps. 3 and 7), it seems reasonable to assume that their evolution in this continent occurred throughout the last 70–75 million years, and perhaps longer. This long period of metatherian evolution in South America occurred under specific tectonic contexts, global and regional climatic parameters, biogeographic constraints, ecosystem developments, and trophic interactions with other groups of animals and plants. In order to understand the timing of metatherian radiations, adaptations, and extinctions, it is obviously important to review these contexts, which, in turn, are strongly interrelated. One of them (tectonics and metatherian dispersals) was reviewed in Chap. 3. Here we focus on the remaining ones.

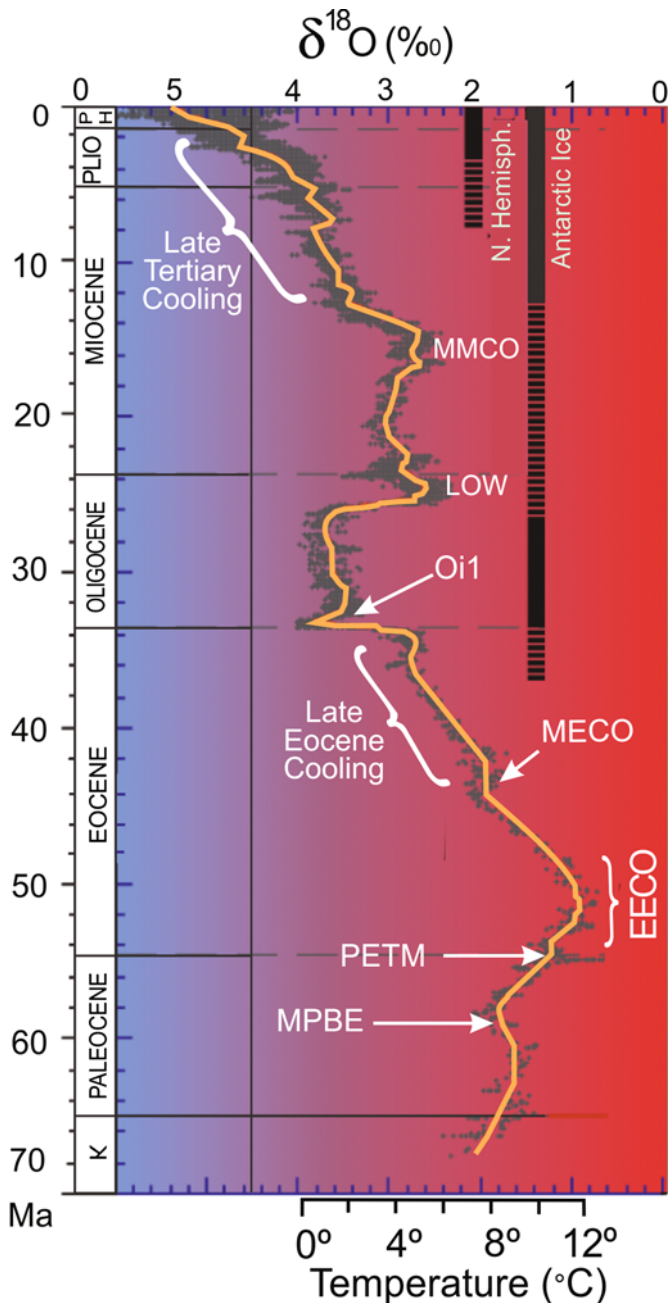
4.1 Climate

During the Cenozoic Era global climates shifted from Greenhouse to Icehouse conditions. This major change was quite obvious by the middle of the Cenozoic, at ca. 33 Ma (the Eocene–Oligocene boundary, or EOB; see, e.g., Zachos et al. 2001). However, several other large-scale changes also occurred prior and subsequent to this shift. As suggested in Chap. 7, metatherian evolution responded in various ways to most, if not all of them.

Many factors are known to affect the global climate, both external (e.g., solar intensity, orbital cycles) and internal (atmospheric circulation, ocean currents, vegetation cover, albedo, tectonics and sea-floor spreading, paleogeography, orographic barriers, etc.) to the Earth's dynamics. Interrelationships among these factors are the norm rather than exceptions. Examples include the relations among plate tectonics, volcanism, and atmospheric dust; vegetation cover and albedo; plate shifts and ocean currents. Most important paleogeographic factors that have been mentioned as Cenozoic triggers of climate changes are the isolation of Antarctica and the inception of the Antarctic Circumpolar Current (ACC) by the EOB (beginning of the Icehouse world); the Eocene to Miocene collision of India with Eurasia (another global cooling event); the late Miocene isolation of the Mediterranean from Thetis (and the further cooling of Europe); finally, the Pliocene separation of the Atlantic and Pacific oceans by means of the Panama land-bridge, which triggered the beginning of the full, bipolar, Icehouse world of the late Cenozoic (see, e.g., Crowley 2012 and literature cited). In turn, high atmospheric greenhouse gas concentrations (GHG) have been cited as crucial factors in several hothouse events such as the Paleocene–Eocene Thermal Maximum (PETM; see Fig. 4.1).

Some of the major climatic events that framed mammalian evolution throughout the last 70 m.y. are as follows (see a review in Crowley 2012 and literature cited):

1. During the latest Cretaceous, hothouse conditions persisted in spite of minor cooling during the late Maastrichtian (ca. 67 Ma; see Gallagher et al. 2008). Warm ocean currents encircled the globe by means of wide ocean gateways, and shallow epicontinental seas acted as climate moderators. In South America there were no high Andes blocking the equatorial easterlies (Crowley 2012). These conditions persisted up to Paleocene times (Danian). By the latest Selandian or earliest Thanetian (ca. 58 Ma) a brief hyperthermal event caused a biotic response, the Mid-Paleocene Biotic Event (MPBE, see Fig. 4.1; Bernaola et al. 2007).
2. The Paleocene–Eocene boundary coincided with the first of a series of Eocene hyperthermals, the Paleocene–Eocene Thermal Maximum (PETM), leading to the Early Eocene Climatic Optimum (EECO; Fig. 4.1). The PETM consisted of a giant release of greenhouse gases (GHG) in a short period (less than 0.3 m.y.; Zachos et al. 2001). In taking place in an already greenhouse world, it triggered a hotter than normal greenhouse phase. The PETM, together with the EECO, marks the highest global average temperatures for the whole Cenozoic. Also, the highest sea levels and warmer ocean waters of the whole Era are recorded in this period (Sluijs et al. 2008, 2011).
3. The isolation and glaciations of Antarctica by the Eocene–Oligocene boundary (EOB) marks the end of the last phase of greenhouse conditions and the beginning of the Icehouse world, at least in mid- and high latitudes north and south of the Equator. The cooling event was triggered by the full opening of the Drake Passage and the widening of the Tasman Sea, which caused oceanic currents to fully encircle the Antarctic continent. A higher albedo and the progressive closing of tropical oceanic gateways have also been cited as concurrent factors in the EOB global cooling (Lawver and Gahagan 2003; Livermore et al. 2005).
4. The late Miocene (Messinian) witnessed the closing of three oceanic gateways: Panama, Gibraltar, and Indonesia. This triggered the full establishment of bipolar Icehouse conditions on Earth; evidence of ice caps appear for the first time in the Northern Hemisphere. The onset of the Northern Hemisphere Glaciation (NHG) is usually taken at 3.6 Ma (Bartoli et al. 2005). India finished its collision course with Asia; Tapponnier et al. (2001) suggest that by the late Miocene began the third, and still in progress, phase of rise and growth of the Tibetan Plateau. In South America, the Central Andes began its final uplift also by the late Miocene (ca 7 Ma); it has been estimated that the Altiplano and Eastern Cordillera had, by 10 Ma, no more than half of their modern elevation (Gregory-Wodzicki 2000). These and other factors set the conditions for a cooler, drier world. Both South America and Africa were completely crossed by arid belts between 15 and 30° South. In South America, this arid belt acted, in Mesozoic and Cenozoic times, as a biogeographic barrier between the Neotropical and Andean regions (see below).
5. During the Pleistocene, a combination of features such as orbital cycles and paleogeography set up the conditions for a continued Ice Age characterized by glacial advances and retreats. The last of these, the Last Glacial Maximum



◀ **Fig. 4.1** Latest Cretaceous–Cenozoic temperatures, polar ice, and thermal events at the global scale. The temperature curve (in orange) fluctuates from warmer (red area) to cooler (blue). Black bars represent ice volume in each hemisphere (dashed bar: periods of minimal ice cover; full bar: close to maximum ice cover). $\Delta^{18}\text{O}$ refers to the deep-sea oxygen record based on data compiled from DSDP and ODP drilling sites. *Abbreviations* EECO, Early Eocene Climatic Optimum; K, Late Cretaceous; LOW, Late Oligocene Warming; MECO, Middle Eocene Climatic Optimum; MMCO, Middle Miocene Climatic Optimum; MPBE, mid-Paleocene Biotic Event; Oi1, earliest Oligocene oxygen isotope excursion that marks the beginning of the ice sheet coverage in Antarctica; PETM, Paleocene–Eocene Thermal Maximum. Modified after Zachos et al. (2001: Fig. 2)

(LGM, ca. 20,000 ybp), was colder and drier than any other interval in the Cenozoic. Continental ice-sheets up to 2–3 km in thickness extended across northern North America and Eurasia; a dramatic fall in sea level gave rise to land bridges linking islands and continents; forested areas greatly decreased, and were replaced by shrublands, grasslands, tundra, and deserts.

