Springer Earth System Sciences

Francisco J. Goin
Michael O. Woodburne
Ana Natalia Zimicz
Gabriel M. Martin
Laura Chornogubsky

A Brief History of South American Metatherians

Evolutionary Contexts and Intercontinental Dispersals

Springer

Springer Earth System Sciences

More information about this series at http://www.springer.com/series/10178

Francisco J. Goin · Michael O. Woodburne
Ana Natalia Zimicz · Gabriel M. Martin
Laura Chornogubsky

A Brief History of South American Metatherians

Evolutionary Contexts and Intercontinental Dispersals

Springer

Francisco J. Goin
CONICET—División Paleontología Vertebrados
Museo de La Plata
La Plata
Argentina

Michael O. Woodburne
Department of Geology
Museum of Northern Arizona
Flagstaff, AZ
USA

Ana Natalia Zimicz
IBIGEO (CONICET)
Universidad Nacional de Salta
Salta
Argentina

Gabriel M. Martin
CIEMEP (CONICET)
Universidad Nacional de la Patagonia San Juan Bosco
Esquel
Argentina

Laura Chornogubsky
CONICET—División Paleontología de Vertebrados
Museo Argentino de Ciencias Naturales
Buenos Aires
Argentina

ISSN 2197-9596 ISSN 2197-960X (electronic)
Springer Earth System Sciences
ISBN 978-94-017-7418-5 ISBN 978-94-017-7420-8 (eBook)
DOI 10.1007/978-94-017-7420-8

Library of Congress Control Number: 2015950891

Springer Dordrecht Heidelberg New York London

Printed on acid-free paper

Springer Science+Business Media B.V. Dordrecht is part of Springer Science+Business Media
(www.springer.com)

Preface

Twenty years ago I attended a conference about an ancient civilization from the Middle East. (By that time I had finished my doctoral studies and I was beginning to understand the diversity of one of the most complex, extinct metatherian faunas of all times: that of Yacimiento Las Flores, in central Patagonia, the levels and fauna of which can be traced to the climax of the Cenozoic greenhouse world–the early Eocene). I remember the increasing sensation of discomfort I felt while listening to the speaker, a venerable, charming old historian with a soft voice and a perfect Oxford accent. He was telling us the development of an ancient, pre-Hittite civilization on the basis of three elements: an unrecognizable piece of pottery, the hilt of a sword, and a piece of a letter written in a clay tablet. I still remember the first few words of the single phrase that historians had managed to translate from that broken tablet: "I give you this sword…" That was almost all. "I give you this sword…" The rest of the sentence was only partially intelligible and difficult to interpret. The remaining hour of that conference was an amazing series of inferences the historian had been able to rescue from those, to say the least, scarce pieces of evidence. The letter had been written by a king; it was directed to another king; it was part of a peace treaty between both the kingdoms, and the story went on and on. The history of a human culture, four thousand years ago, began to unravel before our increasingly marveled eyes.

Still, my feeling of uneasiness persisted, even well afterwards, when I came back home. Only hours later I realized what was going on in my mind. It happened that the old historian and I, a paleontologist, had much in common. To begin with, the fragmentary nature of the evidence we both have to deal with. Just a few bits of evidence, and a whole story to be told; that's the dilemma, and the magic, of trying to understand the past. Any past.

Twenty years later, I am still trying to complete my study of the Las Flores metatherian assemblage (fortunately, a paper on this topic will soon be completed). My bits of evidence for this task are around 500 isolated molars, probably belonging to three dozen species. From time to time, while I am looking at the specimens under the stereomicroscope, I find myself thinking the ominous words: “I give you this sword…”

By the end of the Mesozoic Era, probably during late Campanian or Maastrichtian times (some 75–66 million years ago) a metatherian mammal stepped into the South American continent for the very first time. Possibly, it was not very different from the small opossum shown in Fig. 1.1 of this book. Most probably it came from North America, taking advantage of a land bridge opportunity provided by the oriental margin of the Caribbean Plate, in its constant drift eastwards since the Late Cretaceous. It is not clear whether this single arrival provided the genetic source for the whole radiation of metatherian mammals in South America during the Cenozoic. It has been argued that not one but several lineages were part of the migratory event, possibly in more than one dispersal episode. A few million years later, most of the basic lineages of South American metatherians were already in place, developing some of the most extraordinary adaptive types ever evolved in this continent. Also possibly, a few million years later, the first lineage (lineages?) of South American marsupials arrived at Australia via the Antarctic continent. During the Cenozoic, the once cosmopolitan metatherians would be progressively restricted to the Southern Hemisphere, until the arrival in North America of the Didelphidae by the end of this era.

This short book is a summary of what we know about the evolution of South American metatherians during Cenozoic times. More than a detailed taxonomic typology, it offers a review of the different contexts that framed their evolution in this continent. After the introductory notes (Chap. 1), we examine the biology and natural history of living marsupials as a hint to understanding their past (Chap. 2). We then comment on different aspects of Cenozoic tectonics, climates, and biotas that composed the successive scenarios of metatherian evolution, radiations, dispersals, and extinctions (Chaps. 3 and 4). A brief characterization of each major lineage of South American metatherians is provided (Chap. 5). We also make a number of inferences as to the paleobiology of these lineages during Paleogene times, the most significant period in South American metatherian history (Chap. 6). Finally, we summarize the most significant milestones in the evolution of South American metatherians.

We offer you this book (“I give you this sword…”) in the understanding that several of the hypotheses that have been put forth here probably will be outdated in the next few years. Much research is currently being carried out on the phylogeny, taxonomy, anatomy, macroevolution, and paleobiology of extinct South American metatherians. Exciting new developments are being made in many topics, and a new generation of researchers is taking the lead in each one of them. Hopefully, a more detailed panorama on South American, Cenozoic metatherian evolution will be completed before the end of this decade. We look forward to it.

La Plata
July 2015

Francisco J. Goin

Acknowledgments

We wish to thank the editors of *Springer Briefs in Earth System Sciences*, for their kind invitation to collaborate in this series ("South America and the Southern Hemisphere"): Drs. Gerrit Lohmann, Lawrence A. Mysak, Justus Notholt, Jorge Rabassa, and Vikram Unnithan. Special thanks to Naomi Portnoy, from Springer's Project Coordination Production, for her kindness, help, understanding, and patience.

Each of the authors has many colleagues and students that much helped throughout recent years in the various reasonings that underly all chapters of this book. In particular we wish to thank researchers of the División Paleontología Vertebrados, Museo de La Plata, for their fruitful discussions and support.

The making of the figures that illustrate this volume would have been impossible without the voluntary help of many people: Patricia Sarmiento, Rafael Urréjola, Bruno Pianzolla, Manuel Sosa, Peter Meserve, Brian Lang, Bruce Patterson, Sylvain Pincebourde, Gabriel Martin, Mael Dewynter, Fabrice Schmitt, Jean-Francois Szpigel, Max Bernal Montes, Vitor Rademaker, Francois Catzeflis, Andre Baertschi, Sergio Solari, Joseph Rupert, Guillermo Gabriel Soteras, Sebastien Barrioz, Maurício E. Graipel, Karen Loughrey and "danybehs" (Project Noah), Michael Butcher, Laise Orsi Becker, and Rob Asher. Marcela Tomeo was decisive in the design, drawing, and/or arrangement of most of the final figures. Our special thanks for her professionalism, patience, and friendship.

In the making of Chap. 3, considerable appreciation is extended to the excellent summary provided by Lawver et al. (2013), and the review of Ortiz-Jaureguizar and Pascual (2012; see references in Chap. 3). Michael Hall, Monash University, Victoria, Australia, is greatly acknowledged for his personal communication regarding the late Eocene marine connection between the Gippsland and Bass basins. Ralph Molnar, University of California, Berkeley, and Robin Beck, University of New South Wales, provided valuable comments on an earlier version of the manuscript. None of these individuals necessarily agrees with the interpretations presented.

Much of the work summarized here derives from research funded by various research agencies and foundations. We wish to thank the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina; PIPs 5621 and 0361), Fondo para la Investigación Científica y Tecnológica (FONCyT; PICTO UNDAV 0102, 0105), an instrument of the Agencia Nacional de Promoción Científica y Tecnológica (Agencia, Argentina), the Alexander von Humboldt Foundation (AvH, Germany), and the National Sciences Foundation (NSF, USA).

Finally, most of the authors of this book have benefited, directly or indirectly, by the immense influence of the late Rosendo Pascual, our mentor, teacher, colleague, and friend. This contribution is dedicated to his memory.

Contents

Chapter 1
Introduction

Abstract With more than 100 species, living South American marsupials (Mammalia, Metatheria) give only a glimpse of the much higher taxonomic and ecological diversity acquired by metatherians throughout the Cenozoic Era. The term Metatheria designs a taxon within Mammalia that includes not only Marsupialia but also all therian mammals more related to Marsupialia than to Eutheria. Several features (e.g., epipubic ones) formerly considered as diagnostic of Metatheria are now regarded either a primitive condition or not present in all members of this group. Other derived features, such as the presence of a shelf-like, inflected angular process in the lower jaw, are consistently present in all metatherians. A brief characterization of all major South American, Cenozoic metatherian lineages is given: "basal ameridelphians," Sparassodonta, Didelphimorphia, Paucituberculata, Microbiotheria, and Polydolopimorphia (the latter including Polydolopiformes and Bonapartheriiformes). Three periods can be distinguished in the history of our knowledge of Cenezoic South American Metatheria: the first one (1878–1930) is intimately linked to Florentino Ameghino, Argentina's most notable paleontologist; much of our knowledge on extinct metatherians from South America was elaborated by him. The second period (1930–1977) occurred under the influence of George Gaylord Simpson's ideas. Bryan Patterson and Rosendo Pascual also had an important imprint in South America's Mammalian Paleontology. The third period (1977-present) is currently evolving under new phylogenetic, taxonomic, and paleobiogeographic paradigms; influences are multiple and major reviews of specific lineages are currently in the making. A final note on the incompleteness of Cenozoic South America's fossil record is made: only the mid to high latitudes, basically in the Southern Cone, are moderately well-sampled in their terrestrial fossil record.

Keywords Mammalia · Metatheria · Marsupialia · South America · Cenozoic Era · Diversity · Fossil record

Figure 1.1 shows a young (subadult) specimen of the Pampean, short-tailed opossum, *Monodelphis dimidiata,* in several postures. The specimen was captured at the basal slopes of Sierras Bayas, near the town of Balcarce, in central Buenos

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8_1

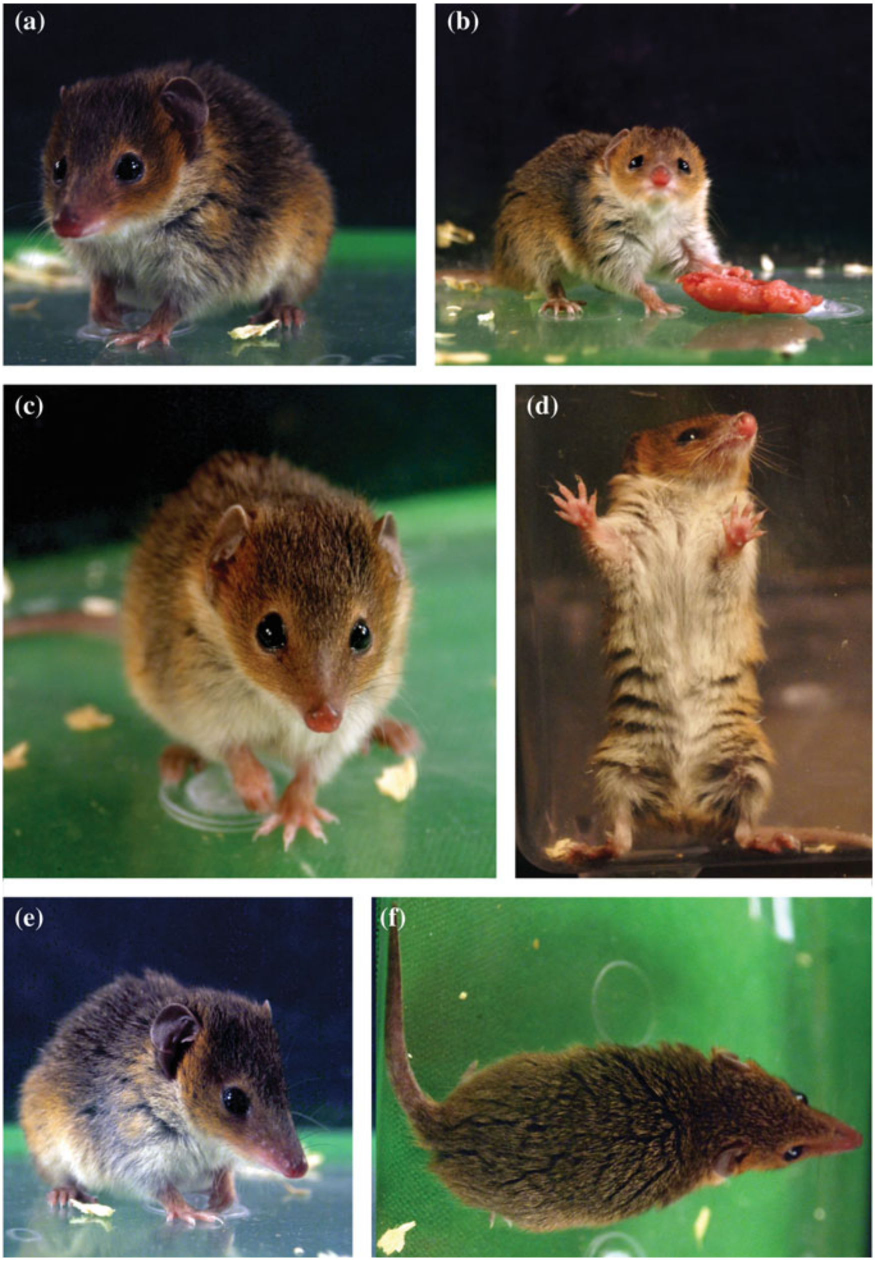


Fig. 1.1 A single, subadult specimen of *Monodelphis dimidiata* from the Balcarce area in Buenos Aires Province, central Argentina. The specimen is shown in frontal (**a**–**c**, **e**), ventral (**d**), and dorsal (**f**) views. Photographs by Bruno Pianzola

Aires Province, Argentina. It is a quite small individual, less than 20 g in body mass and a head and body length of 95 mm. Throughout the Cenozoic Era, many of the metatherians that populated South America were of comparably small size, an inconspicuous aspect, and generalized morphology. Most of them weighed less than 1 kg. Their probably nocturnal or crepuscular habits and, for many, arboreal biotopes, made them even more inconspicuous. This is clearly the case of the single living group of metatherians in South America, the Marsupialia (see below for a characterization of Metatheria and Marsupialia). Australasian marsupials, on the contrary, have developed a much wider variety of taxonomic, morphological, and adaptive types.

When considering the diversity of all Cenozoic metatherians in South America, the panorama widens considerably. This is so even taking in account that metatherians were just one of the three major lineages of therian mammals that evolved in this continent since early Paleogene times—the remaining two being the Xenarthra (armadillos, glyptodonts, sloths, ant-eaters, and related taxa), and the South American native ungulates (abbreviated SANU), a diverse array of medium- to very large-sized herbivores: Litopterna, Notoungulata, Xenungulata, Astrapotheria, and Pyrotheria (no SANU survived to the Recent). Both Xenarthrans and SANU developed numerous types of browsing and grazing herbivores of middle to very large size; that is the main reason why metatherians did not exploit those niches, especially the grazing ones (see, e.g., Simpson 1950; Patterson and Pascual 1968; Pascual 2006). Notwithstanding, the taxonomic, morphological, and adaptive types developed by South American Cenozoic metatherians is still impressive. An idea of this diversity is suggested by the fact that they are currently referred to 33 families and no less than five orders (see Table 5.1).

1.1 Abbreviations and Conventions

The following abbreviations and conventions are used throughout the whole volume.

1.1.1 Abbreviations

AAG	Australo-Antarctic Gulf
ACC	Antarctic Circumpolar Current
BAT	Brown adipose tissue
BMR	Basal metabolic rate
°C	Degree Celsius or centigrade
CTM	Cretaceous Thermal Maximum
CT scan	Computed Tomography Scan
EECO	Early Eocene Climatic Optimum

EOB	Eocene–Oligocene boundary
FABI	First American Biotic Interchange
FMR	Field metabolic rate
g	Grame
GABI	Great American Biotic Interchange
GHG	Greenhouse gases
JD	Relative height of the dentary (or jaw depth)
K-Ar	(^{40}K–^{40}Ar) Potassium–Argon radiometric dating
kg	Kilogram
K/Pg	Cretaceous–Paleogene (boundary)
ky	One thousand years (see Chap. 3 for a definition)
LGM	Last Glacial Maximum
LOW	Late Oligocene Warming
LPTM	Latest Paleocene Thermal Maximum (now regarded as PETM)
Ma	Megannum (see Chap. 3)
MAP	Mean annual precipitation
MAT	Mean annual temperature
MECO	Middle Eocene Climatic Optimum
MLP	Museo de La Plata
mm	Millimeter
MMCO	Middle Miocene Climatic Optimum
MNI	Minimal number of individuals
my	One million years (see Chap. 3)
NALMA	North American Land Mammal Age
ODP	Ocean Drilling Program
Oi1	A basal Oligocene event, associated with extreme cooling, in the oxygen isotope values of marine carbonates
PETM	Palecene–Eocene Thermal Maximum
PS	Relative size of the largest lower premolar
RGA	Relative grinding area
RPS	Relative shape of the largest lower premolar
SALMA	South American Land-Mammal Age
SANU	South American Native Ungulates
SEG	Southeastern Gondwana
SEM	Scanning Electron Microscopy
SST	Sea Surface Temperature
STR	South Tasman Rise
SWG	Southwestern Gondwana
TLV	Thoracolumbar vertebrae
y.b.p.	Years before present

1.1.2 Dental Nomenclature

The generalized dental formula for metatherians is: I/i 5/4, C/c 1/1, P/p 3/3, M/m 4/4, being I, upper incisor; I, lower incisor; C, upper canine; c, lower canine; P, upper premolar; p, lower premolar; M, upper molar; m, lower molar. Figure 1.2 shows a lower (a) and an upper (b) molar of a generalized "opossum-like"

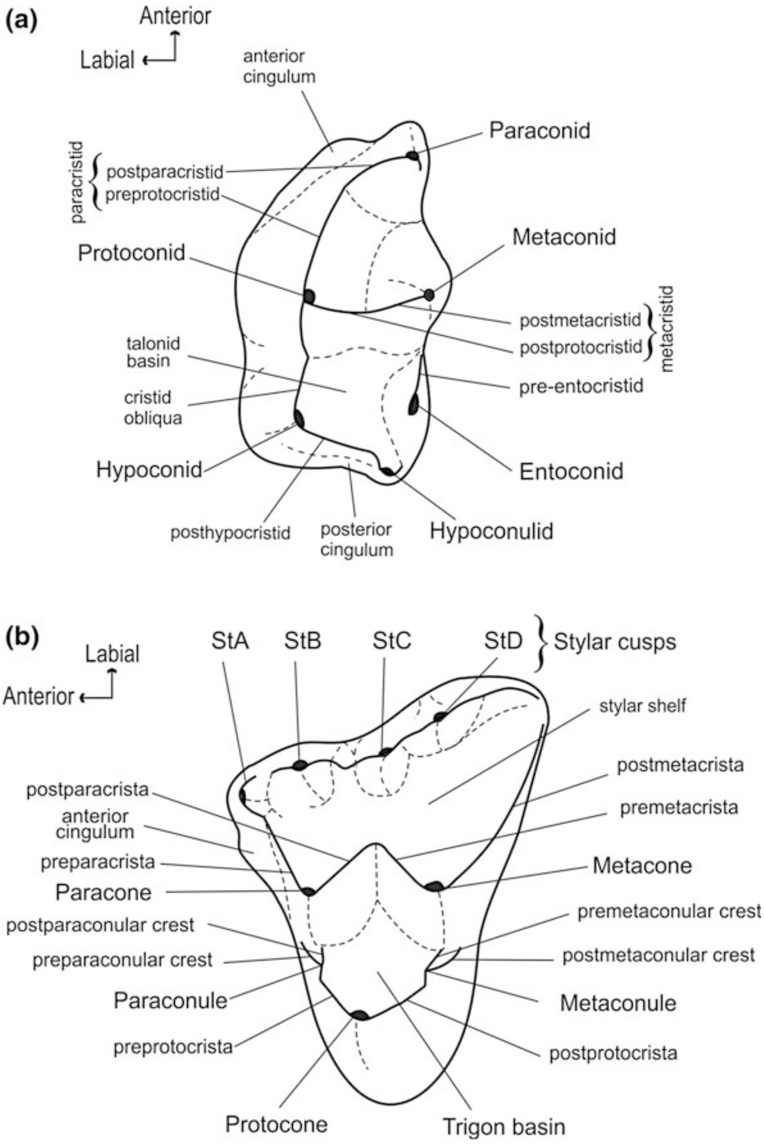


Fig. 1.2 Molar nomenclature used in this work. **a** Lower left molar; **b** upper left molar. In (**b**) the centrocrista includes the postparacrista + the premetacrista

metatherian, with the nomenclature used here for cusps (in upper case letters), crests, cinguli and basins.

1.1.3 Chronology

Figure 1.3 illustrates South America's Cenozoic biochronological succession. We follow the standard chronological scale of Gradstein et al. (2012). South America's biochronological scheme largely follows that of Goin et al. (2012), excepting the ages of the Peligran SALMA and the *Carodnia* Zone, for which we follow Clyde et al. (2014). Late Cenozoic biochronology (latest Miocene onward) follows Tomassini et al. (2013). Late Pleistocene–Holocene chronology follows Tonni (2009).

1.1.4 Classification

Table 5.1 shows the classification of South American metatherians, above the generic level, used in this study. Families including living representatives are marked in bold. See below and Chap. 5 for a brief characterization of extinct groups.

1.2 Metatheria and Marsupialia

1.2.1 Fossils and Radiations

The oldest metatherian known up to now is the Early Cretaceous (ca. 125 Ma) *Sinodelphys szalayi*, from the Yixian Fm of Liaoning Province, northeastern China (Luo et al. 2003). It was a small-sized creature (around 30 g of body mass) with arboreal capabilities. Based on this discovery, Luo et al. (2003) argued in favor of the hypothesis that Asia was the likely center for diversification of metatherians (and of eutherians as well). In turn, Cifelli and Davis (2003) noted striking differences in the patterns of therian diversification between Asia and North America: "Eutherians dominated in Eurasia throughout the Cretaceous, but were absent from North America through most of the Late Cretaceous and did not attain appreciable diversity there until the last ~10 million years of the period" (Cifelli and Davis 2003: 1900). To these authors, this pattern constitutes a puzzle that remains to be solved.

According to Luo et al. (2003), the metatherian fossil record and phylogeny suggest a series of successive, major episodes of diversification: (1) the divergence of metatherians and eutherians in Asia occurred no later than 125 Ma in the Early

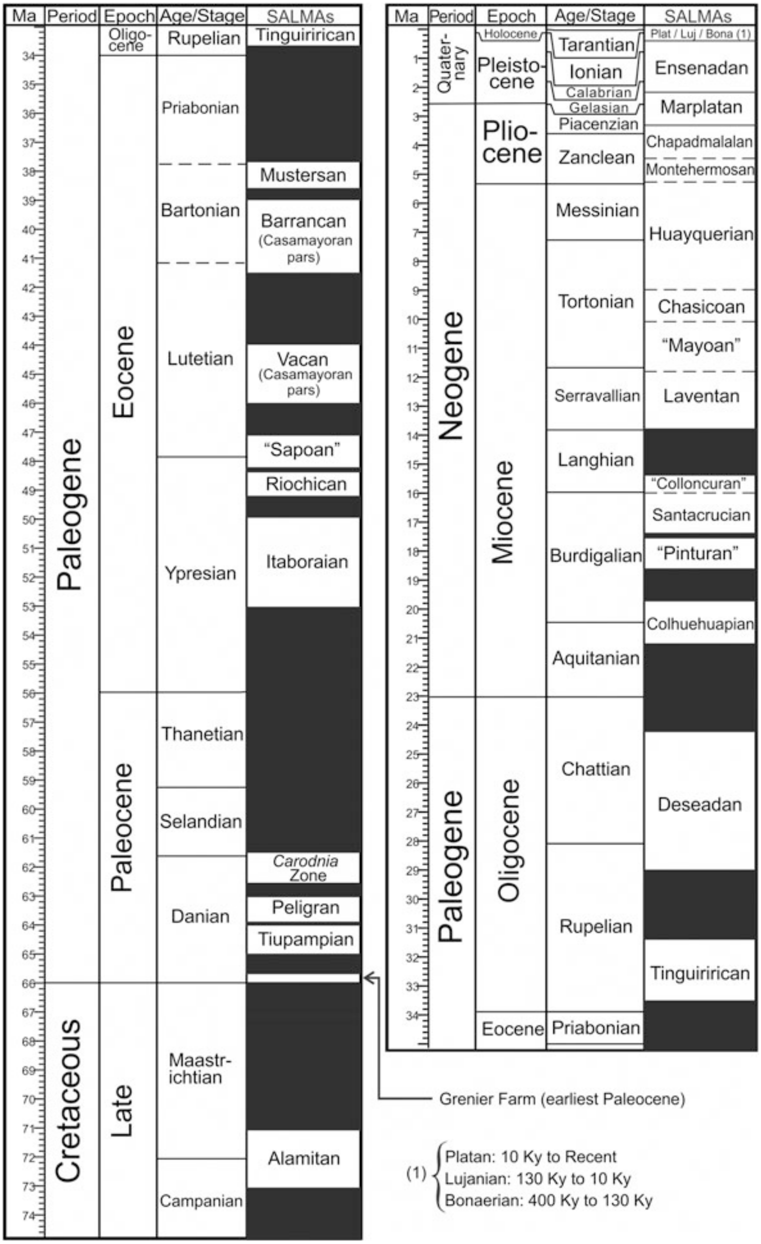


Fig. 1.3 South America's Cenozoicbiochronological succession. After Clyde et al. (2014, early Paleocene), Woodburne et al. (2014a, b, early-middle Eocene), Dunn et al. (2013, late Eocene-early Miocene), Tomassini et al. (2013, late Miocene-Pliocene), Tonni (2009, late Pleistocene-Holocene). The "*Carodnia* Zone," "Sapoan," "Pinturan," "Colloncuran," and "Mayoan" have not been formalized as SALMAs. Vacan and Barrancan are subages of the CasamayoranSALMA. For Paleogene biochronological units, see a review in Woodburne et al. (2014a)

Cretaceous; (2) it was followed by the evolution of deltatheroidan-like metatherians both in Asia and North America during the late Early Cretaceous (120 to 100 Ma); (3) then, a major diversification episode occurred in North America by the early Late Cretaceous (around 100 Ma); and finally (4) the Paleocene diversification of proximal relatives to crown marsupials occurred in South America. (As discussed in Chaps. 3 and 7, it is more probable that this event happened by the Late Cretaceous). To these, we could add a fifth major episode: (5) the (possibly, latest Cretaceous; see Chaps. 3, 4, and 7) for the origin and later radiation of Australidelphians and their dispersal throughout southern South America, Antarctica, and Australia. The history of Southern Hemisphere metatherians involves the last two steps of this succession.

The oldest record of a therian mammal in South America is that of *Cocatherium lefipanum*, from the earliest Paleocene of western Patagonia (Paso del Sapo area, Chubut Province; Goin et al. 2006). It consists of an isolated, worn lower molar (Fig. 1.4) recovered from levels of the Maastrichtian-Danian Lefipán Fm, and referred by Goin et al. (2006) to the Polydolopimorphia (Marsupialia). A striking aspect of *Cocatherium* is that, even though it is the oldest South American metatherian, it is not generalized but instead quite derived in its molar pattern. For instance, (1) it is bunodont, (2) the talonid is relatively short, (3) the labial face of the molar doubles the height of the lingual face, (4) the paraconid is reduced and set close to the metaconid, (5) the protoconid is robust but low, probably of the same height as the also robust metaconid, and finally (6) the talonid has a tall, laterally compressed entoconid. Taking in account that the specimen was found less than 5 m above the inferred Cretaceous-Tertiary boundary at the Lefipán Fm, the degree of specialization shown by *Cocatherium* is suggestive of an earlier (Late Cretaceous) evolution of this and other metatherian lineages. This agrees with the idea of a Late Cretaceous arrival of the first immigrant lineage (lineages? see below) from North America. As suggested in Chap. 3, this arrival could have taken place

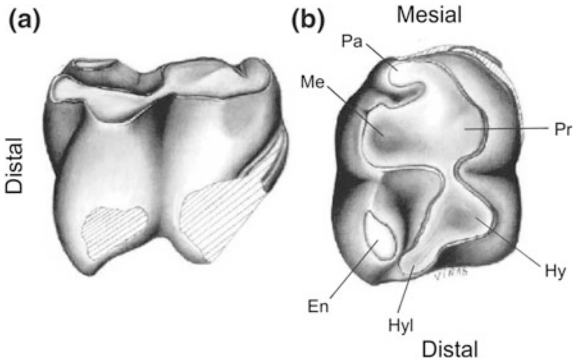


Fig. 1.4 *Cocatherium lefipanum* (Metatheria, Polydolopimorphia), the oldest Cenozoic therian mammal known up to now from South America. Specimen LIEB-PV 1001, an isolated, lower right molar in labial (**a**) and occlusal views. *Abbreviations* Pa, paraconid; Me, metaconid; Pr, protoconid; Hy, hypoconid; En, entoconid; Hyl, hypoconulid. Modified after Goin et al. (2006)

either by Campanian or by Maastrichtian times. In addition, Case et al. (2005) argued that at least “didelphimorphians” (now regarded as basal ameridelphians) and polydolopimorphians (typical South American metatherians), had their origins in North America, probably in southern latitudes of that continent, and then dispersed into South America by the end of the Cretaceous. Forasiepi (2009) also suggested that the Sparassodonta had a Late Cretaceous, North American origin, previous to their dispersal into South America.

In his thorough description of the early Paleocene mammalian assemblage of Tiupampa (Bolivia; Tiupampan SALMA), Muizon (1991) noted that the Tiupampan eutherians show much closer affinities to those of North America (Puercan NALMA) than those shown by metatherians. He concluded that placental mammals arrived in South America in a dispersal event that was not synchronous with, but subsequent to that of metatherians. Other authors agreed with this (e.g., Pascual and Ortiz Jaureguizar 1991) and suggested that during the latest Cretaceous and the earliest Paleocene, there probably were several dispersal events between the Americas, the earliest of which may have involved the metatherian immigration into South America (see Chap. 3). More recently Goin et al. (2012) named this inferred dispersal event as FABI (First American Biotic Interchange), a term that is reminiscent of the complexities and sequential aspect of the late Tertiary GABI, the Great American Biotic Interchange (see Chap. 4).

1.2.2 Definitions and Characteristic Features

Since the last decades of the twentieth century, the term Marsupialia has acquired a more restricted sense than in previous interpretations. Today it is regarded as the crown group including all extant marsupials, their common ancestor, and all of their descendants Rowe (1998). In turn, Metatheria is a more comprehensive term for designing a taxon within Mammalia that includes not only Marsupialia but also all therian mammals more related to Marsupialia (i.e., their stem relatives) than to Eutheria (Rougier et al. 1998; Kielan-Jaworowska et al. 2004; Williamson et al. 2014). Hence, by definition, all non-marsupial metatherians are extinct—as well as many Cenozoic marsupials. Because of this distinction, it is quite difficult to extend to all metatherians the series of features of soft anatomy, reproduction, and physiology that characterize living marsupials (see Chap. 2 for a detailed characterization of these features among living South American marsupials). Notwithstanding, it is reasonable to assume that many of these characters were also present in non-marsupial metatherians. Several features of metatherian physiology (as, for instance, the lack of Brown Adipose Tissue, or BAT) are a potential source of biases in the evolution of the group (see Chap. 2; Sánchez-Villagra 2012).

