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Origins, Radiations, and Distribution of South American Mammals From Greenhouse to Icehouse Worlds

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Abstract

At least five successive phases in South American mammalian evolution can be envisaged, the oldest one being largely hypothetical: (1) Early Gondwanan (?Late Triassic-Early Cretaceous), mammals of Pangaeon (triconodontids with amphilestid affinities) and Gondwanan (australosphenids) origin; (2) Late Gondwanan (Late Cretaceous), strong endemism in most lineages of Pangaeon (Dryolestida) and Gondwanan (Gondwanatheria) origin; (3) Early South American (?latest Cretaceous-latest Eocene), major radiations within Metatheria and Eutheria; (4) Late South American (early Oligocene-middle Pliocene), standardization of relatively few lineages among metatherians and marked radiation of hysodont types among South American native ungulates; and (5) Inter-American (late Pliocene-Recent), mixture of North and South American therian lineages, with progressive decline of native faunas. The biotic and abiotic events that triggered these phases include the last global warming event at the beginning of the Late Cretaceous (between phases 1 and 2); an intermittent connection between North and South America by the Late Cretaceous, enabling the First American Biotic Interchange, and the decline of native nontherians (between 2 and 3); global cooling and full development of the Circumpolar Antarctic Current, and arrival of platyrrhines and caviomorphs (between 3 and 4); and finally, the Panamanian connection between the Americas and the beginning of the Great American Biotic Interchange (between 4 and 5).

3.1 Introduction

Several reviews in recent years have highlighted the historical keystones in our knowledge of South American mammalian successions (e.g., Pascual 2006 and literature cited therein). Others include the works of Ameghino (1906), Ortiz-Jaureguizar (1986), Pascual and Ortiz-Jaureguizar (1990a, 1990b), Pascual et al. (1985), Pascual, Ortiz-Jaureguizar, and Prado (1996), Patterson and Pascual (1972), Reig (1981), and Simpson (1950). Most of these studies have focused

on the better known Cenozoic evolution of South American mammals, even though in the past few years their Mesozoic history has also been considered (Pascual 2006; Pascual and Ortiz-Jaureguizar 2007). These works, especially those following Simpson (1950, 1980), have stressed the episodic nature of the mammalian successions. This is partly a consequence of several important hiatuses in our biochronological knowledge of these successions, which exaggerate the differences between each “stratum,” “stage,” “cycle,” “horofauna,” or “episode,” as they have been variously named. Nevertheless, when the biochronological sequence is relatively well known, as with the Neogene mammalian associations of southern South America, it seems obvious that there are such things as cycles or phases among them, each being characterized by faunal turnovers and a distinctive taxonomic composition. In addition to the intrinsic evolutionary patterns of each mammalian lineage, a few major driving forces of these phases can be recognized, with paleoclimate and tectonics being the most relevant.

Two aspects preclude a better understanding of the early history of South American land mammals (for alternative views of the concepts of *Mammaliomorpha* and *Mammalia*, see Kielan-Jaworowska, Cifelli, and Luo 2004; Luo 2007; Rowe et al. 2008 [whom we follow]; regarding cynodont evolution in South America, see Bonaparte, Martinelli, and Schultz 2005; Martinelli and Rougier 2007). First, the Mesozoic fossil record is extremely fragmentary (see Rougier, Chornogubsky, et al. 2009). Most known Mesozoic taxa come from Late Cretaceous (Campanian-Maastrichtian) sites, in that the pre-Campanian Cretaceous and Jurassic mammal record still is largely unknown. Second, almost all of the Mesozoic and most of the early Cenozoic (Paleocene-Eocene) fossil record in South America comes from its southernmost tip, Patagonia (e.g., Marshall, Hoffstetter, and Pascual 1983; Rougier, Chornogubsky, et al. 2009). Given this limitation, and for reasons discussed more fully later, we need to be cautious in making inferences about the whole South American continent on the basis of Patagonian mammalian sequences. South America and its biotas are and were neither isolated nor homogeneous.

Two recent studies (Pascual 2006; Pascual and Ortiz-Jaureguizar 2007) have considered the evolution of South American land mammals throughout Mesozoic and Cenozoic times. Both recognize two major episodes, a Gondwanan Episode and a South American Episode. “The Gondwanan Episode is so termed because it is exclusively represented by endemic mammals of Gondwanan origin, i.e., Mesozoic lineages. In contrast, the South American Episode is almost exclusively distinguished by endemic therian mammals whose ancestors emi-

grated from the Laurasian North American Continent” (Pascual 2006, 209). As striking as the difference between therian and nontherian assemblages is, we feel that this primary distinction in the mammalian succession obscures other equally important patterns and processes that affected, and are reflected by, South American land mammals. Dispersal events were not the only factors that triggered the significant turnovers that occurred during the continent’s history; a two-episode portrayal of this period simplifies what actually occurred. Moreover, it is not clear that the earliest mammalian phase in South America was strictly of Gondwanan origin. Finally, consideration of South America as a single biogeographical unit hides a more complex, richer evolutionary history whose early phases in tropical and intertropical parts of the continent remain largely unknown.

Here we propose a new model for the successive phases reflected by southern South American mammals throughout history. Our proposal is preliminary and subjective, as we have not attempted a formal analysis of faunal turnovers (e.g., Alroy 2004)—our current knowledge of Mesozoic South American mammals is too incomplete for such an attempt. Instead, we have tried to emphasize the interactions between global climate, tectonics, and South American mammal assemblages, in some cases in a highly speculative manner. In short, we offer a narrative framework for considering the mammalian successions in South America, hoping that future tests of our model will confirm, clarify, and extend its applicability, causes, and consequences. We view it as an initial step in a general, multidisciplinary attempt to understand the evolution of South America’s biota as a whole over the last 250 million years of its history.

3.2 Biogeographical Context

A traditional approach to the biogeography of South America is that it can be referred to as a single, Neotropical unit (e.g., Cox 2001). Following studies by Crisci et al. (1991), and on the basis of panbiogeographic and cladistic biogeographic studies, Morrone (2001a, 2001b, 2002) argued in favor of the composite nature of this continent, “. . . with southern South America closely related to the southern temperate areas (Australia, Tasmania, New Zealand, New Guinea, and New Caledonia), and tropical South America closely related to Africa and North America” (Morrone 2002, 149). Thus, he formally proposed the Andean Region (southern South America and a strip of the Andean Cordillera) as part of an Austral Kingdom. The concept of an Austral biogeographic kingdom (or Austral realm, fig. 3.1) is not new, and can be traced back