All of these climatic turning points had consequences on the world's biotas and ecosystems, including many mammalian lineages. Several turning points may have triggered the successive faunal phases described below. Also, metatherian radiations, taxonomic and functional turnovers, and extinctions, seem to have been influenced by these climatic and ecological events (see below and Chap. 7).

4.2 Ecosystem Evolution

Regardless of their Jurassic or Early Cretaceous origins (see Graham 2011, and literature cited), angiosperms—presently the predominant component of most terrestrial ecosystems—underwent a rapid diversification in mid-Early Cretaceous times (Heimhofer et al. 2005). Based on genetic (molecular clock) data, Ruban (2012) estimates that the radiation of flowering plants peaked three times during the Cretaceous: in the Albian (112–100 Ma), in the early Campanian (83.5–70.6 Ma), and in the Maastrichtian (70.6–65.5 Ma). According to him, the Cretaceous/Paleogene mass extinctions were followed by a strong, abrupt reduction in the radiation intensity of angiosperms (Ruban 2012). These radiation peaks in angiosperm evolution may have been triggered by environmental disruptions. Heimhofer et al. (2005) state that the late Barremian to Aptian diversification of early magnoliids and/or monocots took place within a period of major climatic and environmental destabilization, including several episodes of climate warming and cooling, as well as changes in humidity and hydrological cycling. They also indicate that, judging by the fossil record, angiosperms were already defining most of the Earth's terrestrial ecosystems by the Cenomanian (100 Ma).

Several authors have recently contributed reviews of lineage (taxonomic) or floral diversity in South America throughout the Late Cretaceous–Cenozoic, especially in Paleogene times (see, e.g., Wilf et al. 2003, 2005; Iglesias et al. 2007;

Jaramillo et al. 2006; a more integrative panorama of floristic and faunal relationships was given by Wilf et al. 2013; Woodburne et al. 2014). Focusing instead on an ecosystemic approach, Graham (2011) developed a classification of terrestrial New World ecosystems beginning at 100 Ma. He stated that already by the Cenomanian 8 of the 12 ecosystems recognized for the modern Earth were present: polar broad-leaved deciduous forests, notophyllous broad-leaved evergreen forests, paratropical rain forests, tropical forests, aquatic, herbaceous freshwater bog/marsh/swamp (including lake margins) settings, as well as mangroves, and beach/strand/dunes. From these types, the remaining modern ecosystems evolved. A detail of these ecosystem types, with examples from Latin America, are the following:

1. Desert—Communities receiving less than 120 mm MAP. An extreme South American example is the Atacama desert in northern Chile.
2. Shrubland/chaparral-woodland-savanna. Examples include the Caatinga and the Cerrado in Brazil, or Patagonia in southern Argentina and Chile.
3. Grassland—The most noticeable case is the Pampas in Argentina.
4. Mangroove—Mangrooves border coastal brackish waters, where rivers discharge into the ocean.
5. Beach/strand/dune.
6. Freshwater herbaceous bog/marsh/swamp—It includes the Pantanal of Paraguay, Brazil, and Bolivia.
7. Aquatic.
8. Lowland Neotropical rain forest (Including the Atlantic forest of southeastern Brazil)—It consists of broad-leaved evergreen vegetation, mostly between 10°N and 10°S, lateritic soils, high MAT (ca 24 °C) and MAP (1800–5000 mm), without a pronounced dry season.
9. Lower to upper montane broad-leaved forest—This is Latin America’s deciduous forest ; an ecosystem intermediate between the lowland Neotropical rain forest and the páramo, with a variety of complex subdivisions.
10. Coniferous/gymnosperm forest—In South America, forest ecosystems including *Araucaria*, *Austrocedrus*, *Fitzroya*, *Podocarpus*, etc.
11. Alpine tundra—In South America, the Páramo.
12. Tundra.

According to Graham (2011) among the forcing mechanisms that promoted this ecosystem diversification during the Cretaceous are hothouse (hyperthermal) events, the existence of low-lying and epicontinental seas at various periods, and the subsequent drainage of those inland seas; finally, tectonic events such as the separation of South America from Africa, which triggered a provincialization of their respective biotas. Most important Cenozoic events include the PETM (ca 55Â Ma), the EECO (50â€“53Â Ma), and the EOB global cooling ca. 33Â Ma. TableÂ 4.1 shows the timing of each of the 12 ecosystems in South America. As shown, at least elements, if not early versions of most of them, were already present since the Cretaceous. By the Paleocene-early Eocene, several of the most important types had developed their modern versions, as is the case of the Neotropical forest and the

Table 4.1 Timing of ecosystem appearance in the New World. Light grey: elements of the future ecosystems are already present; dark grey: early versions; black: essentially modern versions

	ECOSYSTEM	CRETACEOUS	PALEOCENE- EARLY EOCENE	MIDDLE EOCENE- EARLY MIOCENE	MIDDLE MIOCENE- PLIOCENE
1	Desert				
2	Shrubland (1)				
3	Grassland				
4	Mangrove				
5	Beach/strand/dune				
6	Freshwater (2)				
7	Aquatic				
8	Neotropical forest (3)				
9	Broad-leaved forest (4)				
10	Coniferous forest				
11	Tundra				
12	Alpine tundra (5)				

Notes (1) Shrubland/chaparral-woodland-savanna; (2) freshwater herbaceous bog/marsh/swamp (lake margin); (3) Lowland Neotropical rain forest; (4) in Latin America, low to upper montane broad-leaved forest; and (5) in Latin America, Páramo. After Graham (2011). Note that Barreda and Palazzesi (2007) state that grasslands were already present in southern South America already in the Oligocene

broad-leaved forest. This agrees well with the recorded metatherian radiation by the early Eocene when the Itaboraian fauna was probably the most diverse metatherian association of all times (Oliveira 1998; Oliveira and Goin 2011). Subsequent cooling from the middle Eocene to the early Miocene gave rise to modern versions of several other ecosystems, such as coniferous forest, or beach/strand dune types, as well as early versions of shrublands, grasslands, tundra, and páramo. Barreda and Palazzesi (2007) indicate that grasslands were already established in southern South America by the late Oligocene.

This also agrees with the recorded evidence of mid-Eocene to early Miocene metatherians, which show a progressive decline in tropical types as well as a functional turnover in feeding habits (see Chap. 6). By the Eocene–Oligocene transition, a sharp taxonomic and adaptive change in metatherian associations was recorded (Goin et al. 2010). Finally, by the Middle-Miocene–Pliocene, modern versions of all 12 ecosystems were already in place in South America. Concomitantly, late Miocene–Pliocene metatherian assemblages in South America support the idea that essentially modern types and lineages were already developed, together with a few, extremely specialized ones, that would face extinction in the Pliocene (see, e.g., Goin 1997; Goin et al. 2000; Goin and Pardiñas 1996).