Several features of the hard parts (skeleton and teeth) of metatherians that have been considered diagnostic of this group are not exclusive of them. This is the case, for instance, of the presence of epipubic bones in the pelvic girdle, a primitive condition as they have also been found in early eutherians (Kielan-Jaworowska 1975).

The presence of an alisphenoid bulla is a derived feature within several lineages rather than a metatherian synapomorphy (see, e.g., Kielan-Jaworowska et al. 2004). In the middle ear, the absence of a groove for the stapedial artery on the promontorium is also present in eutherians and *Vincelestes*, though a few others, such as the lack of a foramen for the superior ramus of the stapedial artery, absence of the related ascending canal, the posterolateral placement of the transverse sinus with respect to the subarcuate fossa, and the separation of the jugular foramen from the inferior petrosal opening, have been referred to as metatherian synapomorphies (Rougier et al. 1998). The presence of an angular process in the rear part of the dentary is also frequently cited as a synapomorphy of Metatheria (it is absent in *Sinodelphys*). Even though this feature is also present in a few Cretaceous eutherians, its shelf-like aspect is exclusive of the group (Averianov and Kielan-Jaworowska 1999).

Luo et al. (2003) listed several derived features of the postcranial skeleton that are quite constant among metatherians: (1) Manus: carpals with a hypertrophied hamate (relative to the capitate and trapezoid), an enlarged triquetrum (relative to the lunate and distal ulna), and an enlarged scaphoid (relative to the lunate and/or trapezium). (2) Pes: tarsals have a transversely broad but anteroposteriorly short navicular; the navicular facet on the astragalar head is spread medially along the length of the neck, such that the head with its navicular facet is asymmetrical with regard to the main axis of the astragalar neck; the calcaneocuboid facet is obliquely oriented with respect to the length of the calcaneus, and is buttressed by a large anteroventral tubercle; the base of the peroneal process is level with the cuboid facet or anterior to it; the sustentacular process forms a pointed triangle. (3) Typical metatherian features in the forelimb are: much wider supraspinous fossa than infraspinous fossa at midlength of the scapula; the cranial border of the scapula has a strongly sigmoidal profile, ending anteriorly in a pronounced supraspinous incisure; the ectepicondylar region of the humerus has a shelf-like supinator crest with a sigmoidal profile.

Several dental features are also common among metatherians but not exclusive of the group: a generalized dental formula of I/i 5/4, C/c 1/1, P/p 3/3, M/m 4/4, molars with a typical tribosphenic aspect, or the sharp morphological break between the premolar and molar series. Kielan-Jaworowska et al. (2004) list two features as synapomorphies of Metatheria: the reduction in the premolar number (from four or five in the ancestral boreosphenidans to three in metatherians), and the reduction of diphyodonty (i.e., the presence of two successive sets of teeth, deciduous and permanent), restricted to the third premolar (Luckett 1993). Some other features listed by Luo et al. (2003; see also O'Leary et al. 2013) as synapomorphies of Metatheria are the presence of an entoconid which is close, or twinned to the hypoconulid in the lower molars, presence of a stylar cusp B (StB, opposite the paracone) at least on the upper second molar; and presence of a stylar cusp D (StD, opposite the metacone) at least on the penultimate upper molar.

In their extensive morphological analysis of 229 dental, cranial, postcranial, and soft tissue characters and selected mammalian taxa, Horovitz and Sánchez-Villagra (2003) listed the following unambiguous apomorphies as diagnostic of Metatheria:

four upper molars; staggered third lower incisor; marsupial pattern of dental replacement; angular process of the dentary medially inflected; the palatal process of the premaxilla reaches the canine alveolus or is immediately posterior to it, and absence of the stapedial artery sulcus on the petrosal. In turn, they regarded the following unambiguous apomorphies as diagnostic of Marsupialia: humerus with equal proximal extension of capitulum and trochlea; spherical distal process of ulna, contributing to a ball and socket articulation; posterior shelf of the tibia present and extending posteriorly beyond the medial astragalotibial facet; dorsal mesiolateral orientation of the calcaneal sustentacular facet; poorly developed alisphenoid tympanic wing; transverse canal foramen anterior to the carotid foramen, and palatal vacuities present in both maxillary and palatine bones.

1.3 South American Metatherians, Living and Extinct

With slightly more than 100 species (Brown 2004; Voss and Jansa 2009; Wilson and Mittermeier 2015), living, South American marsupials account for around 10 % of the terrestrial mammals fauna of South America (i.e., excluding volant and marine mammals; Goin et al. in press). They are currently grouped in three orders: Didelphimorphia , Paucituberculata, and Microbiotheria—several didelphid didelphimorphians are also distributed in Central and North America. Living didelphimorphians are grouped in the family Didelphidae (Didelphoidea); they are, by far, the largest group of living marsupials in the New World (more than 90 species). According to recent systematic accounts, they are classified in four subfamilies: Glironiinae, Caluromyinae, Hyladelphinae, and Didelphinae (Voss and Jansa 2009; see Chap. 2). Extinct didelphimorphians include the Sparassocynidae (also referable to the Didelphoidea), a clade of mesocarnivorous didelphoids around the size of the large living didelphines (500–600 g; Zimicz 2014), as well as the Peradectoidea (Horovitz et al. 2009) with two families: Peradectidae (but see Williamson et al. 2012) and Caroloameghiniidae, the latter bearing several convergent features with small-sized primates (Goin 2006).

Living paucituberculatans are restricted to one family, the relatively generalized, shrew-like Caenolestidae, with around half a dozen species. Extinct paucituberculatans (with around 50 species; Abello 2007) are included in this and three additional families: Pichilipidae, Palaeothentidae, and Abderitidae, the latter bearing some of the most derived dental adaptations for the whole order, as a plagiaulacoid-like first molar (not premolar; Marshall 1980). The earliest record of the Paucituberculata dates back to the early Eocene (Itaboraian SALMA). However, the paucituberculatan record is scarce throughout most of the Eocene. They reached their climax by the early-middle Miocene, when representatives of the Palaeothentidae and Abderitidae underwent a rapid radiation. A recent analysis of the paleoecology of 10 species of Patagonian paucituberculatans of Santacrucian age (late early Miocene) led Abello et al. (2012) to recognize a variety of frugivorous, insectivorous, and a combination of both feeding habits, a relative wide variety of body masses and curso-saltatorial, scansorial, and arboreal locomotor behavior.

Living microbiotherians are restricted to a single species belonging to the family Microbiotheriidae: the highly arboreal *Dromiciops gliroides*, restricted to the Valdivian forests of the Southern Andes (see Chap. 2; Martin 2010). Similarly, most extinct microbiotherians inhabited in the southernmost portion of South America, and in the Antarctic Peninsula as well. They were taxonomically varied, with several representatives of the family Microbiotheriidae flourishing during the early Miocene (Abello et al. 2012, Chornogubsky and Kramarz 2012; Goin and Abello 2013). A less varied, older, larger-sized, and more generalized group is that of the Woodburnodontidae (Goin et al. 2007), from the early Eocene of Patagonia and the early-middle Eocene of Antarctica. Earlier claims (e.g., Muizon 1991) that *Khasia cordillerensis*, from the early Paleocene of Tiupampa (Bolivia) is a microbiotherian, are not followed here (see Chap. 5; Woodburne et al. 2013: Table 1).

Microbiotherians have been subject of intensive research in the last three decades. Following initial studies by Szalay (1982) they are currently grouped in the Cohort Australidelphia, a clade that includes microbiotherians plus the four extant Australasian marsupial orders (Dasyuromorphia, Peramelemorphia, Notoryctemorphia, and Diprotodontia). Numerous studies based on a variety of character systems have supported the monophyly of this clade, although the precise affiliation of the Microbiotheria within it has been matter of debate. Several authors (e.g., Amrine-Madsen et al. 2003) argued that microbiotherians are the sister-group of all Australasian marsupials, while others (e.g., Kirsch et al. 1997) supported a scheme where microbiotherians lie within that group.

The above-mentioned taxa do not exhaust the variety of lineages that inhabited South America during Cenozoic times (see Fig. 1.5). As "basal ameridelphians," we refer here to a series of non-marsupial, non-sparassodontan metatherians that were especially abundant in the Late Cretaceous of North America as well as in the Paleogene of South America. The Pucadelphyidae, Jaskhadelphyidae, and Mayulestidae include several of the earliest Cenozoic metatherians, most of them recovered from Tiupampa (early Paleocene) of Bolivia (see Chap. 3). They were small to very small-sized, mostly of insectivorous habits, and already displayed several specialized features both skeletal and dental (Muizon and Céspedes in press). Several other, more specialized "basal ameridelphians" are known from the late Paleocene-early Eocene of Itaboraí, Brazil: Protodidelphidae, Derorhynchidae, Sternbergiidae (Oliveira 1998; Oliveira and Goin 2011).

Representatives of the Order Polydolopimorphia were quite abundant throughout the Paleogene Period, though much more restricted in the Neogene up to the Pliocene Epoch. Two major lineages (Suborders) compose this group: the Bonapartheriiformes on one hand, and the Polydolopiformes on the other.

Representatives of this order were the first to develop a molar pattern of quadrangular shape, apt for the comminution of plant materials of a variety of shapes, sizes, and hardness. It has been suggested that the Polydolopimorphia were derived from the Microbiotheria (Goin et al. 2009a), thus their tentative inclusion among the Australidelphian marsupials in this book (Table 5.1). The Bonapartheriiformes include two major groups: The (earlier) Bonapartherioidea include the families Prepidolopidae, Rosendolopidae, Bonapartheriidae, and Gashterniidae. The (younger) Argyrolagoidea include the distinctly derived Groeberiidae, Patagoniidae, and Argyrolagidae. The Polydolopiformes include a stem lineage represented by *Roberthoffstetteria nationalgeographica*, plus the Polydolopidae, possibly the most highly derived metatherians ever developed in the New World. Three taxa from the Late Cretaceous of North America, *Glasbius*, *Hatcheritherium*, and *Ectocentrocristus*, have been mentioned as basal either to the whole order (the former two) or to the Polydolopiformes (*Ectocentrocristus*; but see Williamson et al. 2012; Case et al. 2005). This implies that stem polydolopimorphians were already developed in North America before their arrival in South America (Case et al. 2005). Actually, the oldest known South American metatherian, *Cocatherium lefipanum* from the earliest Paleocene of Patagonia, has been regarded as a member of this order (see above and Goin et al. 2006).

The Sparassodonta is another order of strictly South American metatherians that become extinct before the end of the Cenozoic. They occupied a wide variety of hypo-, meso-, and hypercarnivorous niches. Almost 60 species referable to this lineage have been described from Colombia, Brazil, Chile, Uruguay, Bolivia, and Argentina (Forasiepi 2009). The early Paleocene *Allqokirus australis*, from the early Danian (Puercan equivalent; see Gelfo et al. 2009) of Tiupampa, Bolivia, has been referred as a basal Sparassodonta (Muizon 1991). Thus, the Sparassodonta, together with the Polydolopimorphia and several basal “ameridelphians”, can be regarded as the oldest metatherians so far known in this continent.

Five families of Sparassodonta have been recognized up to now. The generalized Hondadelphidae are restricted to the South American tropics (Middle Miocene of Colombia, Marshall 1976). The Hathliacynidae range from Patagonia to Colombia and are mostly Neogene in age; they were relatively small carnivores, several of which had opportunistic feeding habits. The larger Borhyaenidae (up to the size of a modern puma) were also widespread in South America, ranging from the middle Eocene to the Pliocene. Proborhyaenids include the largest known New World metatherian so far known, *Proborhyaena gigantea*, with about 100 kg of body mass (Zimicz 2014). They are known from a few sites in southern and northern Argentina, and Bolivia, of late Eocene-Oligocene age. Finally, the extremely specialized, sabre-toothed Thylacosmilidae are known from Neogene sites of Argentina, Uruguay, and Colombia (Forasiepi 2009).

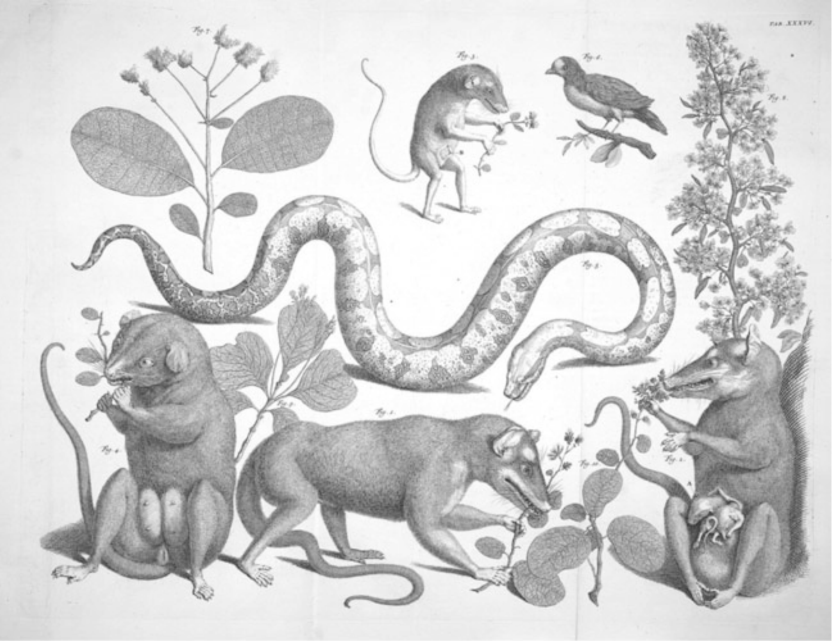

Homo vitruvianus et Metatheria diversitas
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Manuel F. Soca
1 Homo vitruvianus
2 Didelphis
3 Bonapartherium
4 Minusculodelphis
5 Derorhynchus
6 Argyrolagus
7 Groeberia
8 Patagonia
9 Abderites
10 Caroloameghinia
11 Kramadolops
12 Proborhyaena
13 Thylacosmilus
14 Necrolestes (? Metatheria)

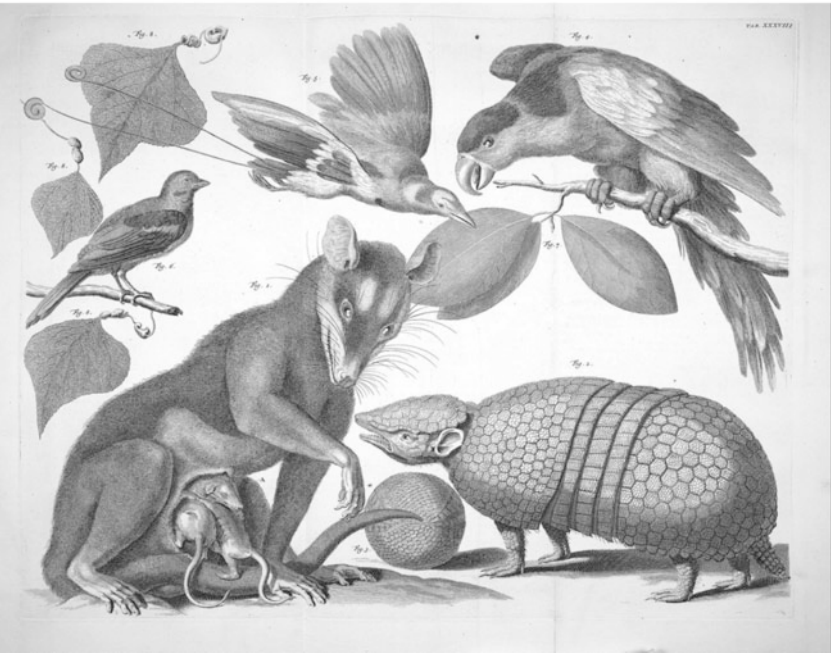
◀ **Fig. 1.5** Extinct South American diversity of metatherian mammals. Leonardo da Vinci's "Vitruvian Man" (1) serves as a parameter for size comparisons. Depicted are the living *Didelphis albiventris* (2), a female specimen with six pouch-young individuals attached to its back, and a hanging subadult), and the extinct *Bonapartherium hinakusijum* (3), *Minusculodelphis minimus* (4), *Derorhynchus singularis* (5), *Argyrolagus scagliai* (6), *Groeberia minoprioi* (7), *Patagonia peregrina* (8), *Abderites meridionalis* (9), *Caroloameghinia mater* (10), *Kramadolops maximus* (11), *Proborhyaena gigantea* (12), and *Thylacosmilus atrox* (13). The phylogenetic affinities of *Necrolestes patagonensis* (14) are still unclear. Goin et al. (2007) regarded it as a Mammalia *incertae sedis* (for a more recent review, see Rougier et al. 2012). Drawings and composition by Manuel Sosa

1.4 A Historical Perspective

The first metatherians known to Western eyes were, of course, not extinct but living. In 1500, the seafarer Vicente Yáñez Pinzón presented to the Catholic Monarchs three juvenile opossums (probably referable to some species of *Didelphis*), as well as the skins of their mother and an additional juvenile, both dead during their trip from Brazil to Spain (Cabrera and Yepes 1960). Since then, many historians, chroniclers, explorers, and naturalists of the sixteenth, seventeenth, and eighteenth centuries mentioned these animals under a variety of names, many of which were derived from aboriginal names. The first Western graphic representation of an opossum is that of the Waldseemüller map of 1516, the "Carta Marina" (see, e.g., http://myloc.gov/exhibitions/earlyamericas/interactives/maps/html/cartamarina1516/view1516.html). There, a rather strange marsupial is depicted within a poorly recognizable South American contour, and near a region labeled as "Cannibal Land" (*Terra Canibalor*, present Brazil). Other representations must have excited the imagination of many naturalists during these early centuries. An outstanding example is that of Albertus Seba's "Cabinet of animal curiosities," one of the most prized natural history books of all times (Seba 1734; Fig. 1.6). Carl Linnaeus' 10th edition of the Systema Naturae already incorporates American opossums, all species known by then included in the genus *Didelphis* (Order Bestiae; Linnaeus 1758). From the nineteenth century onward, an enormous corps of the literature has been devoted to the taxonomy, anatomy, natural history, physiology, ecology, and paleontology of New World marsupials (for the latter, see below).

Less known or studied are the numerous graphic, sculptural, and oral narrative references to American opossums among the native archaeological remains throughout the whole continent (López Austin 1990). Figure 1.7 shows three of them, coming from quite different archaeological context and cultures. From southern North America to central Argentina, opossums have played an important role in creation myths, legends, as well as symbols of specific meaning. In rural areas of northwestern Argentina, for instance, it is not infrequent to see an opossum skin (e.g., *Didelphis albiventris*) close to the beds of a woman in labor due to the small size of pouch young in all marsupial species, it is regarded as an omen of painless birth (Contreras 1983). Several myths throughout Central and South


TAB. XXXVI.


TAB. XXXVIII

◄ **Fig. 1.6** Some of the oldest representations ever made of American marsupials by Western naturalists. Both drawings were included in Albertus Seba's (1734–1765) *Locupletissimi Rerum Naturalium Thesaurus*. The upper figure is from Vol. 1 (1734), Plate XXXVI, while the lower one is from the same volume, Plate XXXVIII. Note the stress made by the artist on the pouch and pouch young of the depicted marsupials (most probably referable to an undetermined species of the four-eyed opossum *Philander*). Images courtesy of the Missouri Botanical Garden, http://www.botanicus.org

America give a fire-gifting role for the opossum, quite similar to that of Prometheus in Greek mythology (López Austin 1990). Finally, aboriginal medicine has usually a number of recipes that include parts of opossums (typically, the tail) for therapeutic purposes (Hartmann 1952).

The history of our scientific knowledge of extinct South American metatherians dates back to the last quarter of the nineteenth century. Paleontological discoveries in the Americas predate by far this date; however, most of these records were largely incidental, as well as related to other lineages of (usually very large) South American mammals: xenarthrans, SANU, proboscideans, etc. One of the earliest records of fossil mammals in this continent is attributed to a Jesuit priest, Father Guevara, who was probably the first one to infer the extinct condition of the "Carcarañá giants" (after Carcarañá River in Santa Fe Province, Argentina): "… These giants, formidable towers of flesh, whose single name awakens the horrors and astonishment of peoples [and] attracts our attention, do not exist in present times; nevertheless, their old traces that from time to time are discovered by the Carcarañá and elsewhere, are evidence of their existence in past times" (Celaya 2005: 7; original in Spanish).

Following a "kuhnean" approach (e.g., Kuhn 1970), Goin (1991) distinguished three periods in our knowledge of South American extinct metatherians. Each of them was characterized, and influenced, by distinct phylogenetic paradigms, available research technologies, and involved scholars. Each period included moments of theoretical effervescence followed by longer, mostly descriptive phases that were conceptually hegemonized by previously established paradigms. Finally, each period was influenced by the historic, political, cultural, and technological avatars of our contemporary history. Boundary dates for each of these periods, especially the latter one, are somewhat arbitrary, as it is hard to separate a process of successive knowledge achievements that were characterized, notably in South America, by their continuity.

1.4.1 *First Period (1878–1930)*

This period or cycle is intimately linked to the genius and figure of Florentino Ameghino (1854–1911), the most notable South American paleontologist of all times and Argentina's father of science. Almost a half of all the genera currently recognized of South American extinct metatherians were described by Ameghino between 1888

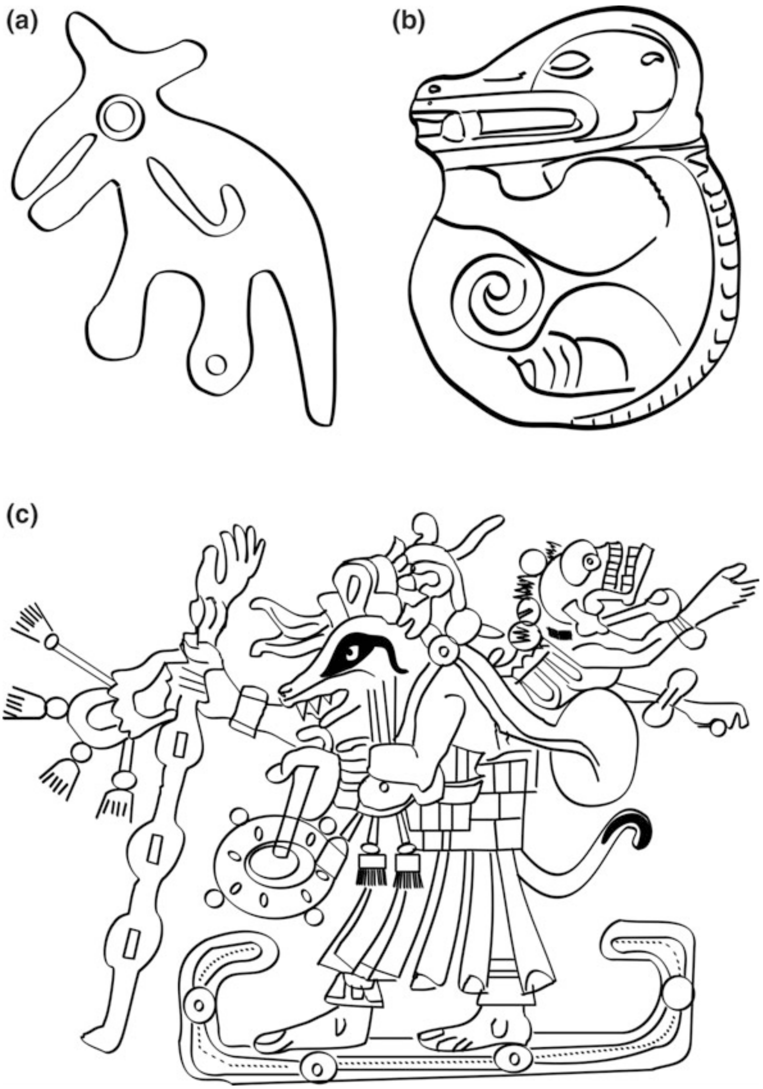


Fig. 1.7 **a**–**c** Schematic drawings of three opossum representations in archaeological objects belonging to different Central and South American cultures. **a** An opossum carved in a stone throne at Complejo Arqueológico Ventarrón-Collud, in northern Perú (see Alva Meneses 2008); **b** schematic drawing of a sculpture in stone of an opossum, belonging to the Tumaco-Tolita culture in the northern Andes, Ecuador (specimen Nr. LT-36-48-70, Museo Banco Central del Ecuador, Esmeraldas; after a photograph in Ugalde 2006); **c** depiction of an opossum in a Mayan Code (Dresden Code; after Gates 1932: Pl. 29). All drawings by Marcela Tomeo

and 1904. Several of his genial intuitions relative to the evolutionary history of our mammals still stand as the most reasonable evolutionary hypotheses. Additionally, we owe him the first biostratigraphic scheme for South America's Cenozoic, mostly based on his brother Carlos' observations and collections made in Patagonia, as well as in central Argentina, especially the Pampean region, made by both of them. He wrote about and discussed most Argentinian fossil localities, biostratigraphical units (his "étagés"), and mammalian taxa known during his lifetime.

Ameghino studied fossils by the naked eye, or at the most with the help of a simple magnifying glass (Sbarra 1963); this is remarkable taking into account the tiny size of some of the fossils he described. A passionate man, he supported some bitter, even almost violent, discussions with contemporary naturalists (e.g., Germán Burmeister, Francisco Moreno, Alcides Mercerat), generally with more abundant and better arguments. He was the largest source of information of his time concerning South American extinct mammals, and the one that elaborated many of the soundest interpretative models regarding their chronologic succession, evolution, and phylogenetic relationships. His was an age of notable scientific production in many disciplines in many South American countries. In some of them, as in Argentina, the hiring of many foreign naturalists by official institutions brought an exponential increase in our knowledge of regional geography, natural resources, as well as the cultural and natural heritage, Paleontology among them. Florentino Ameghino stands as the founder of South America's Vertebrate Paleontology.

Notably enough, Ameghino never regarded the Metatheria as a natural group. A few years before his death, he commented: "…[T]he division of mammals in two subclasses is a great mistake, as it raises impassable barriers that prevent us to recognize the close affinities among animals of such fundamentally identical structures as those of the dog and the thylacine" (Ameghino 1910: 41; Spanish in the original).

To give an idea of the magnitude of his production, and just regarding South American, Neogene "opossum-like" marsupials, Ameghino contributed more than 70 % of the publications of this period (e.g., Ameghino 1882, 1884, 1885, 1888, 1889, 1891a, b, c, 1893a, b, c, 1898, 1900, 1900-1903, 1902a, b, 1904, 1906, 1907, 1908, 1910). Other researchers involved in such studies were Burmeister (1879), Winge (1893), Mercerat (1898), Sinclair (1906), Rovereto (1914), Frenguelli (1921), Cabrera (1927, 1928).

1.4.2 Second Period (1930–1977)

Since the beginnings of the third decade of last century, South American paleomammalogy greatly benefited from the contributions of several North American scientists, most notably from one in particular: George Gaylord Simpson (1902–1984). One of the main figures of the Synthetic Theory of Evolution, Simpson gave light to an impressive scientific production, both empirical and theoretical (see, e.g., Gingerich 1986). Due to several field trips to Patagonia, Simpson got involved in the study of South American extinct mammals; as a consequence, he was able to discuss many of Ameghino's previous ideas. Overall, his thoughts on South American mammalian taxonomy, evolution, succession, biochronology, and turnovers, turned out to constitute a new paradigm. Particularly important are his contributions on the early establishment of mammalian lineages in this continent, as well as the concepts of isolation and of successive, distinct taxonomic associations (his "mammal strata") throughout Cenozoic times (e.g., Simpson 1948, 1950, 1967). Simpson was also active in the description, allocation, and phylogenetic speculation of several major lineages of South American metatherians, most notably polydolopid polydolopimorphians and didelphoid didelphimorphians (for the latter see Goin 1991). Also relevant as major frameworks on mammalian evolution in South America, stand the contributions by Patterson and Pascual (1968, 1972).

This period also saw major improvements in the design of a biochronological scheme for the continental Cenozoic of South America. Efforts were led by Rosendo Pascual and his team at the Museo de La Plata (Pascual et al. 1965, 1966; Pascual and Odreman Rivas 1971, 1973), who refined and completed previews work by Ameghino (e.g., 1906), Kraglievich (1952). Our knowledge of Paleogene metatherians was notably expanded with the discovery and description, by Carlos de Paula Couto, of the early Eocene assemblage of Itaboraí, in southeastern Brazil, largely dominated by stem "ameridelphians" (Paula Couto 1952a, b, c, 1960, 1962, 1970; see a review in Oliveira 1998). Another interesting fauna described in this period is that of the ?late Paleocene of Laguna Umayo in southern Perú (Sigé 1971, 1972; see Sigé et al. 2004 for a reassessment of its age). By the end of this period and the beginning of the third one, the late Oligocene (Deseadan SALMA) Salla-Luribay (Bolivia) assemblages were first discovered and described (Hoffstetter 1968, 1969, 1976; Hoffstetter and Lavocat 1970; Hoffstetter et al. 1971; for a preliminary review on the metatherian taxa, see a review in Villarroel and Marshall 1982). Also, the extraordinary mammalian fauna of the middle Miocene of La Venta, also rich in metatherians, began to be described (e.g., Marshall 1976, 1977).

From a technological point of view, this second period was characterized by the intensive use of now standard optical instruments, as the stereomicroscope, stereoscopic photography, or the micrometric ocular and calipers, for the observation and measurement of the cranial, postcranial, and dental structures of mammals. This prompted a huge advance in our knowledge of the diversity and evolution of many extinct lineages of small-sized mammals, including those of metatherians. Field methods still kept on the long tradition of naked-eye prospecting.

Taking again the example of Neogene "opossum-like" marsupials, there is a quite balanced production among local and foreign researchers: Rusconi (1932), Simpson (1932a, b, 1935a, b, 1938, 1948, 1972, 1974), Kraglievich (1934), Patterson (1937), Riggs and Patterson (1939), Ringuelet (1953, 1966), Reig (1952, 1955a, b, 1957a, b, 1958a, b, c), Hoffstetter (1963), Zetti (1967), Reig and Simpson (1972), Marshall (1976, 1977), Del Corro (1977).

1.4.3 Third Period (1977–Present)

Even though somewhat arbitrary, the date chosen as the beginning of this third period is coincidental with the appearance, within a short period of five years, of a series of highly influential works by two North American researchers. The first one was that of John A.W. Kirsch: "The comparative serology of Marsupialia, and a Classification of Marsupials" (Kirsch 1977). In it, the author introduced a new methodology in the analysis of living metatherians (he compared around a hundred species), and tested his results with those of more traditional, morphological taxonomy. Even though he accepted, with slight modifications, Ride's (1964) multi-ordinal scheme for the arrangement of marsupials, he recognized the uniqueness of microbiotheriids among the South American metatherians. We owe the second major contribution to Frederick Szalay, who a few years later (e.g., Szalay 1982; see also Szalay 1994) would promote a drastic re-arrangement of marsupial affinities based on their tarsal morphology. He recognized the Australidelphia, including microbiotherians and all Australasian lineages, as a natural group.