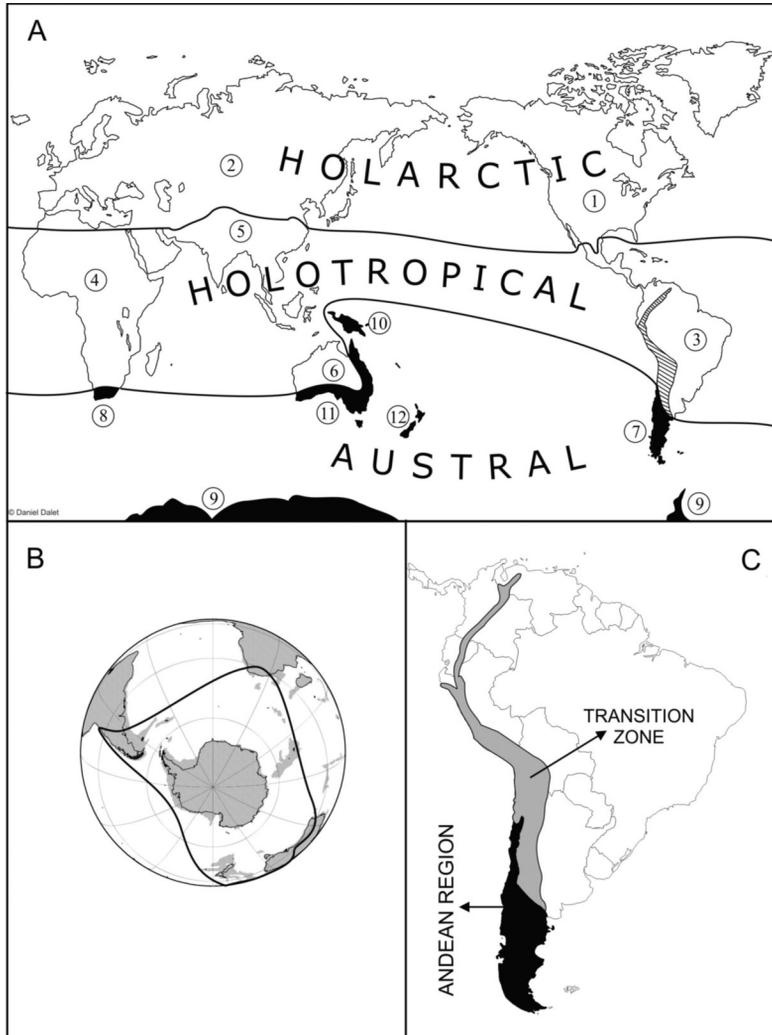


Figure 3.1 (A) World biogeographic kingdoms and regions sensu Morrone (2002). Biogeographic regions are, for the Holarctic Kingdom (=Laurasia): (1) Nearctic, (2) Palearctic; for the Holo-tropical Kingdom: (3) Neotropical, (4) Afrotropical, (5) Oriental, (6) Australotropical; for the Austral Kingdom: (7) Andean, (8) Cape or Afrotemperate, (9) Antarctic, (10) Neoguinean, (11) Australotemperate, and (12) Neozelandic. (B) The Austral biogeographic kingdom in polar projection (based in the ODSN Plate Tectonic Reconstruction Service, <http://www.odsn.de/odsn/services/paleomap/paleomap.html>). (C) map of South America showing the Andean Region and the Transition Zone (from Morrone 2006). Sources for maps in (A) and (C) are: http://dmaps.com/carte.php?lib=mundo_centrado_oceano_pacifico_mapa&num_car=3227&lang=es and http://d-maps.com/carte.php?lib=america_del_sur_mapa&num_car=2313&lang=es, respectively.

to the early nineteenth century (see Moreira-Muñoz 2007). Morrone's (2001a, 2001b) model considers three global biotic realms: The Holarctic Kingdom, the Holotropical Kingdom (essentially Western Gondwana), and the Austral Kingdom (essentially Eastern Gondwana). The latter included southernmost South America and the Andean Range (the Andean Region), Antarctica (Antarctic Region), southernmost Africa (Cape or Afrotropical Region), eastern and southern Australia (Australotropical Region), New Zealand (Neozelandic Region), and New Guinea (Neoguinean Region). Later, Morrone (2004a, 2004b, 2006) restricted the concept of the Andean Region to the southernmost tip of South America (i.e., central and southern Chile, the southern Andes, and Patagonia in Argentina). In turn (Morrone 2006, fig. 1), he regarded the central and northern sections of the Andean Range as a transitional zone between the Neotropical and Andean regions. "Transition zones . . . are located at the boundaries between biogeographic regions . . . and represent areas of mixture of different biotic elements" (Morrone 2006, 469; fig. 3.1C).

The recognition of the dual nature of South America's historical biogeography offers a new insight to the understanding of mammalian evolution in this continent, especially its earlier phases. The general tendency to extrapolate results to a continental scale, based on empirical evidence coming from Patagonia, may prove to be largely inadequate. For instance, analyzing the middle Miocene (Laventan) mammalian fauna of Quebrada Honda, in southernmost Bolivia, Croft (2007, 277) stated that it is "more similar to the slightly older high-latitude fauna of Collón-Curá [Patagonia] than to the contemporaneous low-latitude fauna of La Venta [Colombia], suggesting that isolating mechanisms between the low and middle latitudes were in place during the early and/or middle Miocene." Owing to few comparable taxa and lacking isotopic dates for the faunas at La Venta and Quebrada Honda, it would be difficult to assign both to the same biochronological unit! Interestingly, Quebrada Honda is located at the heart of the Transition Zone between the Neotropical and Andean regions, something that could explain its mix of earlier southern taxa with more modern, middle/low latitude forms. Another example of mammal provinciality is represented by the Cerdas fauna from southwestern Bolivia (Croft et al. 2009). This fauna ranges in age from 16.3–15.1 Ma, but seems to be faunally more like that of Quebrada Honda (13.0–12.7 Ma) than to comparably old faunas of nearby Chile (Chucal; 18.8–17.5 Ma). This indicates that faunas typically found during the Laventan South American Land Mammal Age (SALMA) have an earlier occurrence in Bolivia than would be expected for faunas of Cerdas age based on traditional faunal compositions derived from sites farther south.

In that context, Croft et al. (2009, 193) noted that “significant provinciality was present in South America at least by the early Miocene.” We interpret this to indicate that elements of the modern Holotropical Realm in South America have considerable antiquity.

We elaborate on the historical development of the Austral Kingdom elsewhere. Briefly, we suggest that the initial stages in the development of an Austral realm could date from the Late Triassic. Artabe, Morel, and Spalletti (2003) summarized the relatively well-known paleobotanical evidence in southwestern Gondwana, claiming that the extensive floral extinctions that occurred at the end of the Permian, together with the expansion of northern lineages into southern Gondwana, characterized the main components of the Gondwanan Triassic turnover. The Gondwanan Triassic (floral) Kingdom (defined by the presence of *Dicroidium* floras) can be divided in two main dominions, or areas: the Tropical Area and the “Tethys Wet Corridor” on one side (northern Gondwana), and the Extratropical Area on the other, south of 30° S paleolatitude (the latter is defined by the presence of the Ipswich microfloras; see Zavattieri 2002). In turn, the Extratropical Area includes two major regions, or floral provinces: Southwestern Gondwana, mostly including central and southern South America and Africa, and Southeastern Gondwana, for the remaining landmasses of South Gondwana. Most of Southwestern Gondwana is included within the dry subtropical climatic zone (from 30° to 60° S paleolatitude), while Patagonia in South America, the Karoo Basin in southernmost Africa, and most of Southeastern Gondwana belong to the warm-temperate climatic belt (south of 60° S; Artabe, Morel, and Spalletti 2003; fig. 3.2). Because of their similar latitudinal position and a similar climatic regime, several characteristic lineages were shared between Patagonia and Southeastern Gondwana (e.g., Marattiales; Artabe, Morel, and Spalletti 2003). It is probable that, under these paleolatitude and climatic constraints, the Austral realm began its differentiation in the Late Triassic.