4.3 Biogeography

Traditional biogeographic studies (e.g., Cox 2001) tend to regard South America as a single biogeographical entity, the Neotropical Region. Following previous (mainly botanical) hypotheses that can be traced back two centuries ago (see Moreira Muñoz 2007), and by means of a panbiogeographic approach, Morrone (2002, 2004a, b, 2006) challenged this view and proposed that the southernmost tip of South America belongs to a distinct biogeographical unit, the Andean Region of the Austral Kingdom (Fig. 4.2). This biogeographical kingdom also includes

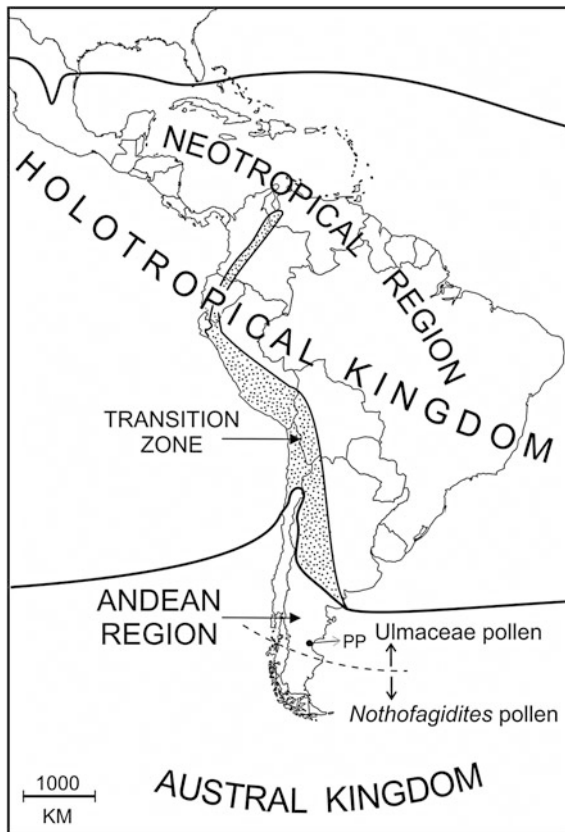


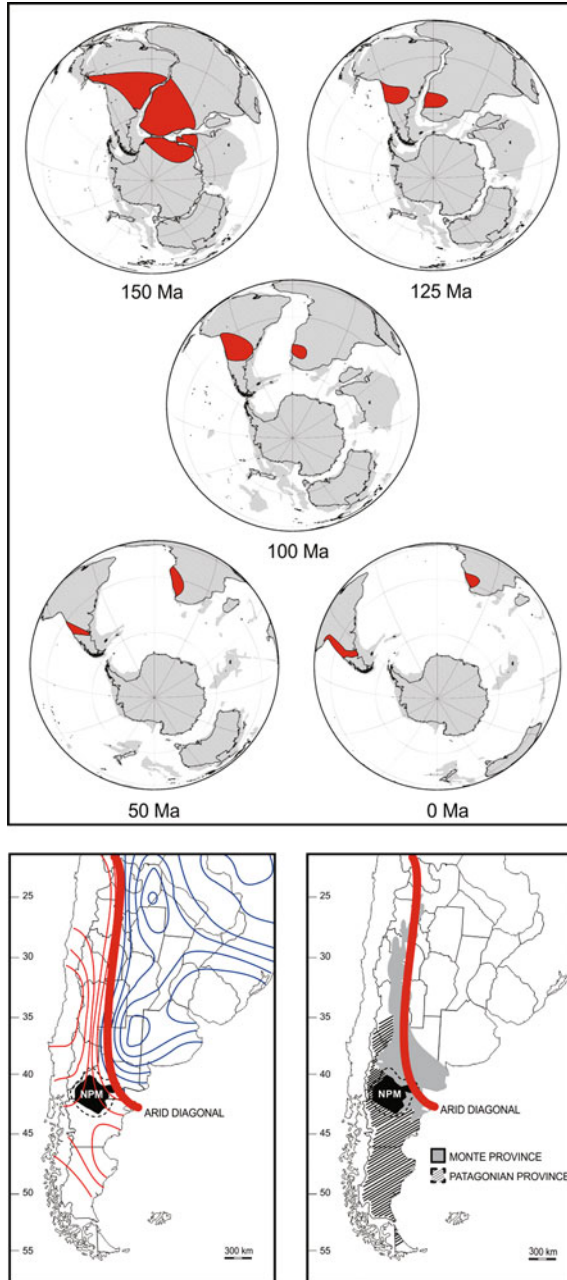
Fig. 4.2 Central and South American biogeography. The map shows the biogeographic boundary between the Andean Region of the Austral Kingdom (south), and the Neotropical Region of the Holotropical Kingdom (north). The dotted area represents the Transition Zone sensu Morrone (2006). The dashed line in central Patagonia indicates the divide between two major palynological provinces by Danian times: the Ulmaceae Province to the north, and the *Nothofagidites* Province to the south (from Quattrocchio and Volkheimer 2000). PP, Punta Peligro local fauna (Peligran SALMA)

several other regions of the Southern Hemisphere: Antarctica (Antarctic Region), southernmost Africa (Cape or Afrotropical Region), eastern and southern Australia (Australotropical Region), New Zealand (Neozelandic Region), and New Guinea (Neoguinean Region). In turn, most of the remaining areas of South America, as well as southernmost North America and the Caribbean, were included in the Neotropical Region of the Holotropical Kingdom (Morrone 2002).

The Neotropical Region, in this more restricted sense, includes most of tropical South America's most distinctive areas, or subregions: Caribbean, Amazonian, Chacoan, and Paranaean. The Andean Region, in turn, includes the Central Chilean, Subantarctic, and Patagonian subregions. Morrone (e.g., 2006) also argued that the central and northern sections of the Andean Range constitute a transitional zone between the Neotropical and Andean regions (Fig. 4.2). In his view, this transition zone is the area where elements of the Neotropical Region and the Andean Region overlap. It comprises the north Andean Páramo (Ecuador and Perú), the coastal Peruvian desert, the Puna and Prepuna (northwestern Argentina), the Atacama Desert (northern Chile), and the Monte (western Argentina, see Fig. 4.3). These six biogeographical provinces composing the transition zone represent areas of biotic "hybridization." "More than a static line between the Neotropical and Andean regions, the South American transition zone is characterized as an area where ecological and historical processes have allowed the evolution of a characteristic, mixed biota" (Morrone 2004b: 41).

Relevant to our review of contexts to metatherian evolution is the recognition that biogeographic zones are not static areas. They contract and expand in historical times, usually following changing abiotic parameters, such as temperature and precipitation. The Neotropical Region, for instance, expanded far north and south in pre-Quaternary times (Morrone 2006).

The initial stages in the development of an Austral realm could be as old an event as the Late Triassic. Briefly, the Triassic saw a rearrangement of floral regions mostly due to the notable climatic changes that occurred since the Late Paleozoic (a bipolar world), to the development of a more equable, monsoon-controlled Triassic (Artabe et al. 2003; Iglesias et al. 2011). By that time southern Gondwana was forming part of the Extratropical Area, a phytogeographic realm south of 30°S paleolatitude. Within this region, all areas south of 60°S (Patagonia, southernmost Africa, and parts of Antarctica and Australia) were characterized as having cooler climates than those of more northern latitudes (although still warm temperate and humid). Even though a distinction between southeastern (SEG) and southwestern (SWG) Gondwana has been made (Artabe et al. 2003), it is noteworthy that two areas geographically belonging to SWG share several floristic traits with SEG: the Karoo in southern Africa and El Tranquilo in southern Patagonia. Also interesting is that, floristically, the Transantarctic Mountains have also been suggested as part of SEG (Artabe et al. 2003). An example of the affinity of (at least southern) Patagonia with the SEG floral province is the distribution of ferns belonging to the Dipteridaceae (typical of SWG) and Marattiales (well represented in SEG). In the Triassic of South America, Marattiales are present mostly in Patagonia.



◀ **Fig. 4.3** Top: areas of dry climates (in red) in the Southern Hemisphere, from the Late Jurassic (150 Ma) to present. Redrawn after Monge-Nájera (1996, roughly similar to the “subtropical seasonal dry” climates elsewhere; see, e.g., Iglesias et al. 2011: Fig. 1). Bottom: southern South America’s Arid Diagonal (thick red line) in present times. In the map at the left, it is shown a projection of mean annual precipitations (MAP) for 2020/2040, based on current levels of GHG emissions (A1b scenario; after Barros 2008: Fig. 4). Isohyets that indicate lower than current MAPs are in red; those that project larger than current MAPs are in blue. Note the general coincidence between the Arid Diagonal and the isohyet boundary between lower and larger MAPs. The right map shows the overlapping, in Argentina, of the Arid Diagonal with the distribution of the Monte biogeographic Province. NPM: North Patagonian Massiff (or North Patagonian High Plateau)

In summary, it can be postulated that the initial steps and regionalization of a biogeographic Austral realm can be traced back to Triassic times.

