

## Chapter 2

# Paleoenvironment, Tectonics, and Paleobiogeography

**Abstract** The Earth experienced dramatic transformations during the Cenozoic, with changing sea levels, climate, and tectonic events having major influences on the global biota. In South America, loss of the connection between Patagonia and Antarctica, Andean orogeny, and formation of the Isthmus of Panama defined the continent, as we know it today. These events had enormous effects on local faunas, with major consequences for their evolution and extinction. The Great American Biotic Interchange (GABI), a major natural experiment in biotic reorganization, was either enabled or at least greatly enhanced by land connections between North and South America during the late Neogene. The outcome of the meeting of previously separated biotas was a drastic change, both for the composition of South American faunas and the terrestrial ecosystems they inhabited.

**Keywords** Paleogeographic changes • Marine transgressions • Montane tectonics • Orogenic rain shadows • Glacial cycles

### 2.1 Historical Factors: An Overview

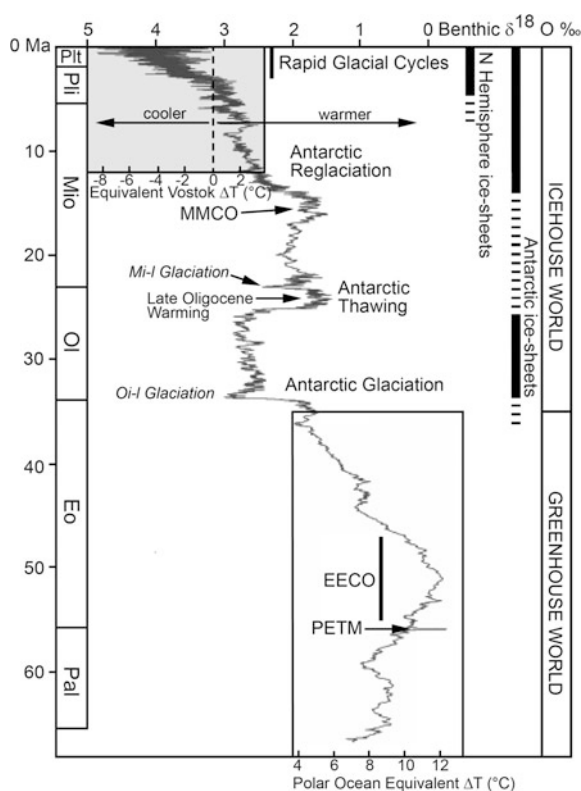
The faunal and floral communities of South America experienced strong climatic, tectonic, and geographic changes during the Cenozoic. These historical causal factors profoundly affected the evolution of South American terrestrial ecosystems during the past 66 Ma. In this chapter, we review key aspects of South American geological history during the Cenozoic, focusing on those features that likely had the greatest influence on the environment and fauna. This chapter is a summary of major patterns of tectonic, climatic, geographic, environmental, and faunal change as they occurred in South America. As part of our scope, we include evaluations of controversies concerning the timing of the establishment of the Panamanian land bridge and the chronology of the GABI.

### 2.1.1 Geography and Climate—from Greenhouse to Icehouse

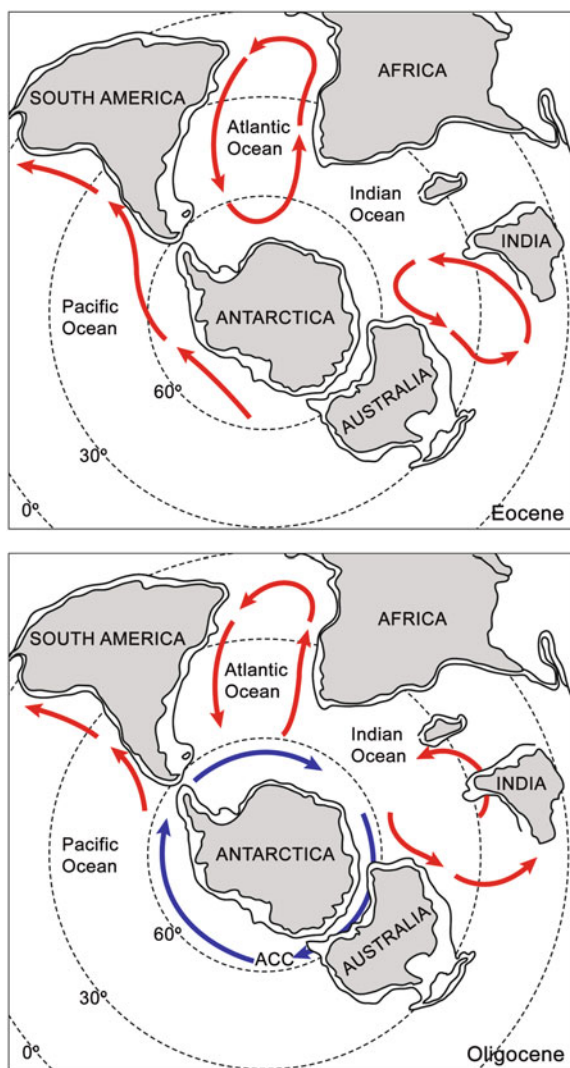
At the beginning of the Cenozoic, South America was separated from North America by a major seaway, but still connected to Antarctica and (at a further remove) Australia. Temperatures were warm worldwide, a persistence of greenhouse conditions from the close of the Mesozoic. The terminal late Paleocene–early Eocene (~59 to ~52 Ma) was a period of unusual warmth even by the standards of previous eras. Global temperatures and atmospheric greenhouse gas levels were higher than they have been at any other point in the past 65 Ma (Fig. 2.1). This hyperthermal period, known as the Paleocene–Eocene thermal maximum (PETM), peaked at ~52–50 Ma, with the early Eocene climatic optimum (EECO) (Woodburne et al. 2014a, b).