Regarding South American mammalian evolution as a whole, the theoretical framework during this period consisted of a series of attempts to relate the different phases in mammalian evolution with the biotic (floral and ecosystemic dynamics) and abiotic (tectonic, temperatures, and rainfall) factors that framed it. Again, a leading figure in this field was the late Pascual (1984, 1996, 2006; Pascual and Ortiz-Jaureguizar 1990, 1991, 2007; Pascual et al. 1996; other contributions include those of Simpson 1980; Flynn et al. 2003; Goin et al. 2012; Woodburne et al. 2013; among others). Several of these studies were triggered as a consequence of improvements in the geochronological calibration of the Cenozoic succession (e.g., Marshall and Pascual 1978; Marshall and Patterson 1981; Marshall et al. 1977, 1981, 1983a, b; Flynn and Swisher 1995; Kay et al. 1999; Flynn and Wyss 1999; Flynn et al. 2003; Tejedor et al. 2009; Ré et al. 2010; Madden et al. 2010). Preliminary attempts to specifically relate metatherian evolutionary phases with global climates were presented by Goin et al. (2010, in press).

This period can be characterized, in technological terms, by the use of a series of tools that greatly improved our capacity for anatomical and taxonomical analysis: the use of plastic casts, especially of dental specimens, for comparative purposes; the application of scanning electron microscopy (SEM), computed tomography scan (CT-scan), digital image managing, etc., in morphological analyses; the use of a variety of cladistic methodologies in the phylogenetic analysis; finally, information technologies hugely expanded the publishing and sharing of scientific knowledge. In the field, various methodologies have proven to be successful in fossil prospecting; regarding small vertebrates, as is the case of most metatherians, the use of dry-screening, or underwater screen-washing of fossil-bearing sediments has exponentially enlarged collections from a number of localities.

Regarding our knowledge of the evolutionary history of South American metatherians, this period is characterized by an exponential growth in available information on both extinct and extant local faunas and isolated taxa, and by the numerous proposals of alternate (and frequently antagonistic) phylogenetic schemes (for the latter, see Chap. 5). Besides numerous works describing isolated metatherian taxa, notable are the discovery of many new faunal assemblages that radically enhanced our knowledge of mammalian evolution in this continent. Among the mammalian associations discovered and/or described during this period, with a significant metatherian content, prominent are those of the early Paleocene of Tiupampa in Bolivia (Marshall et al. 1983a, 1985; Marshall and Muizon 1988; Muizon 1991, 1994, 1998; Muizon and Cifelli 2001), "medial" Paleocene of Punta Peligro in southern Argentina (e.g., Bonaparte et al. 1993; Bond et al. 1995; Gelfo et al. 2009), early to middle Eocene of Paso del Sapo in southern Argentina (Tejedor et al. 2009), ?middle Eocene of the La Meseta Fm in northernmost Antarctic Peninsula (Woodburne and Zinsmeister 1982, 1984; Goin et al. 1999; Chornogubsky et al. 2009), middle-late Eocene of Northwestern Argentina (Pascual 1980a, b, 1981, 1983; Pascual et al. 1981; Goin et al. 1986); middle to late Eocene of Contamana in northeastern Perú (Antoine et al. 2012); ?late Eocene of Santa Rosa in eastern Perú (Campbell 2004; Goin and Candela 2004), latest Eocene-earliest Oligocene of Tinguiririca in central Chile (Wyss et al. 1990, 1994; Flynn et al. 2003; Croft et al. 2008), early Oligocene faunas of La Cancha and La Cantera in southern Argentina (Goin et al. 2010); reviews of the early Miocene, Colhuehuapian SALMA metatherians from Patagonia (Goin et al. 2007; Goin and Abello 2013) and of middle Miocene of La Venta (Colombia) metatherians (Goin 1997a); late Miocene of Cerro Azul Fm and Caleufú in Central Argentina (Goin et al. 2000; Abello et al. 2002). Among post-tertiary faunas discovered and described in this period, can be mentioned the interesting, early to late Holocene successions, including many marsupial specimens, of Tixi Cave in southeastern Pampas, Argentina (Goin 2001) and of several sites in southeastern Brazil (Hadler et al. 2009a, b; Oliveira et al. 2011).

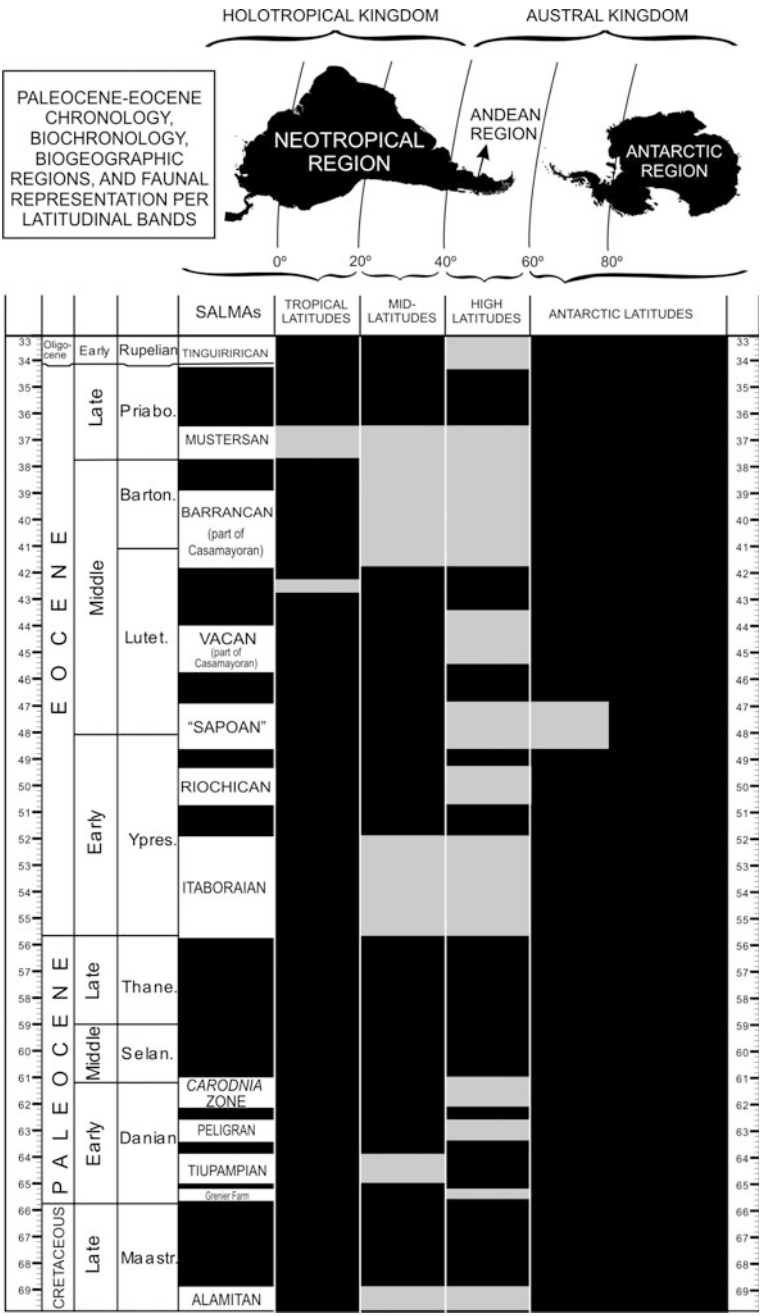
This was also a period of several major reviews of metatherian lineages. Beginning in 1976, Larry G. Marshall would accomplish a remarkable series of reviews of most South American groups known up to then (Marshall 1976b, 1977, 1979, 1980, 1981a, b, 1982a, b, 1987; Marshall et al. 1990). More recent reviews, including the addition of newly described taxa, include those of Goin (1991), Sánchez-Villagra et al. (2000; see also Sánchez-Villagra 2001; Sánchez-Villagra and Kay 1997), Forasiepi (2007), Abello (2007, 2012, 2013), Chornogubsky (2010), Chornogubsky et al. (2009), Goin et al. (2009a, b).

Finally, and taking again the case of Neogene opossum-like marsupials, works in this period show a consolidated production by South American researchers (e.g., Marshall 1976; Villarroel and Marshall 1983; Prado et al. 1985; Goin 1997b, c, 2001; Goin and De Los Reyes 2012; Goin and Montalvo 1989; Goin and Pardiñas 1996; Goin et al. 2009b; Cozzuol et al. 2006; Forasiepi et al. 2009; Oliveira et al. 2011; Abello et al. in press).

1.5 The Incompleteness of the Fossil Record

A final note should be made on the biased, incomplete fossil record of South American metatherians—and of other terrestrial vertebrates as well. Figure 1.8 shows a chart of the first half of the Cenozoic Era, relating periods, epochs, SALMAs, and known extinct South American and Antarctic terrestrial faunas. The latter have been related to their latitude. As can be appreciated, the best known areas are those of mid- to high latitudes up to 50°N. South and north of them, the fossil record is almost a black hole. This lack of records is particularly relevant for metatherians, as they are usually distributed in tropical-subtropical areas of the continent. As argued in Chaps. 4 and 7, metatherian radiations seem to have been triggered by phases of global warming (i.e., the climatic optima) not only in Cenozoic times but also during the Cretaceous.

The best known tropical, extinct metatherian assemblage is, up to now, that of the middle Miocene of La Venta in Colombia (see Marshall 1976a; Goin 1997a). Among the thylacosmilid sparassodonts, which are well represented in specimens and taxa, noteworthy is the persistence of several taxa which are generalized with respect to even earlier assemblages in higher latitudes (e.g., Patagonia). The earliest record of a thylacosmilid sparassodont is that of an isolated upper molar recovered from early Miocene levels of Colhuehuapian age at Gran Barranca, in southern Chubut Province, Patagonia (Goin et al. 2007). Even though it comes from levels at least five million years older than those of La Venta, it already shows morphological specializations as advanced, or even more so, than those of the tropical, middle Miocene *Anachlysictis gracilis*—comparisons have to be made on indirect grounds, as the latter was based on a lower jaw. Moreover, an additional specimen from La Venta, originally referred by Goin (1997a, p. 203) to a "Thylacosmilidae?", could represent the most generalized thylacosmilid so far known. The persistence of generalized types in the tropics, as is the case of the La Venta thylacosmilids, suggests that the lack of records from tropical areas in South America still precludes our better understanding of metatherian's phylogenetic relationships. Many "missing links" are still hiding in the tropics, maybe for ever.


HOLOTROPICAL KINGDOM
AUSTRAL KINGDOM
PALEOCENE-EOCENE CHRONOLOGY, BIOCHRONOLOGY, BIOGEOGRAPHIC REGIONS, AND FAUNAL REPRESENTATION PER LATITUDINAL BANDS
NEOTROPICAL REGION
ANDEAN REGION
ANTARCTIC REGION
0°
20°
40°
60°
80°
SALMAs
TROPICAL LATITUDES
MID-LATITUDES
HIGH LATITUDES
ANTARCTIC LATITUDES
Oligo-cene
Early
Rupelian
TINGUIRIRICAN
EOCENE
Late
Priabo.
MUSTERSAN
Middle
Barton.
BARRANCAN (part of Casamayoran)
Lutet.
VACAN (part of Casamayoran)
"SAPOAN"
Early
Ypres.
RIOCHICAN
ITABORAIAN
PALEOCENE
Late
Thane.
Middle
Selan.
CARODNIA ZONE
Early
Danian
PELIGRAN
TIUPAMPIAN
Grenier Farm
CRETACEOUS
Late
Maastr.
ALAMITAN
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69

◄ **Fig. 1.8** "Black holes" in our knowledge of metatherian faunas in South America. The time span considered here is the first half of the Cenozoic (i.e., Paleocene-Eocene). Areas in black refer to the still unsampled regions of South America for this time span. See Chap. 4 for details on South America's biogeographic regions and kingdoms

References

Abello MA (2007) Sistemática y bioestratigrafía de los Paucituberculata (Mammalia, Marsupialia) del Cenozoico de América del Sur. Unpubl. thesis, Univ Nacional de La Plata

Abello MA (2013) Analysis of dental homologies and phylogeny of Paucituberculata (Mammalia: Marsupialia). Biol J Linn Soc 109:441–465

Abello MA, Montalvo CI, Goin FJ (2002) Marsupiales del Mioceno Superior de Caleufú (La Pampa, Argentina). Ameghiniana 39(4):433–442

Abello MA, Ortiz-Jaureguizar EO, Candela AM (2012) Paleoecology of the Paucituberculata and Microbiotheria (Mammalia, Marsupialia) from the late Early Miocene of Patagonia. In: Vizcaino SF, Kay RF, Bargo MS (eds) Early Miocene Paleobiology in Patagonia. High-latitude paleocommunities of the Santa Cruz Formation. Cambridge University Press, Cambridge

Abello MA, De los Reyes M, Voglino C, Candela AM, Coira B, Galli CI (in press) Primer registro de Marsupialia (Mammalia, Metatheria) para la Formación Maimará (Mioceno Tardío), Quebrada de Humahuaca (Provincia de Jujuy, Argentina). Ameghiniana

Alva Meneses I (2008) Los complejos de Cerro Ventarrón y Collud-Zarpán: del Precerámico al Formativo en el valle de Lambayeque. Bol Arqueol, Pontif Univ Catól Perú 12:97–117

Ameghino F (1882) Catálogo explicativo de las colecciones de antropología prehistórica y de Paleontología, Florentino Ameghino. In: Catálogo de la sección de la Provincia de Buenos Aires en la Exposición Continental Sudamérica. Anexo A, Buenos Aires

Ameghino F (1884) Excursiones geológicas y paleontológicas en la Provincia de Buenos Aires. Bol Acad Nac Cs Córdoba 6:161–257

Ameghino F (1885) Informe sobre el Museo Antropológico y Paleontológico de la Universidad Nacional de Córdoba durante el año 1885. Bol Acad Nac. Cs. Córdoba 8:347–360

Ameghino F (1888) Lista de las especies de mamíferos fósiles del Mioceno Superior de Monte Hermoso hasta ahora conocidos. PE Coni, Buenos Aires

Ameghino F (1889) Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas Acad Nac Cs Córdoba, Vol 4, Buens Aires

Ameghino F (1891a) Las antiguas conexiones del continente sudamericano y la fauna eocena argentina. Rev Arg Hist Nat 1:123–216

Ameghino F (1891b) Burmeister: adiciones al examen crítico de los mamíferos fósiles tratados en el "Examen crítico de los mamíferos y reptiles fósiles, etc". por A. Bravard. Rev Arg Hist Nat 1:259–290

Ameghino F (1891c) Sobre la supuesta presencia de creodontes en el Mioceno Superior de Monte Hermoso. Rev Arg Hist Nat 1:437

Ameghino F (1893a) Les mammifères fossiles de La Patagonie Australe. Rev Sci 51:13–17

Ameghino F (1893b) New discoveries of a fosil Mammalia of Southern Patagonia. Amer Nat 27:445

Ameghino F (1893c) Les premieres mammiferes. Relation entre les mammiféres diprotodontes eocenes de l´Amerique du Nord et deux de la Republique Argentine. Rev Gen Sci Pures et Appliq 4(3):77

Ameghino F (1898) Sinopsis geológico-paleontológica de la República Argentina. In: Segundo Censo de la República Argentina, Vol 1, La Plata

Ameghino F (1900) Presencia de mamíferos diprotodontes en los depósitos terciarios de Panamá. Anal Soc Cient Arg 49:235

Ameghino F (1900–1903) L´age des formations sedimentaires de Patagonie. Anal Soc Cient Arg 50:109–130

Ameghino F (1902a) Línea filogenética de los Proboscídios. Anal Mus Nac Buenos Aires, Ser 3 (1):1–2

Ameghino F (1902b) Premiere contribution a laconnaissance de la faune mammalogique des couches a *Colpodon*. Bol Acad Nac Cs Córdoba 17:71–140

Ameghino F (1904) Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. Anal Soc Cient Arg 57:225–291

Ameghino F (1906) Les formations sedimentaires du Crétacé Supèrieur et du Tertiaire de Patagonie, avec un paralieleentre leurs faunes mammalogiques et celles de l´ancien continente. Anal Mus Nac Hist Nat Buenos Aires 3(8):1–568

Ameghino F (1907) Nota sobre una pequeña colección de huesos de mamíferos, procedente de las grutas calcáreas de Iporanga (Sao Paulo, Brazil). Rev. Mus Paulista 7:59–124

Ameghino F (1908) Las formaciones sedimentarias de la Región litoral de Mar del Plata y Chapadmalal. Anal Mus Nac Hist Nat Buenos Aires 3(10):43–428

Ameghino F (1910) Paleontología Argentina: relaciones filogenéticas y geográficas. Anal Inst Enseñ Gen 1:11–84

Amrine-Madsen H, Scally M, Westerman M, Stanhope MJ, Krajewski C, Springer MS (2003) Nuclear gene sequence provides evidence for the monophyly of *Australidelphian marsupials*. Mol Phylogenet Evol 28:186–196

Antoine P-O, Marivaux L, Croft DA, Billet G, Ganerød M, Jaramillo C, Martin T, Orliac MJ, Tejada J, Altamirano AJ, Duranthon F, Fanjat G, Rousse S, Salas Gismondi R (2012) Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. Proc R Soc B 279(1732):1319–1326

Averianov AO, Kielan-Jaworowska Z (1999) Marsupials from the Late Cretaceous of Uzbekistan. Acta Palaeontol Pol 44:71–81

Bonaparte JF, Van Valen LM, Kramartz A (1993) La fauna local de Punta Peligro, Paleoceno Inferior, de la Provincia del Chubut, Patagonia, Argentina. Evol Monogr 14:1–61

Bond M, Carlini AA, Goin FJ, Legarreta L, Ortiz-Jaureguizar E, Pascual R, Uliana MA (1995) Episodes in South American land mammal evolution and sedimentation: testing their apparent concomitance in a Palaeocene succession from Central Patagonia. VI Congr Arg Paleont Bioestrat Trelew, Actas, pp 47–58

Brown B (2004) Atlas of New World Marsupials. Fieldiana Zool (NS) 102:1–308

Burmeister G (1879) Description Physique de la Republique Argentine. II Animaux Vertebres, Premiere partie. PE Coni, Buenos Aires

Cabrera A (1927) Datos para el conocimiento de los Dasiuroideos fósiles argentinos. Rev Mus La Plata 30:271–315

Cabrera A (1928) Un nuevo marsupial Plioceno de Monte Hermoso. Rev Mus La Plata 31: 335–337

Cabrera A, Yepes J (1960) Mamíferos Sudamericanos, vol 1. Ediar, Buenos Aires

Campbell KE Jr (ed) (2004) The Paleogene mammalian fauna of Santa Rosa, Amazonian Perú. Nat Hist Mus Los Angeles County, Sci Ser 40, Los Angeles

Case JA, Goin FJ, Woodburne MO (2005) "South American" marsupials from the Late Cretaceous of North America and the origin of marsupial cohorts. J Mammal Evol 12:461–494

Celaya RA (2005) Orígenes e inicios de la localidad de Aldao (Depto. San Lorenzo). Congreso Argentino de Inmigración y IV Congreso de la Historia de los Pueblos de la Provincia de Santa Fe. Asoc Amigos Arch Gen Prov, Esperanza, Santa Fe. Unpubl. https://www.google.com.ar/#bav=on.2,or.r_qf.&fp=ef598c4af7830a47&q=+Ricardo+Alberto+Celaya.

Chornogubsky L (2010) Sistemática de la familia Polydolopidae (Mammalia, Marsupialia, Polydolopimorphia) de América del Sur y la Antártica. Unpubl thesis, Univ Buenos Aires

Chornogubsky L, Kramarz AG (2012) Nuevos hallazgos de Microbiotheriidae (Mammalia, Marsupialia) en la Formación Pinturas (Mioceno temprano, Argentina). Ameghiniana 49 (4):442–450

Chornogubsky L, Goin FJ, Reguero M (2009) A reassessment of Antarctic polydolopid marsupials (Middle Eocene, La Meseta Formation). Antarct Sci 21(3):285–297

Cifelli RL, Davis BM (2003) Marsupial origins. Science 302:1899–1900

Clyde WC, Wilf P, Iglesias A, Slingerland RL, Barnum T, Bijl PK, Bralower TJ, Brinkhuis H, Comer EE, Huber BT, Ibañez-Mejia M, Jicha BR, Krause JM, Schueth JD, Singer BS, Raigemborn MS, Schmitz MD, Sluijs A, Zamaloa MC (2014) New age constraints for the Salamanca formation and lower Río Chico Group in the western San Jorge Basin, Patagonia, Argentina: implications for K/Pg extinction recovery and land mammal age correlations. Bull Geol Soc Amer

Contreras JR (1983) La comadreja overa. In: Fauna Argentina, Publ 11. Centro Editor de América Latina, Buenos Aires

Cozzuol MA, Goin FJ, de los Reyes M, Rancy A (2006) The oldest species of Didelphis (Mammalia, Marsupialia, Didelphidae), from the Late Miocene of Amazonia. J Mammal 87 (4):663–667

Croft DA, Flynn JJ, Wyss AR (2008) The Tinguiririca fauna of Chile and the early stages of "modernization" of South American mammal faunas. Arq Mus Nac Rio de Janeiro 66(1):1–21

de Muizon C (1991) La fauna de mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucía) Bolivia. In: Suarez-Soruco R (ed) Fósiles y Facies de Bolivia, vol 1, Vertebrados. Rev Técn Yac Petrolíferos Fiscales de Bolivia 12:575–624

de Muizon C (1994) A new carnivorous marsupial from the Palaeocene of Bolivia and the problem of marsupial monophyly. Nature 370:208–211

de Muizon C (1998) *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. Géodiversitas 20:19–142

de Muizon C, Céspedes R (in press) The beginning of the age of therian mammals in South America: Tiupampa, a transition between Northern and Southern worlds in the basal Paleocene. In: Rosenberger AL, Tejedor MF (eds) Origins and evolution of Cenozoic South American mammals. Springer, New York

de Muizon C, Cifelli RL (2001) A new basal "didelphoid" (Marsupialia, Mammalia) from the early Paleocene of Tiupampa (Bolivia). J Vert Paleontol 21:87–97

de Paula Couto C (1952a) Fossil mammals from the begining of the Cenozoic in Brazil. Marsupialia: Polydolopidae and Borhyaenidae. Amer Mus Novitates 1559:1–27

de Paula Couto C (1952b) Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Didelphidae. Amer Mus Novitates 1567:1–26

de Paula Couto C (1952c) A new name for *Mirandaia ribeiroi* Paula Couto, 1952. J Mamm 33:503

de Paula Couto C (1960) Marsupiais fósseis do Paleoceno do Brasil. An Acad Bras Cs 33(3–4): 321–333

de Paula Couto C (1962) Didelfídeos fósiles del Paleoceno de Brasil. Rev Mus Arg Cs Nat "B. Rivadavia" 112:135–66

de Paula Couto C (1970) News on the fossil marsupials from the Riochican of Brazil. An Acad Bras Cs 42(1):19–34

Del Corro J (1977) Un nuevo microbioterio (Marsupialia) del Eoceno de Patagonia. Rev Mus Arg Cs Nat "B. Rivadavia" 2(2):31–33

Dunn RE, Madden RH, Kohn MJ, Schmitz MD, Strömberg CAE, Carlini AA, Ré GH, Crowley J (2013) A new chronology for middle Eocene–early Miocene South American Land Mammal Ages. GSA Bulletin 125(3/4):539–555

Flynn JJ, Swisher CC III (1995) Cenozoic South American land mammal ages: correlation to global geochronologies. In: Berggren WA, Kent DV, Aubry M-P, Hardenbol J (eds) Geochronology, time-scales and global stratigraphic correlation: a unified framework for an historical geology. Soc Strat Geol Spec Pub 54:317–333

Flynn JJ, Wyss AR (1999) New marsupials from the Eocene-Oligocene transition of the Andean Main Range, Chile. J Vert Paleontol 19:533–549

Flynn JJ, Wyss AR, Croft DA, Charrier R (2003) The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal Age. Palaeogeogr Palaeoclim Palaeoecol 195:229–259

Forasiepi AM (2009) Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. Monogr Mus Arg Cs Nat "B Rivadavia" NS 6:1–174

Forasiepi AM, Goin FJ, Martinelli AG (2009) Contribution to the knowledge of the Sparassocynidae (Mammalia, Metatheria, Didelphoidea), with comments on the age of the Aisol Formation (Neogene), Mendoza Province, Argentina. J Vert Paleont 29(4):1–12

Frenguelli J (1921) Los terrenos de la costa atlántica en los alrededores de Miramar (Pcia. de Buenos Aires). Bol Acad Nac Cs Córdoba 24:325–485

Gates W (1932) The Dresden Codex. Maya Society Publication 2, J Hopkins Univ, Baltimore

Gelfo JN, Goin FJ, Woodburne MO, de Muizon C (2009) Biochronological relationships of the earliest South American Paleogene mammalian faunas. Palaeontology 52:251–269

Gingerich PD (1986) George Gaylord Simpson: empirical theoretician. Contrib Geol Sp Paper 3:3–9

Goin FJ (1991) Los Didelphoidea (Mammalia, Marsupialia, Didelphimorphia) del Cenozoico tardío de la Región Pampeana. Unpubl thesis, Univ Nac La Plata

Goin FJ (1997a) New clues for understanding Neogene Marsupial radiations. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) A history of the neotropical fauna. Vertebrate Paleobiology of the Miocene in Colombia. Smithsonian Institute Press, Washington

Goin FJ (1997b) *Thylamys zettii*, nueva especie de marmosino (Marsupialia, Didelphidae) del Cenozoico tardío de la Región Pampeana. Ameghiniana 34(4):481–484

Goin FJ (1997c) Sobre la edad y afinidades de *Zygolestes paranensis* Ameghino, 1898 (Marsupialia, Didelphidae, Marmosinae). Neotropica 43(109–110):15–19

Goin FJ (2001) Marsupiales (Didelphidae: Marmosinae & Didelphinae). In: Mazzanti D, Quintana C (eds) Cueva Tixi: Cazadores y recolectores de las Sierras de Tandilia Oriental. 1: Geología, Paleontología y Zooarqueología. Lab Arqueol Univ Nac Mar del Plata, Publ Esp 1, Mar del Plata

Goin FJ (2006) A review of the Caroloameghiniidae, Paleogene South American "primate-like" marsupials (?Didelphimorphia, Peradectoidea). In: Kalthoff D, Martin T, Möors T (eds) Festband für Herrn Professor Wighart v. Koenigswald anlässlich seines 65. Geburtstages. Palaeontographica Abt. A 278. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart

Goin FJ, Abello MA (2013) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, edad mamífero Colhuehuapense): Microbiotheria y Polydolopimorphia. Ameghiniana 50(1):51–78

Goin FJ, Candela AM (2004) New Paleogene marsupials from the Amazonian basin, Southeastern Perú. In: Campbell KE Jr (ed) The Paleogene mammalian fauna of Santa Rosa, Amazonian Perú. Nat Hist Mus Los Angeles County, Sci Ser 40, Los Angeles

Goin FJ, de los Reyes M (2012) Contribución al conocimiento de los representantes extintos de *Lutreolina* Thomas, 1910 (Mammalia, Marsupialia, Didelphidae). Rev Hist Natural Fund Félix de Azara 1(2):15–25

Goin FJ, Montalvo C (1989) Revisión sistemática y reconocimiento de una nueva especie del género *Thylatheridium* Reig (Marsupialia, Didelphidae). Ameghiniana 25(2):161–167

Goin FJ, Pardiñas U (1996) Revisión de las especies del género *Hyperdidelphys* Ameghino, 1904 (Mammalia, Marsupialia, Didelphidae). Su significación filogenética, estratigráfica y adaptativa en el Neógeno del Cono Sur Sudamericano. Estud Geol 52:327–359

Goin FJ, Palma RM, Pascual R, Powell JE (1986) Persistencia de un primitivo Borhyeanidae (Mammalia, Marsupialia) en el Eoceno temprano de Salta (Formación Lumbrera, Argentina). Aspectos geológicos y paleoambientales relacionados. Ameghiniana 23(1–2):47–56

Goin FJ, Woodburne MO, Case JA, Vizcaíno SF, Reguero M (1999) New discoveries of "opossum-like" marsupials from Antarctica (Seymour Island, Middle Eocene). J Mamm Evol 6 (4):335–365

Goin FJ, Montalvo C, Visconti G (2000) Los Marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (Provincia de La Pampa, Argentina). Rev Esp Geol 56:101–126

Goin FJ, Pascual R, Tejedor MF, Gelfo JN, Woodburne MO, Case JA, Reguero MA, Bond M, Cione AL, Udrizar Sauthier D, Balarino L, Scasso RA, Medina FA, Ubaldón MC (2006) The earliest Tertiary therian mammal from South America. J Vert Paleontol 26:505–510

Goin FJ, Zimicz AN, Reguero MA, Santillana S, Marenssi SA, Moly JJ (2007) New mammal from the Eocene of Antarctica, and the origins of the Microbiotheria. Rev Asoc Geol Arg 62:597–603

Goin FJ, Candela AM, Abello MA, Oliveira EV (2009a) Earliest South American Paucituberculatans and their significance in the understanding of “pseudodiprotodont” marsupial radiations. Zool J Linn Soc 155:867–884

Goin FJ, Zimicz N, de los Reyes M, Soibelzon L (2009b) A new large didelphid of the genus *Thylophorops* (Mammalia: Didelphimorphia: Didelphidae) from the Late Tertiary of the Pampean Region (Argentina). Zootaxa 2005:35–46

Goin FJ, Abello MA, Chornogubsky L (2010) Middle tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America’s Grande Coupure. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The Paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York

Goin FJ, Gelfo JN, Chornogubsky L, Woodburne MO, Martin T (2012) Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: an 80-million year history of Recent Neotropical mammals. The University of Chicago Press, Chicago

Goin FJ, Zimicz AN, Forasiepi AM, Chornogubsky LC, Abello MA (in press) The rise and fall of South American Metatherians: Contexts, Adaptations, Radiations, and Extinctions. In: Rosenberger AL, Tejedor MF (eds) Origins and evolution of Cenozoic South American Mammals. Springer, Dordrecht

Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (2012) The geologic time scale 2012 (vols 1, 2). Elsevier, Amsterdam

Hadler P, Ferigolo J, Goin FJ (2009a) Mamíferos de pequeno porte (Didelphimorphia, Chiroptera e Rodentia) do Pleistoceno final/Holoceno do Brasil, con énfase o Rio Grande do Sul. In: Ribeiro AM, Bauermann SG, Saldanha Scherer S (eds) Quaternario do Rio Grande do Sul. Integrando conhecimentos. Monograf Soci Brasileira Paleontol Porto Alegre

Hadler P, Goin FJ, Ferigolo J, Ribeiro AM (2009b) Environmental change and marsupial assemblages in Holocene successions of Southern Brazil. Mamm Biol 74:87–99

Hartman C (1952) Possums. University of Texas Press, Austin

Hoffstetter R (1963) La faune Pleistocene de Tarija (Bolivia). Note prelimimaire. Bull Mus Nat d’Hist Naturelle 33(2):152–160

Hoffstetter R (1968) Un gisement de mammiferes deseadiens (Oligocene inferieur) en Bolivie. Compt Rendus Acad Sciences 267:1095–1097

Hoffstetter R (1969) Un primate de l’Oligocene interieur sud-american: Branisella boliviana gen. et sp. nov. Compt Rendus Acad Sciences 269:434–437

Hoffstetter R (1976) Rongeurs caviomorphes de l’Oligocene de Bolivie: Palaeovertebrata 7:1–14

Hoffstetter R, Lavocat R (1970) Decouverte dans le Deseadien de Bolivie des genres pentalophodontes appuyant les affinities africaines des rongeurs Caviomorphes. Compt Rendus Acad Sci 271:172–175

Hoffstetter R, Martínez R, Matteur M, Tomasi P (1971) Lacayani, un nouveau gisement bolivien de mammiferes deseadiens (Oligocene inferieur). Compt Rendus Acad Sciences 273:2215–2218

Horovitz I, Sánchez-Villagra MR (2003) A morphological analysis of marsupial mammal higher-level phylogenetic relationships. Cladistics 19:181–212