By the Early Jurassic, there are already close microfloral similarities between Australia and South America (Quattrocchio et al. 1996). Later (Late Jurassic–Early Cretaceous), a distinction is recorded between a tropical, Northern Gondwana Province and a temperate, Southern Gondwana Province (Quattrocchio and Volkheimer 2000). Already by the Late Cretaceous and Paleogene, Patagonia, together with Antarctica (mainly Western Antarctica), New Zealand, and south-eastern Australia, have been regarded as belonging to the same (“Weddellian”) biogeographic province (Quattrocchio and Volkheimer 2000). Quattrocchio (2006) and Quattrocchio et al. (2005) recognized two major Danian microfloral provinces in Argentina (see Fig. 4.2), an *Ulmaceae* pollen province north of Santa Cruz Province, and a *Nothofagidites* province south of the Chubut–Santa Cruz boundary. Goin et al. (in press) suggested that these palynological provinces correspond to the Neotropical and Austral biogeographic regions, respectively. They also noted that the late Danian faunal assemblage of Punta Peligro, in southeastern most section of the Chubut Province, is very close to this Danian divide. “We wonder whether or not this assemblage actually represents a mixture of faunal elements from both regions. Thus monotremes, for instance, might represent a taxon that evolved in the Austral Region, while therians would originally belong to the Neotropical Region” (Goin et al. in press).

As stated by Goin et al. (in press; see also Chap. 7), the recognition of the composite nature of South America’s biogeography offers new insights in the understanding of metatherian evolution in this continent. It can be postulated, for instance, that the radiation of basal “Ameridelphians” was, in South America, largely a Neotropical event. In turn, the origin, radiation, and dispersals of the Australidelphia occurred mostly within the Austral biogeographic realm.

4.3.1 Development of South America’s Arid Diagonal

We regard South America’s Arid Diagonal as the great biogeographic divide between the Neotropical Region and the Andean Region. The term “Arid Diagonal” refers to a regional belt of arid to very arid climate ranging NW–SE from the Pacific

coasts of southern Perú to the Atlantic coasts of Chubut Province in southern Argentina (see, e.g., Villagrán and Armesto 2005). In terms of regional biomes, the Arid Diagonal includes deserts or semideserts, such as the Atacama Desert in Chile (Marquet et al. 1998) or the Monte (phytogeographic) Province in Argentina (Roig et al. 2009). Climatologically, deserts are defined as arid or hyperarid areas; biologically, as the areas that contain plants and animals with clear adaptations to surviving in arid environments; physiologically, as large, contiguous areas with low vegetation cover and ample extensions of bare soil. Under most definitions of a desert biome, South America's Arid Diagonal is clearly recognizable (Ezcurra et al. 2006: Figs. 1.2 and 1.3).

According to some authors (e.g., Villagrán and Hinojosa 2005), the development of the Arid Diagonal is one of the most significant events in the evolutionary and biogeographic history of all of southern South America's flora –and, we add, to South America's biota as a whole. Briefly, the Arid Diagonal acts as a primary barrier between both of South America's biogeographical regions (see above): the Neotropical Region (Holotropical Kingdom) and the Andean Region (Austral Kingdom). Discussing the development of the Transitional Zone between both regions, Morrone (2004a, b: Fig. 3) reviewed several of the geographical boundaries proposed by various authors since the late nineteenth century onwards (see also Lopretto and Menni 2003). All of the proposed boundaries imply a major NW–SE divide which closely matches South America's Arid Diagonal (see, e.g., Ringuélet 1955, 1961).

The present arid and semiarid regions that compose the Arid Diagonal in South America have a composite origin. The southern coast of Perú and northern Chile (where some of the most hyperarid deserts of the world have developed, such as the Atacama Desert) are a consequence of the cool marine water upwelling of the Humboldt Current which, in its westward movement, generates a cool, dry atmosphere with little evaporation from the sea and very low rainfall. In turn, most of the Monte Desert belt of northern and west-central Argentina owes its dryness to the rainfall shadow of the southern Andean Cordillera (Ezcurra et al. 2006).

Discussing the historical development of aridity in Northern Chile, Kalin-Arroyo et al. (1988 and literature cited) stated that proposed timetables for the development of arid climates in western South America range from the Miocene to the Quaternary, and that maximum aridity may have been achieved quite recently (see also Vargas and Ortlieb 1998). Whereas the setting of modern Pacific Ocean circulation (e.g., the Humboldt Current) and modern Andean tectonics are Neogene events, it has been suggested that the ultimate origins of the Arid Diagonal, as well as the two main biogeographical regions of South America can be traced back to the early Mesozoic (Goin et al. 2012a, b). In this regard, it is notable that the Arid Diagonal has generally coincided areally with the Subtropical Seasonal Dry climate of SW Gondwana since at least the Triassic (Scotese et al. 1999; Iglesias et al. 2011).

The Mesozoic Era was characterized by quite warm climates, with less climatic differentiation than that of the Paleozoic. Five main biomes were recognized for the Triassic: Tropical Seasonal Dry (summerwet), Desert, Subtropical Seasonal Dry

(winterwet), Warm Temperate, and Cool Temperate (Scotese et al. 1999). In the Southern Hemisphere, the Southwest Gondwana province of extratropical Gondwana covered two climatic belts: Subtropical Seasonal Dry and Warm Temperate (Artabe et al. 2003). Rees et al. (2000) identified five basic biomes in the early Jurassic, with the Subtropical Seasonal Dry being one of them. Equatorial regions were markedly drier than they are today, with a large continental interior. A cooling pulse occurred by the Late Jurassic–Early Cretaceous. By the Early Cretaceous, even though new climate belts and biomes were added (Cold Temperate and Tropical Everwet), the Subtropical Seasonal Dry was consistently present, though less expanded, as a boundary between the Southern Cone (South America south of Bolivia) and northern South America. By mid- and Late Cretaceous times the opening of the Atlantic Ocean was continuous and rapid, as was the Pacific subduction of western South America and Antarctica. The southern monsoon breakdown in the Cretaceous generated an increase of precipitation in northern and southwestern South America (Iglesias et al. 2011). The zonal climatic model was enhanced, and temperatures began to increase at high latitudes. Again, the Subtropical Seasonal Dry belt was present, already foreshadowing the Arid Diagonal's current outline (Fig. 4.3). Global paleoclimatic distributions throughout the Paleogene were approximately similar to those of the latest Cretaceous. It was already mentioned that the Danian floristic divide in Ulmaceae and *Nothofagidites* pollen provinces (Quattrocchio and Volkheimer 2000; Quattrocchio et al. 2011; Fig. 4.2) may reflect the location of the Arid Diagonal by early Paleocene times. Also, the presence of the North Patagonian Massif (or North Patagonian High Plateau) in northern Patagonia may have acted as an additional biogeographic barrier, thus enhancing the isolation between northern (Neotropical) and southern (Andean) regions by the Late Cretaceous–Paleogene (Aragón et al. 2011). The strengthening of the zonal climatic model continued and the increase in temperatures at high latitudes was reinforced by the global early Paleogene warming (Zachos et al. 2001). Patagonia had a relative climatic uniformity as it was situated in the Warm Temperate belt. In the latest Cretaceous (65 Ma) and the early Paleogene (65–57 Ma), sea levels remained high and sea incursions fragmented the geographical continuity of the South American continent (see below).

The distributions of numerous biotic elements have their northern or southern boundaries at South America's Arid Diagonal. A clear example among floral elements is that of trees (see, e.g., Quiroga 2010); among animals there is a wide variety of examples, from invertebrates (e.g., Onychophora; Monge-Nájera 1996) to vertebrates (e.g., fish; Menni 2004). Following climatic data by Condie (1982) and Parrish (1993), Monge-Nájera (1996) reconstructed climatic belts including the Southern Hemisphere regions since the Early Jurassic. The distribution of the arid-semiarid belts for SW Gondwana closely matches the distribution of the Subtropical Seasonal Dry climatic belt (cf. Monge-Nájera 1996 with Iglesias et al. 2011). In summary, South America's Arid Diagonal can be traced back to early Mesozoic times, both in its current geographic location as in its functional significance: South America's great biogeographical divide. Aragón et al. (2011) stressed that the North Patagonian High Plateau (or North Patagonian Massif; Fig. 4.3) also acted as a

biogeographic barrier between Patagonia, on one side, and the rest of the continent, on the other, thus reinforcing the Arid Diagonal at its southern end.

As a final note, it is interesting to point out that the current global pulse of climate warming could maximize the climatic tendencies on both sides of the Arid Diagonal. Recent projections of climatic models for the 2020–2040 interval in Argentina, run under “A1 scenario” assumptions (see, e.g., IPCC 2008), suggest that precipitations for that future period would increase in the Chaco–Pampean plains, while decrease west (Cuyo and Northwestern Argentina) and south (Patagonia) of it (Barros 2008; Barros et al. 2006). The divide between increasing and decreasing isohyets quite accurately coincides with the itinerary in Argentina of the Arid Diagonal, where most of the Monte Desert is located (Fig. 4.3).