By the early Eocene, global surface ocean currents were warm, with saline concentrations similar to those at depth. Equatorial waters circulated with those of the South Pacific and South Atlantic, keeping ocean temperatures uniform between high and low latitudes (Fig. 2.2).

**Fig. 2.1** Changes in atmospheric CO<sub>2</sub> levels and global climate during the Cenozoic. Abbreviations: EECO, early Eocene climatic optimum; MMCO, middle Miocene climatic optimum; PETM, Paleocene–Eocene thermal maximum (based on Zachos et al. 2001)



**Fig. 2.2** Ocean circulation pattern in the Southern Hemisphere at the early Eocene and early Oligocene. The Antarctic Circumpolar Current (CCA, in blue) is a clockwise cold ocean current defined after the separation of Antarctic, Australia, and South America. (based on Benedetto 2010)



The EECO was followed by a long trend toward cooler conditions from 50 to 34 Ma. This cooling event peaked at the Eocene–Oligocene Boundary ( $\sim 34$  Ma), and the world then began to change from greenhouse to icehouse (Fig. 2.1). Ice sheets previously present at higher altitudes in the Antarctic expanded, ushering in the first major Cenozoic glaciation on that continent (Oi-1 Glaciation). Temperatures declined  $7^{\circ}\text{C}$  in deep seas (from  $\sim 12$  to  $\sim 4.5^{\circ}\text{C}$ ) (Zachos et al. 2001; Reguero et al. 2013), and significant temperature gradients appeared from the equator to the poles.

The sea floor between Antarctica and Australia started forming by the middle/early late Eocene. By the early Oligocene ( $\sim 32$  Ma), ocean depth permitted deep-water communication between the Pacific and Indian Oceans, setting the stage for the development of a major Antarctic ice cap and the largest Cenozoic sea level drop ( $\sim 30$  Ma; Haq et al. 1987). The current oceanic configuration was complemented by the opening of the Drake Passage. The precise timing of the separation of Antarctica and South America is difficult to establish. The evidence indicates that by the late Oligocene ( $\sim 24$  Ma; Pfuhl and McCave 2005), the deep-water connection between the Pacific and Atlantic Oceans was fully established. However, studies based on seafloor magnetic anomalies indicated that a shallow-water opening ( $<1000$  m deep) was present as early as  $\sim 50$  Ma (early Eocene; Livermore et al. 2007; see also Scher and Martin 2006; Reguero et al. 2013). This configuration resulted in the formation of the Antarctic Circumpolar Current (ACC), a clockwise current flowing around Antarctica (Fig. 2.2) that thermally isolated the continent for the remainder of the Cenozoic and profoundly influenced worldwide climate.

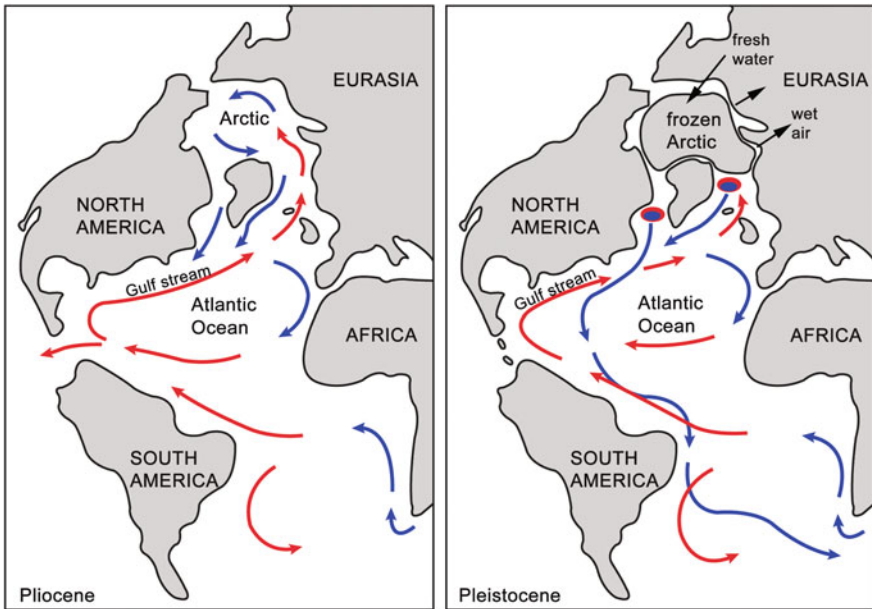
The Eocene–Oligocene boundary is marked by biotic changes on a global basis, including major diversification/extinction and immigration/emigration events (Prothero 1994; Sluijs et al. 2007; Wing et al. 1995). In Europe, this episode was recognized by the Swiss paleontologist Hans Stehlin as “La Grande Coupure,” or the great break, in what was perceived as previous long-term faunal continuity. Similar faunal reorganizations were later recognized for North America by Henry F. Osborn (Prothero 1994), Asia with the concept of the “Mongolian Remodeling” (Meng and McKenna 1998), and South America with the “Patagonian Hinge,” based on an abrupt change within metatherian-dominated associations in Patagonia (Goin et al. 2010, 2016).

Climatic deterioration at the start of the Oligocene and the formation of semipermanent ice sheets in Antarctica persisted until the late Oligocene (26–27 Ma; Zachos et al. 2001), when a warming trend reduced Antarctic ice cover. Another hypothermal peak is recorded in the early Miocene (Mi-1 Glaciation). From this point onward until the middle Miocene, warmer conditions prevailed. Global ice volume remained low, and bottom water temperatures trended slightly higher. This warm phase peaked in the middle Miocene ( $\sim 17$  to  $\sim 15$  Ma) with the middle Miocene climatic optimum (MMCO) (Fig. 2.1). Global temperatures gradually decreased once more, with the initiation of the modern phase of Antarctic glaciation, reestablishing permanent ice cover by 10 Ma (Zachos et al. 2001). Global temperatures decreased gradually through the late Miocene until the early Pliocene (6 Ma), with additional cooling and ice sheet expansion in West Antarctica and the Arctic.