3.3 Phases in the Evolution of Austral South American Mammals

We distinguish five successive phases in the evolution of South American southern mammals: (1) Early Gondwanan (?Late Triassic–Early Cretaceous), (2) Late Gondwanan (Late Cretaceous), (3) Early South American (?latest Cretaceous–latest Eocene), (4) Late South American (early Oligocene–Middle Pliocene), and (5) Inter-American (late Pliocene–Recent). Because of their scarcity in the fossil record, we provide a short overview of our knowledge regarding Mesozoic

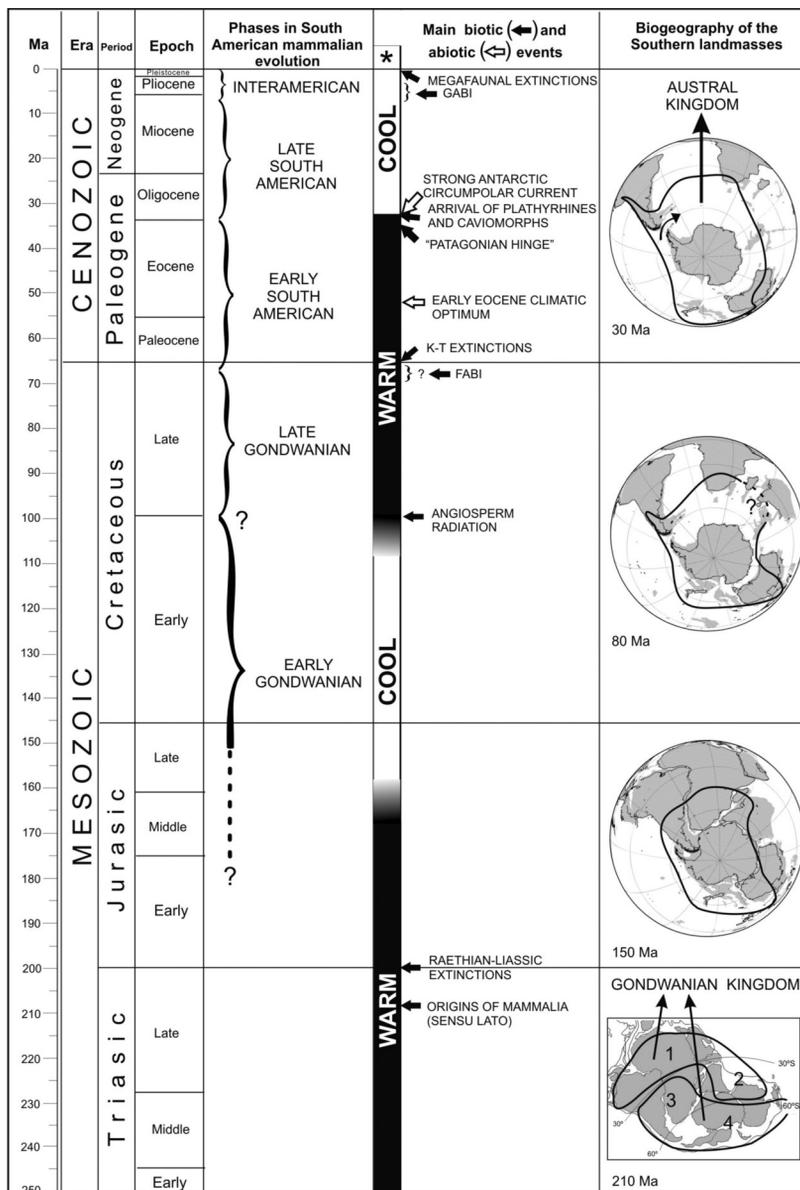


Figure 3.2 Phases in the evolution of South American mammals. Maps at the right show plate reconstructions at 30 Ma, 80 Ma, 150 Ma (based in the ODSN Plate Tectonic Reconstruction Service (<http://www.odsn.de/odsn/services/paleomap/paleomap.html>), and 210 Ma (*). Temperatures (long waves) modified after Scotese, Boucot, and McKerrow (1999). The arrow in the uppermost map indicates the full opening of the Drake Passage. Floral areas and provinces of the Gondwanan Floristic Kingdom in the lowermost map: (1) tropical area, (2) wet warm corridor of Tethys, (3) southwestern Gondwana, and (4) southeastern Gondwana (after Artabe, Morel, and Spalletti 2003, fig. 3).

mammals (phases 1 and 2). Regarding phases 3 through 5, we briefly mention only the main processes undergone by marsupials and native ungulates, which are better known than xenarthrans in the early Tertiary. Much more detailed reviews of these and other lineages of South American therians are cited in the introduction. Regarding the Inter-American phase, we detail relatively recent information on the timing of arrival of several mammalian lineages (see also fig. 3.3).