Horovitz T, Bloch MJ, Ladevèze S, Kurz C, Sánchez-Villagra MR (2009) Cranial anatomy of the earliest marsupials and the origin of opossums. PLoS ONE 4(12):e8278. doi:10.1371/journal.pone.0008278

Kay RF, Madden RH, Vucetich MG, Carlini AA, Mazzoni MM, Re GH, Heizler M, Sandeman H (1999) Revised age of the Casamayoran South American Land Mammal ‘Age’ -climatic and biotic implications. Proc Nat Acad Sci 96(23):13235–13240

Kielan-Jaworowska Z (1975) Possible occurrence of marsupial bones in Cretaceous Eutherian mammals. Nature 255:698–699

Kielan-Jaworowska Z, Cifelli RL, Luo ZX (2004) Mammals from the age of dinosaurs. Origin, evolution, and structure. Columbia University Press, New York

Kirsch JAW (1977) The comparative serology of Marsupialia, and a classification of marsupials. Australian J Zool Suppl Ser 52:1–152

Kirsch JAW, Lapointe FJ, Springer MS (1997) DNA-hybridisation studies of marsupials and their implications for metatherian classification. Australian J Zool 45:211–280

Kraglievich JL (1934) La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. El Siglo Ilustrado, Buenos Aires

Kraglievich JL (1952) El perfil geológico de Chapadmalal y Miramar, provincia de Buenos Aires. Rev Mus Municip Cs Nat Tradicional Mar del Plata 1:8–37

Kuhn TS (1970) The structure of scientific revolutions, 2nd edn. The University of Chicago Press, Chicago (Enlarged)

Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10 edn, vol 1, Holmiae. Salvius, Stockholm

López Austin A (1990) The myths of the Opossum. Pathways of Mesoamerican mythology. University of New Mexico Press, Albuquerque

Luckett WP (1993) An ontogenetic assessment of dental homologies in therian mammals. In: Szalay FS, Novacek MJ, McKenna MC (eds) Mammal phylogeny: mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials. Springer, New York

Luo ZX, Ji Q, Wible JR, Yuan CX (2003) An Early Cretaceous tribosphenic mammal and metatherian evolution. Science 302:1934–1940

Madden RH, Kay RF, Vucetich MG, Carlini AA (2010) Gran Barranca: a 23 million-year record of middle Cenozoic faunal evolution in Patagonia. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The Paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University of Press, New York

Marshall LG (1976a) New didelphine from the la Venta fauna (Miocene) of Colombia, South America. J Paleontol 50(3):402–418

Marshall LG (1976b) Evolution of the Thylacosmilidae, extinct saber-toothed marsupials of South America. PaleoBios 23:1–30

Marshall LG (1977) A new species of *Lycopsis* (Borhyaenidae: Marsupialia) from the La Venta Fauna (Late Miocene) of Colombia, South America. J Paleontol 51(3):633–642

Marshall LG (1979) Review of the Prothylacyninae, an extinct subfamily of South American "Dog-like" Marsupials. Fieldiana NS 3:1–50

Marshall LG (1980) Systematics of the South American Marsupial Family Caenolestidae. Fieldiana NS 5:1–145

Marshall LG (1981a) Review of the Hathlyacyninae, an extinct subfamily of South American "Dog-like" Marsupials. Fieldiana NS 7:1–120

Marshall LG (1981b) The Families and Genera of Marsupialia. Fieldiana NS 8:1–65

Marshall LG (1982a) Systematics of the South American Marsupial Family Microbiotheriidae. Fieldiana NS 10:1–75

Marshall LG (1982b) Systematics of the Extinct South American Marsupial Family Polydolopidae. Fieldiana NS 12:1–109

Marshall LG (1987) Systematics of Itaboraian (middle Paleocene) age "opossum-like" marsupials from the limestone quarry at São José de Itaboraí, Brazil. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty & Sons Pty Lted, Chipping Norton (R Zool Soc New South Wales)

Marshall LG, de Muizon C (1988) The dawn of the age of mamals in South America. Nat Geogr Res 4:23–55

Marshall LG, Pascual R (1978) Una escala temporal radiométrica preliminar de las Edades - mamífero del Cenozoico medio y tardío sudamericano. In: Obra del Centenario del Museo de La Plata, vol 5. La Plata

Marshall LG, Patterson B (1981) Geology and geochronology of the mammal-bearing tertiary of the Valle de Santa Maria and Rio Corral Quemado, Catamarca Province, Argentina. Fieldiana NS 9:1–80

Marshall LG, Pascual R, Curtis GH, Drake RE (1977) South American geochronology: radiometric time scale for Middle to Late Tertiary mammal-bearing horizons in Patagonia. Science 195(4284):1325–1328

Marshall LG, Butler RF, Drake RE, Curtis DH (1981) Calibration of the beginning of the age of mammals in Patagonia. Science 212:43–45

Marshall LG, de Muizon C, Sigé B (1983a) Late Cretaceous mammals (Marsupialia) from Bolivia. Géobios 16:739–745

Marshall LG, Hoffstetter R, Pascual R (1983b) Geocronology of the continental mammal-bearing tertiary of South America. Palaeovertebrata, Mém Extraord:1–93

Marshall LG, de Muizon C, Sigé B (1985) The "Rosetta stone" for mammalian evolution in South America. Nat Geogr Res 1:274–288

Marshall LG, Case JA, Woodburne MO (1990) Phylogenetic relationships of the families of marsupials. In: Genoways H (ed) Current mammalogy, vol 2. Plenum Press, New York

Martin GM (2010) Geographic distribution and historical occurrence of *Dromiciops gliroides* Thomas (Marsupialia, Microbiotheria). J Mamm 91:1025–1035

Mercerat A (1898) Sur de nouveaux restes fossils de Carnassiers primitifs de Monte Hermoso. An Soc Cient Arg 47:56–60

O'Leary MO, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg SL, Kraatz BP, Luo Z-X, Meng J, Ni X, Novacek MJ, Perini, Randall ZS, Rougier GW, Sargis EJ, Silcox MT, Simmons NB, Spaulding M, Velazco PM, Weksler M, Wible JR, Cirranello AL (2013) The placental mammal ancestor and the post–K-Pg Radiation of Placentals. Science 339 (662). doi:10.1126/science.1229237

Oliveira EV (1998) Taxonomia, filogenia e paleobiogeografia de marsupiais "poliprotodontes" do Mesopaleoceno da Bacia de Itaboraí, Rio de Janeiro, Brasil. Unpub thesis, Univ Fed Rio Grande do Sul

Oliveira EV, Goin FJ (2011) A reassesment of bunodont metatherians from the Paleogene of Itaboraí (Brazil): Systematics and age of the Itaboraian SALMA. Revista Brasileira de Paleontologia 14(2):105–136

Oliveira EV, Villa Nova P, Goin FJ, Dos Santos Avilla L (2011) A new hyladelphine marsupial (Didelphimorphia, Didelphidae) from cave deposits of northern Brazil. Zootaxa 3041:51–62

Pascual R (1980a) Prepidolopidae, nueva familia de Marsupialia Didelphoidea del Eoceno sudamericano. Ameghiniana 17(3):216–242

Pascual R (1980b) Nuevos y singulares tipos ecológicos de marsupiales extinguidos de América del Sur (Paleoceno tardío o Eoceno temprano) del Noroeste argentino. Actas 2 Congr Arg Paleontol Bioestrat, 1 Congr Latinoam Paleontol Buenos Aires 3:151–173

Pascual R (1981) Adiciones al conocimiento de *Bonaparterium hinakusijum* (Marsupialia, Bonapartheriidae) del Eoceno temprano del Noroeste argentino. Ann 2 Congr Latinoam Paleontol Porto Alegre 2:507–520

Pascual R (1983) Novedosos marsupiales paleógenos de la Formación Pozuelos (Grupo Pastos Grandes) de la Puna, Salta, Argentina. Ameghiniana 20(3–4):265–280

Pascual R (1984) La sucesión de las Edades-mamífero, de los climas y del diastrofismo sudamericanos durante el Cenozoico: fenómenos concurrentes. Anal Acad Nac Cs Exact Fís Nat 36:15–37

Pascual R (1996) Late Cretaceous-recent land-mammals. An approach to South American geobiotic evolution. Mastozool Neotr 3(2):133–152

Pascual R (2006) Evolution and geography: the biogeographic history of South American land mammals. Ann Missouri Bot Gard 93:209–230

Pascual R, Odreman Rivas O (1971) Evolución de las comunidades de los vertebrados del Terciario argentino, los aspectos paleozoogeográficos y paleoclimáticos relacionados. Ameghiniana 8(3–4):372–412

Pascual R, Odreman Rivas O (1973) Las unidades estratigráficas del Terciario portadoras de mamíferos. Su distribución y sus relaciones con los acontecimientos diastróficos. Acts 5 Congr Geol Arg 3:293–338

Pascual R, Ortiz-Jaureguizar E (1990) Evolving climates and mammal faunas in Cenozoic South America. J Human Evol 19(1–2):23–60

Pascual R, Ortiz-Jaureguizar E (1991) El Ciclo Faunístico Cochabambiano (Paleoceno Temprano): su incidencia en la historia biogeográfica de los mamíferos sudamericanos. In: Suáres Soruco R (ed) Fósiles y facies de Bolivia, vol 1: Vertebrados. Rev Técn Yacimientos Petrolíferos Fiscales, Bolivia 12(3–4), Santa Cruz de la Sierra

Pascual R, Ortiz-Jaureguizar E (2007) The South American mammalian history: two major unrelated episodes. J Mamm Evol 14:75–137

Pascual R, Ortega Hinojosa EJ, Gondar D, Tonni EP (1965) Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio bonaerense. An Com Invest Cient Prov Buenos Aires 6:165–193

Pascual R, Ortega Hinojosa EJ, Gondar D, Tonni EP (1966) Las edades del Cenozoico mamalífero de la provincia de Buenos Aires. In: Borrello AV, Pascual R (eds) Paleontografía Bonaerense, 4: Vertebrata 2. Com Invest Cien Prov Buenos Aires, La Plata, pp 3–12

Pascual R, Bond M, Vucetich MG (1981) El Subgrupo Santa Bárbara (Grupo Salta) y sus vertebrados. Cronología, paleoambientes y paleobiogeografía. Actas 8 Congr Geol Arg 3: 743–758

Pascual R, Ortiz-Jaureguizar E, Prado JL (1996) Land mammals: paradigm of Cenozoic South American geobiotic evolution. In: Arratia G (ed) Contributions of Southern South America to vertebrate paleontology München Geowiss Abh (A) 30, München

Patterson (1937) Didelphines from the Pliocene of Argentine. Proc Geol Soc Amer:379

Patterson B, Pascual R (1968) Evolution of mammals in southern continents. V. Fossil mammal fauna of South America. Quart Rev Biol 43(4):409–451

Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast A, Erk FC, Glass B (eds) Evolution of mammals and Southern continents. State Univesity of New York Press, Albany

Prado JL, Goin FJ, Tonni EP (1985) *Lestodelphys halli* (Mammalia, Didelphidae) in Holocene sediments of Southeastern Buenos Aires Province (Argentina): morphological and palaeoenvironmental considerations. Quatern South Amer Antarct Penins 3:93–107

Ré GH, Bellosi ES, Heizler M, Vilas JF, Madden RH, Carlini AA, Kay RF, Vucetich MG (2010) A geochronology for the Sarmiento Formation at Gran Barranca. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York

Reig OA (1952) Descripción previa de nuevos ungulados y marsupiales fósiles del Plioceno y del Eocuartario argentinos. Rev Mus Mun Cs Nat Trad Mar del Plata 1:119–129

Reig OA (1955a) Noticia preliminar sobre la presencia de microbiotherinos vivientes en la fauna sudamericana. Invest Zool Chilenas 2:121–130

Reig OA (1955b) Un Nuevo género y especie de cenolestinos del Plioceno de la Provincia de Buenos Aires. Rev Asoc Geol Arg 10(1):60–71

Reig OA (1957a) Nota previa sobre los marsupiales de la formación Chasicó. Ameghiniana 1 (3):27–31

Reig OA (1957b) Sobre la posición sistemática de Zygolestes paranensis Amegh. Y de Zygolestes entrerrianus Amegh., conuna reconsideración sobre la edad y la correlación del “Mesopotamiense“. Holmbergia 5:209–226

Reig OA (1958a) Comunicación preliminar sobre nuevas especies del género *Thylatheridium* Reig (Mammalia, Didelphidae). Neotropica 4(15):89–95

Reig OA (1958b) Notas para una actualización el conocimiento de la fauan de la formación Chapadmalal. I. Lista faunística preliminar. Acta Geol Lilloana 2:251–254

Reig OA (1958c) Notas para una actualización el conocimiento de la fauan de la formación Chapadmalal. II. Amphibia, Reptilia, Aves, Mammalia (Marsupialia; Didelphidae, Borhyaenidae). Acta Geol Lilloana 2:255–283

Reig OA, Simpson GG (1972) *Sparassocynus* (Marsupialia, Didelphidae), a peculiar mammal from the late Cenozoic of Argentina. J Zool London 167:511–539

Ride WDL (1964) A review of Australian fossils marsupials. J R Soc Western Australia 47:97–131

Riggs E, Patterson B (1939) Stratigraphy of late Miocene and Pliocene deposits os the Province of catamarca (Argentina), with notes on the faunae. Physis 14:143–162

Ringuelet AB (1953) Revisión de los Didélfidos fósiles argentinos. Rev Mus Cs Nat La Plata NS 2:265–308

Ringuelet AB (1966) Marsupialia. In: Borrello AV, Pascual R (eds) Paleontografía Bonaerense, Vol 4 Vertebrata. Com Invest Cient Prov Bsuenos Aires, La Plata

Rougier GW, Wible JR, Novacek MJ (1998) Implications of *Deltatheridium* specimens for early marsupial history. Nature 396:459–463

Rougier GW, Wible JR, Beck RMD, Apesteguía S (2012) The Miocene mammal *Necrolestes* demonstrates the survival of a Mesozoic nontherian lineage into the late Cenozoic of South America. PNAS 109:20053–20058

Rovereto R (1914) Los estratos araucanos y sus fósiles. Anal Mus Hist Nat Buenos Aires 25:1–249

Rowe T (1998) Definition, diagnosis, and origin of mammalia. J Vert Paleontol 8(3):241–264

Rusconi R (1932) Una nueva especie de comadreja fósil *Didelphys seneti* n. sp. An Soc Cient Arg 113:213–215

Sánchez-Villagra MR (2001) The phylogenetic relationships of argyrolagid marsupials. Zool J Linn Soc 131:481–496

Sánchez-Villagra MR (2012) Why are there fewer marsupials than placentals? On the relevance of geography and physiology to evolutionary patterns of mammalian diversity and disparity. J Mammal Evol. doi:10.1007/s10914-012-9220-3

Sánchez-Villagra MR, Kay RF (1997) A skull of *Proargyrolagus*, the oldest argyrolagid (Late Oligocene Salla Beds, Bolivia), with brief comments concerning its paleobiology. J Vert Paleontol 17:717–724

Sánchez-Villagra MR, Kay RF, Anaya-Daza F (2000) Cranial anatomy and palaeobiology of the miocene marsupial *Hondalagus altiplanensis* and a phylogeny of argyrolagids. Palaeontol 43 (2):287–301

Sbarra N (1963) La Plata tuvo una Universidad al aire libre. In: Universidad nueva y ámbitos culturales platenses. Ed. UNLP, La Plata

Seba A (1734) Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam. Opus, cui, in hoc rerum genere, nullum par exstitit. Ex toto terrarum orbe collegit, digessit, et depingendum curavit, vol I. Wetstenium. Smith & Janssonio-Waesbergios, Amsterdam

Sigé B (1971) Les Didelphoidea de Laguna Umayo (Formation Vilquechico, Crétacé supérieur, Pérou), et le peuplement marsupial d'Amérique du Sud. Compt Rendus Acad Sci 273:2479–2481

Sigé B (1972) La faunule de mammifères du Crétacé supérieur de Laguna Umayo (Andes péruviennes). Bull Mus Nat Hist Nat 99 Sc Terre 19:375–409

Sigé B, Sempere T, Butler RF, Marshall LG, Crochet J-Y (2004) Age and stratigraphic reassessment of the fossil-bearing Laguna Umayo red mudstone unit, SE Peru, from regional stratigraphy, fossil record, and paleomagnetism. Géobios 37:771–794

Simpson GG (1932a) Some new or little known mammals from the *Colpodon* beds of Patagonia. Amer Mus Novit 575:1–12

Simpson GG (1932b) The supposed occurrences of Mesozoic mammals in South America. Amer Mus Novit 530:1–9

Simpson GG (1935a) Descriptions of the oldest known South American mammals, from the Río Chico formation. Amer Mus Novit 793:1–25

Simpson GG (1935b) Note of the classification of Recent and fossil opossums. J Mammal 16: 134–137

Simpson GG (1938) A new marsupial from the Eocene of Patagonia. Amer Mus Novit 989:1–5

Simpson GG (1948) The beginning of the age of mammals in South America, Part 1. Bull Amer Mus Nat Hist 91:1–232

Simpson GG (1950) History of the fauna of Latin America. Am Sci 38:361–389

Simpson GG (1967) The beginning of the age of mammals in South America, Part 2. Bull Amer Mus Nat Hist 137:1–259

Simpson GG (1972) Didelphidae from the Chapadmalal Formation in the Museo Municipal de Ciencias Naturales of Mar del Plata. Publ Mus Cs Nat Trad Mar del Plata 2:1–40

Simpson GG (1974) Notes on the Didelphidae (Mammalia, Marsupialia) from the Huayquerian (Pliocene) of Argentian. Amer Mus Novit 2259:1–15

Simpson GG (1980) Splendid isolation: the curious history of South American mammals. Yale Univesity Press, New Haven

Sinclair E (1906) Marsupialia of the Santa Cruz beds. In: Reports of the Princeton University Expeditions to Patagonia, 1896–1899, 4 (Paleontology). Princeton

Szalay FS (1982) A new appraisal of marsupial phylogeny and classification. In: Archer M (ed) Carnivorous marsupials, vol 2. R Zool Soc New South Wales, Sydney

Szalay FS (1994) Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge University Press, New York

Tejedor MF, Goin FJ, Gelfo JN, López G, Bond M, Carlini AA, Scillato-Yané GJ, Woodburne MO, Chornogubsky L, Aragón E, Reguero M, Czaplewski N, Vincon S, Martin GM, Ciancio M (2009) New Early Eocene mammalian fauna from Western Patagonia, Argentina. Amer Mus Novit 3638:1–42

Tomassini RL, Montalvo CI, Deschamps CM, Manera T (2013) biochronology of the Monte Hermoso formation (early Pliocene) at its type locality, Buenos Aires Province, Argentina. J South Ameri Earth Sci 48:31–42

Tonni EP (2009) Los mamíferos del Cuaternario de la región pampeana de Buenos Aires, Argentina. In: Ribeiro AM, Girardi Bauermann C, Saldanha Scherer C (eds) Quaternario do Rio Grande do Sul. Integrando Conhecimentos. Monogr Soc Brasileira Paleontol, Porto Alegre

Ugalde MF (2006) Difusión en el período de Desarrollo Regional: algunos aspectos de la iconografía Tumaco-Tolita. Bull Instit Français d'Études Andines 35(3):397–407

Villarroel C, Marshall LG (1982) Geology of the Deseadan (early Oligocene) age Estratos Salla in the Salla-Luribay basin, Bolivia, with description of new Marsupialia. Geobios Mem Spec 6:201–211

Villarroel C, Marshall LG (1983) Two new late Tertiary marsupials (Hathlyacyninae and Sparassocyninae) from the Bolivian Altiplano. J Paleontol 57:1061–1066

Voss RS, Jansa SA (2009) Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. Bull Amer Mus Nat Hist 322:1–177

Williamson TE, Brusatte SL, Carr TD, Weil A, Standhardt BR (2012) The phylogeny and evolution of Cretaceous-Palaeogene metatherians: cladistic analysis and description of new early Palaeocene specimens from the Nacimiento Formation, New Mexico. J Syst Palaeontol 10(4):625–651

Williamson TE, Brusatte SL, Wilson GP (2014) The origin and early evolution of metatherian mammals: the Cretaceous record. ZooKeys 465:1–76. doi:10.3897/zookeys.465.8178

Wilson DE, Mittermeier RA (eds) (2015) Handbook of the Mammals of the World, vol 5, Monotremes and Marsupials. Lynx Edicions, Barcelona, p 799

Winge A (1893) Jordfundne og nulevende Pungdyr (Marsupialia) fue Lagoa Santa, Minas Gerais, Brasilien. Med, Udsigt over Pungdyrenes Slaegtskab. E Mus Lund 11(2):1–149

Woodburne MO, Zinsmeister WJ (1982) Fossil land mammal from Antarctica. Science 218:284–286

Woodburne MO, Zinsmeister WJ (1984) The first land mammal from Antarctica and its biogeographic implications. J Paleontol 58:913–948

Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN, LÃ³pez GM, Iglesias A, Zimicz AN (2013) Paleogene Land Mammal Faunas of South America; a response to global climatic changes and indigenous floral diversity. J Mamm Evol. doi:10.1007/s10914-012-9222-1

Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN, López GM, Iglesias A, Zimicz AN (2014a) Paleogene Land Mammal Faunas of South America; a response to global climatic changes and indigenous floral diversity. J Mamm Evol. doi:10.1007/s10914-012-9222-1

Woodburne MO, Goin FJ, Raigemborn MS, Heizler M, Gelfo JN, Oliveira EV (2014b) Revised timing of the South American early Paleogene land mammal ages. J S Am Earth Sci 54:109–119

Wyss AR, Norell MA, Flynn JJ, Novacek MJ, Charrier R, Salinas P, McKenna M, Meng J (1990) A new Early Tertiary mammal fauna from central Chile: implications for Andean tectonics. J Vert Paleontol 10:518–522

Wyss AR, Flynn JJ, Norell MA, Swisher CCIII, Novacek MJ, McKenna MC, Charrier R (1994) Paleogene mammals from the Andes of Central Chile: a preliminary taxonomic, biostratigraphic, and geochronologic assessment. Amer Mus Novit 3098:1–31

Zetti A (1967) Sobre la presencia del género *Marmosa* (Didelphidae, Marsupialia) en sedimentos de la Formación Epecuén (Plioceno Medio). Ameghiniana 5(5):169–173

Zimicz AN (2014) Avoiding competition: the ecological history of metatherian carnivores. J Mamm Evol 21(4):383–393

Chapter 2
South American Living Metatherians: Physiological Ecology and Constraints

Abstract South American living metatherians are relatively inconspicuous and comprise ca. 10 % of the region's mammal species richness. Most of them are small-sized (<150 g), with long tails and grasping hands and feet, and resemble one another in their general appearance. Individuals are solitary, nocturnal or crepuscular, and most of them are arboreal or scansorial. Two orders are exclusive of South America (Microbiotheria and Paucituberculata), while a third (Didelphimorphia) ranges from Patagonia (Argentina) to the border between USA and Canada. The ecology, physiology, and reproductive traits of living South American marsupials have been poorly studied. This chapter describes several aspects of their natural history and how they influence their recent distribution, as they probably did so throughout the Cenozoic. Physiological constraints include variable energetic costs for regulating metabolic processes, due to low rates of metabolism, the possibility to enter torpor/hibernation, and the storage of different types of fat tissues available for those varied processes. Reproduction, which can be characterized by a short gestation period and long, energy-demanding, breeding period, shows specific differences in strategies (e.g., semelparity, partial semelparity, iteroparity) and their main traits (e.g., litters per year and litter size, teat number). South American marsupials make a complete use of the habitat available to them and have a broad, generally opportunistic and omnivorous diet. These adaptations, combined with a general small size, small energy expenditure on foraging and other daily activities, limit their distribution. Despite these constraints, South American marsupials seem to thrive in environments where competition with other animals might be strong (e.g., tropical and subtropical climates), or where a few small mammals can survive (e.g., temperate and temperate-cold climates) due to several environmental limitations.

Keywords Marsupialia · South America · Physiology · Ecology · Distribution · Reproductive strategy · Life histories · Ecological constraints

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8_2

2.1 Introduction

Our knowledge of the natural history of South American living metatherians is still very incomplete, despite a long history since their discovery (Hershkovitz 1987). Living New World marsupials were some of the first animals to receive the attention of naturalists after the early voyages of exploration to central and northern South America, back in the 1500s (Hershkovitz 1987; Tyndale-Biscoe and Renfree 1987). Taking into account their size and habits, they are relatively inconspicuous components of the mammal fauna of this continent, comprising ca. 10 % of the region's species richness (Streilen 1982; Birney and Monjeau 2003). Most of them are solitary, nocturnal or crepuscular, live in tropical and subtropical ecosystems (Tyndale-Biscoe 2005; Gardner 2008), and are arboreal or scansorial (Eisenberg 1981; Vieira 2006a, b). They are generally small-sized (<150 g), with long tails and grasping hands and feet, and resemble one another in their general appearance (Nowak 1999; Tyndale-Biscoe 2005).

Of the three currently recognized orders of new World marsupials, two are exclusive to South America (Microbiotheria and Paucituberculata) (Figs. 2.1 and 2.5b, c). The remaining one, the Didelphimorphia (Figs. 2.2, 2.3, 2.4 and 2.5a), is distributed throughout all of South and Central America, and the southern and eastern portion of North America to the border between USA and Canada. The Order Microbiotheria includes a single living species, the "*monito del monte*" *Dromiciops gliroides* Thomas, which is restricted to the Valdivian Temperate Rainforest (sensu Olson et al. 2001; Martin 2010) (Fig. 2.5b). The Order Paucituberculata includes six or seven species allocated in three genera: *Caenolestes*, *Lestoros* and *Rhyncholestes*, with a distribution concentrated in the Andean "*páramos*" and "*subpáramos*", the upper stratum of the *Yungas* in Perú, Bolivia and adjacent areas (for *Caenolestes* and *Lestoros*), and the Valdivian Temperate Rainforest (for *Rhyncholestes*; Brown 2004; Martin 2008, 2011; Myers and Patton 2008; Patterson 2008; Timm and Patterson 2008) (Fig. 2.5c). Recent didelphimorphs are grouped in the family Didelphidae , which has been recently subdivided into four subfamilies: Glironiinae, Caluromyinae, Hyladelphinae, and Didelphinae (Voss and Jansa 2009). The subfamily Didelphinae is distributed from 48°N to 48°S, with the highest diversity in tropical and subtropical South America (Brown 2004; Birney and Monjeau 2003; Martin 2012; Fig. 2.6a). Species of the subfamily Caluromyinae range from 18°N to 30°S (Fig. 2.6b), in forested habitats of the Neotropical Region (sensu Morrone 2004, 2006; see Chap. 4). A few records fall within the South American Transition Zone (sensu Morrone 2004, see Chap. 4), representing low altitude localities (<2000 m) in Venezuela, Colombia and Ecuador, which have a Neotropical affinity (Brown 2004). The distribution of representatives of the subfamilies Glironiinae and Hyladelphinae is restricted to South America, ranging from 10°N to 15°S and 0° to 17°S, respectively (Bernarde and Machado 2008; Voss et al. 2001; Astúa 2006; Fig. 2.6c, d, respectively).

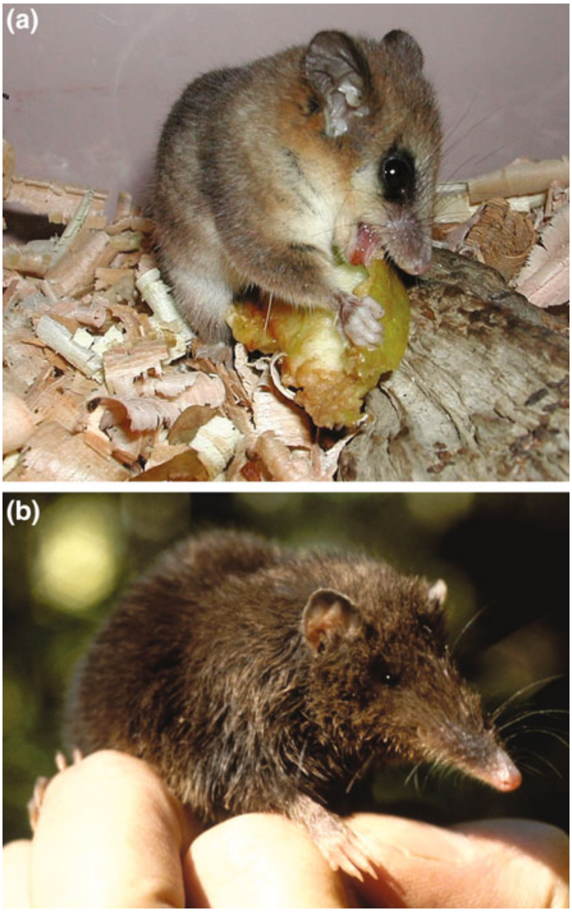
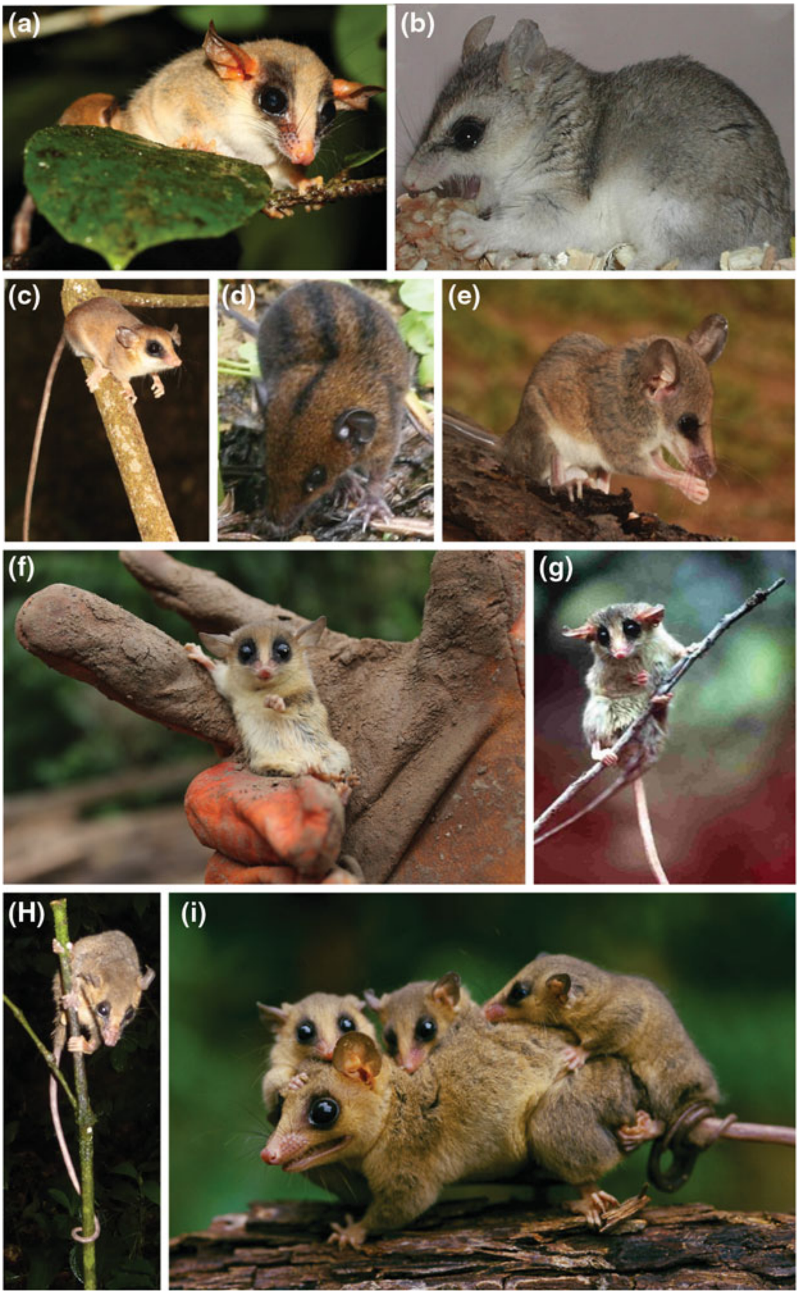


Fig. 2.1 Non-didelphid South American marsupials: **a** *Dromiciops gliroides* (Microbiotheria, Microbiotheriidae), northwestern Patagonia, Argentina (photograph by Gabriel Martin). **b** *Rhyncholestes raphanurus* (Paucituberculata, Caenolestidae), La Picada, Chile (photograph by Peter Meserve, Brian Lang, and Bruce Patterson)

The ecology, physiology, and reproductive traits of living South American marsupials have been poorly studied for most species (e.g., Eisenberg and Wilson 1981; Willig and Gannon 1997; Birney and Monjeau 2003; Martin in preparation), although an increasing number of works has been produced in the last 30 years (e.g., O'Connell 1979; Atramentowicz 1986; Monteiro-Filho and Cáceres 2006).