The early Pliocene is marked by a subtle warming trend until  $\sim 3.2$  Ma when temperatures abruptly decreased, marking the onset of Northern Hemisphere Glaciation (NHG). Since then, temperature curves show contrasting peaks and valleys, correlated with the pattern of repeated glaciations and interglaciations that characterize the Ice Ages of the last 2.6 Ma. The amplitude of these changes greatly increased at the beginning of the Middle Pleistocene 0.7 Ma (Zachos et al. 2001).

This event has been previously correlated with the completion of the Isthmus of Panama (but see below) and consequent changes in oceanic circulation (Fig. 2.3). Closure of the seaway between the Pacific and Atlantic Oceans enhanced the Gulf Stream, the warm Atlantic current that passes from the Gulf of Mexico along the North American Atlantic seaboard before departing for northern Europe. Enhanced production of water vapor from evaporation of the warm waters of the Gulf Stream triggered increased snowfall in Europe, Asia, and North America and the consequent formation of thick snow cover (Haug and Tiedemann 1998).

In Patagonia, glaciations had begun to occur in the southern Andes (Santa Cruz Province) by the late Miocene–early Pliocene  $\sim 7$ –4.4 Ma (Rutter et al. 2012). After this, 15 successive expansion/retreat events have been documented for southern South America, some of which can be recognized worldwide (Rutter et al. 2012). During the late Pliocene (4.8–4.7 Ma, 3.5–2.79 Ma), extra-Andean ice sheets formed in Patagonia, with major expansions (the so-called Great Patagonian Glaciation) dating to  $\sim 2.4$  Ma and  $\sim 1$  Ma (Rabassa 2008; Rutter et al. 2012). Evidence of early Pleistocene expansions ( $\sim 2.6$  Ma) has been recovered in the Andes of Bolivia and Colombia, while that for the mid-Pleistocene glaciation ( $\sim 1$  Ma) has been recovered from the Bogota basin of Colombia (Rutter et al. 2012). The Last Glacial Maximum (LGM) in the Northern Hemisphere is recorded



**Fig. 2.3** Ocean circulation pattern before and after the closure of the Panama Isthmus. The Gulf Stream is a warm Atlantic Ocean current from the Gulf of Mexico to northern Europe enhanced by the closure of Panama Isthmus. The water vapor from evaporation of the warm waters of the Gulf Stream triggered increased snowfall in Europe, Asia, and North America and the consequent formation of thick snow cover (based on Benedetto 2010)

from  $\sim 80$  to 20 Ka (Wisconsinan glaciation), while in South America it ranges from  $\sim 48$  to 25 Ka (Rutter et al. 2012). In South America, evidence for this later advance is restricted to the cordilleras and valleys of the Andes (Clapperton 1993; Rabassa 2008; Rutter et al. 2012). Ice sheets reached their maximum  $\sim 26,500$  years ago, with deglaciation starting  $\sim 19,000$  years ago (Clark et al. 2009), ushering in the current interglacial period from about 11,700 years ago.

### 2.1.2 Tectonics—Rise of the Andes

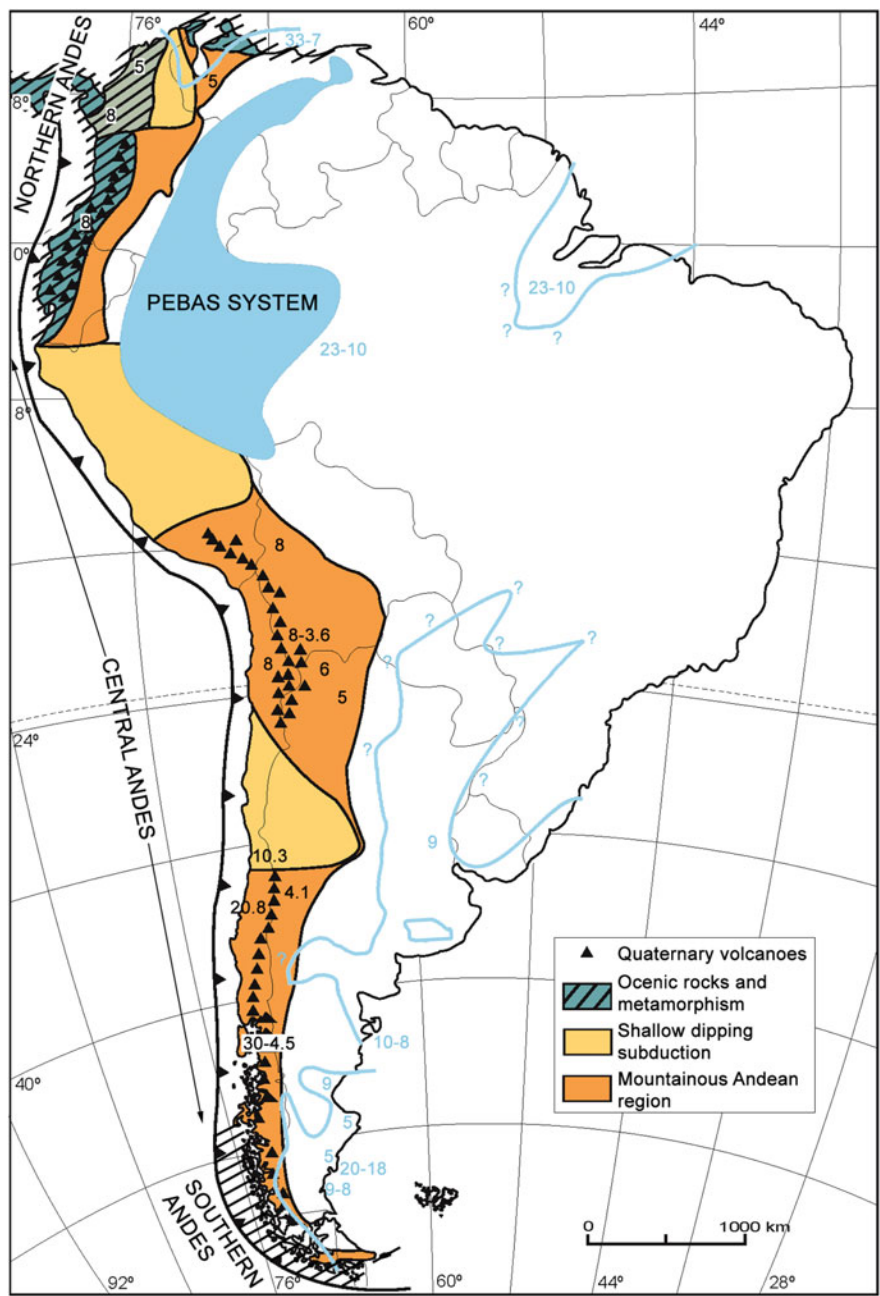
The Andes, originating by subduction of oceanic crust underneath the Pacific margin of South America, constitutes the world's longest active orogenic system (Ramos 2009). Its range extends more than 8000 km, from the Caribbean Sea in the north to Tierra del Fuego in the south, with an average height of about 4000 masl and maximum elevations up to 7000 masl (Ramos 1999).