3.3.1 EARLY GONDWANAN PHASE

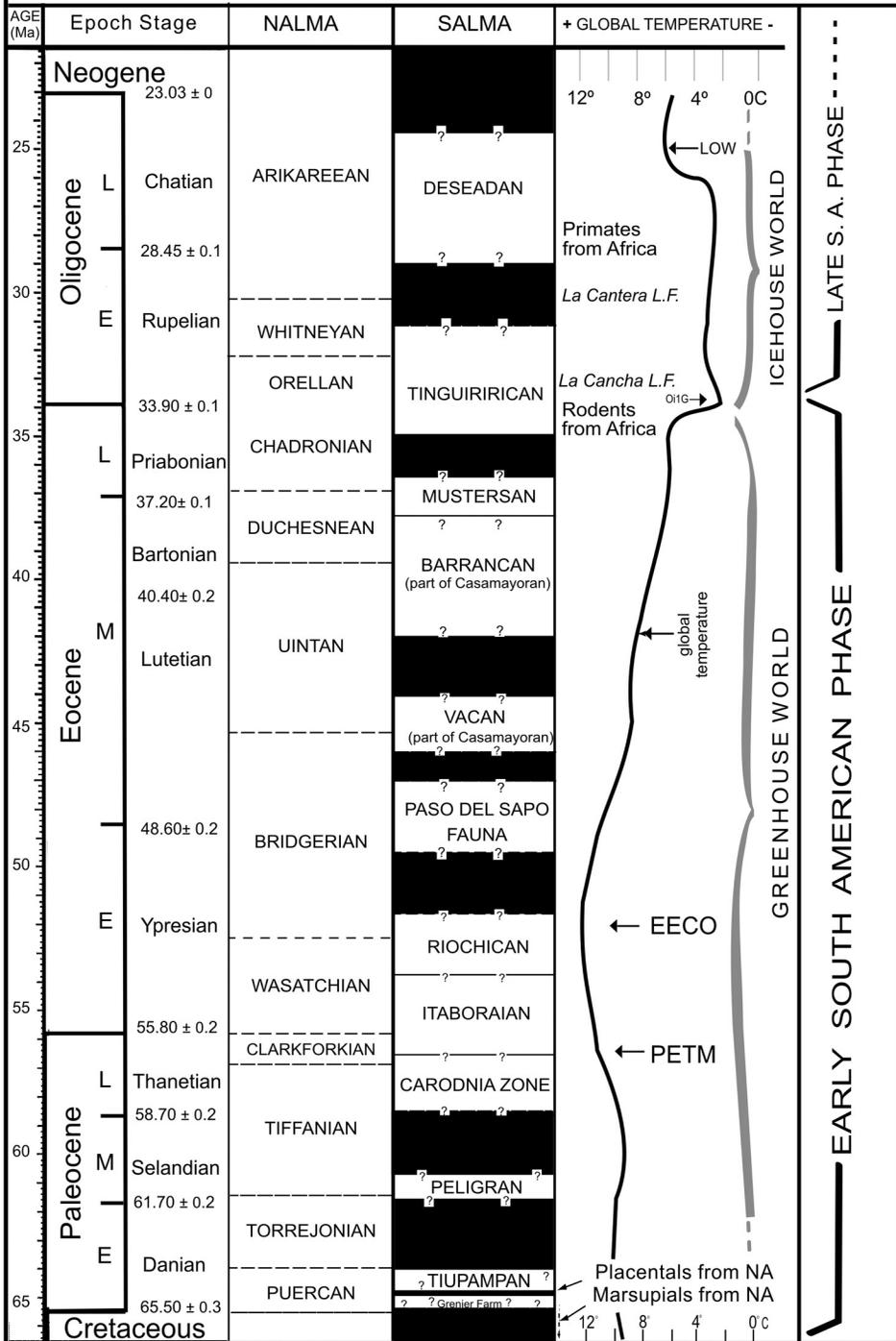
From the Late Triassic up to the late Early Jurassic, Pangaea persisted as a single supercontinent. By the Middle Jurassic, the early phases of Pangaean breakup had already begun, with several plates beginning to drift from Gondwana toward Eurasia. During the Early Cretaceous, Gondwana separated from Laurasia. Climate during the Late Triassic was warm (10° C warmer than present), polar ice caps were absent, and there was a gradual gradient from the Equator toward the poles (Scotese 2001). The Middle Jurassic climate of the Austral realm was warm-temperate. From the Late Jurassic up until the end of the Early Cretaceous, there was a steep decrease in global temperatures. However, these new icehouse conditions were not extreme, as extended polar ice caps and glacial systems did not develop. Most of the Austral realm during the Early Cretaceous was in the cool-temperate climate zone (Scotese, Boucot, and McKerrow 1999).

The earliest records of fossils probably belonging to a Mesozoic South American mammal are also the oldest: the ichnogenus *Ameghinichnus patagonicus* (Casamiquela 1961) from Middle Jurassic levels in Santa Cruz Province, southern Patagonia. Its mammalian status has been recently supported by De Valais (2009), who cited alternative views of *Ameghinichnus* as an advanced therapsid.

Middle Late Jurassic mammals from the Queso Rallado locality near Cerro Cónдор (Cañadón Asfalto Formation, Chubut Province, central Patagonia) are represented by the eutriconodont *Argentoconodon fariatorum* (Rougier, Garrido, et al. 2007) and the australosphenidans *Asfaltomylos patagonicus* and *Henosferus molus* (Rauhut et al. 2002; Rougier, Forasiepi, et al. 2007). The concept, contents, and phylogenetic position of the Gondwanan Australosphenida are still a matter of debate (contrast Luo, Kielan-Jaworowska, and Cifelli 2002; Martin and Rauhut 2005; Rauhut et al. 2002; and Rougier, Garrido, et al. 2007 with Rowe et al. 2008 and Woodburne, Rich, and Springer 2003).

Early Cretaceous (Hauterivian-Barremian) South American mammals are

Paleogene time scale, global temperature, NALMAs, SALMAs, and faunal events in South America



solely represented by *Vincelestes neuquenianus* (La Amarga Formation, Neuquén Province, northern Patagonia; Bonaparte 1986a). *Vincelestes* was first related to the Zatheria (Rougier 1992), although more recently Bonaparte (2008) made a case for australosphenidan relationships.

In general terms, despite the still spotty record, Jurassic and Early Cretaceous mammals from Patagonia seem to represent a combination of cosmopolitan (eutricodontids) and Austral (australosphenidan) taxa.

3.3.2 LATE GONDWANAN PHASE

Before the end of the Early Cretaceous, South America and Africa were already separated (see a discussion in Krause et al. 2006). However, paleogeographic bridges between South America and Antarctica persisted until the Paleogene (Woodburne and Case 1996), and Antarctica and Australasia remained connected throughout the Late Cretaceous. The timing of the separation of Antarctica and Indo-Madagascar is controversial. Case (2002) and Krause et al. (2006) suggested that links between these landmasses were maintained until 80 Ma (i.e., Campanian). As previously mentioned, global greenhouse conditions persisted during the whole period (up to the late Eocene). Burgoyne et al. (2005) suggested a slight cooling phase at the end of the Cretaceous and a transient warming at the Cretaceous/Tertiary boundary.

Several mammals from the early Late Cretaceous (Cenomanian-Coniacian) locality of La Buitrera (Candeleros Formation, Río Negro Province) remain undescribed (Rougier and Apesteguía 2004). One, represented by several partial skulls, belongs to a long-snouted dryolestoid superficially resembling living elephant shrews. “It is probably part of a Gondwanan dryolestoid lineage that [subsequently gave rise to] the latest Cretaceous and Paleocene South American forms” (Apesteguía, Gaetano, and Rougier 2009, 26).

Figure 3.3 (facing page) Paleogene time scale, global temperatures, North American Land Mammal Age (NALMA), and South American Land Mammal Age (SALMA). Marsupials immigrated to South America in the latest Cretaceous, with the earliest records preserved in the early Paleocene Grenier Farm site. Placental mammals immigrated in the Tiupampian. Rodents, presumably from Africa, are recorded in the Tinguiririan. The La Cancha and La Cantera Local Faunas are known from the Gran Barranca of Argentina (Goin, Abello, and Chornogubsky 2010). Primates are recorded from the Deseadan, but may have arrived in South America concurrently with rodents. The Paleogene time scale is after Luterbacher et al. (2004). The NALMA chronology is after Woodburne (2004) and Woodburne, Gunnell, and Stucky (2009a, 2009b), while SALMA chronology follows Gelfo et al. (2009), with Tinguirirican after Goin, Abello, and Chornogubsky (2010) and Deseadan after Ré, Geuna, and Vilas (2010). Global temperature, PETM (Paleocene-Eocene Thermal Maximum), EECO (Early Eocene Climatic Optimum), and OiG (initiation of Antarctic glaciations) are after Zachos et al. (2001).