This chapter introduces several aspects of the physiology and ecology of living South American marsupials. It illustrates how these constraints limit their distribution in South America and, probably, did so throughout the Cenozoic (see also Chap. 6). The taxonomic arrangement follows mostly that of Voss and Jansa (2009), with the exception of recently described species.


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(H)
(i)

◀ **Fig. 2.2** South American small-sized marsupials referable to the family Didelphidae (Didelphimorphia) : **a** *Hyladelphys kalinowskii*, La Trinidad Mountains, French Guiana; **b** *Lestodelphys halli*, central Patagonia, Argentina; **c** *Gracilinanus emiliae*, Petit-Saut, Sinnamary, French Guiana; **d** *Monodelphis gardneri*, Central Andes, Perú; **e** *Marmosops parvidens*, Tresor Natural Reserve (Kaw-Roura), French Guiana; **f** *Marmosa murina*, Ecuador; **g** *Gracilinanus microtarsus*, southeastern Brazil; **h**, **i**, *Micoureus demerarae*, Tresor Natural Reserve (**h**), and Madidi National Park, Bolivia (**i**). Photographs by Sylvain Pincebourde (**a**), Gabriel Martin (**b**), Mael Dewynter (**c**), Fabrice Schmitt (**d**), Jean-Francois Szpigel (**e**), Max Bernal Montes (**f**), Vitor Rademaker (**g**), Francois Catzeflis (**h**), Andre Baertschi (**i**). Drs. Francois Catzeflis and Sergio Solari facilitated several of the photos here displayed

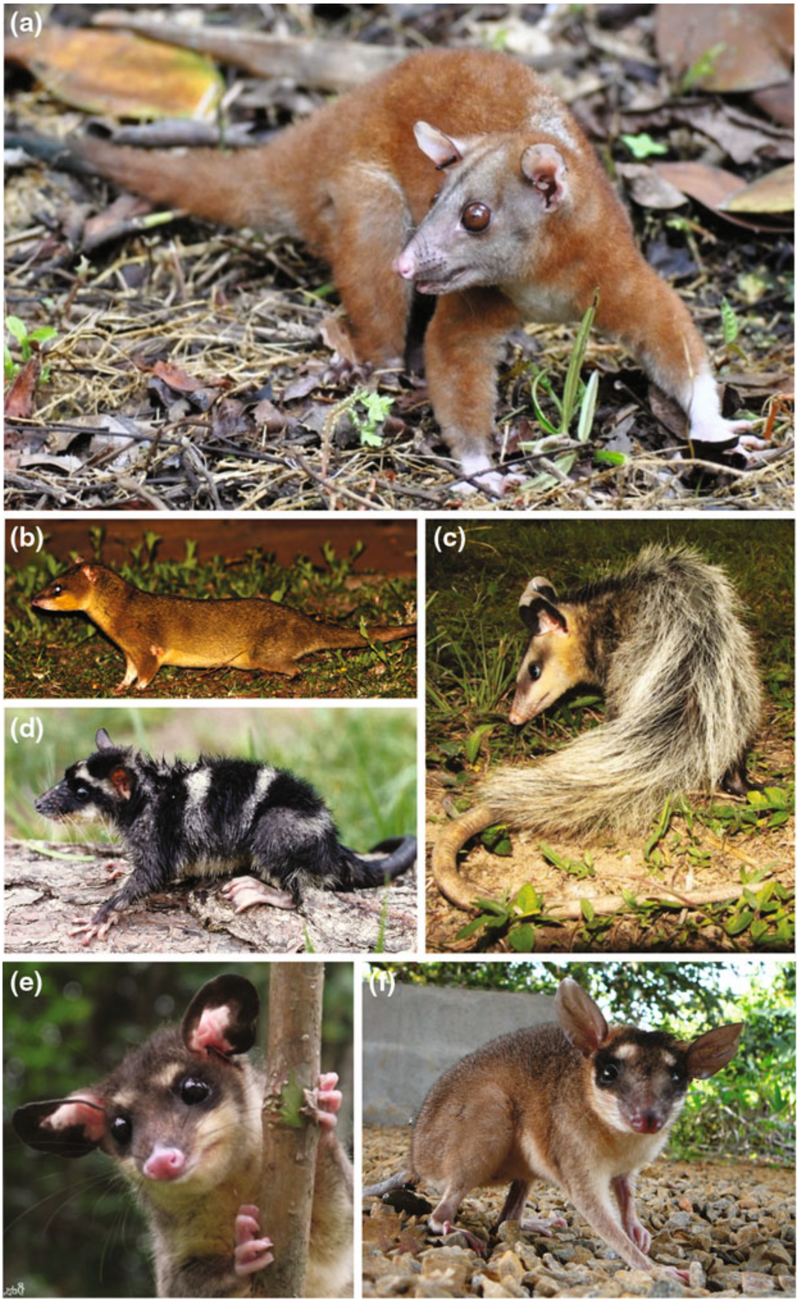
2.2 Thermal Constraints

Most South American living marsupials are nocturnal and/or crepuscular, being active during the coldest part of the day and facing high thermoregulatory costs during foraging, feeding, and other physiologically demanding activities (Geiser 2003). Despite this, a few studies on the thermal biology of South American marsupials have documented a high capacity for thermal regulation and the ability to achieve metabolic rates higher than most placentals (Dawson and Olson 1987; Bozinovic et al. 2004, 2005; Ribeiro and Bicudo 2007).

Marsupials can be characterized as having low basal metabolic rates (BMR), high thermal conductance due to a large surface area/volume ratio, and low body temperatures (McNab 1982; Hume 1999; Geiser 2003; Tyndale-Biscoe 2005). Several studies have found different correlation values between BMR and ambient temperature, climate, substrate use, and the ability to enter torpor and/or hibernation (McNab 2005), with body mass being pointed out as the main determinant in the ability of New World marsupials to thermoregulate (Harder and Fleck 1997; McNab 2005). Feeding preferences and/or diet show little or no direct relationship to BMR (Hume 1999).

Apart from this, marsupials have been found to use different mechanisms for thermogenesis than those of placentals (Riek and Geiser 2014). The main source for non-shivering thermogenesis in placentals is brown adipose tissue (BAT) (Jastroch et al. 2008; Riek and Geiser 2014). However, some studies in marsupials show that BAT is absent, while others show BAT is present but nonfunctional (Hope et al. 1997; Rose et al. 1999). Therefore BAT and its adaptive use in marsupials remains controversial. Also, marsupials are able to use vasoconstrictor-induced non-shivering and shivering thermogenesis in skeletal muscles (Geiser et al. 2003 and literature cited therein), which in turn might represent the most common adaptation as a response to cold exposure. Several of these adaptations have been documented for Australian marsupials but little or no information is available for South American species.

Despite differences in size, habitat use and diet, data on BMR has been found to be similar among marsupials in general (Dawson and Hulbert 1970; Hulbert and

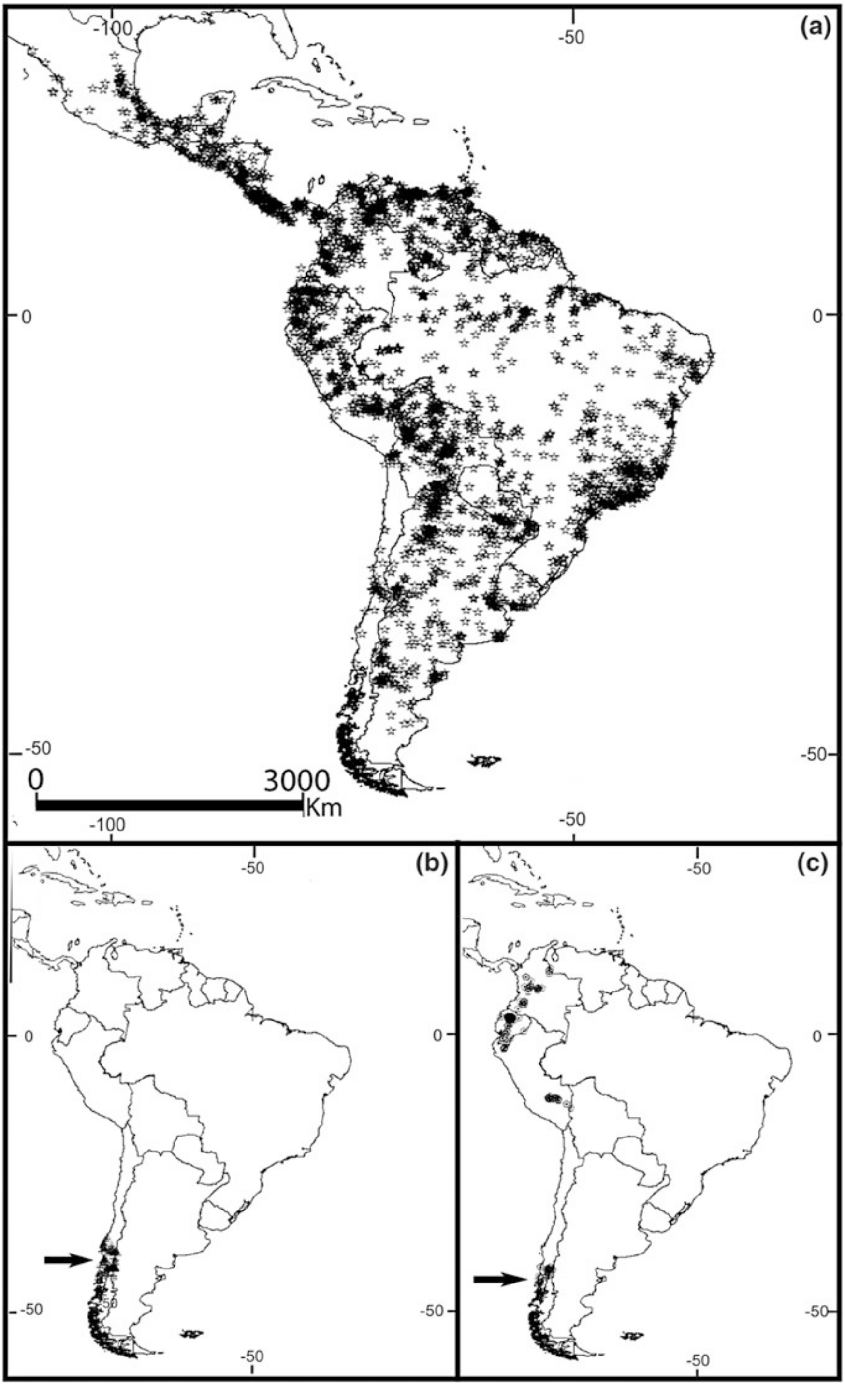

(a)
(b)
(c)
(d)
(e)
(f)

◀ **Fig. 2.3** South American medium-sized marsupials referable to the Family Didelphidae (Didelphimorphia): **a** *Caluromys derbianus*, Costa Rica; **b** *Lutreolina crassicaudata*, Corrientes Province, Argentina; **c** *Didelphis imperfecta*, Petit Saut (Sinnamary), French Guiana; **d** *Chironectes minimus*, Mata Atlantica, southeastern Brazil; **e** *Philander frenatus*, Santa Catarina, Brazil; **f** *Metachirus nudicaudatus*, Cacao, French Guiana. Photographs by Joseph Rupert (**a**), Guillermo Gabriel Soteras (**b**), Sebastien Barrioz (**c**), Maurício E. Graipel (**d**), "danybehs" (Project Noah) (**e**), Francois Catzeflis (**f**). Michael Butcher, Francois Catzeflis and Karen Loughrey (Project Noah) facilitated several of the photos here displayed

Dawson 1974; Dawson and Wolfers 1978; McNab 1978, 1986; Thompson 1988; Wallis and Farrell 1992; Ribeiro and Bicudo 2007). The BMR of South American marsupials varies from 50.6 to 99.1 % of that expected for mammals, with only one species showing a marginally high basal rate by mammalian standards (i.e., *Didelphis marsupialis* with 105 %) (McNab 2005). Predicted values of BMR from allometric equations show that marsupials have substantially lower BMR than similar sized placentals living in similar environments, especially at small body masses (Geiser 2003; McNab 2005). Low BMRs have often been described as a poor adaptation to tolerate temperate-cold climates and, hence, a factor limiting the distribution of marsupials on a continental scale. It has also been argued that low BMRs reflect primitive thermoregulatory characteristics of ancestral mammals. Recently, and in contrast to this, it has been suggested that a low BMR in marsupials might be influenced by physiological and ecological constraints (e.g., water balance, feeding, predation), or climate unpredictability (e.g., daily and/or seasonal temperature variation, rainfall) (Geiser 2003 and literature cited therein). Lovegrove (2000) has argued that BMR is mainly determined by resource availability during certain periods of time, and throughout a limited space (i.e., the areas where individuals forage for food). Clearly, several factors might influence energy balance in marsupials depending on their size, thermoregulation ability, environmental constraints, and phylogenetic affinities (Geiser 2003; McNab 2005; Riek and Geiser 2014).

Most studies show that American marsupials are similar in physiology and metabolism to Australian marsupials, especially dasyurids (Hume 1999; McNab 2005; Tyndale-Biscoe 2005). Several studies point to a relationship between thermal regulation and BMR, especially for Australian marsupials which are very competent homeotherms, but these studies have not been replicated in American marsupials (Dawson and Dawson 1982). In general, New World marsupials show a higher BMR than Old World marsupials (McNab 1978), an exception being *D. gliroides*, which seems to be closer in physiological ecology to Australian marsupials (Bozinovic et al. 2004). This particular fact could be a result of the phylogenetic affinities of Microbiotheria with Australian marsupials, adding support to the idea in which critical temperatures, as measured by thermoneutral zones (in turn, highly related to BMR), are all influenced by phylogeny (Riek and Geiser 2014).

Fig. 2.4 **a**–**c** A female specimen of *Lutreolina crassicaudata* showing seven pouch-young attached to its nipples. **a** handling of the specimen by researchers for sexing and measuring; **b** a view of its ventral side; **c** the same specimen and view, with completely relaxed pouch. The specimen was captured at Fazenda Experimental da Ressacada (Universidade Federal do Santa Catarina), Florianópolis, Santa Catarina, Brazil. Photographs by Laise Orsi Becker


(a)
-100
-50
0
0
-50
-50
0
3000
Km
-100
-50
(b)
-50
0
-50
-50
(c)
-50
0
0
-50
-50
-50

◀ **Fig. 2.5** Distribution (known localities) of the three orders of New World marsupials: Didelphimorphia (**a**), Microbiotheria (**b**), and Paucituberculata (**c**). Didelphimorphia does not include North American localities, referrable to *Didelphis virginiana*

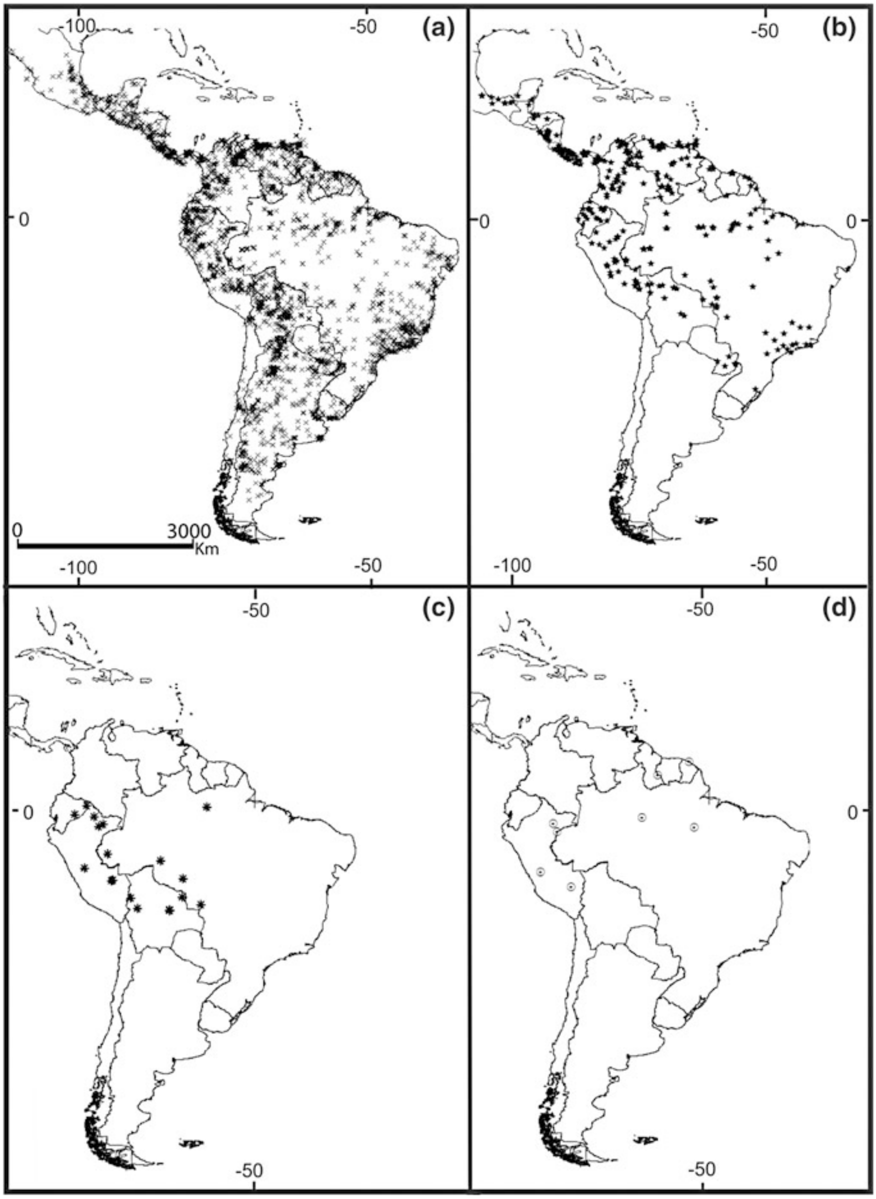


Fig. 2.6 Distribution of the four subfamilies of Didelphidae: Didelphinae (**a**), Caluromyinae (**b**), Glironiinae (**c**), and Hyladelphinae (**d**). Didelphimorphia does not include North American localities, referrable to *Didelphis virginiana*

2.3 Feeding Constraints

Feeding habits of South American marsupials were, until recently, mostly based on qualitative data and, to certain extent, are still poorly known (Cordero and Nicolas 1987, Lee and Cockburn 1987, Hume 1999, 2003). Traditionally considered to represent the ancestral and generalized omnivore/insectivore pattern of food consumption (Lee and Cockburn 1987), recent quantitative studies have revealed a large variation in the preferences of living New World marsupial diets (e.g., Carvalho et al. 1999; Astúa de Moraes et al. 2003; Ceotto et al. 2009; García et al. 2009).

Studies on the diet of South American marsupials conform to a series of feeding categories (Eisenberg 1981, Martin in preparation), ranging from predominantly frugivorous to a diet that can be mostly characterized as animalivorous, with several species which can be included in animalivore/omnivore and animalivore/frugivore categories. Proportionately, the diets of South American marsupials show that 14 genera (63.6 %) fall into the animalivore/frugivore category, three (13.6 %) in the animalivore/omnivore category, three (13.6 %) in the frugivore/animalivore category, one (4.5 %) in the animalivore category (*Lestodelphys*), and one (4.5 %) in the omnivore category (*Didelphis*) (Table 2.1). Diet information is available, mainly from tropical/subtropical environments, for medium/large-sized species and a few small-sized ones (e.g., Atramentowicz 1988; Busch and Kravetz 1991; Freitas et al. 1997; Carvalho et al. 1999; Fernandes et al. 2006; Ceotto et al. 2009; Pires et al. 2009; Bocchiglieri et al. 2010; Macedo et al. 2010). However, it is not clear whether data on a single species from polytypic genera can be extrapolated to the rest of the species (e.g., *Monodelphis domestica* to some *Monodelphis* spp.), especially considering the variation in habitats, latitude, and altitude in many of them (e.g., *Monodelphis*, *Thylamys*). Also, several of these polytypic genera conform to a similar craniodental and anatomically conservative pattern of mastication, despite living in different environments, showing how versatile and efficient the tribosphenic molar and food processing in these marsupials is. Despite the information presented above, the inclusion of species in feeding categories should be used with caution due to overlaps in general consumption patterns (Astúa de Moraes et al. 2003).

In recent years, the role of marsupials as seed dispersers especially in tropical and subtropical environments has been acknowledged (Thielen et al. 1997; Amico and Aizen 2000; Cáceres 2000; Cáceres and Monteiro-Filho 2000; Cáceres et al. 2002; Amico et al. 2009; García et al. 2009; Cantor et al. 2010), a role which was previously attributed to birds, bats, monkeys, and some rodents. In order to be a good disperser, seeds must pass undamaged through the digestive tract and be deposited at places favorable to germination (Cáceres 2006). Under some circumstances, the passage through the gut is critical in the development of a “holdfast” mechanism which affects the seed’s attachment to the host plant (Amico and Aizen 2000;

Table 2.1 Feeding and foraging categories of South American marsupial genera (n = number of species within each genera)

Genus (*n*)	Feeding category	Foraging category
Caluromys (3)	Frugivore/animalivore[a]	Arboreal
Caluromysiops (1)	Frugivore/animalivore	Arboreal
Chacodelphys (1)	Animalivore/frugivore	Scansorial
Chironectes (1)	Animalivore/frugivore	Semiaquatic
Cryptonanus (5)	Animalivore/frugivore	Scansorial
Didelphis (6)	Omnivore[a]	Scansorial
Glironia (1)	Frugivore/animalivore	Arboreal
Gracilinanus (6)	Animalivore/frugivore[a]	Arboreal
Hyladelphys (1)	Animalivore/frugivore	Scansorial
Lestodelphys (1)	Animalivore	Scansorial
Lutreolina (1)	Animalivore/frugivore[a]	Terrestrial
Marmosa (15)[b]	Animalivore/frugivore[a]	Arboreal
Marmosops (15)	Animalivore/frugivore[a]	Arboreal
Metachirus (1)	Animalivore/frugivore[a]	Terrestrial
Monodelphis (22)	Animalivore/frugivore[a]	Terrestrial
Philander (7)	Animalivore/frugivore	Scansorial
Thylamys (13)	Animalivore/frugivore	Scansorial
Caenolestes (5)	Animalivore/omnivore	Terrestrial
Lestoros (1)	Animalivore/omnivore	Terrestrial
Rhyncholestes (1)	Animalivore/omnivore	Terrestrial
Dromiciops (1)	Animalivore/frugivore[a]	Arboreal

Adapted from Eisenberg (1981) and Martin (in prep.)

[a] Species involved in seed dispersion

[b] *Marmosa* includes species in the subgenus *Micoureus* sensu Voss and Jansa (2009)

Nickrent and Musselman 2004). Seasonal fruit availability in tropical and subtropical environments is directly related to the use of these resources as food items, fluctuating from high to low proportions during humid and dry periods, respectively (Cáceres et al. 2002; Cáceres 2006; Leiner and Silva 2007). Nine genera of New World marsupials (ca. 41 %) have been reported as seed dispersers, eight of them from tropical and/or subtropical environments (Table 2.1). In the only study made in a southern temperate environment (i.e., *D. gliroides* in the Valdivian ecoregion), fruit availability was found to be related to summer temperature, becoming a highly seasonal resource (Amico and Aizen 2000).

Through the study of marsupial feeding, Hume (1999) proposed a relationship between food quality and digestibility, and described a series of constraints: (1) optimal digestion time will vary depending on the type of food ingested (i.e., longer for poor quality items like adult insects, shorter for high-quality items like larvae, earthworms, or soft fruits); (2) animals with longer digestion times will have longer digestive tracts than those eating easily/quickly digestible food; (3) young animals with limited gut capacity will consume only high-quality food items; (4) animals should maximize food retention in order to extract the most energetic value out of the consumed items. Studies of the alimentary tract in South American marsupials show a relationship between relative length of the stomach, caecum and colon, with species' feeding habits (Hume 1999; Astúa de Moraes et al. 2003 and literature cited therein). The observed variation in craniodental anatomy and diet is directly related to differences in the species' digestive tracts, but only subtle differences were found between them (Santori and Astúa de Moraes 2006).

According to the information presented above, most South American marsupials can be considered, within certain limits and a few exceptions, opportunistic omnivores in a broad sense. This generalization has a strong influence on both ecological and physiological traits. For example, species might present seasonal variations related to food availability (e.g., feeding on fruits and insects during the rainy and dry seasons, respectively), and individual development (e.g., young individuals might feed on insects at one point in life, and shift to feeding on vertebrates as adults). This in turn, would influence their reproductive strategy (e.g., seasonal, aseasonal), energetic balance (e.g., use of torpor bouts, tail incrassation), reproduction and habitat use (see below).

In comparison to Australian marsupials, New World species occupy relatively broad ecological niches when it comes to feeding categories, with only a few of them showing feeding specializations (Vieira and Astúa de Moraes 2003; Tyndale-Biscoe 2005). The consumption of variable proportions of animal material and fruits in their diet is comparable, in many cases, to Australian dasyurid species (Strahan 1991; Hume 1999). Species within Caluromyinae are similar in feeding preferences to ringtails, gliders, brushtails and cuscuses (Petauridae and Phalangeridae), while *D. gliroides* can be easily compared to pygmy possums (Burramyidae; Strahan 1991). Noticeably, Caenolestids have feeding preferences that resemble (or are similar to) that of shrews (Soricidae) (Vaughan et al. 2011). The generalized feeding habits of living New World marsupials contrast with those inferred for extinct metatherian lineages, which included several types of hypercarnivorous, granivorous, strictly frugivorous, and even folivorous forms (see Chap. 6).

2.4 Reproductive Constraints

The reproduction pattern found in marsupials differs consistently from that of placentals with respect to gestation length, lactation, and neonate size (Cockburn and Johnson 1988). Originally considered primitive, recent studies have shown that the "marsupial mode of reproduction" is a highly derived condition, and not the ancestral pattern of a primitive Therian mammal (Hayssen et al. 1985). Marsupials are born in a much earlier stage of development and have a shorter duration of gestation relative to lactation, with a general average of $\sim 12\ \%$ (Hayssen et al. 1985;

Tyndale-Biscoe and Janssens 1988). Despite their small size (usually weighing less than 0.01 % of the mother's weight at birth) and poorly developed appearance, newborn marsupials show a mixture of well-developed functional organs and embryonic structures (Clark and Smith 1993; Tyndale-Biscoe 2005). Amongst the first well-developed organs are a relatively large head with large mouth and tongue, well-developed shoulders and forelimb skeleton. Embryonic or poorly developed structures include comparatively small hind legs and hip, a short and poorly developed tail, and ears and eyes concealed by membranes (or shut; Tyndale-Biscoe 2005). The well-developed structures are crucial during what is considered the most vulnerable period for the newborn marsupial (i.e., the transition from an intrauterine life to an external world), where it migrates from the vagina to the teat, mostly unaided. The young are wholly dependent on the mother during this period, and remain attached to the teat for a variable period of time (e.g., 48 days in *Didelphis virginiana*; 20 days in *Marmosa robinsoni*; 14 days in *M. domestica*), or detach briefly during this period (Tyndale-Biscoe and Renfree 1987 and literature cited therein, R. Cerqueira, personal communication).

The common name given to marsupials implies the presence of a pouch/marsupium enclosing the teat area (Fig. 2.4). In the Didelphimorphia , this morphological feature is present only in some of the larger (i.e., Didelphini) and medium-sized species (i.e., Caluromyinae), but is not developed in the remaining taxa (e.g., Glironiinae, Hyladelphinae, Marmosini, Metachirini, Thylamyini), which includes all small and a few medium-sized species (Voss and Jansa 2009). The absence or poor development of a pouch in most groups is probably the ancestral condition for New World species, and might be related to a nesting phase in the development of the young, with a well-developed pouch being a derived feature (Tyndale-Biscoe and Renfree 1987; Merritt 2010). The pouch opening in Didelphini is medially oriented, except in *Chironectes* where it opens posteriorly, an adaptation that has been related to its peculiar semiaquatic lifestyle (Nowak 1999). A pouch is not present in the Caenolestidae and Microbiotheria, where lateral folds of skin tend to enclose the teat area, at least partially (Tyndale-Biscoe and Renfree 1987; Hershkovitz 1999).

Only a few studies have documented the gestation period in South American marsupials, most of them from tropical/subtropical environments and from large/medium-sized didelphids, with the exception of *Lutreolina crassicaudata*, *M. robinsoni,* and *Monodelphis dimidiata* (Table 2.2). The gestation period found for most species is of 13–15 days, with the exception of *Caluromys philander* in which data of up to 20 days was recorded (Table 2.2).