Subduction, initiated in the late Proterozoic, has been episodic up to the present (Ramos 2009). In southern South America, several phases of Cenozoic Andean orogeny are denoted as the Incaica ( $\sim 30$  Ma), Pehuenche ( $\sim 25$  Ma), Quechua ( $\sim 15.5$  Ma), and Diaguita Phases ( $\sim 4.5$  Ma) (Yrigoyen 1979; Leanza and Hugo 1997). These events, defined at the latitudinal level of northern Patagonia (Neuquén Province), are diachronic along the major segments, usually identified as the northern, central, and southern Andes (Fig. 2.4). Each segment has its own history with regard to tectonics, including convergence rate of oceanic and continental plates, collision with allochthonous terrains, subduction angle, age and rigidity of oceanic crust, magmatism, and sedimentation. Normal subduction (angle about  $30^\circ$ ) is characterized by intense vulcanism. Flat-slab subduction, with inclination between  $5^\circ$  and  $10^\circ$  (subhorizontal), is characterized by significant seismic activity, minor vulcanism, and substantial compression forces (Ramos 1999) (Fig. 2.4).

With regard to diachronicity, the Principal Cordillera (about  $33^\circ\text{S}$ ) was raised between 20 and 8.6 Ma, the Frontal Cordillera between 10 and 3 Ma, and the Precordillera after 4 Ma (Ramos 1999). The Cordillera Oriental was fully uplifted  $\sim 8$  Ma in the extreme northwest of Argentina (Jujuy and Salta Provinces), while the Sierras Subandinas did not achieve maximum uplift until the early Pliocene (Ramos 1999). The level of uplift was such that the northwestern Argentinean Andes reached altitudes greater than 6000 m prior to 6 Ma.

The central Andes (the Altiplano of Bolivia, northern Chile, and southern Peru) underwent a steep uplift starting  $\sim 9$  Ma, with the northern part reaching modern altitudes by  $\sim 8$  Ma and the south by 3.6 Ma (Garzzone et al. 2008; Bershaw et al. 2010).

In northern central and northern Andes (north of  $20^\circ\text{S}$ ), present-day elevations were achieved during or soon after 10–8 Ma. Andean orogeny in Ecuador, Colombia, and Venezuela included collision with island arcs and oceanic plateaus (Iturralde-Vinent and MacPhee 1999; Coates et al. 2004; Ramos 2009; Farris et al. 2011; Montes et al. 2012; Coates and Stallard 2013). The Venezuelan Andes



**Fig. 2.4** Major segments of the Andes, Quaternary volcanic zones and tectonic processes, and in the blue lines, major Neogene marine ingressions (adapted from Ramos 1999; Hoorn et al. 2010; Del Río et al. 2013). Dating of the events are expressed in Ma



experienced rapid uplift and widening during the late Miocene (Erikson et al. 2012), with uplift in Merida, Sierra de Perija, Santa Marta, Lara-Falcón, and Guajira occurring  $\sim 5$  Ma.

In Colombia, the rise of the Eastern Cordillera was complex, involving several steps. Depending on the area, uplift occurred at intervals between the Oligocene and late Miocene ( $\sim 30$ – $26$  Ma,  $\sim 23$ – $20$  Ma, and  $\sim 10$ – $6$  Ma) and involved an overall rise of more than 1000 m (Ochoa et al. 2012). The Western and Central Cordilleras had emerged by the Paleocene–Eocene, with rejuvenation in the Miocene (Borrero et al. 2012). The Bogota basin in Colombia was less than 1000 m above sea level until the early Pliocene, when it rose to 1500 m. Between the late Pliocene and early Pleistocene, it reached its modern height of about 2500 m (Rutter et al. 2012).

For obvious reasons, the Andes constitutes an important biogeographic structure in South America. Its physiographic structure, in combination with the drastic environmental changes occasioned by their uplift, has long acted as biogeographic barriers for some taxa and corridors for others (Webb 1985, 1991; Woodburne 2010). In consequence, they have, in effect, ruled the later Cenozoic evolution of most terrestrial ecosystems in South America (Hoorn et al. 2010; Patterson et al. 2012).

### 2.1.3 *Sea Level Changes and Marine Ingressions*

South America experienced several marine ingressions between the late Miocene and Pleistocene. Marine deposits dating between 10 and 9 Ma in Patagonia and to  $\sim 9$  Ma in the Pampean Region (Entre Rios Province) establish the occurrence of a late Miocene marine ingressions in the southern cone (Del Río et al. 2013; Pérez 2013; Marengo 2015; for older transgressions, see Guerstein et al. 2010; Tambussi and Degrange 2013; Woodburne et al. 2014a). Evidence of another more recent marine ingressions in Patagonia date to  $\sim 5.1$  Ma (Del Río et al. 2013).