4.3.2 Late Maastrichtian–Danian Paleogeography of Southern-South America

Several paleogeographic reconstructions of South America suggest that the continent was split into northern and southern portions by means of epeiric seas due to marine transgressions. Uliana and Biddle (1988) suggested that maximum epeiric flooding transpired during the Maastrichtian. It has been proposed (see above) that this shallow marine barrier promoted the development of distinct northern and southern South American biotas, the former more closely resembling other equatorial biotas, while the latter was more closely related to austral biotas (e.g., Wilson and Arens 2001). Even though, as shown above, the origins of these biogeographic distinctions largely predate the Late Cretaceous, it is clear that the splitting of the continent by means of epeiric seas reinforced the isolation of northern and southern South America, already split by climatic barriers (i.e., the Arid Diagonal; see above).

In southernmost South America, the paleogeography resulting from marine transgressions led to a very complex, almost archipelagic continental configuration. Four successive shallow, ephemeral Atlantic transgressions flooded Patagonia during the Late Cretaceous and Cenozoic: Maastrichtian–Danian, late middle Eocene, late Oligocene–early Miocene, and middle Miocene, with the first being the largest (Malumián and Náñez 2011). The coastal shape and extension of each transgression were modulated by the surrounding positive areas: the North Patagonian (or Somuncurá) and Deseado massifs, the eastern Patagonian Atlantic Dorsal, and the Fuegian orocline (proto-Andean uplift) on the west. (The first phase of mountain building, representing the beginning of the Andean uplift, has been dated as Late Cretaceous–Paleocene; see Quattrocchio 2009). During the Maastrichtian–Danian transgression (Fig. 4.4), and at its maximum flooding, the sea reached mid platform depths in central northern Patagonia (Malumián and Náñez 2011). By Danian times several deposits in western Patagonia already reflect deltaic origins, as with the Lefipán Fm (Ruiz 2006).

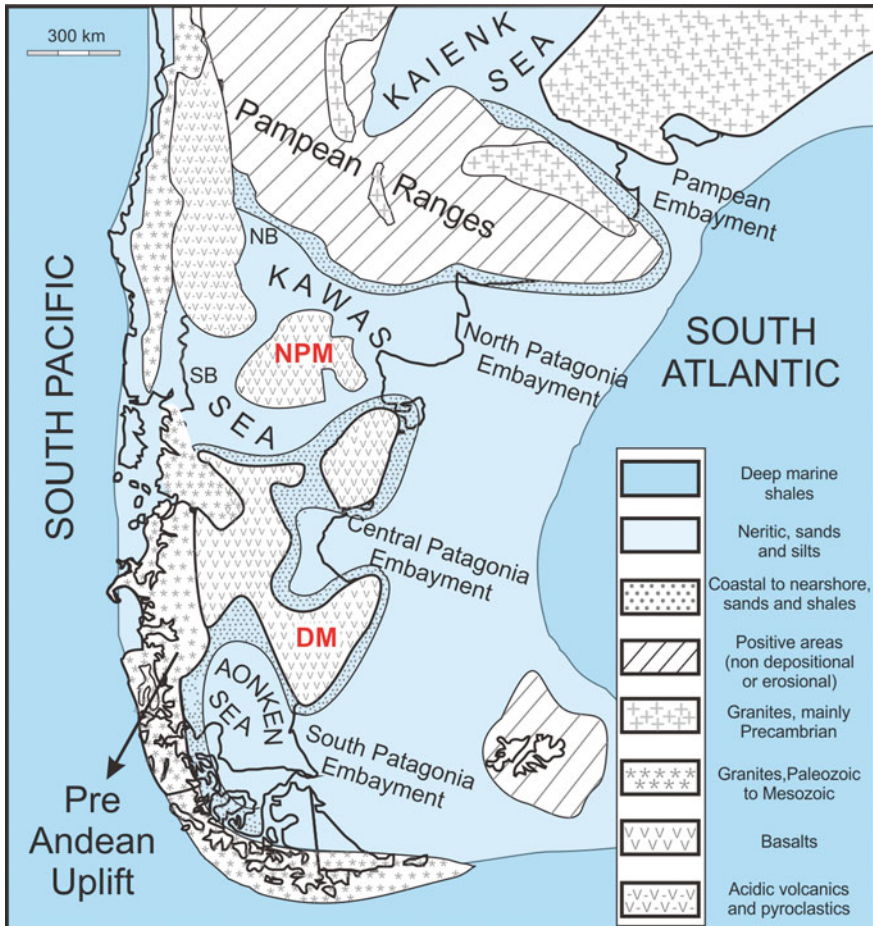


Fig. 4.4 Paleogeography of southern South America during the Late Cretaceous (Maastrichtian) – early Paleocene (Danian). Abbreviations DM, Deseado Massif; NB, northern branch; NPM, North Patagonian Massif; SB, southern branch. The name of Kawas Sea follows Casamiquela (1979); names of the Kaienk and Aonken seas derive from the Tehuelchian (meaning “north” and “south,” respectively). Redrawn after Urien et al. (1995) and Quattrocchio (2009)

Figure 4.4 depicts a paleogeographic reconstruction of southern South America by Maastrichtian–Danian times (see Urien et al. 1995; Casamiquela 1979; Quattrocchio 2009; Malumián and Náñez 2011). This temporal interval was crucial for metatherian evolution in the Southern Hemisphere, as it probably saw their immigration into South America (see Chap. 3) and, shortly afterwards, the radiation of the Australidelphia (see Chap. 7) and dispersal into Australia. It can be appreciated that the Patagonian landscape was more of an archipelago than a peninsula.

Also, as mentioned above, it was a region of a biogeographical divide (Quattrocchio et al. 2011). In this geographic context, it is probable that several endemisms evolved among stem metatherians. This was, possibly, the evolutionary theatre for the origins of the Australidelphia (see Chap. 7).

4.4 Phases in South American Mammalian Evolution

Goin et al. (2012a) recognized five successive phases in the evolution of Mesozoic–Cenozoic South American mammals. Here we add a sixth one and briefly summarize all of them. Metatherian evolution in South America involved the last four phases. Each of them is characterized by a distinct taxonomic composition, established after a faunal turnover triggered by a major climatic–environmental event.

4.4.1 *Early Gondwanian Phase*

This phase extends from the Late Triassic to the Early Cretaceous. Due to the scarcity of the fossil record, it is a largely theoretical episode in South America's mammalian history. Actually, a better record will probably lead to the realization that more than one phase is involved. The oldest mammalian record for South America is the ichnospecies *Ameghinichnus patagonicus* (Casamiquela 1961), from Middle Jurassic levels in Santa Cruz Province, southern Patagonia (De Valais 2009). Eutriconodonts and australosphenidans include all other mammalian record of this long phase in South America, exclusively known from Patagonian fossil localities. Briefly, Jurassic and early Cretaceous mammals from Patagonia comprise a mixture of cosmopolitan (eutriconodontids) and Austral (australosphenidan) taxa (see above for the concept of an Austral biogeographic Kingdom).

4.4.2 *Late Gondwanian Phase*

The Late Gondwanian Phase ranges throughout the Late Cretaceous, probably not including the latest Cretaceous (?latest Campanian–Maastrichtian). Again, most of the record of South American Late Cretaceous mammals comes from Patagonia in southern Argentina (see Table 3.1 in Chap. 3). Several patterns can be discerned among the mammalian associations: (1) As in the previous one, no therian mammal has been recorded during this phase (therians were dominant in the Northern Hemisphere during the Late Cretaceous). (2) Even though dryolestoids flourished in the Northern Hemisphere during the Late Jurassic and Early Cretaceous, it is in

this phase (Late Cretaceous) that they reached their climax in South America, showing high endemism and the development of some remarkable adaptive morphological types (e.g., mesungulats, reigitheriids). (3) Among the most notable mammals of this phase, stand out the Gondwanatheria, a group of uncertain affinities (see Goin et al. 2012b). Goin et al. (2012a) suggested that the radiation of gondwanatherians probably dates back to the early late Cretaceous, concomitant with the beginning of the last greenhouse cycle (Late Cretaceous–latest Eocene). (4) Although with no Mesozoic record in South America, they also hypothesized that monotremes could have been present in South America already by Late Cretaceous times.