Bonaparte and Soria (1985) and Bonaparte (1986a, 1986b) executed a series of studies on one of the richest and diverse Mesozoic localities for mammals, the Late Cretaceous (Campanian-Maastrichtian, Alamitan SALMA) Los Alamitos site in Río Negro Province, northern Patagonia. These specimens provided completely new insights into the evolution of mammals in the Southern Hemisphere, as most previous ideas had been made exclusively from the Northern Hemisphere record. In the north, tribosphenic mammals dominated mammalian assemblages of the Late Cretaceous; the multituberculates and triconodonts being exceptions. Strikingly, in the Los Alamitos assemblage, only nontribosphenic mammals are represented, including: a variety of symmetrodonts, triconodonts, dryolestoids, and gondwanatheres (Bonaparte 1986a, 1986b, 1987, 1990, 1992; see alternative views of gondwanatherian affinities in Gurovich and Beck 2008; Kielan-Jaworowska, Cifelli, and Luo 2004; Pascual et al. 1999). Representatives of this locality include the gondwanatherians *Ferugliotherium* and *Gondwanatherium* and a number of dryolestoids including *Mesungulatum*, *Groebertherium*, *Brandonia*, *Leonardus*, and *Reigitherium* (the latter formerly regarded as a docodont; Pascual et al. 2000). At least one group of dryolestoids, the Mesungulatae, had a dentition in some ways functionally convergent on that of tribosphenic mammals (Bonaparte 1996). Two additional faunas of similar (Late Cretaceous) age have been reported subsequently: La Colonia in Chubut Province, central Patagonia (Kielan-Jaworowska et al. 2007; Pascual et al. 2000; Rougier et al. 2000; Rougier, Forasiepi, et al. 2009), and Cerro Tortuga (Allen Formation, Río Negro Province, northern Patagonia; Rougier, Chornogubsky, et al. 2009). La Colonia produced the first records for multituberculates from South America (Kielan-Jaworowska, Cifelli, and Luo 2004; Kielan-Jaworowska et al. 2007). From the Late Cretaceous site of Paso Córdoba (Río Colorado Formation, Río Negro Province), an edentulous mandible probably belonging to a metatherian was reported by Goin, Carlini, and Pascual (1986). However, Martinelli and Forasiepi (2004) suggested this specimen could be a dryolestoid. Rougier, Forasiepi, et al. (2009) described several petrosals tentatively assigned to the mesungulatid *Coloniatherium cilinskii*, and suggested its phylogenetic position is close to *Vincelestes*.

Mesozoic mammals are known from some additional South American localities far north of Patagonia. A fragmentary mandible with one premolar was recovered from the Late Cretaceous Adamantina Formation at Santo Anastasio, Brazil. Bertini et al. (1993) suggested its affinities lay with eutherians, while its fragmentary nature led Candeiro et al. (2006) to treat it as *Mammalia incertae sedis*. Several isolated molars referable to tribosphenic and nontribosphenic

mammals have been reported from the Late Cretaceous of Pajcha Pata, El Molino Formation, in western Bolivia; some dryolestoid teeth apparently show affinities with those of contemporary strata in Patagonia (Gayet et al. 2001; Rougier, Forasiepi, et al. 2009). The Tiupampa fauna, also in Bolivia, originally referred to the Late Cretaceous, is currently regarded as early Paleocene in age (Muizon 1991; reviewed in Gelfo et al. 2009). Sigé (1968, 1971) reported the Laguna Umayo site and fauna in southern Peru as late Cretaceous, but more recently, Sigé et al. (2004) suggested the fauna dates from the late Paleocene or early Eocene.

Late Cretaceous mammals from Patagonia (and hypothetically all the Austral kingdom) differ from those of Laurasia in two important respects. First, dryolestoids are mostly known from the Late Jurassic and Early Cretaceous of Laurasian landmasses, but southern South America's dryolestids apparently reached their climax during the Late Cretaceous (Cenomanian-Maastrichtian). Second, "To date, no unequivocal cranial or dental remains of therian mammals are known from the Late Cretaceous of South America" (Rougier, Forasiepi, et al. 2009, 207); the same can be said for all other Mesozoic localities and levels of this continent. In contrast, therian mammals were dominant during the Late Cretaceous in all Laurasian continents.

Although the roots of some lineages can be traced back to the Jurassic of Laurasia (e.g., dryolestoids; Bonaparte 1994), Late Cretaceous mammals from Patagonia show high endemism and the development of some remarkable adaptive morphological types (e.g., mesungulatids, reigitheriids, gondwanatherians). Mesungulatids ". . . achieve a dentition reflecting omnivorous and herbivorous habits, with a progressive reduction of the orthal component during mastication culminating finally with the acquisition of an almost lophodont dentition in [the Paleocene dryolestoid] *Peligrotherium*" (Rougier, Forasiepi, et al. 2009, 208; see also Gelfo and Pascual 2001). Gondwanatherians were one of the earliest mammals to develop hypsodont cheek-teeth having thick cementum surfaces (Koenigswald, Goin, and Pascual 1999). We suggest that the radiation of these endemic mammalian lineages coincided with the global warming trend that had begun by the early Late Cretaceous, roughly contemporaneous with the radiation of angiosperms (Gurovich and Beck 2008; Koenigswald, Goin, and Pascual 1999; Rougier, Forasiepi, et al. 2009). We also hypothesize that the radiation of several, if not most, of these Patagonian lineages was an event biogeographically restricted to the Austral Kingdom. Testing this last hypothesis will require more prospecting in other Austral fossiliferous levels of contemporary age, as well as in northern (Neotropical) South America. The dis-

covery of other Austral elements of the mammalian fauna (e.g., monotremes) is expected in Late Cretaceous strata of Patagonia. Rowe et al. (2008) estimated that the platypus and echidna clades were already distinct by the Early Cretaceous. Paleocene monotremes have already been recorded in central Patagonia (e.g., Pascual and Ortiz-Jaureguizar 2007; Pascual et al. 1992).

3.3.3 EARLY SOUTH AMERICAN PHASE

At the end of the Cretaceous, there was an intermittent connection between North and South America. Case, Goin, and Woodburne (2005) summarized previous data on the Caribbean tectonics and discussed several alternatives regarding land bridges between the Americas. They concluded that the best candidate for a pathway for biotic dispersal was the Aves Ridge and adjacent Cuba during the Campanian and especially the Maastrichtian. A major consequence of this development was the arrival of the first therian mammals in South America (but see Rich 2008), as well as other vertebrate groups (e.g., hadrosaurs, neoceratopsians). We call this dispersal event between the Americas as the First American Biotic Interchange (FABI). Rage (1978) reported at least one group of snakes (Boidae) as having dispersed northward at this time. The South America and Antarctica connection was interrupted by the early Eocene (48.6–55.8 Ma), as happened between Antarctica and Australia with the opening of the Tasmanian Gate (Woodburne and Case 1996). There were widespread tropical conditions in the global climate, especially during the Early Eocene Climatic Optimum (~50–53 Ma; Zachos et al. 2001). Patagonian climates from the early Paleocene through the late Eocene were warm-temperate (Bijl et al. 2009).