Several authors have supported the contention that the late Miocene (“Paranaense” and “Enterrriense”) ingressions in the southern part of the continent communicated with coeval incursions in the north, resulting in a shallow epicontinental sea covering extensive portions of lowland South America (Räsänen et al. 1995; Ramos 1999; Hovikoski et al. 2007; Uba et al. 2009). The evidence for such widespread inundation is, however, either inconclusive (Hoorn et al. 2010; Marengo 2015) or contradictory (Latrubesse et al. 2010; Gross et al. 2011). By contrast, other authors have maintained that during the late Miocene, a giant lake, the Pebas system, occupied western Amazonia (Fig. 2.4). About 10 Ma this was replaced by a large fluvial system that connected several isolated basins (e.g., Amazon and Parana). In the Pliocene, the Amazonian region was elevated and the current river-systems became entrenched (Campbell et al. 2006; Cozzuol 2006; Hoorn et al. 2010).

Pleistocene glaciations produced recurrent changes in sea level (above the present level in interglacial periods, below in glacial stages). Rises caused brief marine ingressions, mainly limited to coastal areas and river basins (Clapperton 1993; Ponce et al. 2011; Rabassa and Ponce 2013). On the east coast of southern South



America, low sea levels during glacial periods exposed a large portion of the continental platform, considerably increasing the extent of environments available for the terrestrial fauna (Ponce et al. 2011; Rabassa and Ponce 2013) (Fig. 2.5).

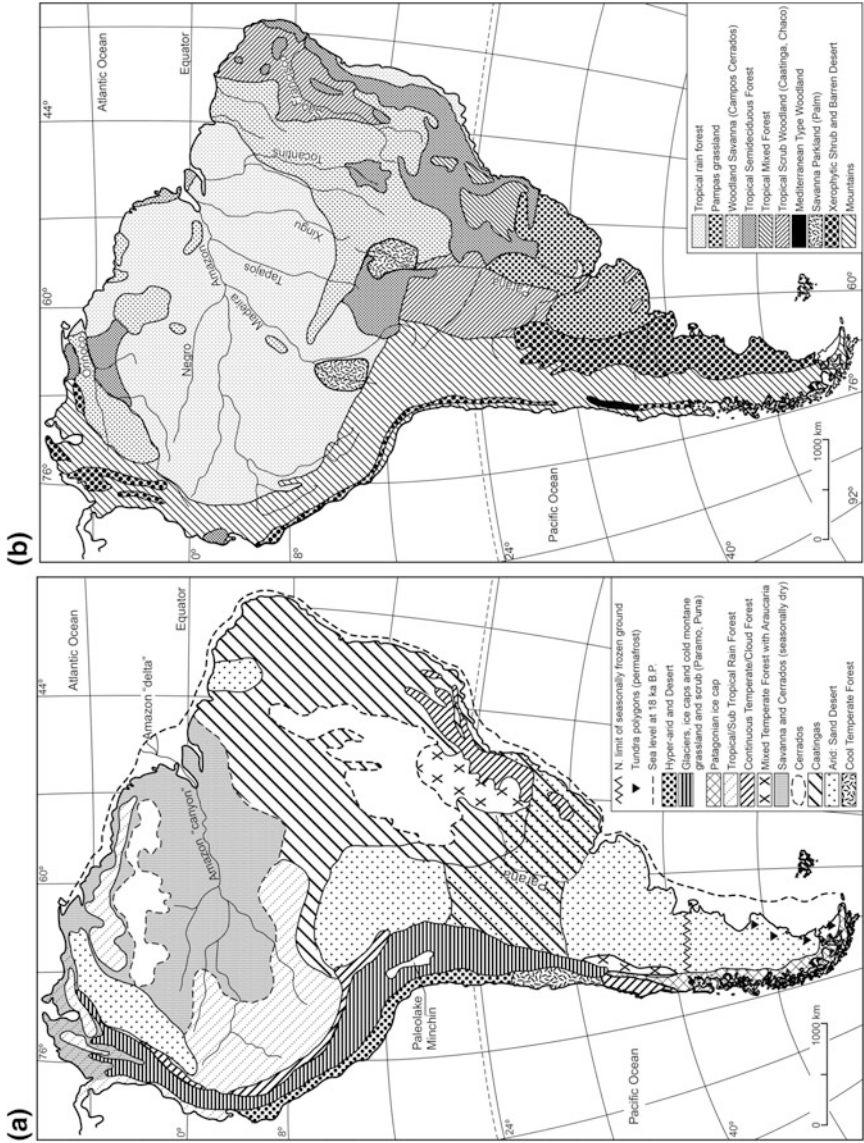


**Fig. 2.5** Changes of the Atlantic coast of Pampa and Patagonia from the LGM to the middle Holocene (based on Ponce et al. 2011). The numbers correspond to different terraces or levels present at the continental shelf, indicating the sea level position. I: –140 m, corresponding to the Last Glacial Maximum (LGM) or an earlier glaciation; II: –120 m, equivalent to the LGM; III: –90 m, corresponding with 15 ka (calibrated); IV: –30 m, around 11–10 ka (calibrated)

## 2.2 The South American Biota

The paleontologist Simpson (1950, 1980) recognized three phases/strata in South American mammalian evolution that, despite new discoveries, additions, and corrections, remain in use. The first stratum was characterized by the evolution of indigenous archaic forms, like pouched marsupials and their extinct relatives (Didelphimorphia, Microbiotheria, Paucituberculata, Polydolopimorphia, Sparassodonta; Chap. 3), archaic South American native ungulates—collectively, the SANU—(Notoungulata, Litopterna, Astrapotheria, Pyrotheria), sloths, anteaters, and armadillos (Pilosa and Cingulata). To this group was added a crew of immigrants from Africa (rodents and monkeys), defining the second stratum. Fossil evidence establishes that caviomorph rodents and platyrrhine primates have been in South America since the Eocene (Antoine et al. 2012; Woodburne et al. 2014b; Bond et al. 2015). Collectively, the mammalian groups composing Simpson's first two strata are “natives.” Their splendid isolation (but see Wilf et al. 2013) ended during the late Neogene following the arrival of new placental groups from North America (see next section). The “invaders” included pumas, jaguars, foxes, bears, deer, llamas, horses, gomphotheres, mice, and humans (Carnivora, Artiodactyla, Perissodactyla, Gomphotheriidae, Cricetidae, and Hominidae), defining the third stratum of Simpson.