4.4.3 *Early South American Phase*

This phase, ranging from the latest Cretaceous to the EOB, is characterized by the arrival of therians, most probably from North America and in several, successive waves (Pascual 2006 and literature cited). By the end of the Cretaceous, an intermittent connection between North and South America by means of the eastern margin of the Caribbean Plate led to a biotic interchange, named the First American Biotic Interchange (FABI) by Goin et al. (2012a; see Chap. 3 and Case et al. 2005). Many non-therian mammals, such as those characterizing the Late Cretaceous Alaman SALMA, did not survive the Cretaceous Tertiary extinction event. Therians rapidly expanded and became dominant among South American mammals, as shown by the early Paleocene assemblage of Tiupampa (Tiupampa, Fig. 4.5). Metatherians would constitute the most taxonomically diverse group of therians up to the mid-Eocene, where the first cooling pulses gave rise to a variety of eutherians (see Fig. 4.5). Summarizing the key events of this phase in South American mammals, Goin et al. (2012a) noted (1) the arrival of therian mammals; (2) a rapid decline of non-therian lineages probably since mid-Paleocene times; (3) major radiations of therian lineages, especially among metatherians, during the late Paleocene and early Eocene; (4) since the end of the early Eocene, the first cooling pulses promoted some taxonomic and ecologic turnover among the mammalian associations, including metatherians; and (5) at the end of this phase, probably by the late Eocene, the first caviomorph rodents arrived in South America (Antoine et al. 2011), and, we suggest, platyrrhine primates. The ultimate origin of both lineages is most probably Africa; a matter of debate is whether these immigration events took place in synchrony or in asynchronous waves (Poux et al. 2006). Paleoreconstructions of the South Atlantic led Oliveira et al. (2009) to suggest that the most favorable period for a possible dispersal was between 50 and 40 Ma (i.e., late early to early late Eocene). Even though the timing and impact of the arrival of caviomorphs and platyrrhines is yet to be confirmed, in southern South America, already by the early Oligocene, at least caviomorph rodents were fully integrated in the mammalian associations.

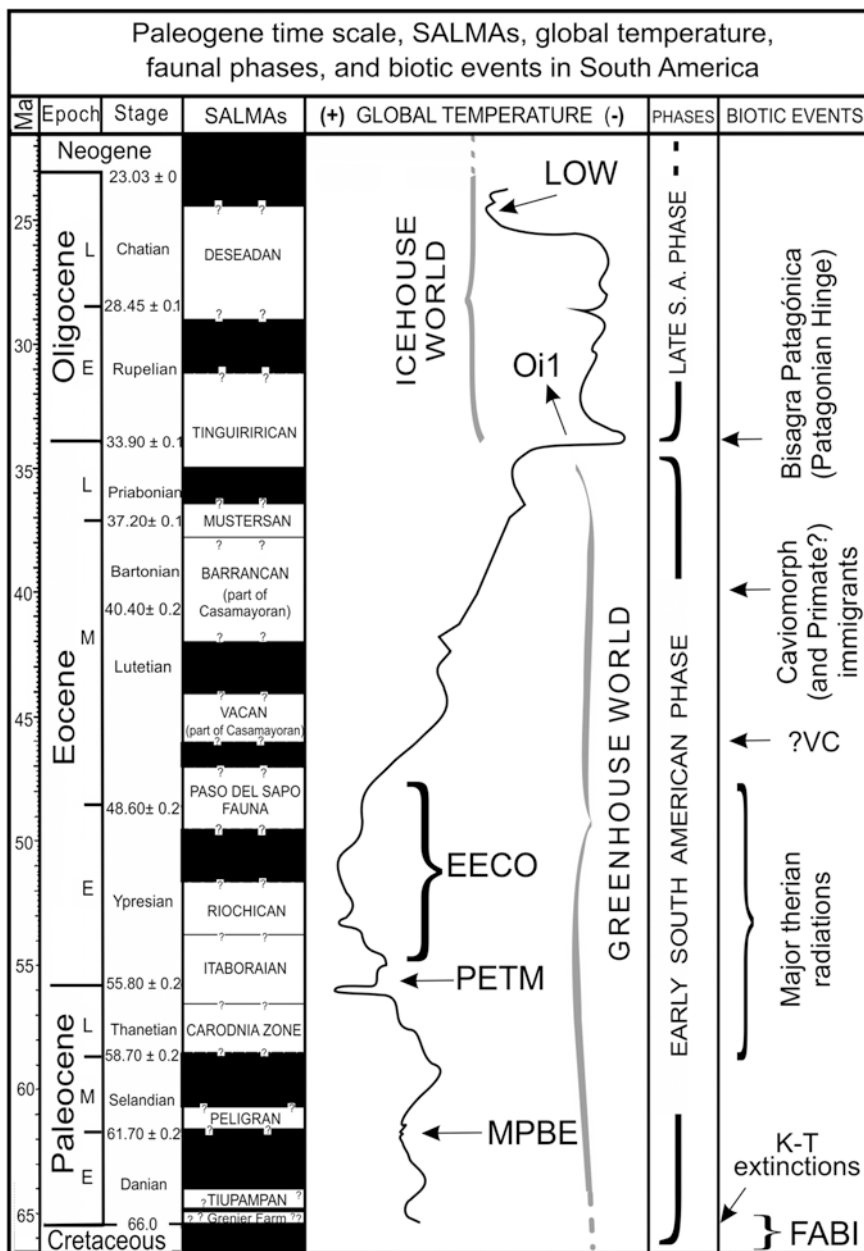


Fig. 4.5 Paleogene time scale, South American land-mammal ages (SALMAs), global temperatures, and biotic events. For most abbreviations, see legend to Fig. 4.1. Other abbreviations FABI, First American Biotic Interchange; K-T, Cretaceous-Tertiary; Ma, Megannum; ?VC, “Vacan Crash?” (see Chap. 7)

4.4.4 *Late South American Phase*

This phase extends from the EOB up to the late Miocene, and was signaled by a major biotic turnover (Flynn et al. 2003; Goin et al. 2010), concomitant with one of the most important global cooling events of the Cenozoic Era (see above). Goin et al. (2010, 2012a) coined the name *Bisagra Patagónica* (“Patagonian Hinge”), for the evolutionary event represented by the major taxonomic and ecological shift in land mammal composition of southern South America at the EOB. *Bisagra Patagónica* was the regional expression of similar phenomena occurring in other parts of the World, such as Europe’s *Grande Coupure* or Central Asia’s Mongolian Remodeling (see Goin et al. 2010 and literature cited).

The Tinguirirican SALMA, abundantly recorded both in central Chile and in Patagonia, attests to the world’s oldest eutherian assemblage dominated by hypsodont herbivores, especially notoungulates (Archaeohyracidae, Interatheriinae, Hegetotheriidae and Mesotheriidae, among others). Metatherians show a functional turnover (see Chap. 6) as well as a sharp decline in diversity, comprising only 30 % of the mammalian fauna (Fig. 4.5). Already by early Miocene times, the modern lineages of metatherians essentially were already established (Goin et al. 2007; Goin and Abello 2013). Goin et al. (2010 and in press; see also Chap. 7) stated that, among the most notable changes among South American metatherians, are the following: (1) last record of basal “Ameridelphians” (e.g., Sternbergiidae, Caroloameghiniidae (Didelphimorphia), Glasbiidae, Bonapartherioidea, and Polydolopidae (Polydolpimorphia)); (2) first record of Argyrolagoidea (Polydolpimorphia); (3) decline and posterior extinction of the Proborhyaenidae (Sparassodonta), and of all basal sparassodonts (sensu Forasiepi 2009); (4) hypothesized origin of the Thylacosmilidae (Sparassodonta), and of modern didelphimorphians (Didelphidae) (first known record for both lineages is in the early Miocene, see Goin et al. 2007); and (5) rapid expansion of Palaeothenoid paucituberculatans, Borhyaenid sparassodontans, and of Microbiotheriid microbiotherians (see Chap. 7). As can be appreciated, the sum of these changes implies a drastic rearrangement, both taxonomic as well as functional, among metatherian associations from the EOB onwards. Briefly, the Late South American Phase can be characterized as the adjustment of native mammalian associations to the icehouse world conditions imposed at the EOB.