As mentioned, no unequivocal therian remains have been discovered in the South American Mesozoic. The earliest known Cenozoic therian is, most probably, a polydolopimorphian marsupial represented by an isolated lower molar. The specimen comes from early Paleocene levels of the Lefipán Formation in Chubut Province, Argentina, just 5 m above a level referred to as the Cretaceous-Tertiary boundary (Goin et al. 2006). It is noteworthy that the specimen does not belong to a generalized “opossum-like” marsupial but instead shows several derived features common among bonapartheriiform polydolopimorphians. Its discovery strongly suggests that the diversification of metatherians in South America can be traced back to the Late (probably latest) Cretaceous. Alternatively, because of the dual nature of South America’s biogeography, the first therians may have arrived on this continent earlier in the Neotropical Region (e.g., Campanian; Case, Goin, and Woodburne 2005), only arriving later (e.g.,

Late Maastrichtian) in the Andean Region. Present evidence suggests that the faunal turnover that marked the beginning of the Early South American Phase happened sometime between the Late Cretaceous (Alamitian Age; Bonaparte 1986a) and the earliest Paleocene (Tiupampian age, 65–64 Ma; Ortiz-Jaureguizar 1996; Ortiz-Jaureguizar and Pascual 2007; Pascual and Ortiz-Jaureguizar 1990a, 1990b; see Gelfo et al. 2009 on the age of the Tiupampian).

Three major events in the evolution of southern South American mammals took place during the Early South American Phase: (1) the rapid decline and extinction of the nontherian native lineages, probably by mid-Paleocene times (but see Goin et al. 2004); (2) the arrival of therians, probably in several waves (Gelfo et al. 2009), already by the Late Cretaceous; and (3) major radiations of therians during the late Paleocene-early Eocene, possibly coincident with the Early Eocene Climatic Optimum (see fig. 3.4).

During the Paleocene and early Eocene, marsupials were dominant in Patagonian faunas. Tiupampian marsupials (early Paleocene) reveal that they had already undergone a rapid diversification, probably in the Late Cretaceous (Muizon 1991). Mid-Paleocene marsupials of Peligran age are already quite derived. Between the late Paleocene and early middle Eocene, polydopimorphians reached their climax. A wide variety of opossum-like marsupials (e.g., Derorhynchidae, Peradectidae, Protodidelphidae, Sternbergiidae), many still of uncertain affinities, developed by the Itaboraian (here regarded as latest Paleocene-early Eocene in age; Gelfo et al. 2009). The earliest microbiotherians and paucituberculates are also of Itaboraian age, and sparassodonts of this time are small-to-medium in size. Marsupials of this phase exploited a variety of adaptive zones and diets: insectivorous, omnivorous, frugivorous, carnivorous, or a combination of them.

The earliest record of eutherians dates from the early Paleocene of Tiupampa and pertains to North American groups (Pantodonta, Mioclaenidae). Native ungulates also appear at Tiupampa, in the form of an indeterminate notoungulate referred to henricosbornids or oldfieldthomasiids (Muizon and Cifelli 2000; Muizon and Marshall 1992; Muizon, Marshall, and Sigé 1984). Medial Paleocene to early Eocene ungulates developed a wide variety of forms that characterized the first radiation of native South American ungulates. They developed low-crowned dentitions of various types: strictly bunodont (i.e., Didolodontidae, Protolipternidae), bilophodont (i.e., Xenungulata), bunolophodont (e.g., Notonychopidae, Trigonostylopidae, Henricosborniidae, Oldfieldthomasiidae, notopithecine Interatheriidae), and more lophoselenodont

(e.g., Sparnotheriodontidae). Middle and late Eocene ungulates show the first trend toward hypsodonty, particularly among archaeohyacid Typotheria from the Casamayoran (late Eocene; Bond and López 1993, 1995). About the time of the late Eocene-early Oligocene global cooling (see later), there was an increase in grass phytoliths and volcanic activity, which generated volcanic ash that deposited upon vegetation. Both generated positive selective pressures in favor of higher-crowned dentitions among ungulates (Madden et al. 2010; Scarano 2009).

A marked biogeographic distinction between northern (Neotropical) and southern (Andean) regions was also apparent during this phase. Among the best known Paleogene faunas are those of Itaboraí (Brazil) and Las Flores (southern Argentina), of contemporary age (Itaboraian SALMA; late Paleocene-early Eocene; see Bergqvist, Lima Moreira, and Ribeiro Pinto 2006). Marsupials are the best represented taxa in both local associations. While polydolopid polydolopimorphians are the most diverse and abundant marsupials throughout the Patagonian and Antarctic Paleogene, including the Las Flores association, they are completely absent in Itaboraí.

3.3.4 LATE SOUTH AMERICAN PHASE

By the Eocene-Oligocene boundary (33.9 Ma), climatic conditions changed again toward a new icehouse phase. The opening of the Southern Ocean with the Drake Passage (i.e., the disconnection of South America and Antarctica) led to the formation of the Antarctic Circumpolar Current (Livermore et al. 2004). The result was the first major expansion of Antarctic ice in the Cenozoic. The sharp decrease in global temperatures was the primary driving force causing generalized turnovers in Paleogene marine and terrestrial biota. Probably, soon after these shifts, a major dispersal event occurred: the arrival of caviomorph rodents and platyrrhine primates in South America.

Goin, Abello, and Chornogubsky (2010) called the major taxonomic and ecologic shift in land-mammal faunas of southern South America at the Eocene-Oligocene boundary the *Bisagra Patagónica* (Patagonian Hinge; see also Flynn et al. 2003). They regarded the Hinge as equally important as other contemporary, major biotic events as the European *Grand Coupure* or the Central Asian *Mongolian Remodeling*. Recalling a more general statement made by the late Stephen Gould, Pascual (2006, 221) summarized the major differences in the early-to-late Cenozoic mammalian successions as follows (brackets added): “At this point, the history of South American mammals passed from ‘Early Ex-

perimentation' [our Early South American Phase] to 'Modern Standardization' [our Late South American Phase]."

The recently discovered mammalian faunas of La Cancha and La Cantera, in central Patagonia (~33 Ma and 31–29 Ma, respectively; Goin, Abello, and Chornogubsky 2010), offer a detailed panorama of faunal changes at the beginning of this phase. Marsupials, especially sensitive to low temperatures, had already experienced a major turnover by the earliest Oligocene, including the last records of Caroloameghiniid peradectoids (Didelphimorphia), Sternbergiidae opossum-likemarsupials (Didelphimorphia), Hatcheriformes (Polydolopimorphia), bonapartherioid Bonapartheriiformes (Polydolopimorphia), and all Polydolopiformes (Polydolopimorphia), as well as the beginning of a rapid diversification of the "shrew opossums" (Paucituberculata), the radiation of large, modern borhyaenoids (Sparassodonta), and the origins of the Argyrolagoidea (Polydolopimorphia; Goin, Abello, and Chornogubsky 2010). This reflects a modernization of the marsupial fauna and extinction of some of the earlier, archaic taxa. Records of the first modern opossums (Didelphidae sensu stricto, possibly including also a caluromyine), the first Thylacosmiliidae sparassodonts, as well as major radiations within the Microbiotheria and Paucituberculata all appear by the early Miocene (Colhuehuapian, 19–20 Ma; Goin et al. 2007).