During the Paleogene, forests were widespread in South America, including the southern tip of the continent and the Antarctic Peninsula. Paleobotanical evidence from middle latitudes ( $\sim 50^\circ\text{S}$ ) indicates that floras were extraordinarily diverse at that time, such as that of the early Eocene Laguna del Hunco (Chubut Province), which included ferns, conifers, and flowering plants. During the early Miocene, the Patagonian flora was characterized by *Nothofagus* trees (relatives of ñire, coihue, and lenga), araucarias, laurel, similar to current Andean-Patagonian forests from Chile and Argentina (Brea et al. 2012). The dry, windy, and sparsely vegetated environments so characteristic of central Patagonia today were at that time quite moist, with high rainfall and moderate temperatures. In lowland Patagonia, Andean uplift and long-term Cenozoic temperature reduction forced the replacement of earlier forest formations with more open and xerophytic vegetation during the middle–late Miocene. By late Miocene, Patagonian forests were dominated by *Schinus*, *Prosopis*, *Celtis*, with shrubby Ephedraceae and Asteraceae (Barreda et al. 2008; Dozo et al. 2010; Palazzesi et al. 2014). In north of Patagonia, evidence of mixed floras with C3–C4 species at localities between  $21^\circ$  and  $35^\circ\text{S}$  in Bolivia and Argentina indicates the presence of extensive grasslands (MacFadden et al. 1996) by 8 Ma. In central and northwestern Argentina, northern Chile, and at higher altitudes in the Colombian Andes, the percentage of high-altitude plants increased following the late Miocene–Pliocene, with the “Paramo” vegetation having become well established by the late Pliocene (Van der Hammen, 1973; Helmens and Van der Hammen 1994; Wijninga 1996; Starck and Anzotegui 2001). In the late Miocene ( $\sim 9$  Ma), the southern part of the Parana basin (Entre Ríos, Argentina) was occupied by seasonal tropical forest (Brea et al. 2013), which may indicate a southward extension of warmer conditions (Cozzuol 2006).



**Fig. 2.6** Distribution of the different vegetation coverage in South America during the Last Glacial Maximum (a) and today (b) (based on Clapperton 1993)

In the Pleistocene, glacial–interglacial climatic cycling strongly affected vegetation coverage (Fig. 2.6). During colder glacial phases, more arid conditions were present, with an overall retreat of forests and their replacement by open environments (Clapperton 1993; Cione et al. 2003, 2008, 2015; Woodburne et al. 2014a; and bibliography cited there). On the other hand, the warmer interglacial phases recorded conditions more similar to those of the present (Clapperton 1993; Cione et al. 2008, 2015).

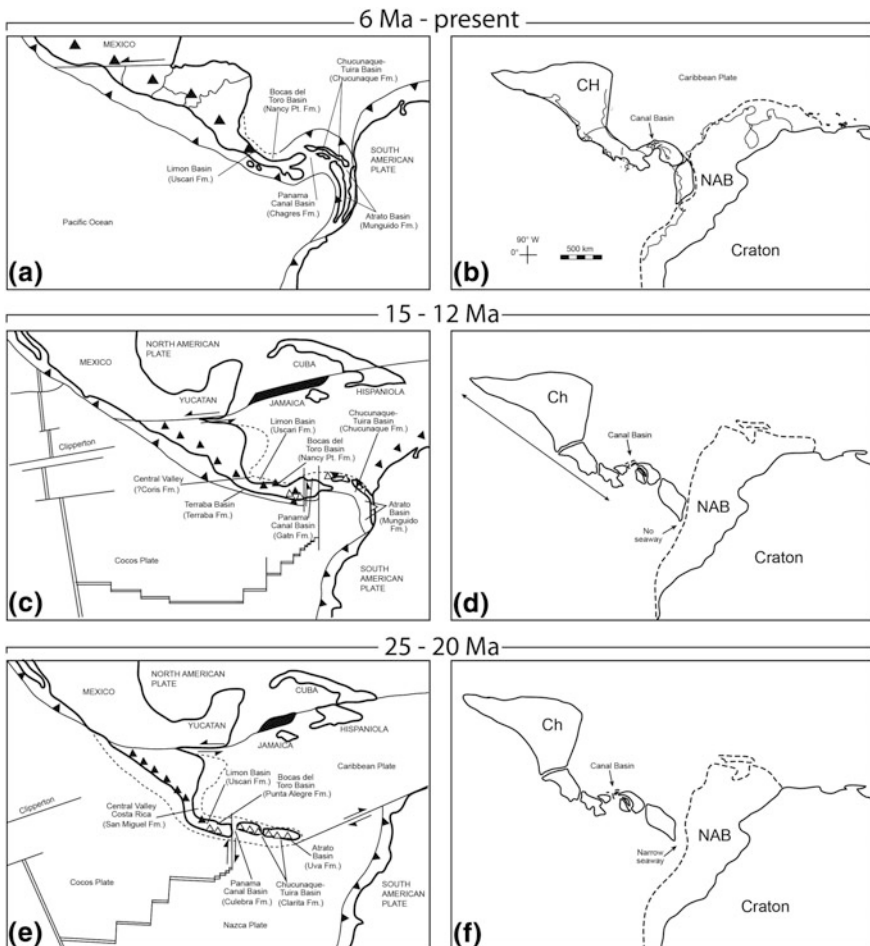
These environmental and floristic changes from the middle Miocene–Pliocene onward had notable impacts on several autochthonous groups of mammals (e.g., Pascual and Ortiz Jaureguizar 1990). Although several groups of SANU (e.g., Astrapotheria, Leontinidae, Adiantidae, Notohippidae) became completely extinct in the middle Miocene, some xenarthran taxa radiated extensively (Megalonychidae, Megatheriidae, and Mylodontidae) (Marshall and Cifelli 1990). A few lineages of SANU continued and even produced restricted radiations (e.g., Toxodontidae), but their later history was one of continuing decline during the middle Miocene–Pleistocene, followed by further steep reductions in the Pliocene and finally their complete disappearance with the Pleistocene–Holocene transition and associated megafaunal extinctions (Marshall and Cifelli 1990; Bond et al. 1995).