4.4.5 *Interamerican Phase*

The full establishment of bipolar Icehouse conditions by late Miocene (Messinian) times triggered another global cooling pulse. Several native mammalian lineages became extinct by Huayquerian (latest Miocene) times, including metatherians. Also, the initial phases of the closing of the Panama isthmus led to a first migratory pulse between the Americas: the “heralds” of the Great American Biotic

Interchange (GABI; Patterson and Pascual 1972; Webb 1976, 1985, 2006; Pascual 2006; Woodburne et al. 2006; Morgan 2008; Woodburne 2010). GABI's main pulse occurred 2.6–2.4 Ma (Fig. 4.6). It is unclear to what extent metatherians of Central and South America were affected by the GABI. Goin et al. (2012a) suggested that, since it involved mainly temperate, savanna-adapted taxa, its influence was probably not dramatic. As a consequence of these events, South America acquired its modern mammalian composition.

Woodburne et al. (2006) and Woodburne (2010) updated our current knowledge of the biotic and tectonic GABI dynamics, including its chronology, sea level changes, and climatic context that facilitated the transisthmian exchanges. In their view, the interchange of GABI “heralds” (sensu Webb 1985, or pre-GABI dispersals sensu Woodburne et al. 2006) took place under generally tropical conditions. On the contrary, the four phases involving the “legions” interchange (sensu Webb 1985, or sensu stricto GABI dispersals of Woodburne et al. 2006) took place under cooler conditions. Woodburne (2010) formally named these phases as GABI 1, 2, 3, and 4; see Fig. 4.6).

The first late Cenozoic North American mammals to immigrate to South America were representatives of Procyonidae carnivores (ca. 7 Ma) and Sigmodontinae rodents (ca. 6 Ma; see Woodburne 2010). Later immigrants into South America included representatives of Camelidae and Tayassuidae (3.3–3.5 Ma). GABI 1, the first significant episode of faunal exchange, took place concurrently with the initiation of major Northern Hemisphere Glaciation (at 2.6–2.4 Ma). Newcomers to South America included several taxa of Mustelidae, Canidae, Equidae, and Gomphotheriidae (for an earlier, 9 Ma arrival of the latter, see Campbell 2010). In GABI (around 1.8 Ma) two more taxa dispersed southward than the reverse, and included new representatives of Ursidae, Felidae, Machairodontidae, Cervidae and Tapiridae, among others. GABI 3 (around 0.8 Ma) was a relatively minor interchange; it included the arrival to South America of new taxa referable to Felidae, Tayassuidae, and Cervidae; dispersal to North America seems to have been restricted to didelphine opossums. Finally, GABI 4 (by the end of the Pleistocene) consisted of a diverse, one way (southward) dispersal: Mustelidae, Canidae, Felidae, Leporidae, Equidae, and Glyptodontidae.

4.4.6 *Hypoamerican Phase*

Following suggestions by Croft (2012) while commenting on Goin et al. (2012a) scheme of faunal phases, we add here a sixth one: the Hypoamerican Phase (Fig. 4.6). The beginning of this last phase is marked by end of the Last Glacial Maximum (LGM) and the arrival of humans to South America, i.e., at some unspecified moment of the latest Pleistocene. (One of the earliest dates of human settlements in South America is that of Monte Verde, in southern Chile:

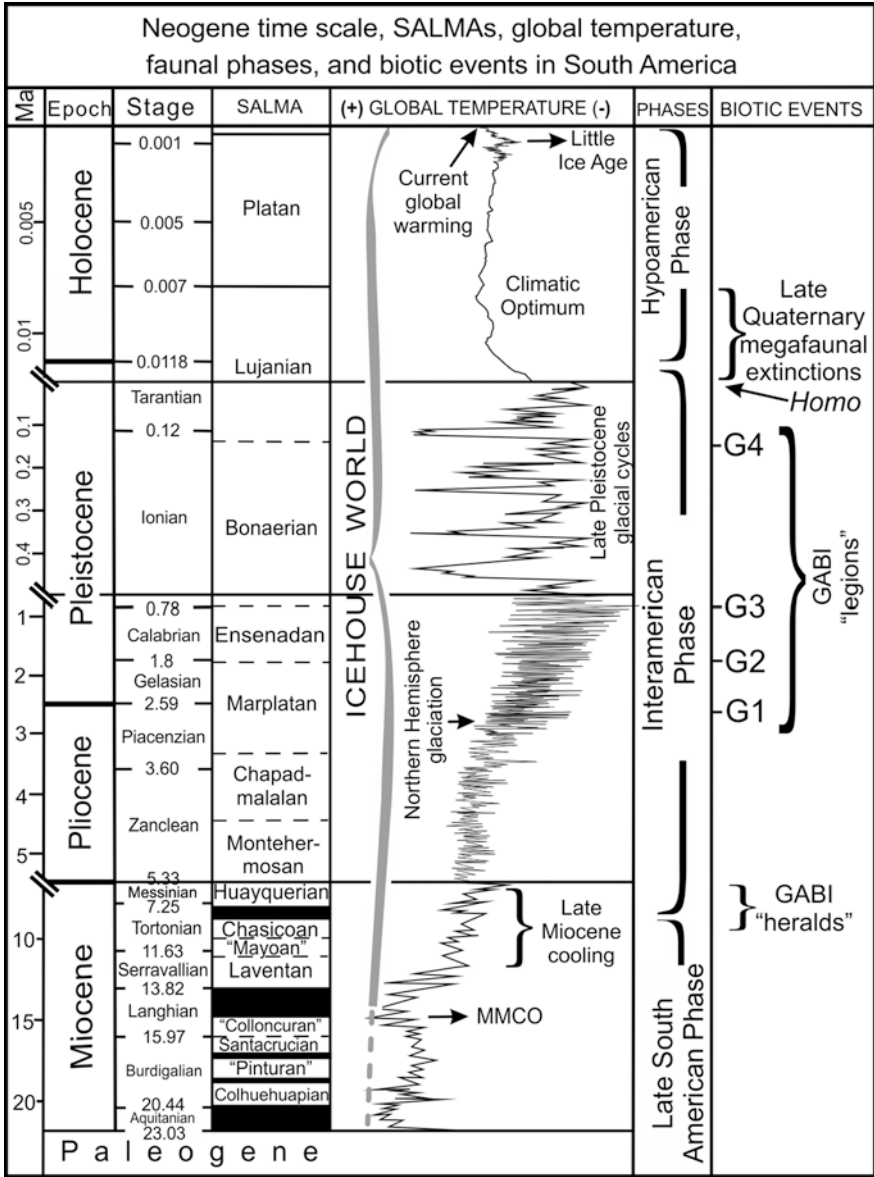


Fig. 4.6 Neogene time scale, South American land-mammal ages (SALMAS), global temperatures, and biotic events. For most abbreviations, see legend to Fig. 4.1. Other abbreviations GABI, Great American Biotic Interchange; G1, G2, G3, G4, mayor dispersal events within GABI (see Woodburne 2010); Ma, Meganumm. The arrow near "Homo" marks the latest Pleistocene arrival of humans in South America. The concept of GABI "heralds" and "legions" is from Webb (1985, 2006), but see Woodburne (2010)

14,000 ybp; see Saint Pierre et al. 2012 and literature cited). This last episode in South America's mammalian evolution is marked by the extinction of several lineages of xenarthrans and SANU, as well as many GABI immigrants (Cione et al. 2009, and literature cited). As a consequence, all native megaherbivores, and many large- and medium-sized mammals became extinct (the largest herbivore mammal that survived to the Recent is *Tapirus*, weighing less than 400 kg). Causal hypotheses related to this last, large extinction event of the Cenozoic Era have been varied, though climate changes, diseases, and/or human activity are the most frequently cited. In our view, a more balanced explanation of the latest Pleistocene extinctions was given by Cione et al. (2003, 2009) with their "Broken Zig-Zag" hypothesis.

Metatherians of this last phase are restricted to the Marsupialia: didelphimorphs, paucituberculatans, and microbiotherians, the latter two restricted to the Andean Cordillera. It is unlikely that the late Pleistocene megafaunal extinctions affected South American marsupials. In turn, it can be argued that the setting of the last interglacial (i.e., warmer) cycle most probably affected marsupial (as well as many other mammalian) distributions all over the continent, and especially in its more temperate regions. An example of this is that of the Holocene faunal successions recorded at Tixi Cave in eastern Buenos Aires Province, Argentina (Table 4.2). Tixi deposits are arranged in five strata, with radiocarbon dates of around 10,000, 5000, 3200, 700, and 170 ybp (Mazzanti and Quintana 2001). They probably represent the most comprehensive set of Holocene small mammal associations known for the whole South American continent. All but one species of this sequence are living ones, but not all of them occur in this region today. *Lestodelphys halli*, for instance, is almost completely absent after 5000 ybp—its current distribution is far south, in Patagonia. On the contrary, *Lutreolina crassicaudata*, *Didelphis albiventris*, *Monodelphis dimidiata*, and *Thylamys pallidior* are currently living in this region. The succession of didelphid associations in Tixi Cave shows that, already by 3000 ybp, their distribution in the Pampean region was essentially as that of Recent times. The only exception is that of *Monodelphis* sp. which became extinct after 700 ybp (Goin 2001).