Among native ungulates, there was a noticeable increase in the diversity of hypsodont notoungulates (e.g., Archaeohyracidae, Interatheriinae, Hegetotheriidae, and Mesotheriidae) after the early Oligocene. Low-crowned, bunodont ungulate types (i.e., megadolodine *Litopterna*) became scarce and were completely restricted to the lower latitudes of the Miocene of Colombia and Venezuela (Carlini, Gelfo, and Sánchez 2006; Cifelli and Villarroel 1997). Astrapotheria and Pyrotheria developed their larger forms during the Oligocene-Miocene and disappeared by the middle late Miocene (see Vizcaíno et al., chapter 5, this volume). In some lineages, limb specialization was convergent on that of equids; lophoselenodont dentitions (e.g., in proterotheriid *Litopterna*) were well developed by the Miocene (Soria 2001).

The oldest record of a platyrrhine in South America is *Branisella* from the Deseadan of Salla, Bolivia (late Oligocene, ~26 Ma; Kay et al. 1998). The oldest records of caviomorphs come from Tinguirirican levels of central Chile (Wyss et al. 1993). The age of the Tinguirirican SALMA has been estimated as 33.4–31 Ma (latest Eocene-early Oligocene; Goin, Abello, and Chornogubsky 2010). Both lineages probably arrived from Africa, although there is still debate on

whether this took place in synchrony or in asynchronous waves (e.g., Poux et al. 2006). The early records of caviomorphs are far more abundant than those of platyrrhines. Recently, Vucetich et al. (2010) described several taxa of relatively generalized, pre-Deseadan caviomorphs from the post-Tinguirirican (early Oligocene) levels of La Cantera, in central Patagonia (ca. 31–29 Ma), and estimated that the arrival of caviomorphs into South America “was not much before the early Oligocene” (Vucetich et al. 2010, 189). A recent molecular dating of early divergences within Hystricognathi, using a Bayesian “relaxed clock” approach and multiple fossil calibrations, suggested that the split between phiomorphs and caviomorphs occurred around 36 Ma (late Eocene; Sallam et al. 2009). Again, we propose an alternative hypothesis that takes into account the dual nature of South America’s biogeography: rodents and primates arrived earlier in the Neotropical Region, by middle or late Eocene times (e.g., Frailey and Campbell 2004), only arriving later in the Andean Region.

3.3.5 INTER-AMERICAN PHASE

The Great American Biotic Interchange (GABI) (Stehli and Webb 1985) refers to the establishment of the strongest biogeographic linkage between North and South America ever (Marshall et al. 1982; Morgan 2008; Simpson 1953; Webb 1976, 1985; Woodburne, Cione, and Tonni 2006). Although the Panamanian region was an upland isthmus as early as 6 Ma, permitting limited dispersals from about that time, the main pulse of the interchange began about 2.6 Ma, essentially coeval with the onset of major Northern Hemisphere glaciation (Mudelsee and Raymo 2005), and persisted to ~2.4 Ma. Traditional views on the GABI regard this process as a response to the tectonic closure of the Panamanian seaway. It is now clear from geological evidence that this closure was under way by ~12 Ma and effectively completed by ~6 Ma (Coates et al. 2004), with final closure of the Central American seaway transpiring by ~2.8 Ma (Bartoli et al. 2005). By 6 Ma, a few mammalian lineages known as the “heralds” of the GABI (Webb 1985) dispersed throughout the Americas. However, the main thrust of the GABI was the multitaxon exchanges that began ~2.6 Ma when

Figure 3.4 (*facing page*) Neogene time scale, NALMA, SALMA, Great American Biotic Interchange (GABI), global temperatures, and taxa that dispersed from South America to North America during this time. The Neogene time scale is after Lourens et al. (2004), the NALMA chronology follows Woodburne (2004), while the SALMA chronology is based on Woodburne, Cione, and Tonni (2006) and Flynn and Swisher (1995). Taxa that dispersed to North America are from Woodburne, Cione, and Tonni (2006). Global temperature scale is after Zachos et al. (2001).

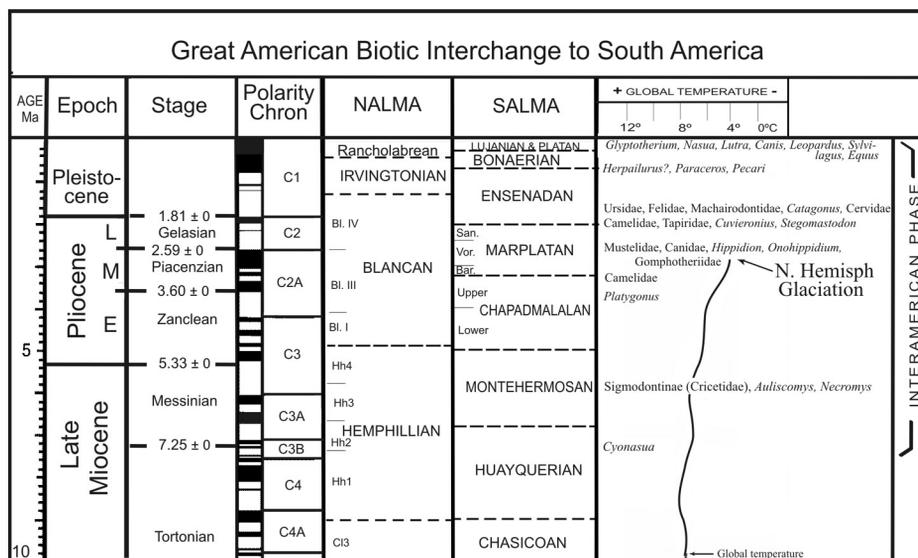


Figure 3.5 Great American Biotic Interchange to South America, NALMA and SALMA chronology, and global temperature. Taxa that dispersed to South America are from Woodburne, Cione, and Tonni (2006), Cione et al. (2007), and Woodburne (2010).

climate changed with Northern Hemisphere glaciations, permitting temperate-adapted taxa to cross the Panamanian isthmus (fig. 3.5).

The traditional viewpoint has been that GABI signaled the development of an overland corridor across the Panamanian region, and that this transpired ~3.0 Ma. A more persuasive interpretation now seems to be that these dispersal episodes reflect the onset and presence of glacial conditions in the Northern Hemisphere (Webb 1991). This stems not only from paleobotanical and other evidence, but also reflects the more temperate, versus tropical, adaptations of the taxa making the crossings. In fact, Coates et al. (2004) reconstructed the geological evolution of the Panamanian region and indicated that it was an upland isthmus as early as 6 Ma, with the former Central American Seaway being interrupted by an evolving volcanic arc as early as ~12 Ma.