South American marsupials have a variable number of teats, ranging from 4 to 19 (Table 2.2). The plesiomorphic number within American marsupials appears to be 4 teats, as found in Microbiotheria, Paucituberculata (e.g., *Lestoros inca*), and three subfamilies within Didelphidae (i.e., Caluromyinae, Glironiinae and Hyladelphinae). Small species from the tribes Marmosini and Thylamyini show most of the variation, with some genera having smaller teat numbers (e.g., *Marmosops* spp. with 5–9 teats) and others with the highest amongst New World marsupials (*Cryptonanus* spp., *Gracilinanus* spp., and *Thylamys* spp. with 9–15

Table 2.2 Reproductive information on South American marsupials

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Caluromys derbianus	–	3.3 (2–4)	–	2?	Biggers (1967), Phillips and Knox Jones (1968)
Caluromys lanatus	–	3.7	–	–	Cáceres (2000)
Caluromys philander	14–20+	3.6–6	4–7	2–3	Davis (1947), O'Connell (1979), Atramentowicz (1986), Perret and Atramentowicz (1989), Julien-Lafèrriere and Atramentowicz (1990), Cáceres and Monteiro-Filho (1997), Emmons and Feer (1997)
Chironectes minimus	–	2–4.5	5	–	Enders (1966), Hunsaker (1977), Marshall (1978b), Eisenberg (1980), Crespo (1982), Hershkovitz (1997), Cáceres (2000)
Cryptonanus chacoensis	–	12	9	–	Massoia and Fornes (1972), Voss et al. (2005), but see Gardner (2008)
Cryptonanus guahybae	–	–	15	–	Tate (1933)
Didelphis albiventris	–	4.2–9.1	8–13	–	Hershkovitz (1997), Tyndale-Biscoe and Mackenzie (1976), Streilen (1982), Monteiro-Filho (1987), Rigueira et al. (1987), Regidor and Gorostiague (1996), Catzeflis et al. (1997)
Didelphis aurita	–	6.5–8.1	11	–	Hill (1918), Davis (1947), Cerqueira et al. (1993), Bergallo and Cerqueira (1994), Cherem et al. (1996), Cáceres and Monteiro-Filho (1997), D'Andrea et al. (1999)
Didelphis marsupialis	–	4–9	9–13	–	Fleming (1973), Tyndale-Biscoe end Mackenzie (1976), O'Connell (1979), Eisenberg (1980), Atramentowicz (1986), Julien-Lafèrriere and Atramentowicz (1990), Hershkovitz (1997)

(continued)

Table 2.2 (continued)

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Gracilinanus agilis	–	–	13	–	Tate (1933)
Gracilinanus marica	–	–	11	–	Hershkovitz (1992a)
Gracilinanus microtarsus	–	–	15	–	Tate (1933)
Hyladelphys kalinowskii	–	–	4	–	Voss et al. (2001)
Lutreolina crassicaudata	13–15	5–11	9–11	2	Monteiro-Filho and Dias (1990), Hershkovitz (1997), Regidor et al. (1999), Iodice et al. (2010)
Marmosa lepida[a]	–	–	7	–	Tate (1933)
Marmosa murina[a]	–	–	7–13	–	Thomas (1888), Tate (1933), Hershkovitz (1992a)
Marmosa quichua[a]	–	–	11	–	Hershkovitz (1992a)
Marmosa robinsoni[a]	14	10–14	15 (11–19)	–	Barnes and Barthold (1969), Fleming (1973), Godfrey (1975), O'Connell (1979), Eisenberg (1980), Eisenberg and Wilson (1981), Hershkovitz (1992a)
Marmosa rubra[a]	–	–	7–9	–	Hershkovitz (1992a)
Marmosa tyleriana[a]	–	–	4	–	Tate (1933)
Marmosa xerophila[a]	14	7.9 (3–11)	–	1–3	Thielen et al. (1997)
Marmosa alstoni[b]	–	–	9–11	–	Tate (1933)
Marmosa cinerea[b]	–	–	9–15	–	Tate (1933), Hershkovitz (1992a)
Marmosa constantiae[b]	–	–	15	–	Tate (1933)
Marmosa demerarae[b]	–	10	9–11	–	Hershkovitz (1992a), Monteiro-Filho and Cáceres (2006)

(continued)

Table 2.2 (continued)

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Marmosa phaea[b]	–	–	9	–	Hershkovitz (1992a)
Marmosops bahiensis	–	–	7	–	Tate (1933)
Marmosops carri	–	–	7–9	–	Tate (1933)
Marmosops caucae	–	–	7–9	–	Tate (1933)
Marmosops handleyi	–	–	9	–	Hershkovitz (1992a)
Marmosops impavidus	–	–	9	–	Tate (1933), Hershkovitz (1992a)
Marmosops incanus	–	–	7	–	Tate (1933)
Marmosops noctivagus	–	–	5–9	–	Tate (1933), Hershkovitz (1992a)
Marmosops parvidens	–	–	7–9	–	Pine (1981), Hershkovitz (1992a)
Marmosops paulensis	–	–	–	1	Leiner et al. (2008)
Metachirus nudicaudatus	–	4–9	9	–	Fonseca and Kierulff (1989), D'Andrea et al. (1999), Cáceres (2000), Gardner and Dagosto (2008)
Monodelphis americana	–	–	15	–	Thomas (1888)
Monodelphis brevicaudata	–	7.5	11	–	Thomas (1888), O'Connell (1979), Eisenberg and Wilson (1981)
Monodelphis dimidiata	–	11	16	–	O'Connell (1979), Eisenberg (1980)
Monodelphis domestica	14	7–8	13–16	–	Thomas (1888), VandeBerg (1983), Kraus and Fadem (1987), Bergallo and Cerqueira (1994), Pfiegler and Cabana (1996), Harder and Fleck (1997)
Monodelphis sorex	–	–	13	–	Carlsson (1903)
Philander andersoni	–	–	4–7	–	Hershkovizt (1997)

(continued)

Table 2.2 (continued)

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Philander frenatus	13–14	4.5–5.4	7	–	Davis (1947), Crespo (1982), Fonseca and Kierulff (1989), Cerqueira et al. (1993), Hingst et al. (1998), D'Andrea et al. (1999), Cáceres (2000)
Philander opossum	–	4–5	7	–	Fleming (1973), Eisenberg (1980), Atramentowicz (1986), Julien-Lafèrriere and Atramentowicz (1990), Hershkovizt (1997)
Thylamys elegans	–	17 (embryos)	11–15	–	Tate (1933), Mann (1958)
Thylamys janetta	–	–	15		Tate (1933)
Thylamys karimii	–	–	–	2?	Carmignotto and Monfort (2006)
Caenolestes fuliginosus	–	3.4	–	–	Osgood (1921), Kirsch and Waller (1979), Tyndale-Biscoe (1980)
Lestoros inca	–	–	4	–	Osgood (1924)
Rhyncholestes raphanurus	–	–	7	1	Patterson and Gallardo (1987)
Dromiciops gliroides	–	1–4	4	1	Philippi (1893), Krieg (1924), Osgood (1943), Mann (1955), Greer (1965), Muñoz-Pedreros et al. (2005)

[a]Subgenus *Marmosa*
[b]Subgenus *Micoureus*

teats; *Monodelphis* spp. with 11–16 teats; *Marmosa* spp. with 7–19; Mann 1958; Hershkovitz 1992a; Bergallo and Cerqueira 1994; Voss et al. 2005; Martin in preparation). Large- to medium-sized species of the tribes Didelphini and Metachirini show intermediate numbers, between 4–13 and 9 teats, respectively (Julien-Lafèrriere and Atramentowicz 1990; Catzeflis et al. 1997; Cáceres 2000). Despite variation in teat number, two reproductive strategies appear to be common: one in which more young are born than the available number of teats (e.g., *Didelphis*), and one in which young are less or equal to the number of teats (e.g., *Caluromys*) (Tyndale-Biscoe 2005). Unfortunately, no information on this aspect of reproduction in species with higher teat numbers is available.

Information on the average litter size is available for less than 20 species (Table 2.2), but this data should be taken carefully as it has been demonstrated that wide ranging species (in latitude) have variable litter sizes, with smaller ones registered toward the periphery of their distribution (Fleming 1973; Rademaker and Cerqueira 2006). The available information has a high bias toward medium/large-sized marsupials from tropical environments, with little information on specialized taxa (e.g., *Caluromysiops*, *Glironia*, *Lestodelphys*) and species-rich genera (e.g., *Marmosops*, *Monodelphis*, *Thylamys*) (Table 2.2).

Another reproductive aspect that has been poorly studied in South American marsupials is the number of litters per year (Table 2.2). Two litters per year have been documented for *Caluromys philander*, *Didelphis albiventris, D. aurita* and *L. crassicaudata* (Catzeflis et al. 1997; Emmons and Feer 1997; D'Andrea et al. 1999; Regidor et al. 1999). One litter per year has been documented for *Philander frenatus*, *D. gliroides* and *Rhyncholestes raphanurus* (Patterson and Gallardo 1987; Cáceres 2000; Muñoz-Pedreros et al. 2005). Because semelparity or partial semelparity (see below) has been described as the reproductive strategy for *M. dimidiata*, *Gracilinanus microtarsus*, *Marmosops incanus* and *Marmosops paulensis,* a single litter per year can be inferred for all these species. In the same context, and given that many species of South American marsupials inhabit highly seasonal habitats, it could be argued that most species would reproduce once a year, and conform to a semelparous or partially semelparous life cycle. From an energetic/metabolic point of view, this would represent a substantial advantage over species with multiyear life cycles (especially in small species), in which individuals should have to regulate and/or balance their energy input to cope with significant seasonal fluctuations in food availability, energy storage (e.g., in the form of interstitial and inner body fat reserves), and resuming reproductive activities on a year-round basis. A reproductive "strategy" that has been recorded for Australian diprotodonts , shows that at least two different aged young can be found at any one time inside the pouch. This has not been documented for New World marsupials, even in species with two or three breeding cycles throughout a year.

The first stages in the life of newborn marsupials were reviewed by Tyndale-Biscoe (2005), who divided postnatal development in three consecutive phases in which different processes take place: (1) acquisition of immune competence, eyes, ears, whiskers and cerebral cortex differentiate, functions of the nervous system develop, and the brain grows fast; (2) acquisition of homeothermality with the increased growth of fur, the development of the thyroid, liver, kidney, and the hormones that control each organ's function; and (3) facultative detachment from teats until they are weaned, changes in diet from milk to other "adult" items, changes in energy balance and metabolism, modifications of the stomach and intestine, and the need for water as the young becomes physiologically independent. Different studies in New World marsupials contribute to validate these phases (e.g., Pine et al. 1985; Muñoz Pedreros et al. 2005; Krause and Krause 2006; Monteiro-Filho and Cáceres 2006), phases which have been based on studies of mostly large-sized Australian marsupials.

When young start detaching from the teat and enter into phase 3, they are left in a den or nest while the mother forages, and later on cling to her back until they are weaned (Tyndale-Biscoe and Renfree 1987). A nesting phase was reported for

D. gliroides (Mann 1955), *M. paulensis* (Leiner et al. 2008) and *Metachirus nudicaudatus* (Loretto et al. 2005), showing this might be a more common feature of South American marsupials than previously thought, even in medium/large sized species.

The reproductive strategies of South American marsupials have been poorly studied, and have been mostly concentrated on a few small-sized species from tropical/subtropical environments (Martins et al. 2006; Leiner et al. 2008), and *M. dimidiata* from temperate grasslands (Pine et al. 1985). In didelphids, different reproductive strategies have been documented, from multiyear cycles with no post-reproductive die-off to complete semelpartity (e.g., Pine et al. 1985; Hingst et al. 1998; Martins et al. 2006; Leiner et al. 2008). Semelparity, also known as senescence, involves a post mating die-off (generally of males), and/or a decline in reproductive fecundity (generally of females) after one reproductive cycle (Braithwaite and Lee 1979; Lee and Cockburn 1987). In semelparous species reproduction occurs once in a lifetime and leads to nonoverlapping discrete generations (Cole 1954; Martins et al. 2006). This reproduction mode has been intensively studied in many Australian species (e.g., *Antechinus* spp., *Phascogale* spp., *Dasyurus hallucatus*) showing some variation in life histories, from complete to partial semelparity (Lee et al. 1982; Cockburn 1997; Oakwood et al. 2001, but see Pine et al. 1985). In South American marsupials, complete semelparity has been inferred based on seasonal weight and marked sexual dimorphism in *M. dimidiata* (Pine et al. 1985). Well-marked sexual dimorphism has been correlated with a high reproductive effort and semelparity (Williams 1966), which relates to males investing in growth associated to reproductive success (and therefore aging at a faster speed and shorter time), and females growing at a slower rate due to breeding and raising the young (Gardner 1973, fide Pine et al. 1985). Complete semelparity has been also inferred based on age classes of museum specimens in *M. incanus* (Lorini et al. 1994), and has been recently reported in an ecological study of *M. paulensis* where both males and females did not survive to breed for a second season (Leiner et al. 2008). Partial semelparity, a different strategy in which males die-off after reproduction but females survive over a period of time, albeit gradually disappearing from the population, has been documented for *G. microtarsus* (Martins et al. 2006).

Braithwaite and Lee (1979) noted a predominance of semelparous marsupials in coastal regions of Australia, and associated this strategy with highly seasonal and predictable environments. If this hypothesis was true, one would expect semelparity as the predominant reproductive strategy in highly dimorphic species that inhabit seasonal environments. Unfortunately, our present knowledge on the reproductive strategies in species living in seasonal environments (both warm and temperate-cold) is very limited, and most South American marsupials are not highly dimorphic. This does not allow for a good interpretation of how climatic factors are involved (or not) in their life cycles. A recent approach proposed by Bradley (2003), involves the study of physiological changes that are likely to occur before males die, those of which could indicate a semelparous reproductive strategy. Although these studies are lacking for most South American marsupials, the combination of environmental and physiological factors at different levels could provide answers onto why semelparity evolved convergently in such different lineages (i.e., Marmosini and Thylamyini in America; Dasyuridae in Australia).

Even though several aspects of New World marsupial reproductive strategies are still poorly understood, different studies show that species tie their reproduction to photoperiod, rainfall or food availability (Julien-Laferrière and Atramentowicz 1990; Bergallo and Cerqueira 1994; Cerqueira 2004). Comparisons between different sized species of didelphid marsupials from Brazil show that photoperiod appears to be the most important proximal factor to influence the onset of the reproductive cycle, instead of meteorological events like rainfall (Cerqueira 2004).

Despite the available data, it is not clear how these factors would influence species with a broad latitudinal distribution (e.g., *Thylamys pallidior, D. albiventris*). For these species, shortening of their reproductive cycle, growth period, and a delay in the onset of the breeding season should be associated to a faster sexual maturity rate and an increase in developmental timing, for which we lack information. The effects of a broad latitudinal range on litter size have been partially explored for the genus *Didelphis* by Rademaker and Cerqueira (2006), showing a positive correlation, and a negative one between breeding season and latitude. This pattern of reproduction and growth would also have consequences in the development of the young, which should have a faster growing curve from tropical to more temperate climates. The time in which species attain sexual maturity would also be critical and should decrease with the distance from the equator (i.e., shorter lived species living far from the equator should reach sexual maturity faster, especially if they were to live for shorter periods of time). Many questions remain to be answered in this respect. For example, what would happen in species that inhabit temperate environments exclusively (e.g., *D. gliroides*, *Lestodelphys halli*), where differences in photoperiod are highly marked in comparison to tropical and subtropical environments studied so far? Would species of widespread distribution along a longitudinal pattern (east-west) show the same reproductive pattern throughout their range despite other variables like rainfall and altitude (e.g., *D. albiventris* from eastern Brazil and eastern Perú or Bolivia)? Would feeding resources influence any of these parameters? As with many of the subjects treated before, our knowledge of the reproductive strategies of South American marsupials is still fragmentary, with no information for caenolestids and very scarce, anecdotal information for *D. gliroides* and most of the species living in temperate ecosystems.

2.5 Size and Anatomical Constraints, Locomotion and Habitat Use

South American marsupials range in size from ca. 10 g to 1.4 kg (*Chacodelphys formosus* and *D. albiventris/D. marsupialis,* respectively) (Gordon 2003; Voss and Jansa 2009). Compared to other living mammals, they are somewhat externally homogeneous, their main morphological variation being body size, with subtle variations in general form, tail and limb proportions, and toe disposition patterns (Voss and Jansa 2009). Of the three extant South American orders, Didelphimorphia shows the largest variation in size, habitat use, and anatomical adaptations (Palma 2003; Tyndale-Biscoe 2005; Gardner 2008). Despite this variation, most didelphids have a surprisingly similar body plan: grasping hindfeet with opposable thumbs and a prehensile or semiprehensile tail (Szalay 1994; Martin 2008). The only living microbiotheriid, *D. gliroides*, is very similar to small didelphids (e.g., *Marmosa* s.l.) in body form, and is highly arboreal. Caenolestids are clearly different from didelphids in their shrew-like appearance, mostly terrestrial (semifossorial?) adaptations and procumbent lower incisors.

Morphological variation in didelphids is also accompanied by subtle variations in postural behavior, locomotion and locomotor performance, with posterior limbs more developed than anterior ones, even in arboreal species (Vieira 1997, 2006a, b). When comparing body and limb weights, hindlimb muscle weight was found to be highest in *Metachirus* and *Chironectes*, two species living in clearly different substrates (i.e., terrestrial and semiaquatic, respectively) (Carvalho et al. 2000; Argot 2001, 2002, 2003). Differences between scansorial/arboreal from generally terrestrial species have also been found in the use and shape of the pelvic girdle (Argot 2002, 2003; Vieira 2006a, b). Terrestrial forms show a larger development of muscular insertions with a somewhat reduced mobility, while arboreal/scansorial forms have more muscular mobility and greater articulation (Argot 2002). The vertebral column, especially in the lumbar region, has also become different in relation to the species' habits: arboreal forms tend to have a thinner and narrower vertebral column, with plenty of freedom in movement (e.g., *Caluromys*, *Marmosa*; Works 1950; Grand 1983), while terrestrial species show more robust muscular insertions and a more developed lower back musculature (e.g., *Metachirus*; Argot 2003). Two main patterns in the scapulae of living New World marsupials were found, one with a triangular shape, present in arboreal species and also in small-sized marsupials (e.g., *Caluromys*, "*Marmosa*" [=*Micoureus*], *Dromiciops*); and the other with a quadrangular shape, present in terrestrial and generalist species (e.g., *Metachirus*, *Didelphis* , *Monodelphis*; Argot 2001, Martin pers. obs.). This difference can be related to the rotation of the anterior limbs and protraction/retraction of the humerus, which is in turn related to muscular mass and therefore to locomotion (Vieira 1997, 2006a, b; Argot 2001).

A primitive pattern of foot morphology is characteristic of didelphids and microbiotheriids, with minor deviations related to toe size and predominance (Szalay 1982a, b, 1994; Voss and Jansa 2003). The hand of didelphids and *Dromiciops* do not reflect major differences in locomotor habits, and are used in a similar stereotyped behavior common to most species, especially the smaller sized ones (e.g., *Dromiciops*, *Lestodelphys*, *Monodelphis*; Streilen 1982; Martin 2008; Martin and Udrizar Sauthier 2011). Extant caenolestids deviate from this pattern, probably in response to a scansorial way of life, by having a reduced hallux (*contra* Szalay 1994).

Studies on foot articulation have led to the assumption that living metatherians (especially Didelphidae) are, in general, highly arboreal (e.g., Szalay 1982a, b, 1994; Szalay and Sargis 2001); and were therefore considered plesiomorphic in their locomotor adaptations. This view has been challenged by recent work (e.g., de Muizon and Argot 2003), supporting the idea that living New World marsupials appear to be more specialized than their Paleogene ancestors, especially in relation to their climbing abilities. Most didelphids and *Dromiciops* share a hindfoot with a powerful grasping mechanism and scansorial adaptations (Grand 1983; Szalay 1994), including the use of the tail as a "fifth member" (see below). Exceptions to this generalized pattern include *Chironectes, Metachirus,* and caenolestids, which are clearly distinct from the rest by having a unique foot morphology with more terrestrial adaptations. Toe length is also directly related to differences in substrate locomotion, where arboreal species (e.g., *Marmosa*, *Caluromys*, *Dromiciops*) have longer ones than terrestrial species (e.g., *Monodelphis*, *Metachirus*).

Locomotion presents different constraints depending on substrate use and the individual's size, especially when moving in inclines (Pridmore 1992, 1994; Hildebrand 1995; Santori et al. 2005; Delciellos and Vieira 2006; Vieira 2006a, b). Terrestrial environments, on one hand, are perceived in different ways by small or medium/large animals, with smaller individuals having to sort out larger obstacles and longer, more sinuous paths when moving around, in proportion to larger ones (Vieira 2006a, b). Arboreal environments, on the other hand, pose considerable constraints to size in mammals, which are related to living in a highly complex three-dimensional habitat which includes gathering food, escaping from predators, and moving through different sized branches and open spaces, amongst others (Szalay 1994; Hildebrand 1995).

Marsupial locomotion has been described as mostly quadrupedal (also called grasp climbing by Szalay 1994), both on terrestrial and arboreal substrates (Grand 1983; Vieira 2006a, b). South American marsupials move at a slow pace, regardless of the substrate, exploring with their heads up and "sensing" the environment (Streilen 1982; Martin and Udrizar Sauthier 2011). Despite this common pattern, differences between lineages show most didelphids move in a lateral sequence (Pridmore 1992; Hildebrand 1995), while *D. gliroides* and *Caluromys philander* use a diagonal sequence, which has been associated (mostly) with locomotion on narrow substrates (Pridmore 1994; Lemelin et al. 2003). The pattern of lateral sequence changes to a diagonal one when starting to run or trot (McManus 1970; Pridmore 1992; Vieira 2006a, b), which is typical for arboreal mammals (Hildebrand 1995; Lemelin et al. 2003). Diagonal sequencing apparently produces a more stable stride in arboreal mammals, probably due to the fact that lateral sequences make thin branches shake in an uncontrolled manner (sideways for the animal). Both diagonal and lateral sequences are symmetrical in Didelphidae (Lemelin et al. 2003; Vieira 2006a, b), meaning that limbs move in pairs. This is also true for the diagonal sequence found in *Caluromys philander* (Caluromyidae) and the microbiotheriid *D. gliroides* (Pridmore 1994; Lemelin et al. 2003). All studied species (except *C. philander*) move to an asymmetrical half-bound and transverse gallop or trot when fleeing (Pridmore 1992, 1994; Lemelin et al. 2003).

These changes in locomotion patterns have been recorded in substrates resembling trees, even with different inclination angles (Vieira 1997, 2006a, b). What does this locomotion pattern imply, and does it resemble the ancestrally inferred pattern of locomotion? It is interesting to note that two lineages of arboreal South American marsupials which are not related (*Caluromys* and *Dromiciops*), share the same diagonal pattern of locomotion, and that this pattern is found in running Didelphidae. Although further studies are required, this could mean that living Didelphidae evolved from an arboreal species with a diagonal sequence, and that a lateral sequence derived when animals ventured onto the ground, with the diagonal sequence retained by "older" lineages.

Compared to other arboreal/scansorial mammals, marsupials move slowly when in trees, grasping the surface and positioning themselves as vertical to the substrate as they can. Also, the position of their limbs is distinct from other arboreal mammals, placing the forefeet close to each other and supporting much of the weight, using the head and tail as balancing organs, and placing the hindfeet a little apart from the gravity center as a way to support the moving individual. Most New World marsupials have long and well-developed tails, with the exception of caenolestids and some terrestrial forms in which the tail is clearly shorter than head-body length (e.g., *Monodelphis*). The presence of a long tail plays an important role as a balancing organ in which the center of gravity is moved backwards and allows for quick movements on uneven substrates without the use of the forelimbs (Argot 2003; Muizon and Argot 2003). Anatomically, arboreal forms are characterized by caudal bones with well-developed neural and mammillary processes, coupled with robust transverse processes and strong abductors at the base of the tail (Argot 2003). In these species, the tail is heavy and muscular at its base, with a lengthening of the posterior caudals and prehensility toward the posteriormost end, where the development of a series of plicas add to the grasping capacity (Hershkovitz 1992b, 1997, 1999). In terrestrial forms, the distal caudal vertebrae are much more slender, presumably not able to support the body weight of the animal (Argot 2003, but see Martin 2008). The use of the tail as a "fifth member," even in highly terrestrial species like *L. halli* (Szalay 1994, but see Argot 2002; Martin and Udrizar Sauthier 2011), would add support to this arboreal ancestry in living didelphids (Enders 1935; McManus 1970).

Although marsupials (with the exception of *Chironectes*) use water habitats only on rare occasions (i.e., when fleeing from predators, encounter them as obstacles during foraging activities or floods), they can be active swimmers. Locomotion in water has been studied for *D. virginiana*, *Chironectes minimus,* and *L. crassicaudata* (Fish 1993; Santori et al. 2005). Main differences were found in the propulsion of these species, *Chironectes* using only its hindfeet while the other two use underwater paddling, which is different between them as well. The use of hindlimbs for swimming in *Chironectes* also has the advantage of leaving the forelimbs free for foraging, capturing, and manipulating prey (Hamrick 2001). *Lutreolina* has a higher stride frequency than *Didelphis*, similar buoyancy and swimming posture to *Chironectes*, but swimming speed similar to that of *Didelphis.* As opposed to that of *Didelphis*, the fur of *Chironectes* and *Lutreolina* is non-wettable and provides a certain degree of buoyancy (Fish 1993; Marshall 1978a), which is associated with a more efficient control of swimming movements. Anecdotal information on swimming capabilities is available for *M. nudicaudatus, P. frenatus, D. albiventris, D. aurita,* and *M. domestica* (Hershkovitz 1997; Santori et al. 2005 and literature cited therein). Mammals with semiaquatic adaptations are not very common due to thermal (and also anatomical) restrictions, especially those with low BMRs (McNab 2005). Heat loss in water through convection is probably a strong limitation and other than *Chironectes*, no other marsupial has "ventured" into this niche.

Although marsupials comprise ca. 10 % of the mammal species of South America, our knowledge on their ecology and behavior is mostly anecdotal. South American marsupials can be found throughout all the region's biomes, and occupy different ecological niches while making use of a variety of substrates (Eisenberg and Wilson 1981; Streilen 1982; Corvalán 2004; Cáceres 2006; Vieira 2006a, b; Martin 2008; Martin and Udrizar Sauthier 2011).

Habitat use has been studied in tropical and subtropical species, most of them from forested biomes (e.g., Charles-Dominique et al. 1981; Charles-Dominique 1983; Pires and Fernandez 1999; Vieira 2006a, b). A few exceptions include *D. albiventris* and *M. domestica* in the Cerrado and Caatinga (Streilen 1982); *M. dimidiata* in the Pampa (Pine et al. 1985); *T. pallidior* in the Monte (Corvalán 2004) and *D. gliroides* in the Temperate Rainforest (Patterson et al. 1990; Rodríguez-Cabal et al. 2007). Studies show that most species make a "complete" use of the habitat by moving throughout most of the space available to them, even if they are mostly arboreal, scansorial or mostly terrestrial. Smaller species, with the exception of *Monodelphis* spp. and *L. halli*, are arboreal or scansorial, and those from tropical or subtropical forests can be found living in microsympatry with similar body-sized species and sharing the same resources (Eisenberg and Wilson 1981; Emmons and Feer 1997; Pires and Fernández 1999; Delciellos and Vieira 2006; Vieira 2006a, b). This has provided unique opportunities to test for hypothesis of vertical stratification and resource partitioning. Comparing different areas in the Brazilian Atlantic Forest, Vieira (2006a, b) found that substrate use was influenced by: (1) seasonal patterns related to food availability, (2) intraspecific segregation (e.g., young from adults, males from females), (3) changes in patterns of community composition according to substrate, and (4) ecological processes involving habitat use in relation to the species' daily activities (e.g., foraging, resting). Many of these factors are influenced by others mentioned above, some of them intrinsic (e.g. diet , reproduction, locomotion, and population density), others extrinsic (e.g., climate, type, and condition of habitat). Two separate studies on *M. incanus* and *M. paraguayanus* in the Brazilian Atlantic forest have shown space use to be the same for both males and females in the former but different in the latter, with females of *M. paraguayanus* exploring the vertical strata of the forest more frequently than males (Loretto and Vieira 2008; Prevedello et al. 2009). Unfortunately, these are the only studies documenting space use at this scale and for one ecoregion, with no information on other spatially/vertically complex environments. Species living in somewhat "simpler" environments (i.e., less vertically stratified) still show a complex habitat use (e.g., *T. pallidior* in the Monte desert of Argentina, Corvalán 2004).

The behavior of South American marsupials is generally comprised of anecdotical accounts in works with a broad scope that might include one or several species. Streilen (1982) presented a lengthy description of activity patterns in *D. albiventris* and *M. domestica*, including activity period, exploration, sleeping, prey manipulation, grooming, and other socially related behavior. Both species have nocturnal and crepuscular activity patterns, concentrated during the first hours after dawn and with bouts throughout the night, depending on foraging activities and food intake. In relation to this, both species move with their noses close to the substrate, stopping for brief moments and sniffing the air, to continue moving with their noses close to the substrate. When an item is located, a moment is spent calculating distance and possible movements, and followed by a quick grasp with its mouth. If the item is a live vertebrate, it is bitten in the neck and immobilized. After this, a semierect feeding position is assumed. Manipulation of the prey is generally done by one or both paws, depending on its size. Grooming of the head and forepaws is often a previous activity to prey manipulation and consumption. Grooming patterns start with the forepaws around the head, which have been previously and extensively licked, and then proceed onto the rest of the body. The hindfeet are used to scratch the body and head, in a similar manner as the forefeet, but with restricted mobility. These stereotyped patterns were found typical, with minor variations, for other species [e.g., *M. dimidiata* (González and Claramunt 2000), *Philander* spp. (Hershkovitz 1997), *D. gliroides* (Mann 1955, 1958; Martin 2008), *Thylamys fenestrae* (Bruch 1917), *Thylamys elegans* (Palma 1997), *L. halli* (Martin and Udrizar Sauthier 2011)].

A combination of anatomical features including size and locomotion, along with a series of common patterns of behavior, results in minor differences between habitat use and other related adaptations in South American marsupials. Most species show variable levels of integration with the habitat in which they live, and the way they use it. Vertical stratification in structurally complex habitats is mostly related to resource availability, while species mobility might influence habitat use in simpler environments.

2.6 Integrating Physiological and Ecological Constraints

As described above, several factors appear to be relevant when analyzing the physiological and ecological constraints of South American marsupials. The BMR and other physiological adaptations (e.g., field metabolic rate), diet and food availability, foraging activities and habitat use, are all related and can be indicative of how different species cope with the availability of food resources and climatic variations (Tyndale-Biscoe and Renfree 1987; Green 1997; Hume 1999; McNab 2005). Apart from the direct relationship to food items, energy expenditure during foraging activities is a critical factor that should maximize, ideally, the net rate of energy balance (Townsend and Hughes 1981). One of the strategies documented in both New and Old World old world marsupials is related to the way in which animals make use of their energetic resources, and includes hibernation and/or daily torpor (McNab 1978, 2005; Geiser 1994, 2003; Bozinovic et al. 2004, 2005), and the storage of those accumulated resources, both as body or caudal fat (Morton 1980; Krause and Krause 2006; see below). Torpor and/or hibernation are common (but not exclusive) adaptations in mammals that experience seasonal food shortages and sometimes low environmental temperatures, to counterbalance the negative results between foraging activities and food intake (Geiser 2003; Bozinovic et al. 2004). While hibernation in New World marsupials is only known to occur in *D. gliroides* (Bozinovic et al. 2004), daily torpor appears to be a common strategy, especially in smaller species (e.g., *L. halli*, *Monodelphis brevicaudata*, *T. elegans*; Morrison and McNab 1962; McNab 1978; Bozinovic et al. 2005; Martin 2008; Geiser and Martin 2013). Torpor can be induced by food deprivation and low ambient temperatures, proving this adaptation is an opportunistic (and facultative) response to unpredictable biotic and abiotic conditions (Geiser 1994; Bozinovic et al. 2004, 2005; Martin 2008; Martin and Udrizar Sauthier 2011; Geiser and Martin 2013). Torpor may also occur in tropical or subtropical environments, even when food is available, as a way of maximizing energy use (Geiser 1994). This has only been documented in small species (e.g., *G. microtarsus*, *M. robinsoni*), suggesting a strong relationship between size (i.e., body mass) and heterothermy (McNab 2005). Recent work on torpor and hibernation in marsupials shows that torpor intensity varies from juveniles to adults, being longer in the former (Geiser et al. 2008). This appears to be an important adaptation in growing individuals to survive periods of energy shortage, and may facilitate somatic growth because valuable nutrients are not wasted in thermoregulation (Geiser et al. 2008). No indication of torpor or hibernation was found in recent observations of several individuals of *Caenolestes fuliginosus*, maintained in captivity during variable periods of time (1 to 12 consecutive days; Martin and González Chávez, in prep.).

A complimentary behavior to torpor that was recently discovered to occur in Australian marsupials is basking (Geiser et al. 2008). A few species of desert dasyurids employ this strategy during rewarming from torpid states, a process that can reduce the energy costs of this process by 85 % (Geiser et al. 2008). Although this behavior is yet to be recorded in South American marsupials, species living in highly seasonal environments (e.g., Patagonian Steppe, Puna, Cerrado, Caatinga) could be expected to show this adaptation as well.