4.5 Faunal Interactions

Recently Woodburne et al. (2014) analyzed South America's Paleogene floral and land mammal faunal dynamics. They offered several new insights, and confirmed previous hypotheses, on a topic that has been extensively treated in South American paleontology (see Woodburne et al. 2014 and literature cited). In that the Paleogene is such a crucial interval in mammalian evolution, it is interesting to compare the dynamics within the mammalian assemblages, especially between metatherians and eutherians (Fig. 4.7). The following comments are mostly extracted from their conclusions.

Table 4.2 Holocene marsupials from the archaeological site Tixi Cave, in southeastern Buenos Aires Province, Argentina

Stratum	Years before present	<i>Lestodelphys halli</i>	<i>Thylamys</i> sp.	<i>Monodelphis</i> sp.	<i>Monodelphis dimidiata</i>	<i>Lutreolina crassicaudata</i>	<i>Didelphis</i> sp.
"B"	170	–	3	–	14	3	–
"C"	715	–	3	4	6	1	1
"D"	3,255	?1	2	4	14	–	1
Upper "E"	4,865	12	5	15	16	1	–
Lower "E"	10,210	6	4	3	–	–	–

Specimen numbers are expressed in MNI (minimal number of individuals). The age of stratum Lower "E" is an average of two radiocarbon datings: 10,045 ± 95, and 10,375 ± 90. Species currently living in the region are *Thylamys pallidior*, *Monodelphis dimidiata*, *Lutreolina crassicaudata*, and *Didelphis albiventris*. *Thylamys* sp. from Tixi Cave could prove to be referable to the living species *T. pallidior*. Modified after Goin (2006: Table 6)

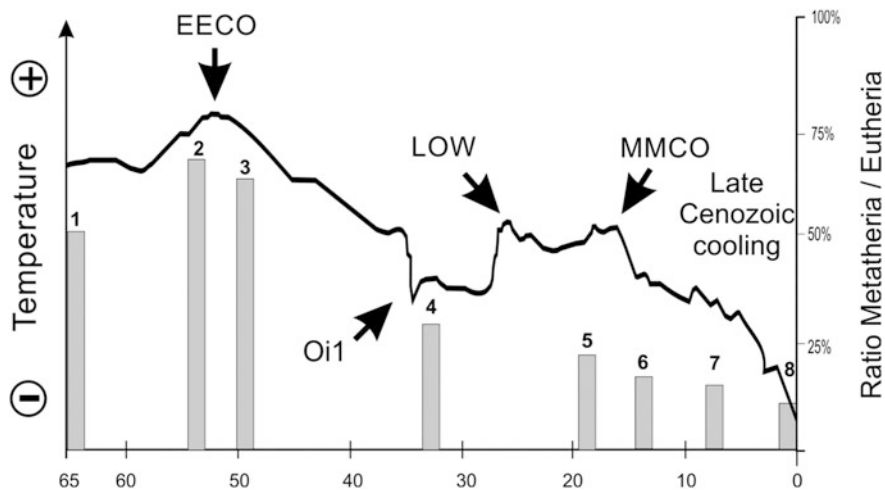


Fig. 4.7 Relative diversity of the South American metatherians throughout the Cenozoic. Columns represent the percentage of metatherian species in relation to the whole terrestrial mammalian faunas in selected SALMAS/faunas. The curve (from Zachos et al. 2001) indicates global surface temperatures for the whole Cenozoic. Columns indicate the Metatheria/Eutheria ratio for single faunas, or associations referable to, a specific SALMA. 1, Tiupampian SALMA (Early Paleocene); 2, Itaboraí and Las Flores (Itaboraian SALMA, latest Paleocene–early Eocene); 3, Paso del Sapo (early–middle Eocene); 4, La Cancha and Tinguiririca (Tinguirirican SALMA, early Oligocene); 5, Gaiman and Puesto Almendra at Gran Barranca (Colhuehuapian SALMA, early Miocene); 6, La Venta (Laventan SALMA, middle Miocene); 7, Cerro Azul Formation (Huayquerian SALMA, late Miocene); 8, South America, Recent. After Goin et al. (in press)

Briefly, Woodburne et al. (2014) concluded that both plants and mammals responded at a rate and extent generally comparable to that portrayed by the global climate pattern of the Paleogene. A result of their study is the confirmation that the initial (i.e., early Paleocene), as well as subsequent Paleogene floral diversity in South America was much greater than that of North America. In turn, the mammalian faunas of South America (both Neotropical and Austral) neither matched nor exceeded the diversity seen in North America. They concluded that this diminished diversity was probably due to a stronger presence of non-mammalian vertebrates (e.g., large crocodiles, predatory birds) in the exploitation of niches targeted by mammals in other continents.

It is important to note that, in order to compare the mammalian responses to climatic, floral, and ecosystem changes in North and South America, the basal taxonomic associations were quite different in both continents. The initial associations found in South America (e.g., the early Paleocene Tiupampa assemblage) consist of a limited variety of metatherians, “condylarths,” and a pantodont. No carnivoran, insectivoran, primate or rodent taxa were present in the Paleocene. Ecological counterparts did evolve in South America (e.g., large metatherian carnivores, rodent-like notoungulates), but they didn’t appear until the late Eocene.

Even though the South American record is much less detailed than that of North America, it seems that the overall pre- and syn-EECO patterns are comparable. In South America, together with the first record of (presumably older) xenarthrans, an important radiation of basal “Ameridelphian” metatherians and of polydolopimorphians, can be recognized, as well as for several SANU lineages (Itaboraian and Riochican SALMAs, and the Paso del Sapo, or “Sapoan” fauna). Among the latter stand out increases in the diversity of astrapotheres, didolodontid ‘condylarths,’ litopterns, and a growing importance of notoungulates.

The decline in temperatures during post-EECO times took place in both continents, but it was less marked in South America, which also retained a higher rate of precipitation. Xenarthrans, which are unknown prior to the Itaboraian SALMA, show a growing diversity from the “Sapoan” (late early Eocene) to the “Barrancan” (late Eocene). They peak in the Mustersan (latest Eocene), and subside in the Tinguirirican and into the Deseadan. That is, the group peaks subsequent to the EECO, and continues in diversity until the Tinguirirican. The endemic didolodontid “condylarths” show a similar pattern, reaching a peak during the late Eocene (“Barrancan” and Mustersan). A similar pattern was observed among isotemnid and henricosbornid notoungulates, with a post-EECO growth in diversity. Several “Vacan” SANU include large-sized taxa as well. Woodburne et al. (2014) suggest that the post-EECO (Riochican) decline in other lineages could mirror the event known as “Bridgerian Crash” in North America (“?Vacan Crash in South America; see also Chap.7). In short, it can be observed that metatherian and eutherian evolutionary responses to the EECO and post-EECO lapses were dissimilar to some extent, while metatherians show a decline in diversity and a functional turnover after the EECO (Fig. 4.7), the radiation of several eutherian lineages was a post-EECO event.

A final step in the modernization of mammalian lineages was the drastic taxonomical and functional turnover that occurred at the EOB, which mirrored the global cooling (O1 event). Among many South American mammals, this event is clearly exposed in Tinguirirican SALMA assemblages (latest Eocene–early Oligocene), as well as in those of the early Oligocene La Cancha and La Cantera local faunas. For metatherians it was a decisive moment (see above), marking the last appearance of many lineages, and the beginning of the radiation of modern lineages. Already by early Miocene times (Colhuehuapian SALMA), all lineages that would exist through the Neogene were established (Goin et al. 2007; Goin and Abello 2013). Goin et al. (2010) coined the term “Patagonian Hinge” (*Bisagra Patagónica*) for this turnover, indicating that it was similar in nature and extent to the European’s *Grande Coupure* (Stehlin 1909) and central Asia’s “Mongolian Remodeling” (Meng and McKenna 1998). According to these authors, contrary to what happened in the *Grande Coupure* event, those of the Patagonian Hinge and Mongolian Remodeling did not involve immigration events. “Therefore, changes occurred across whole faunas, not just in potentially competing lineages” (Goin et al. 2010: 93).

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