Even under Isthmian tropical conditions, North America was a beneficiary of the tectonic process, with the first South American immigrants being the mylodontid sloth, *Thinobadistes*, and the megalonychid sloth, *Pliometanastes*, found in tropical (Florida) to more temperate sites (California) of early Hemphillian age (~9 Ma; Morgan 2008). Island-hopping across short marine barriers apparently did not deter these edentates from colonizing. Subsequently, at

~7 Ma, *Pliometanastes* was the sister taxon to *Megalonyx*, which became a relatively common constituent of late Miocene to Pleistocene faunas of southern North America (Bell et al. 2004). As summarized by Morgan (2008), a variety of other edentates entered North America and successfully inhabited temperate regions across the southern part of North America. Also at about 7.2 Ma, the procyonid carnivore *Cyonasua* dispersed to South America.

From about 6 Ma, the pre-GABI pace of dispersal began to accelerate (Cione et al. 2007; Woodburne 2010). Sigmodontine rodents apparently dispersed to South America by 6 Ma, and at about 4.7 Ma, pampathere (*Plaina*) and mylodont (*Glossotherium*) edentates are recorded in Mexico. Somewhat later (3.0 Ma), *Glossotherium* is recorded in Florida, which was still subtropical. This is one of a number of instances (Flynn et al. 2005) in which Mexico appears to have been a waiting room for taxa that subsequently completed their dispersal to the continental United States, despite the lack of known physical or ecological barriers (Woodburne, Cione, and Tonni 2006). Although Verzi and Montalvo (2008) presented a very interesting scenario regarding the early dispersal of rodents and carnivores in the Hayquerian SALMA, we follow the interpretation of Prevosti and Pardifias (2009) and place the colonization of sigmodontines in this timeframe.

At 3.8 Ma, *Nechoerus* was a northward immigrant to Mexico and, until its discovery in North Carolina strata of the same age (Sanders 2002), was considered one of the Mexican laggards. This genus, a hydrochoerid rodent, is considered to have been an inhabitant of tropical to subtropical conditions. The peccary *Platygonus* is recorded in Argentina at 3.7 Ma, so it apparently dispersed about that time, and *Pampatherium* (Cingulata) is recorded then in Mexico. At 3.3 Ma, Camelidae dispersed to South America: A *Lama* precursor and the peccary apparently are the first savanna-adapted taxa to disperse southward, and the camel record appears coeval with the advent of Northern Hemisphere glaciation. Just prior to GABI, at 3.0 Ma, the mylodont *Glossotherium* appears in Florida (after an earlier presence in Mexico).

As documented by the GABI chronology, at least part of the tropical rain forests of the isthmus shifted toward savanna-like habitat (Webb, 1991); this is reflected in the ecologic diversity of the dispersing taxa. South American records of mustelid and canid carnivores, equid perissodactyls, and a gomphothere appear at about 2.6 Ma. An immigrant to North America at about this time (2.7 Ma), the porcupine *Erethizon* is now adapted to cool temperate conditions.

At 2.4 Ma, the pampathere *Pampatherium* enters from Mexico (a laggard)

along with its through-moving relatives *Holmesina*, armadillos (*Dasybus*, *Pachyarmatherium*), and a megatheriid (*Eremotherium*). Of these, *Dasybus* still inhabits temperate regions in the Gulf Coast region and formerly occurred as far north as Iowa in the Pleistocene (Morgan 2008). Overall, this appears to be a savanna-adapted group of taxa.

An apparent gap in dispersals lasted from 2.4 to 1.8 Ma, which seems to have been a tropical holding pattern for hydrochoerid rodents. *Hydrochoerus* was present in Florida about 2.2 Ma in presumably wet conditions and might have lingered in local sites in the Isthmian region. But about 1.8 Ma, South America experienced a strong pulse of immigration that included ursids, canids, felids, machairodontids, peccaries, deer, camels, tapirs, and proboscideans. Together, they document the presence of (or perhaps a return to) savanna-like conditions in the Isthmian region and adjacent South America. Another apparent gap in dispersal lasted from just after 1.8 Ma to about 0.7 Ma, but immigrants to North America included a toxodont to El Salvador (1.5 Ma) and a megatheriid sloth, *Nothrotheriops* (1.3 Ma).

At about 0.8 Ma *Didelphis* entered North America, followed at ~ 0.7 Ma by the dispersal to South America by a mustelid, a deer, and a peccary. Finally, at ~ 0.125 Ma, a major southward dispersal is recorded by a xenarthran, procyonid, mustelid, canid, and felid carnivores, a sylvilagine rabbit, and the equid *Equus*, a diversified if not balanced assemblage.

In summary, the GABI can be resolved as a series of pulses, possibly reflecting glacial versus interglacial conditions in the Northern Hemisphere. A major exchange from 2.7–2.4 Ma resulted in a variety of edentates and a porcupine arriving in North America and a larger group of carnivores, ungulates, and a gomphothere colonizing South America coincident with major Northern Hemisphere glaciations (Mudelsee and Raymo 2005). A dispersal gap from ~ 2.4 –1.8 Ma saw limited northward dispersal of a hydrochoerid rodent, possibly reflecting its earlier presence in the Isthmian tropics. Renewed dispersals to South America at ~ 1.8 Ma entailed a diversity of carnivores and various artiodactyls, perissodactyls, and proboscideans, with a myrmecophagid entering North America as well. Another gap from ~ 1.8 –0.8 Ma saw limited dispersal to North America by a toxodont to El Salvador at 1.5 Ma and a megatheriid sloth at 1.3 Ma. A more limited exchange at 0.8–0.7 Ma is recorded by a marsupial going north and a mustelid, a deer, and a peccary to the south. The last major GABI at 0.125 Ma saw the southward dispersal of an edentate, a diversity of carnivores, a sylvilagine rabbit, and *Equus*. The foregoing indicates that more taxa went south than went north; Webb (1991) explained this numerical domi-

nance of North American taxa as a reflection of the sixfold difference in the source area of open country habitats in North America versus those in the south.

Beginning in 2000, K. E. Campbell and colleagues have presented a series of articles that propose a modification of the early phase of the aforementioned scenario. In essence, the gomphotheriid proboscidean *Amahuacatherium peruvianum* is considered to have entered South America in the late Miocene, where it is found in Peruvian sediments along with mammal fossils of Huayquerian age (Campbell, Frailey, and Romero-Pittman 2000, 2009). The paleontological age is supported by both radioisotopic and paleomagnetic evidence (Campbell et al. 2001, 2010), with the fossil site considered to be ~9.5 Ma old. Campbell, Frailey, and Romero-Pittman (2000) also suggest that camels, peccaries, and tapirs are part of the immigrant mammalian component at this time. Although the chronologic setting for these taxa seems established, a persistent difficulty is that there is as yet no subsequent record of their pre-GABI presence anywhere in South America (e.g., Pascual and Ortiz-Jaureguizar 1990b; Pascual 2006; Patterson and Pascual 1972), regardless of the potential biogeographic considerations mentioned earlier (Croft 2007; Croft et al. 2009). Thus, the intriguing anomaly suggested by *Amahuacatherium* and its faunal associates remains incompletely understood.

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