Caudal fat storage has been documented as an adaptation to highly seasonal environments acting as energy reserves during periods of food shortage (Morton 1980). This feature is common in many of the small dasyurids living in central Australia, and is also present in some rodents, insectivores, and lemurs. It has also been found to occur in small didelphids from xeric environments (e.g., *L. halli, Thylamys* spp.) and, convergently, in *D. gliroides* and *R. raphanurus*, both from the Valdivian Temperate Rainforest (Morton 1980; Birney and Monjeau 2003; Solari 2003; Martin 2008). Even though *Caenolestes* spp. and *L. inca* inhabit extreme environments (the *páramos* and *subpáramos* above 1800 m) there is no record of tail incrassation in these species (Albuja and Patterson 1996, Tyndale-Biscoe 2005). Tail incrassation has been mentioned in *D. virginiana*

(Krause and Krause 2006), and might also occur in other didelphids that live in highly seasonal environments (e.g., Caatinga, Cerrado, Chaco). Unfortunately, little is known about the occurrence of this adaptation in other didelphids and no information is available on the total amount of energy stored as caudal fat. Also, the speed at which this fat is consumed or metabolized remains unknown. In specimens of *L. halli* maintained in captivity for over two months and with a constant food supply, the tail quickly became incrassated changing its shape from dorsoventrally flattened to "carrot-like" in less than a week (Martin and Udrizar Sauthier 2011). When deprived of food, caudal fat was consumed in a matter of 7–10 days, which is indicative of a quickly available energy resource. High-energy resources like this might provide an important advantage when rewarming from daily or multiday torpor, an adaptation that could also maximize energy use for short foraging activities during harsh environmental conditions. These adaptations would be directly related to the need to prolong fat reserves, keeping the body functioning with a minimum waste of energy to maintain vital processes needed to survive (Morton 1980; Geiser 1994, 2003; Bozinovic et al. 2004, 2005).

The occurrence of physiological adaptations as those mentioned above are generally combined with a selective habitat use. Many species also rely on tree cavities, burrows, and other protected locations during the day and between foraging bouts. While these areas within the environment can be used as resting places and would provide protection from predators, they are also important for buffering thermal extremes (Geiser 2003). In many ways, these adaptations are somewhat related and are a direct consequence of most South American species being small-sized (Lee and Cockburn 1987; Geiser 2003). Locomotor and anatomical features characteristic of New World marsupials influence the species' habitat use and preferences, resulting in most species being arboreal or scansorial. This in turn, can be associated with a generally opportunistic and omnivorous diet , giving these species the capacity to cope with fluctuating resources due to different environmental constrains, including those related to seasonality and complex habitats. While moving away from multi-stratified habitats into simpler ones, resource availability also decreases. Marsupials living in more simple and sometimes extreme habitats should therefore "concentrate" on strategies to minimize energy use during physiological processes (e.g., homeothermy) and foraging activities by entering torpor (daily or multiday bouts), while maximizing energy input by shifting their feeding preferences and fat storage. Most South American marsupials are nocturnal, which represents an additional energetic problem. It is during the night that lowest temperatures are recorded, increasing heat loss and energy expenditure to maintain a constant internal temperature. It is also during the night that "mobile" food resources (mainly arthropods and rodents) are active and easily available, while "static" resources might be available due to other animals not being active during the night (e.g., frugivorous monkeys and birds in tropical and subtropical environments). Another critical factor, especially for species living in xeric environments, is related to hydric balance (Díaz and Cortés 2003). Concentrating foraging activities during the night would maximize the chances of finding food items quicker and with less energy expenditure, while the water balance remains positive avoiding evapoperspiration (Schmidt-Nielsen 1964).

The reproductive strategies of South American marsupials are most likely to be influenced by these ecological and physiological constraints as well. As a result, different strategies might evolve, resulting in species that live for more than one year and reproduce seasonally or throughout the year, and species that only reproduce once in their life (i.e., are truly semelparous). Although our information is very limited in this respect, species with broader distributions appear to have marked seasonal reproduction patterns, especially toward their distribution extremes. These species tend to produce one litter per year and/or reduce their litter size when away from their optimal range, especially towards the South. Thermal constraints would have a direct influence on the reproductive cycles of these broad-ranging species, while resource availability and other ecological factors (i.e., intraspecific competition) might influence tropical and subtropical species more acutely. The advantage of a single reproductive cycle in non-semelparous species living in temperate environments would allow individuals to reduce the energy expenditure related to breeding and allocate resources into metabolic processes for surviving to reproduce yet another season.

The distribution of living South American marsupials is a result of all these constraints, along with historical factors. In this context, two separate lineages (i.e., Microbiotheria and Paucituberculata) adapted to living in temperate or temperate-cold environments would be remnants of once diverse groups, while a separate, and highly diversified lineage (i.e., Didelphimorphia) mainly lives in humid tropical/subtropical environments and has recently adapted to (colonized?) a diversity of habitats (e.g., warm-dry habitats like the Chaco and Caatinga; cold-dry habitats like Patagonia and Puna; cool-humid habitats like the Humid Pampas). Due to this combination of physiological ecology and historical factors, the area between 40°S/70° 30′W and 41° 30′S/72° 30′W (Fig. 2.7) is the only one where the three extant New World marsupial Orders coexist (with five species): Didelphimorphia (*L. halli*, *T. pallidior* and *D. albiventris*); Microbiotheria (*D. gliroides*); and Paucituberculata (*R. raphanurus*) (Martin 2008, 2010, 2011).

South America shows unique environmental conditions, including steep environmental gradients mostly due to acute altitudinal differences, which have no correlation in Australia, providing a magnificent opportunity to study the anatomical and physiological adaptations of these marsupials. Intrinsic (i.e., physiological, ecological) and extrinsic (i.e., climatic) thermal constraints strongly influence their feeding preferences and reproductive strategies, which are bounded within several anatomical constraints, and related to habitat use and, ultimately, their distribution patterns. Several constraints appear to be critical as part of the life strategies of South American marsupials: (1) variable energetic costs for regulating metabolic processes, due to a low rate of metabolism, the possibility to enter torpor/hibernation, and the storage of different types of fat tissues available for those varied processes; (2) a broad, generally opportunistic and omnivorous diet; (3) a reproduction cycle that shares a short gestation period and long, energy-demanding, breeding period, but with specific differences in reproductive strategies

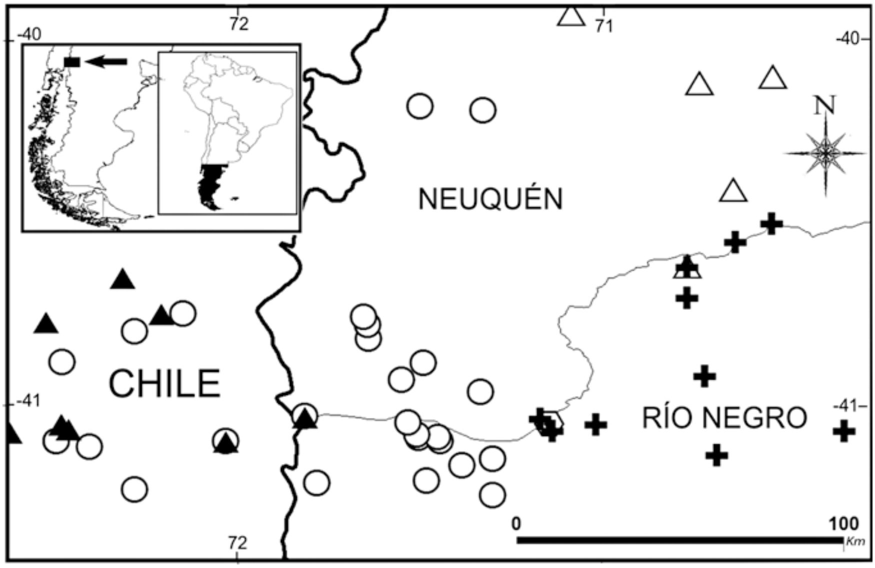


Fig. 2.7 Map of the area between 40°S/70° 30′W and 41° 30′S/72° 30′W where representatives of the three extant New World marsupial orders coexist: Didelphimorphia [*Lestodelphys halli*, black crosses; *T. pallidior*, open triangles; *Didelphis albiventri*s, open hexagon]; Microbiotheria [*Dromiciops gliroides*, open circles]; and Paucituberculata [*Rhyncholestes raphanurus*, black triangles]

(e.g., semelparity, partial semelparity, iteroparity), and their main traits (e.g., litters per year and litter size, teat number); (4) arboreal/scansorial habits and a complete use of the available habitat. These adaptations, added to a generally small size, small energy expenditure on foraging and other daily activities, most of which take place during night hours, allow South American marsupial species to thrive in environments where competition with other animals might be strong (e.g., tropical and subtropical climates), or where a few small mammals can survive (e.g., temperate and temperate-cold climates), due to several environmental limitations.

Future studies should aim at filling the many gaps in our knowledge of their natural history, and integrate them into a body of work which should provide some insight on the evolutionary history of these peculiar groups of mammals.

References

Albuja L, Patterson BD (1996) A new species of northern shrew-opossum (Paucituberculata: Caenolestidae) from the Cordillera del Cóndor, Ecuador. J Mammal 77:41–53

Amico G, Aizen MA (2000) Mistletoe seed dispersal by a marsupial. Nature 408:929–930

Amico G, Rodríguez-Cabal MA, Aizen MA (2009) The potential key seed-dispersing role of the arboreal marsupial *Dromiciops gliroides*. Acta Oecol 35:8–13

Argot C (2001) Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 247:51–79

Argot C (2002) Functional-adaptive analysis of the hindlimb anatomy of extant marsupials, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 253:76–108

Argot C (2003) Functional-adaptive anatomy of the axial skeleton of some extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 255:279–300

Astúa de Moraes D (2006) Range extension and first Brazilian record of the rare *Hyladelphys kalinowskii* (Hershkovitz, 1992) (Didelphimorphia, Didelphidae). Mammalia 70:174–176

Astúa de Moraes D, Santori RT, Finotti R, Cerqueira R (2003) Nutritional and fibre contents of laboratory-established diets of neotropical opossums (Didelphidae). In: Jones M, Dickman C, Archer M (eds) Predators with pouches: The Biology of Carnivorous Marsupials. CSIRO Publishing, Victoria

Atramentowicz M (1986) Dynamique de population chez trois marsupiaux didelphidés de Guyane. Biotropica 18:136–149

Atramentowicz M (1988) La frugivorie opportuniste de trois marsupiaux didelphidés de Guyane. Rev Ecol (Terre et Vie) 43:47–57

Barnes RD, Barthold SW (1969) Reproduction and breeding behavior in an experimental colony of *Marmosa mitis* Bangs (Didelphidae). J Reprod Fertility 6:477–482

Bergallo HG, Cerqueira R (1994) Reproduction and growth of the opossum *Monodelphis domestica* (Mammalia: Didelphidae) in northeastern Brazil. J Zool 232:551–563

Bernarde PS, Machado RA (2008) Mammalia, Didelphimorphia, Didelphidae, *Glironia venusta* Thomas, 1912: Distribution extension to the state of Acre, Brazil. Checklist 4:151

Biggers JD (1967) Notes on reproduction of the woolly opossum (*Caluromys derbianus*) in Nicaragua. J Mammal 48:678–680

Birney EC, Monjeau JA (2003) Latitudinal variation in South American marsupial biology. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Bocchiglieri A, Mendonca AF, Campos JB (2010) Diet composition of *Gracilinanus agilis* (Didelphimorphia, Didelphidae) in dry woodland areas of Cerrado in central Brazil. Mammalia 74:225–227

Bozinovic F, Ruiz G, Rosenmann M (2004) Energetics and torpor of a South American "living fossil", the microbiotheriid *Dromiciops gliroides*. J Comp Physiol (B) 174:293–297

Bozinovic F, Ruiz G, Cortés A, Rosenmann M (2005) Energetics, thermoregulation and torpor in the Chilean mouse-opossum *Thylamys elegans* (Didelphidae). Rev Chilena Hist Nat 78:199–206

Bradley AJ (2003) Stress, hormones and mortality in small dasyurid marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Braithwaite RW, Lee AK (1979) A mammalian example of semelparity. Amer Nat 113:151–155

Brown B (2004) Atlas of new world marsupials. Fieldiana Zool NS 102:1–308

Bruch C (1917) La Comadrejita *Marmosa elegans*. Rev Jard Zool Buenos Aires 51(52):208–214

Busch M, Kravetz FO (1991) Diet composition of *Monodelphis dimidiata* (Marsupialia, Didelphidae). Mammalia 55:619–621

Cáceres NC (2000) Dieta, adaptações morfológicas à alimentação e dispersão de sementes por marsupiais do Sul do Brasil. PhD thesis, Univ Fed Paraná

Cáceres NC (2006) O papel de marsupiais na dispersão de sementes. In: Cáceres NC, Monteiro Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. UFMS Editora, Campo Grande

Cáceres NC, Monteiro-Filho ELA (1997) Reproductive biology of the common opossum *Didelphis marsupialis* (Mammalia: Marsupialia), in southern Brazil. Brenesia 47–48:97–104

Cáceres NC, Monteiro-Filho ELA (2000) The common opossum, *Didelphis aurita*, as a seed disperser of several plants in south Brazil. Ciência e Cultura 52:41–44

Cáceres NC, Ghizoni-Jr IR, Graipel ME (2002) Diet of two marsupials, *Lutreolina crassicaudata* and *Micoureus demerarae*, in a coastal Atlantic Forest island of Brazil. Mammalia 66:331–340

Cantor M, Ferreira LA, Silva WR, Setzl EZF (2010) Potential seed dispersal by *Didelphis albiventris* (Marsupialia, Didelphidae) in highly disturbed environment. Biota Neotropical 10:45–51

Carlsson A (1903) Beitrage zur Anatomic der Marsupial Region bei den Beuteltherien. Zoologische Jahrbiicher, Abteilung Anatomic und Ontogenie der Thiere 80:489–505

Carmignotto AP, Monfort T (2006) Taxonomy and distribution of the Brazilian species of *Thylamys* (Didelphimorphia, Didelphidae). Mammalia 70:126–144

Carvalho FMV, Fernandez FAS, Nessimian JL (1999) Diet of small mammals in Atlantic forest fragments in southeastern Brazil. Rev Brasilera Zoociências 1:91–101

Carvalho RVC, Delciellos AC, Vieira MV (2000) Medidas externas dos membros de marsupiais didelfídeos: una comparção com medidas do esqueleto pós-craniano. Bol Mus Nac NS Zool 438:1–8

Catzeflis F, Richard-Hansen C, Fournier-Chambrillon C, Lavergne A, Vié JC (1997) Biométrie, reproduction, et sympatrie chez *Didelphis marsupialis* et *D. albiventris* en Guyane française (Didelphidae: Marsupialia). Mammalia 61:231–243

Ceotto P, Finotti R, Santori R, Cerqueira R (2009) Diet variation of the marsupials *Didelphis aurita* and *Philander frenatus* (Didelphimorphia, Didelphidae) in a rural area of Rio de Janeiro State, Brazil. Mastozool Neotropical 16:49–58

Cerqueira R (2004) Fatores ambientais e a reprodução de marsupiais e roedores no leste do Brasil1. Arqu Mus Nac 63:29–39

Cerqueira R, Gentile R, Fernandez FAS, D'Andrea PS (1993) A five year study of an assemblage of small mammals in southeastern Brazil. Mammalia 57:507–517

Charles-Dominique P (1983) Ecology and social adaptations in didelphid marsupials: comparison with eutherians of similar ecology. Amer Soc Mammal Sp Publ 7:395–422

Charles-Dominique P, Atramentowicz M, Charles-Dominique M, Gérard H, Hladik A, Hladir CM, Prévost MF (1981) Les memifères frugivores arboricols nocturnes d'une forêt guyanaise: interrelations plantes-animaux. Rev Ecol (Terre et Vie) 35:341–435

Cherem JJ, Graipel ME, Menezes ME, Soldateli M (1996) Observações sobre a biologia do gambá (*Didelphis marsupialis*) na Ilha de Ratones Grande, Estado de Santa Catarina, Brasil. Biotemas 9:47–56

Clark CT, Smith KK (1993) Cranial Osteogenesis in *Monodelphis domestica* (Didelphidae) and *Macropus eugenii* (Macropodidae). J Morpholgy 215:119–149

Cockburn A (1997) Living slow and dying young: senescence in marsupials. In: Saunders NR, Hinds LA (eds) Marsupial biology: recent research, New perspectives. Univ New South Wales Ltd, Sydney

Cockburn CN, Johnson A (1988) Patterns of Growth. In: Janssens PA (ed) Tyndale-Biscoe CH. The developing marsupial. Models for biomedical research. Springer, Berlin

Cole LC (1954) The population consequences of life history phenomena. Quart Rev Biol 29:103–137

Cordero AG, Nicolas RA (1987) Feeding habits of the opossum (*Didelphis marsupialis*) in northern Venezuela. In: Patterson BD, Timm RM (eds) Studies in neotropical mammalogy, essays in honor of Philip Hershkovitz. Fieldiana Zool NS 39:125–131

Corvalán VE (2004) Uso del hábitat y ecología poblacional de pequeños mamíferos del desierto del monte central, Mendoza, Argentina. PhD thesis, Univ Nacional de La Plata

Crespo JA (1982) Ecología de la comunidad de mamíferos del parque Nacional Iguazú, Misiones. Rev Mus Arg Cs Nat "B. Rivadavia" Ecol 3:45–162

D'Andrea PS, Gentile R, Cerqueira R, Grelle CEV, Horta C, Rey L (1999) Ecology of small mammals in a Brazilian rural area. Rev Bras Zool 16:611–620

Davis DE (1947) Notes on the life histories of some Brazilian mammals. Bol Mus Nac 76:1–8

Dawson TJ, Dawson WR (1982) Metabolic scope and conductance in response to cold of some dasyurid marsupials and Australian rodents. Comp Biochem Physiol 71:59–64

Dawson TJ, Hulbert AJ (1970) Standard metabolism, body temperature, and surface areas of Australian marsupials. Am J Phys 218:1233–1238

Dawson TJ, Olson JM (1987) Thermogenic capacities of the opossum *Monodelphis domestica* when warm and cold acclimated: similarities between American and Australian marsupials. Comp Biochem Physiol 89:85–91

Dawson TJ, Wolfers JM (1978) Metabolism, thermoregulation and torpor in shrew sized marsupials of the genus Planigale. Comp Biochem Phy A 59:305–309

Delciellos AC, Vieira MV (2006) Arboreal walking performance in seven didelphid marsupials as an aspect of their fundamental niche. Austral Ecol 31:449–457

Díaz GB, Cortés A (2003) Pequeños mamíferos en ambientes desérticos: los problemas de conservación de agua. In: Bozinovic F (ed) Fisiología Ecológica y Evolutiva, Teoría y casos de estudio en animales. Univ Católica de Chile, Santiago

Eisenberg JF (1980) The density and biomass of tropical mammals. In: Soulé ME, Wilcox BA (eds) Conservation biology. Sinauer Associates, Sunderland

Eisenberg JF (1981) The mammalian radiations: an analysis of trends in evolution, adaptation and behavior. Univ Chicago Press, Chicago

Eisenberg JF, Wilson D (1981) Relative brain size and demographic strategies in didelphid marsupials. Amer Nat 118:1–15

Emmons LH, Feer F (1997) Neotropical rainforest mammals: a field guide, 2nd edn. Univ Chicago Press, Chicago

Enders AC (1966) Attachment, nursing, and survival of young in some Didelphids. In: Rowlands JW (ed) Comparative biology of reproduction in mammals. Academic Press, New York

Enders RK (1935) Mammalian life-histories from Barro Colorado Island, Panama. Bull Mus Comp Zool 78:385–497

Fernandes MEB, Andrade FAG, Silva Júnior JS (2006) Dieta de *Micoureus demerarae* (Thomas) (Mammalia, Didelphidae) associada às florestas contíguas de mangue e terra firme em Bragança, Pará, Brasil. Rev Bras Zool 23:1087–1092

Fish FE (1993) Comparison of swimming kinematics between terrestrial and semiaquatic opossums. J Mammal 74:275–284

Fleming TH (1973) The reproductive cycles of three species of opossum and other mammals in the Panamá Canal Zone. J Mammal 54:439–455

Fonseca GAB, Kierulff MCM (1989) Biology and natural history of Brazilian Atlantic forests of different sizes. Bull Florida Mus Nat Hist Biol Sci 34:99–152

Freitas SR, Astúa de Moraes D, Santori RT, Cerqueira R (1997) Habitat preference and food use by *Metachirus nudicaudatus* and *Didelphis aurita* (Didelphimorphia, Didelphidae) in a restinga forest at Rio de Janeiro. Rev Bras Biol 57:93–98

García D, Rodríguez-Cabal MA, Amico GC (2009) Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. J Ecol 97:217–229

Gardner AL (1973) The systematics of the genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America. Spec Publ Mus Texas Tech Univ 4:1–81

Gardner AL (2008) Mammals of South America, Volume 1: marsupials, xenarthrans, shrews, and bats. Univ Chicago Press, Chicago

Gardner AL, Dagosto M (2008) Tribe Metachirini. In: Gardner AL (ed) Mammals of South America, Vol 1: marsupials, xenarthrans, shrews, and bats. Univ Chicago Press, Chicago

Geiser F (1994) Hibernation and daily torpor in marsupials: a review. Aus J Zool 42:1–16

Geiser F (2003) Thermal biology and energetics in carnivorous marsupials. In: Jones M, Dickman C, Archer M (eds), Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Geiser F, Martin GM (2013) Torpor in the Patagonian opossum (*Lestodelphys halli*): implications for the evolution of daily torpor and hibernation

Geiser F, Drury RL, McAllan BM, Wang DH (2003) Effects of temperature acclimation on maximum heat production, thermal tolerance, and torpor in a marsupial. J Comp Phyisiol 173:437–442

Geiser F, Christian N, Cooper CE, Körtner G, McAllan BM, Pavey CR, Turner JM, Warnecke L, Willis CKR, Brigham M (2008) Torpor in marsupials: recent advances. In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: hibernation, torpor and cryobiology. Univ KwaZulu-Natal, Pietermaritzburg

Godfrey GK (1975) A study of oestrus and fecundity in a laboratory colony of mouse opossums (*Marmosa robinsoni*). J Zool 175:541–555

González EM, Claramunt S (2000) Behavior of captive short-tailed opossums, *Monodelphis* dimidiata (Wagner, 1847) (Didelphimorphia, Didelphidae). Mammalia 64:271–285

Gordon CL (2003) A first look at estimating body size in dentally conservative marsupials. J Mammal Evol 10(1–2):1–21

Grand TI (1983) Body weight: relationships to tissue composition, segmental distribution of mass, and motor function. III. The Didelphidae of French Guyana. Aust J Zool 31:299–312

Green B (1997) Field energetics and water fluxes in marsupials. In: Saunders NR, Hinds LA (eds) Marsupial biology: recent research, new perspectives. Univ New South Wales Ltd, Sydney

Greer JK (1965) Mammals of Malleco Province, Chile. Publ Mus Mich State Univ Biol Ser 3: 81–149

Hamrick MW (2001) Morphological diversity in digital skin microstructure of didelphid marsupials. J Anatomy 198:683–688

Harder JD, Fleck DW (1997) Reproductive ecology of New World marsupials. In: Saunders NR, Hinds LA (eds) Marsupial biology: recent research, new perspectives. Univ New South Wales Ltd, Sydney

Hayssen V, Lacy RC (1985) Basal metabolic rates in mammals: taxonomic differences in the allometry of and body mass. Comp Biochem Physiol 81:741–754

Hershkovitz P (1987) A history of the recent mammalogy of the Neotropical region from 1492 to 1850. In: Patterson BD, Timm RM (eds) Studies in neotropical mammalogy essays in honor of Philip Hershkovitz. Fieldiana Zool NS 39:11–98

Hershkovitz P (1992a) The South American gracile mouse opossums, genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notes on general morphology and relationships. Fieldiana Zool NS 70:1–56

Hershkovitz P (1992b) Ankle bones: the Chilean opossum *Dromiciops gliroides* Thomas, and marsupial phylogeny. Bonner Zool Beitr 43:181–213

Hershkovizt P (1997) Composition of the family Didelphidae Gray, 1821 (Didelphoidea: Marsupialia), with a review of the morphology and behavior of the included four-eyed opossums of the genus *Philander* Tiedemann, 1808. Fieldiana Zool NS 86:1–103

Hershkovitz P (1999) *Dromiciops gliroidesThomas*, 1894, last of the Microbiotheria (Marsupialia), with a Review of the family Microbiotheriidae. Fieldiana ZoolNS 93:1–60

Hildebrand M (1995) Analysis of vertebrate structure. Wiley, New York

Hill JP (1918) Some observations on the early development of *Didelphis aurita* (contributions to the embryology of the marsupialia V). Quart J Microsc Sci 63:93–139

Hingst E, D'Andrea PS, Santori R, Cerqueira R (1998) Breeding of *Philander frenata* (Didelphimorphia, Didelphidae) in captivity. Lab Anim 32:434–438

Hope PJ, Pyle D, Daniels CB, Chapman I, Horowitz M, Morley JE, Trayhurn P, Kumaratilake J, Wittert G (1997) Identification of brown fat and mechanisms for energy balance in the marsupial, Sminthopsis crassicaudata. Am J Physiol 273:161–167

Hulbert AJ, Dawson TJ (1974) Standard metabolism and body temperature of perameloid marsupials from different environments. Comp Biochem Phys A 47:583–590

Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge

Hume ID (2003) Nutrition of carnivorous marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Hunsaker D (1977) Ecology of New World marsupials. In: Hunsaker D (ed) The biology of marsupials. Academic Press, New York

Iodice OH, Cervino CO, Affanni JM (2010) Manejo y reproducción de *Lutreolina crassicaudata* (Marsupialia, didelphidae) en condiciones de bioterio. Rev Electrón Vet 11:1695–7504

Jastroch M, Withers KW, Taudien S, Frappell PB, Helwig M, Fromme T, Hirschberg V, Heldmaier G, McAllan BM, Firth BT, Burmester T, Platzer M, Klingenspor M (2008) Marsupial uncoupling protein 1 sheds light on the evolution of mammalian nonshivering thermogenesis. Physiol Genomics 32:161–169

Julien-Laferrière D, Atramentowicz M (1990) Feeding and reproduction of three didelphid marsupials in two neotropical forests (French Guiana). Biotropica 22:404–415

Kirsch JAW, Waller PF (1979) Notes on the trapping and behavior of the Caenolestidae (Marsupialia). J Mammal 60:390–395

Kraus DB, Fadem BH (1987) Reproduction, development, and physiology of the gray short-tailed opossum (*Monodelphis domestica*). Lab Animal Sci 37:478–482

Krause WJ, Krause WA (2006) The opossum: its amazing story. Department of Pathology and Anatomical Sciences, School of Medicine, University of Missouri

Krieg H (1924) Biologische Reisestudien in Südamerika. III. Chilenische Beutelratten. Z Morphol Okol Tiere 3:169–176

Lee AK, Cockburn A (1987) Evolutionary ecology of marsupials. Monographs on marsupial biology. Cambridge University Press, Cambridge

Lee AK, Wooley P, Braithwaite RW (1982) Life history strategies of dasyurid marsupials. In: Archer M (ed) Carnivorous Marsupials. Royal Zoological Society of New South Wales, Sydney

Leiner NO, Silva WR (2007) Seasonal variation in the diet of the Brazilian slender opossum (*Marmosops paulensis*) in a montane Atlantic forest area, southeastern Brazil. J Mammal 88:158–164

Leiner NO, Setz EZF, Silva WR (2008) Semelparity and factors affecting the reproductive activity of the Brazilian slender-opossum (*Marmosops paulensis*) in southeastern Brazil. J Mammal 89:153–158

Lemelin P, Schmitt D, Cartmill M (2003) Footfall patterns and interlimb co-ordination in opossums (Family Didelphidae): evidence for the evolution of diagonal-sequence walking gaits in primates. J Zool 260:423–429

Loretto D, Vieira MV (2008) Use of space by the marsupial *Marmosops incanus* (Didelphimorphia, Didelphidae) in the Atlantic Forest, Brazil. Mamm Biol 73:255–261

Loretto D, Ramalho E, Vieira MV (2005) Defense behavior and nest architecture of *Metachirus nudicaudatus* Desmarest, 1817 (Marsupialia, Didelphidae). Mamm 69(3–4):417–419

Lorini ML, Oliveira JA, Persson VG (1994) Annual age structure and reproductive patterns in *Marmosa incana* (Lund, 1841) (Didelphidae, Marsupialia). Z Sauegetierkunde 59:65–73

Lovegrove BG (2000) The zoogeography of mammalian basal metabolic rate. Am Nat 156:201–219

Macedo L, Fernandez FAS, Nessimian JL (2010) Feeding ecology of the marsupial *Philander frenatus* in a fragmented landscape in Southeastern Brazil. Mamm Biol 75:363–369

Mann G (1955) Monito del Monte. Dromiciops australis Philippi. Invest Zool Chilenas 2:159–166

Mann G (1958) Reproducción de *Dromiciops australis* (Marsupialia, Didelphydae). Invest Zool Chilenas 4:209–213

Marshall LG (1978a) *Lutreolina crassicaudata*. Mamm Sp 91:1–4

Marshall LG (1978b) *Chironectes minimus*. Mamm Sp 109:1–6

Martin GM (2008) Sistemática, Distribución y Adaptaciones de los Marsupiales Patagónicos. PhD thesis, Univ Nacional de La Plata

Martin GM (2010) Geographic distribution and historical occurrence of *Dromiciops gliroides* Thomas (Marsupialia, Microbiotheria). J Mammal 91:1025–1035

Martin GM (2011) Geographic distribution of *Rhyncholestes raphanurus* Osgood, 1924 (Paucituberculata: Caenolestidae), an endemic marsupial of the Valdivian Temperate Rainforest. Aust J Zool 59:118–126

Martin GM (2012) Distribución geográfica de marsupiales americanos. II Congreso Latinoamericano de Mastozoología y XXV Jornadas Argentinas de Mastozoología, Buenos Aires

Martin GM (in preparation) Living New World marsupials. What do we know? In: Goin FJ, Forasiepi A (eds) New World Marsupials and their Extinct Relatives: One Hundred Million Years of Metatherian Evolution. Springer, Berlin

Martin GM, Udrizar Sauthier DE (2011) Observations on the captive behavior of the rare Patagonian opossum *Lestodelphys halli* (Thomas, 1921) (Marsupialia, Didelphimorphia, Didelphidae). Mammalia 75281–286

Martins EG, Bonato V, da-Silva CQ, Reis SF (2006) Partial semelparity in the Neotropical didelphid marsupial *Gracilinanus microtarsus*. J Mammal 87:915–920

Massoia E, Fornes A (1972) Presencia y rasgos etoecológicos de *Marmosa agilis chacoensis* Tate en las provincias de Buenos Aires, Entre Ríos, y Misiones (Mammalia-Marsupialia-Didelphidae). Rev Invest Agropec, Ser 1. Biol Prod Animal 9:71–82

McManus JJ (1970) Behavior of captive opposums, *Didelphis marsupialis virginiana*. Amer Midland Nat 84:144–169

McNab BK (1978) The comparative energetics of neotropical marsupials. J Comp Physiol 125:115–128

McNab BK (1982) The physiological ecology of South American mammals. In: Mares MA, Genoways HH (eds) Mammalian biology in South America. Pymatuning Lab of Ecol, Spec Publ Ser 6. Univ Pittsburgh

McNab BK (1986) Food habits, energetics, and the reproduction of marsupials. J Zool 208: 595–614

McNab BK (2005) Uniformity in the basal metabolic rate of marsupials: its causes and consequences. Rev Chilena Hist Nat 78:183–198