Within this broad interval, a marked faunal turnover occurred during the mid-Pliocene (e.g., Kraglievich 1952; Tonni et al. 1992; Vizcaíno et al. 2004). Turnover has been attributed to environmental changes resulting from Andean orogeny (e.g., Ortiz Jaureguizar et al. 1995; Cione and Tonni 2001) as well as to the catastrophic effects of a bolide that apparently struck somewhere in or near the Atlantic coast ~3.3 Ma (Schultz et al. 1998; Vizcaíno et al. 2004). Another cause of particular interest here is the arrival of Holarctic invaders, to which discussion will now turn.

## 2.3 The Panamanian Isthmus and the “Great American Biotic Interchange”

Tectonism during the Miocene–Pliocene finally resulted in the establishment of a continuous terrestrial bridge between Central and South America (Coates et al. 2004; Farris et al. 2011) and triggered one of the most important biogeographic events of the Cenozoic: the “Great American Biotic Interchange.” The biotic exchange between the Americas is typically portrayed as principally affecting mammals, birds, and turtles, but of course other vertebrates, invertebrates, and plants were also involved (Stehli and Webb 1985; Woodburne 2010; Tambussi and Degrange 2013; Bagley and Johnson 2014; De la Fuente et al. 2014; Gutiérrez-García and Vázquez-Domínguez 2013; Leigh et al. 2014). Nor were the effects of closure of the seaway limited to the land; disconnection between the Caribbean Sea and the Pacific Ocean had wide repercussions for marine biotas as well (Leigh et al. 2014).

Subduction of the Cocos and Nazca Plates under the Caribbean large igneous province produced a volcanic arc that collided with northwestern South America  $\sim 12$  Ma, reducing the distance between Central and South America, and creating an interstitial island chain (Coates et al. 2004; Fig. 2.7). Recent evidence suggests that the collision between Central and South America started around 25–23 Ma. By this time, Central America was a continuous peninsula, leaving only a narrow, shallow strait between the continents in the Miocene (Farris et al. 2011; Montes et al. 2012). Detrital zircons recovered from the northern Andes (Colombia) in northwestern South America have been interpreted as evidence of a terrestrial connection between



**Fig. 2.7** Comparative diagrams models of the closure of the Isthmus of Panama based on Coates and Stallard (2013) for 6 Ma–present (a, b), 15–12 Ma (c, d), and 25–50 Ma (e, f). Standard model at the left, based on Coates et al. (2004) (a, c, e). New model at the right, based on Montes et al. (2012) (b, d, f)

present-day Panama and Colombia by 13–10 Ma (Montes et al. 2015; Fig. 2.7). Some biological data also suggested an emergence of the Panamanian land bridge earlier than the previous estimate of  $\sim 3$  Ma. Divergence estimates for key Neotropical plants and animals (including marine taxa) suggested that several waves of dispersal to South America occurred between the interval  $\sim 20$  and 6 Ma following Bacon et al. (2015). This challenging interpretation has been recently criticized based on the available geological and biological data (e.g., Marko et al. 2015; O’Dea et al. 2016) while acknowledging a more classical, younger age for the establishment of the Panama bridge and associated massive migration events. However, the interesting review of O’Dea et al. (2016) introduced some inaccurate data and mistakes (e.g., Fig. S3): (1) the dates for most immigration events should be taken with caution since the majority of first records of North American taxa in South America are not precisely dated (see Chaps. 4 and 5); (2), several immigration events to South America are incorrect (e.g., *Lontra* is present since the Ensenadan but not since the Lujanian; *Galictis* since the Vorohuean but not since the Ensenadan, *Canis* is only known since the latest Pleistocene but not since the Middle Pleistocene; see Chap. 4); and (3), the first record of Neotropical carnivorans has to be analyzed in the context of the bias in the SA Pleistocene fossil record (see Chap. 5, Prevosti and Soibelzon 2012).

The picture of land bridge development is still far from conclusively resolved, and there are other possible interpretations (Coates et al. 2004; Coates and Stallard 2013, 2015; Leigh et al. 2014). Coates and Stallard (2013, 2015) argued that narrow but deep marine barriers existed between the island arc and the Americas 15–12 Ma and that the final connection was not established until  $\sim 3$  Ma. Furthermore, it is uncertain to what degree the Central American peninsula was actually subaerial at this time (Leigh et al. 2014). There is also evidence for a persistent shallow-water connection between the Pacific and the Caribbean through the 10–3.5 Ma interval, with complete interruption occurring only around 3 Ma (Coates et al. 2004; Osborne et al. 2014). Even if the interpretation of Montes et al. (2015) concerning the early connection of the Panama arc with South America is accepted, their data cannot confirm the existence of a complete terrestrial corridor between Central and South America. Equally, the divergence dates and immigration rates reported by Bacon et al. (2015) do not constitute conclusive support for an early southward irruption of North American mammals interpreted as a kind of “advance” GABI (Woodburne 2010; Cione et al. 2015). Roughly, their results are congruent with the traditional interpretation of the vertebrate fossil record, with the addition of a few dispersals in the Miocene and possibly a larger event occurring during the early and late Pliocene. Obviously, any estimates of age of clade divergences are contingent on assumptions made in the construction of models or the choice of calibrations, and the relevant cladogenetic events may have occurred outside South America.

In any case, it is clear that the new datasets indicate that the rise of the Panamanian land bridge is much more complex than previously thought and that the evanescent existence of terrestrial connections between Central and South America before 3 Ma is quite plausible. Changes in sea level, climate, and



vegetation must have affected the Panamanian faunal highway in a multitude of ways over time (e.g., Leigh et al. 2014; Bagley and Johnson 2014).

Lower sea levels presumably resulted in the existence of a temporary or nearly complete isthmus in the late Miocene, with a permanently complete terrestrial bridge in place by  $\sim 3$  Ma (produced by a sea level reduction related to increased northern glaciation) and later Pleistocene glaciations enhancing its permeability (Woodburne 2010; Leigh et al. 2014; Bagley and Johnson 2014). This situation was reversed during the interglacials, when higher sea levels could reconnect the Atlantic and Pacific Oceans (Bagley and Johnson 2014). Pacific dry forests in lower Central America were established in the early Pliocene ( $>4$  Ma); remnants were present until the Late Pleistocene when these areas became savannas with patchy forest (Bagley and Johnson 2014). Northern temperate tree species were present in lowland Central America in the late Miocene–Pliocene, suggesting that the composition of tropical rainforests was recurrently affected by cooler and drier climates (Woodburne 2010). During the last glacial maximum, montane forests were found at lower altitudes. A high-altitude Paramo corridor was thus established, which could have assisted the migration of mammals adapted to grasslands and other open landscapes (Webb 1985, 1991, 2006; Woodburne 2010; Bagley and Johnson 2014; but see Colinvaux et al. (1996) for an alternative interpretation).

The classic interpretation places the GABI as having occurred subsequent to  $\sim 3.0$  Ma, with pulses at 2.6–2.4 Ma (Marplatan), a major event of faunal exchange at  $\sim 1.8$  Ma (early Ensenadan), followed by still other, younger events (Woodburne 2010; Prevosti and Soibelzon 2012). Some early migration events toward North America recorded around 9 Ma and toward South America at  $\sim 7.3$  Ma and  $\sim 5$  Ma are exemplified by ground sloths, procyonids, and cricetids, respectively (Woodburne 2010; Prevosti and Soibelzon 2012; Cione et al. 2015). Recently, several North American mammal taxa have been reported from  $\sim 9.5$  Ma deposits in the Amazon basin. The presence of a dromomerycine artiodactyl, gomphotheres, peccaries, and tapirs in these contexts constitutes evidence of an earlier terrestrial interchange between North and South America (Campbell et al. 2009, 2010; Frailey and Campbell 2012; Prothero et al. 2014). However, the taxonomy of some of these fossils and, in particular, their age has been questioned (Alberdi et al. 2004; Ferretti 2008; Lucas and Alvarado 2010; Lucas 2013; Mothé and Avilla 2015). Compounding the problem is that their provenance is indeterminate in some instances (e.g., the dromomerycine artiodactyl was found in reworked deposits; see Prothero et al. 2014). Other than the aforementioned, North American taxa recorded in the South American Neogene begin with procyonids at  $\sim 8$  Ma, cricetid rodents in the early Pliocene ( $\sim 5.3$ – $4$  Ma), peccaries in the mid-Pliocene ( $\sim 3.3$  Ma), and camelids, canids, equids, gomphotheres, and weasels in the late Pliocene (2.8–2.6 Ma). The Quaternary fossil record shows a massive migration in the early Pleistocene ( $\sim 1.8$  Ma) with the first records of cervids, tapirs, ursids, felids, large canids, and otters (Pardiñas 1999; Prevosti et al. 2006; Woodburne et al. 2006; Prevosti and Pardiñas 2009; Woodburne 2010; Prevosti and Soibelzon 2012; Cione et al. 2015) (Fig. 2.8). Further migrations followed in the Late Pleistocene and the





**Fig. 2.8** South American carnivores. During most of the Cenozoic principal predators from the terrestrial ecosystems were marsupial relatives (Sparassodonta), terror birds (Phorusrhacidae), giant crocodiles (Sebecidae), and giant snakes (Madtsoiidae). In relation to the GABI and since the late Miocene, several placental groups (Procyonidae, Mustelidae, Mephitidae, Canidae, Ursidae, Felidae) started occupying different niches, while native predators declined. From the SA native carnivores only terror birds reached NA. Reconstructions from Jorge Blanco; carnivorans adapted from Forasiepi et al. (2007)

Holocene (Woodburne 2010), including a very important increase in carnivoran diversity  $\sim 12$  Ka (Prevosti and Soibelzon 2012; Prevosti et al. 2013).

Migrations from South to North America occurring in the interval  $\sim 9$ –7 Ma (late Miocene) include ground sloths and terror birds (Fig. 2.8), followed by other groups of ground sloths and giant armadillos in the early Pliocene ( $\sim 5$  Ma), hydrochoerids (capybaras), megatherids, and porcupines in the late Pliocene ( $\sim 2.7$  Ma), and anteaters, toxodonts, and opossums in the Pleistocene (Woodburne 2010; Cione et al. 2015). These southern migrants proved to be less successful than their northern counterparts in South America, with limited speciation followed by extinction of most taxa of South American origin (Woodburne 2010; Carrillo et al. 2015). In contrast, northern lineages diversified in South America—sometimes spectacularly, as in the case of canids—and have now become a fully integrated part of the extant mammalian fauna of South America (Woodburne 2010; Prevosti and Soibelzon 2012; Leigh et al. 2014; Cione et al. 2015).

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