Merritt JF (2010) The biology of small mammals. Johns Hopkins Press, Baltimore

Monteiro-Filho ELA (1987) Biologia reprodutiva e espaço domiciliar de Didelphis albiventris em uma área perturbada na região de Campinas, Estado de São Paulo. Master thesis, Universidade Estadual de Campinas

Monteiro-Filho ELA, Cáceres NC (2006) Biología Reproductiva de Fêmeas de Marsupiais Didelfídeos. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Monteiro-Filho ELA, Dias VS (1990) Observações sobre a biologia de *Lutreolina crassicaudata* (Mammalia: Marsupialia). Rev Bras Biol 50:393–399

Morrison PR, McNab BK (1962) Daily torpor in a Brazilian murine opossum (*Marmosa*). Comp Physiol Biochem 6:57–68

Morrone JJ (2004) Panbiogeografía, componentes bióticos y zonas de transición. Rev Bras Entomol 48:149–162

Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. Ann Rev Entomol 51:467–494

Morton SR (1980) Ecological correlates of caudal fat storage in small mammals. Aust Mammal 3:81–86

Muizon C, Argot C (2003) Comparative anatomy of the didelphimorphs marsupials from the early Palaeocene of Bolivia (*Pucadelphys*, *Andinodelphys*, and *Mayulestes*). Palaeobiologic implications. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Muñoz Pedreros A, Lang BK, Bretos M, Meserve PL (2005) Reproduction and development of *Dromiciops gliroides* (Marsupialia: Microbiotheria) in the temperate rainforests of Southern Chile. Gayana 69:225–233

Myers P, Patton JL (2008) Genus *Lestoros* Oehser, 1934. In: Gardner A (ed) Mammals of South America, vol 1. Marsupials, Xenarthrans, Shrews, and Bats. Univ Chicago Press, Chicago

Nickrent DL, Musselman LJ (2004) Introduction to parasitic flowering plants. The Plant Health Instruct. doi:10.1094/PHI-I-2004-0330-01

Nowak RM (1999) Walker's mammals of the World, 6 edn, 2 vols. The Johns Hopkins Univ Press, Baltimore

O'Connel MA (1979) The ecology of didelphid marsupials from northern Venezuela. In: Eisenberg JF (ed) Vertebrate ecology in the northern neotropics. Smithsonian Inst Press, Washington

Oakwood M, Bradley AJ, Cockburn A (2001) Semelparity in a large marsupial. Proc R Soc London 268:407–411

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51:933–938

Osgood WH (1921) A monographic study of the American marsupial *Caenolestes*. Field Mus Nat Hist Zool Ser 16:1–162

Osgood WH (1924) Review of living caenolestids with description of a new genus from Chile. Field Mus Nat Hist Zool Ser 14:165–173

Osgood WH (1943) The mammals of Chile. Field Mus Nat Hist Zool Ser 30:1–268

Palma RE (1997) *Thylamys elegans*. Mammal Sp 572:1–4

Palma RE (2003) Evolution of American marsupials and their phylogenetic relationships with Australian metatherians. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Patterson BD (2008) Genus *Rhyncholestes* Osgood, 1924. In: Gardner A (ed) Mammals of South America, Vol. 1: Marsupials, Xenarthrans, Shrews, and Bats. Univ Chicago Press, Chicago

Patterson BD, Gallardo MH (1987) *Rhyncholestes raphanurus*. Mammal Sp 286:1–5

Patterson BD, Meserve PL, Lang BK (1990) Quantitative habitat associations of small mammals along an elevational transect in temperate rain-forests of Chile. J Mammal 71:620–633

Perret M, Atramentowicz M (1989) Plasma concentrations of progesterone and testosterone in captive woolly opossums (*Caluromys philander*). J Reprod Fert 85:31–41

Pfiegler JF, Cabana T (1996) The vestibular primary afferents and teh vestibulospinal projections in the developing and adult opossum, *Monodelphis domestica*. Anat Embryol 194:75–88

Philippi F (1893) Un nuevo marsupial chileno. Anales de la Universidad de Chile 85:31–34

Phillips CJ, Knox Jones J (1968) Additional comments on reproduction in the woolly opossum (*Caluromys derbianus*) in Nicaragua. J Mammal 49:320–321

Pine RH (1981) Reviews of the mouse opossums *Marmosa parvidens* Tate and *Marmosa invicta* Goldman (Mammalia: Marsupialia: Didelphidae) with description of a new species. Mammalia 45:55–70

Pine RH, Dalby PL, Matson JO (1985) Ecology, postnatal development, morphometrics, and taxonomic status of the short-tailed opossum, *Monodelphis dimidiata*, an apparently semelparous annual marsupial. Ann Carnegie Mus 54:195–231

Pires AS, Fernandez FAS (1999) Use of space by the marsupial *Micoureus demerarae* in small Atlantic forest fragments in southeastern Brazilian. J Tropical Ecol 15:279–290

Pires MM, Cruz LD, Fernandes FR, Martins EG, dos Reis S (2009) Omnivory by *Micoureus paraguayanus* (Didelphimorphia: Didelphidae) in a Brazilian Cerrado remnant: diet composition and dietary seasonality. Ann, 3 Congr Latino Americano de Ecol, São Lourenço, Minas Gerais

Prevedello JA, Rodrigues RG, Monteiro-Filho ELA (2009) Vertical use of space by the marsupial *Micoureus paraguayanus* (Didelphimorphia, Didelphidae) in the Atlantic forest of Brazil. Acta Theriol 54:259–266

Pridmore PA (1992) Trunk movements during locomotion in the marsupial *Monodelphis domestica* (Didelphidae). J Morphol 211:137–146

Pridmore PA (1994) Locomotion in *Dromiciops australis* (Marsupialia: Microbiotheriidae). Aust J Zool 42:679–699

Rademaker V, Cerqueira R (2006) Variation in the latitudinal reproductive patterns of the genus *Didelphis* (Didelphimorphia: Didelphidae). Austral Ecol 31:337–342

Regidor HA, Gorostiague M (1996) Reproduction in the white-eared opossum (*Didelphis albiventris*) under temperate conditions in Argentina. Stud Neotropical Fauna Environ 31:133–136

Regidor HA, Gorostiague M, Sühring S (1999) Reproduction and dental age classes of the little water opossum (*Lutreolina crassicaudata*) in Buenos Aires, Argentina. Rev Biol Tropical 47 (1–2):271–272

Ribeiro P, Bicudo EPW (2007) Oxygen consumption and thermoregulatory responses in three species of South American marsupials. Comp Biochem Physiol A 174:658–664

Riek A, Geiser F (2014) Allometry of thermal variables in mammals: consequences of body size and phylogeny. J Zool 292:74–85

Rigueira SE, Valle CMC, Varejão JBN, Albuquerque PV, Nogueira JC (1987) Algumas observações sobre o ciclo reproductivo anual de fêmeas do gambá *Didelphis albiventris* (Lund, 1841) (Marsupialia, Didelphidae) em populações naturais no Estado de Minas Gerais, Brasil. Rev Bras Zool 4:129–137

Rodríguez-Cabal MA, Aizen MA, Novaro A (2007) Habitat fragmentation disrupts a plant–disperser mutualism in the temperate forest of South America. Biol Conservation 139:195–202

Rose RW, West AK, Ye JM, McCormack GH, Colquhoun EQ (1999) Nonshivering thermogenesis in a marsupial, the Tasmanian bettong (Bettongia gaimardi) is not attributable to brown adipose tissue. Physiol Biochem Zool 72:699–704

Santori RT, Astúa de Moraes D (2006) Alimentação, nutrição e adaptações alimentares de marsupiais brasileiros. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Santori RT, Rocha-Barbosa O, Vieira MV, Magnan-Neto JA, Loguercio MFC (2005) Locomotion in aquatic, terrestrial, and arboreal habitat of the thick-tailed opossum, *Lutreolina crassicaudata* (Desmarest 1804). J Mammal 86:902–908

Schmidt-Nielsen K (1964) Animal physiology, 2nd edn. Prentice Hall Inc, London

Solari SA (2003) Diversity and distribution of *Thylamys* (Didelphidae) in South America, with emphasis on species from the western side of the Andes. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Strahan R (1991) Complete book of Australian mammals. Cornstalk Publishing, New South Wales

Streilein KE (1982) Behavior, ecology, and distribution of South American marsupials. In: Mares MA, Genoways HH (eds) Mammalian biology in South America. Special Publications Series, Vol. 6. Pymatuning Laboratory of Ecology, Univ Pittsburgh

Szalay FS (1982a) Phylogenetic relationships of the marsupials. In: Buffetant E, Janvier P, Rage JC, Tassy P (eds) Philogenie et palengeographie: livre jubilaire de Robert Hoffstetter. Géobios Mém Spéc 6:177–190

Szalay FS (1982b) A new appraisal of marsupial phylogeny and clasification. In: Archer M (ed) Carnivorous marsupials. R Zool Soc of New South Wales, Sydney

Szalay FS (1994) Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge Univ Press, New York

Szalay FS, Sargis EJ (2001) Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaborai (Brazil) and the phylogenetics and biogeography of Metatheria. Geodiversitas 23:139–302

Tate GHH (1933) A systematic revision of the marsupial genus *Marmosa*, with a discussion of the adaptive radiation of the murine opossums (*Marmosa*). Bull Amer Mus Nat Hist 66:1–250

Thielen DR, Arends A, Segnini S, Fariñas M (1997) Food availability and population dynamics of *Marmosa xerophila* Handley and Gordon 1979 (Marsupialia: Didelphidae). Zoocriaderos 2:1–15

Thomas O (1888) Catalogue of the Marsupialia and Monotremata in the collection of the British Museum of Natural, History edn. Trustees of the British Museum, London

Thompson SD (1988) Thermoregulation in the water opossum (*Chironectes minimus*): an exception that "proves" a rule. Physiol Zool 61:450–460

Timm RM, Patterson BD (2008) Genus *Caenolestes* O. Thomas, 1895. In: Gardner A (Ed), Mammals of South America, vol. 1. Marsupials, Xenarthrans, Shrews, and Bats. Univ Chicago Press, Chicago

Townsend, CR, Hughes RN (1981) Maximizing net energy returns from foraging. In: Townsend CR, Calow P (eds) Physiological ecology: an evolutionary approach to resource use. Sinauer Associates, Sunderland Massachusetts

Tyndale-Biscoe CH (1980) Observations on the biology of marsupials in Colombia and Venezuela. Nat Geogr Soc Res Report 12:711–720

Tyndale-Biscoe CH (2005) Life of marsupials. CSIRO Publishing, Victoria

Tyndale-Biscoe CH, Janssens PA (1988) The developing marsupial. Models for biomedical research. Springer, Berlin

Tyndale-Biscoe CH, MacKenzie RB (1976) Reproduction in *Didelphis marsupialis* and *Didelphis albiventris* in Colombia. J Mammal 57:249–265

Tyndale-Biscoe CH, Renfree MB (1987) Reproductive physiology of marsupials. Cambridge Univ Press, Cambridge

VandeBerg JL (1983) The gray short-tailed opossum: a new laboratory animal. Inst Lab Animal Resources News 26:9–12

Vaughan TA, Ryan JM, Czaplewski NJ (2011) Mammalogy, 5th edn. Jones and Bartlett Publishers, Sudbury, Massachusetts

Vieira MV (1997) Body size and form in two neotropical marsupials, *Didelphis aurita* and *Philander opossum* (Marsupialia: Didelphidae). Mammalia 61(2):245–254

Vieira EM (2006a) Padrões de Uso Vertical do Habitat por Marsupiais Brasileiros. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Vieira MV (2006b) Locomção, Morfologia e Uso do Habitat em Marsupiais Neotropicais: Uma Abordagem Ecomorfológica. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Vieira EM, Astúa de Moraes D (2003) Carnivory and insectivory in Neotropical marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Voss RS, Jansa SA (2003) Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. Bull Am Mus Nat Hist 276:1–82

Voss RS, Jansa SA (2009) Phylogenetic relationship and classification of Didelphid marsupials an extant radiation of New World metatherian mammals. Bull Amer Mus Nat Hist 332:1–177

Voss RS, Lunde DP, Simmons NB (2001) The mammals of Paracou, French Guina: a Neotropical lowland rainforest fauna. Part. 2 nonvolant species. Bull Amer Mus Nat Hist 263:1–236

Voss RS, Lunde DP, Jansa SA (2005) On the contents of *Gracilinanus* Gardner and Creighton, 1989, with the description of a previously unrecognized clade of small didelphid marsupials. Amer Mus Novit 3482:1–34

Wallis IR, Farrell DJ (1992) Energy metabolism in potorine marsupials. J Comp Physiol B 162:478–487

Williams GC (1966) Adaptation and natural selection. Princeton Univ Press, Princeton

Willig MR, Gannon MR (1997) Gradients of species density and turnover in marsupials: a hemispheric perspective. J Mammal 78:756–765

Chapter 3
Dispersal of Vertebrates from Between the Americas, Antarctica, and Australia in the Late Cretaceous and Early Cenozoic

Abstract The early Paleocene diversity of metatherians in Tiupampan faunas of South America and the pre-Tiupampan Paleocene polydolopimorphian *Cocatherium* speak in favor of an earliest Paleocene or Late Cretaceous dispersal of metatherians from North America. No Late Cretaceous metatherian or eutherian mammals have been recovered to date in South America, but the late Campanian to Maastrichtian hadrosaurine dinosaurs in Argentina, as well as the late Maastrichtian of the Antarctic Peninsula, is evidence of a biotic connection to North America. Placental ‘condylarths’ in the Tiupampan may have been related to, and dispersed southward relative to, Puercan taxa in North America and perhaps reflect a somewhat later event in comparison to metatherians. Other than hadrosaurine dinosaurs, Late Cretaceous vertebrates of South America are basically Gondwanan in affinities and reflect (and survived) the pre-106 Ma connection between South America, Africa, and Antarctica. The potential for a Late Cretaceous dispersal of metatherians would be compatible with a continued dispersal to Australia at that time, also supported by plate tectonic relationships, notwithstanding the basically endemic coeval Australian dinosaur fauna, and recognizing the essential absence of a Late Maastrichtian land vertebrate record there. An early Paleocene connection between at least Antarctica and South America is documented by the presence of a monotreme in the Peligran fauna of Patagonia. This, coupled with the fact that post-Peligran mammal faunas in South America and the Antarctic Peninsula (from at least 52 Ma in that location) are composed of derived metatherian as well as placental mammals, suggests that dispersal of metatherians to Australia had been achieved prior to the Eocene. Such timing is compatible with the still plesiomorphic level of Australian metatherians from the early Eocene Tingamarra fauna of Australia, the marine sundering of the Tasman Gate at about 50 Ma and the development of a continuously marine southern coastline of Australia from about 45 Ma effectively foreclosed overland mammal and other vertebrate dispersal to Australia thereafter.

Keywords Metatheria · South America · Late cretaceous · Paleogene · Dispersals · North America · Australia · Antarctica

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8_3

3.1 Introduction

Woodburne and Case (1996) and Case et al. (2005) presented a dispersal scenario that utilized contemporaneous plate tectonic and faunal comparisons to suggest a biogeographic connection between North and South America in the Late Cretaceous, based largely on the record provided by metatherian mammals (to South America) and snakes (to North America). The initial dispersal apparently was followed in the early Paleocene by eutherian mammals expanding their range to South America. These events set the stage for the subsequent endemic evolution of South America's unique therian mammal faunas, with episodes of later immigration of placental mammals during the Neogene (summarized in Woodburne 2010; Woodburne et al. 2014). The appraisal also suggested that the most likely dispersal of metatherians to Australia took place prior to 64 Ma when the South Tasman Rise was considered to be flooded.

The following provides an update of faunal and plate tectonic information to move toward a more complete understanding of biogeographic and tectonic aspects of mainly mammalian dispersal between North and South America, Antarctica, and Australia. To this end, considerable recognition is given to the excellent portrayal of these aspects in Lawver et al. (2013).

3.1.1 Definitions and Abbreviations

EECO	Early Eocene Climatic Optimum. This is the interval of highest mean ocean temperature of the Cenozoic Era (Wolfe 1978; Zachos et al. 2001, 2008). It began about 53 Ma and persisted to about 50 Ma (Tsukui and Clyde 2012), and occurred in the contexts of generally warm conditions that characterized the early Cenozoic Era from the Paleocene to about middle Eocene
k.y.	A segment of geologic time one thousand years in duration or the age of an event (e.g., ten thousand years ago), without reference to a point or set of points on the radioisotopic time scale
Ma	Megannum. One million years in the radioisotopic time scale (e.g., 10 Ma refers to the ten million year point on the time scale)
MAT	Mean Annual Temperature (as inferred from paleobotanical leaf margin and other data)
MECO	Mid-Eocene Climatic Optimum; a hyperthermal warming event at about 41.6 Ma (Zachos et al. 2008; Figueirido et al. 2012)
m.y.	A segment of geologic time one million years in duration or the age of an event (e.g., ten million years ago) without reference to a point or set of points on the radioisotopic time scale

NALMA	North American Land Mammal Age (Woodburne 2004); an interval of time based on mammalian biochronology. Units discussed here are Puercan and Torrejonian
PETM	Paleocene–Eocene Thermal Maximum. A short-term hyperthermal pulse of global warming at the Paleocene–Eocene boundary (Zachos et al. 2008; McInerney and Wing 2011). This is the earliest Eocene hyperthermal event, calibrated at 55.33 Ma (Westerhold et al. 2009). It had a duration of 120–220 k.y. (Murphy et al. 2010), with an initial pulse of about 10 k.y. during which global sea surface temperatures rose 5–9 °C
SALMA	South American Land Mammal age; comparable to NALMA; see Pascual et al. (1965), Simpson (1971), Patterson and Pascual (1972), Marshall et al. (1983). Units discussed here include Tiupampan, Peligran, “Carodnian,” Itaboraian, Riochican, and “Sapoan.” Units such as “Sapoan” are given between quotation marks due to their currently informal status.

3.2 Dispersals Between North and South America

3.2.1 Cretaceous Background

Prior to about 106 Ma (late Albian) when South America and Africa finally broke apart (Lawver et al. 2013), Gondwana was still essentially intact, and land vertebrate dispersal was basically possible throughout South America, Africa, Madagascar, India, Australia, and Antarctica. Figure 3.1 shows a late Aptian reconstruction of continental positions, after Lawver et al. (2013; Fig. 4a). Figure 3.2 shows the stratigraphic disposition of faunal-bearing successions in Patagonia during the Late Cretaceous and Paleocene. Land vertebrates are recognized from the Brazilian Baurú Group in the Turonian/Coniacian to Santonian (Adamantina and Uberaba formations, ca 93–83 Ma) and the late Maastrichtian (Marília Fm., ca 67–65 Ma; 1 Fig. 3.3), as well as from the Late Cretaceous of Patagonia. The taxa in the Brazilian assemblages were basically endemic to South America (Candeiro et al. 2004, 2006, 2008; de la Fuente et al. 2007; Candeiro and Rich 2010), with a diversity of fish, lepidosaurian frogs, aniloid snakes, podocnemid turtles, mesoeucrocodylians, spinosaurid, carcharodontosaurid, abelisaurid, and titanosaurid ‘dinosaurs,’enatiornithine birds, and a mammal of uncertain allocation. Overall, the assemblage is typically of Gondwanan affinity and is closely related to coeval biota in Madagascar, India, and continental Africa (Candeiro et al. 2004; Candeiro and Rich 2010). Even though a trans-Caribbean pathway to North America may have been available during at least parts of the Albian-Santonian interval (Pindell and Kennan 2001), little northern affinity was developed as regards these faunal elements. Candeiro and Rich (2010) note a possible northern origin for

Fig. 3.1 Reconstruction of Aptian continental positions at 120 Ma. Modified from Lawver et al. (2013: Fig. 4a)

a Turonian (ca 90 Ma) carcharodontosaurid from Argentina. The depauperate late Maastrichtian Marília Formation contains no hadrosaurian dinosaurs or mammals of North American affinity.

Gayet et al. (2001) discussed the land vertebrate fauna from the early Late Maastrichtian Pajcha Pata site, El Molino Formation, Bolivia (7, Fig. 3.3), correlated to about 69 Ma. The fauna includes frogs, salamanders, turtles, snakes, crocodiles, coelurosaur and sauropod saurischians, and indeterminate mammals. As yet, there is no evidence in the fauna of taxa having affinity beyond South America.

The Campanian–Maastrichtian vertebrate record of Argentina is considerably more diverse than that of the partly coeval Marília Formation of Brazil and has many of the same vertebrate groups found in the Uberaba–Marília formations to the north. These include frogs, turtles, lepidosaurs, mesoeucrocodilians, abelisaurids, carcharodontosaurids, spinosaurids, and titanosaurids recorded in the Allen and Los Alamitos (2, Fig. 3.3), and La Colonia (3, Fig. 3.3) formations (LA, LC in Fig. 3.2). Leanza et al. (2004) considered that Allen Formation hadrosaurine and lambeosaurine ornithopods and ankylosaurine ornithischians likely to be of northern origin and to have immigrated to Argentina at that time (late Campanian or early Maastrichtian), ca 75–70 Ma. Salgado and Gasparini (2006) reviewed the presence of Campanian ankylosaurian dinosaurs from the Antarctic Peninsula, but refrained from proposing a South American connection, which is comparable to Agnolin et al. (2010). Case et al. (2007) recorded the early Maastrichtian presence of an Antarctic Peninsula dromaeosaur, considered it to be endemic and of Gondwanan origin, comparable to the Santonian megalasaurid theropod, a late Campanian nodosaur, and early Maastrichtian hypsilophodontid and a similarly aged

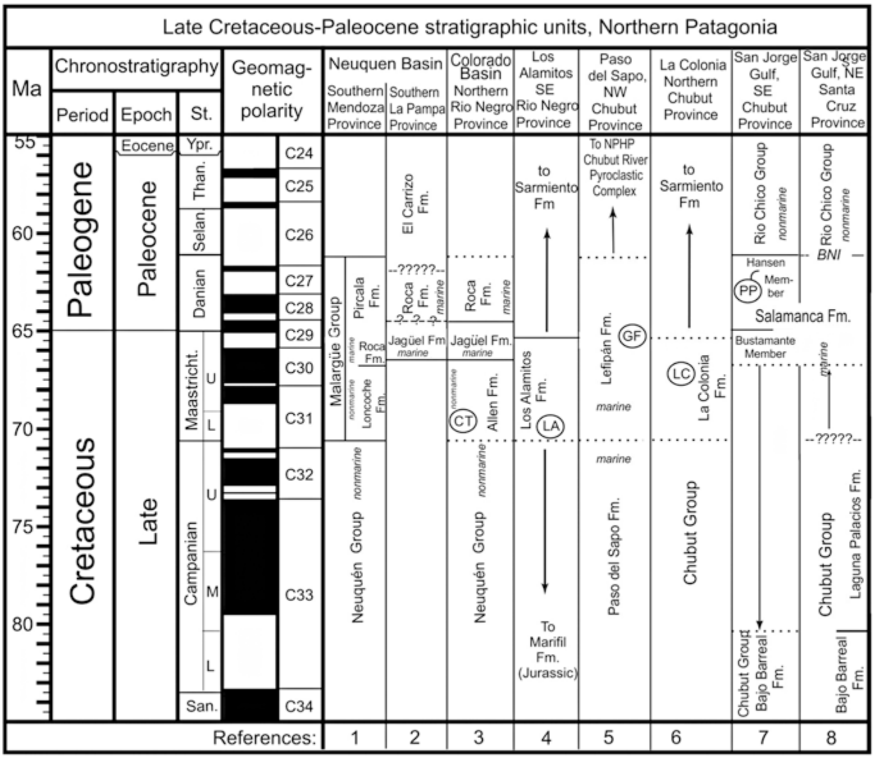


Fig. 3.2 Late Cretaceous stratigraphic units, Northern Patagonia. Modified from Woodburne et al. (2014: Fig. 3). Peligran after Clyde et al. (2014). *References* (1) Neuquén Basin (Leanza et al. 2004, Massabie 1995); (2) Northern Río Negro Province (Rougier et al. 2009a); CT = Cerro Tortuga mammal site. (3) Los Alamitos, southeastern Río Negro Province, (after Bonaparte 1987; Spalletti et al. 1999); LA = Los Alamitos mammal site; (4) Paso del Sapo, NW Chubut Province (after Ruiz 2006); GF = Grenier Farm mammal site; (5) La Colonia, northern Chubut Province (after Pascual et al. 2000); LC = La Colonia mammal site; (6) Golfo San Jorge Basin, SE Chubut Province (after Andreis et al. 1975; Iglesias et al. 2007; Clyde et al. 2014 for the age of the Bajo Barreal Formation); (7) Golfo San Jorge Basin (Clyde et al. 2014, for the age of the Bajo Barreal Formation)

iguanodontid also known from the James Ross Island area of the Antarctic Peninsula (4, Fig. 3.3). The lambeosaurine (Powell 1987) was included in a new hadrosaur genus, *Willinakage*, by Juárez-Valieri et al. (2010), so the presence of lambeosaurs in South America is not supported. Case et al. (2000) reported the late Maastrichtian presence of a hadrosaurian dinosaur from the Antarctic Peninsula and viewed it in the context of an ultimate dispersal from North America. Based on the above considerations, the reptilian dispersal to from North to South America appears to have been accomplished in the late Campanian-early Maastrichtian and involved only hadrosaurs.

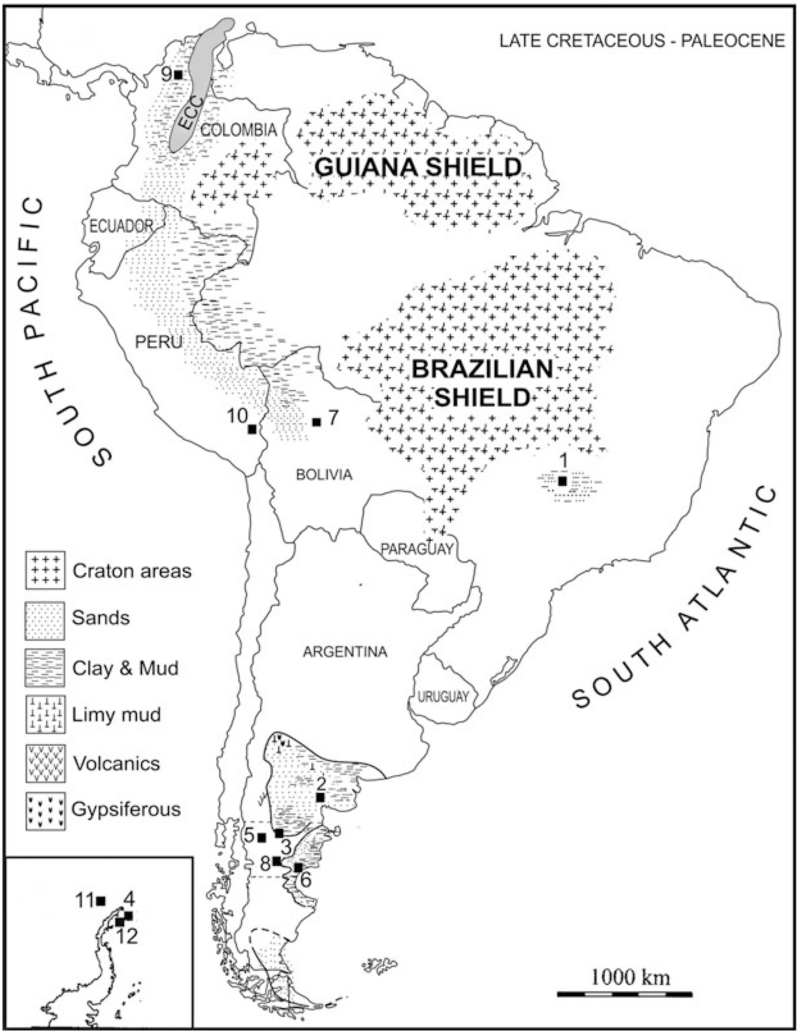


Fig. 3.3 Map of South America showing localities discussed in the text. Modified from Woodburne et al. (2014), Fig. 2B. (1) Baurú Basin, Adamantina and Uberaba formations (Santonian–Coniacian), and Marília Formation (Late Maastrichtian). (2) Allen and Los Alamitos formations (Maastrichtian). (3) La Colonia Formation (Maastrichtian). (4) La Meseta Formation (Eocene), Seymour Island, Antarctic Peninsula. (5) Grenier Farm site, early Paleocene, Chubut Province, Argentina. (6) Punta Peligro, Peligran SALMA, Paleocene, Argentina. (7) Tiupampa Fauna, Paleocene, Bolivia. (8) Palacio de los Loros flora, Salamanca Formation, Paleocene, Argentina. (9) Cerrejón flora, Paleocene, Colombia. (10) Laguna Umayo, late Paleocene or early Eocene, Peru. (11) South Shetland Islands, Antarctic Peninsula; Eocene plants (Poole et al. (2005). (12) James Ross Basin, Antarctic Peninsula, Late Cretaceous to Paleocene plants (Poole et al. (2005)

3.2.2 Alamitan SALMA

As reviewed by Woodburne et al. (2014) and paraphrased here, the Late Cretaceous Alamitan SALMA is based on the mammals of the Los Alamitos and Allen formations, Río Negro Province, as well as the La Colonia Formation, Chubut Province, Argentina, (LC, Figs. 3.2 and 3.3; see also Pascual and Ortiz-Jaureguizar 2007). The Alamitan is considered to be of Campanian-Maastrichtian (Bonaparte 1987) or Maastrichtian, but not latest (LA, Fig. 3.2) Maastrichtian age (Pascual et al. 2000; Rougier et al. 2009a, b). The Alamitan fauna contains 17 genera of mammals, all pertaining to non-tribosphenic groups that include a 'symmetrodont' 13 dryolestoids, and a sudamericid as well as a ferugliotheriid gondwanatheria (Pascual and Ortiz-Jaureguizar 2007; Rougier et al. 2009a, 2011; see Table 3.1). A single multituberculate also was recorded (Kielan-Jaworowska et al. 2007; but see Gurovich and Beck 2009). Even though the number of dryolestids may be reduced, their meridiolestid order is a distinct South American group (Rougier et al. 2011) and illustrative of the general pattern in which all Alamitan taxa are of endemic origin, with no antecedent and very few subsequent forms known.

The Alamitan fauna is clearly dominated by the 13 dryolestoids, distributed among seven families. Of these, casamiquelids comprise the most diverse family (3 genera), with mesungulatids, dryolestids, and barbereniids each represented by two genera. The Sudamericidae is of Gondwanan distribution in the Late Cretaceous through the mid-Paleocene in South America (and mid-Eocene of the Antarctic Peninsula; Goin et al. 2006). This, along with the Late Cretaceous South American endemic Ferugliotheriidae, reflects a major gondwanatheria influence here (Goin et al. 2012b). If correctly identified, the Alamitan multituberculate recovered from levels of the La Colonia Fm. (LC, Fig. 3.2) would reflect—along with those of the Early Cretaceous of Australia (Rich et al. 2009)—the rare Gondwanan occurrence of the group that is much better known in faunas of Jurassic and Cretaceous age in North America (and Holarctica; McKenna and Bell 2002). The Early Cretaceous record of the group in Africa (Morocco; Sigogneau-Russell 1991; Hahn and Hahn 2003) has been disputed (Hahn and Hahn 2006).

With the possible exception of multituberculates, this diverse group of non-tribosphenic taxa had its origin in late Jurassic faunas of Gondwana and underwent a successful radiation in the Cretaceous (Rougier et al. 2009a), during an interval termed the Gondwanan Episode by Pascual and Ortiz-Jaureguizar (2007). Goin et al. (2012a) suggested that the radiation of these endemic mammals was a Late Cretaceous (Cenomanian–Maastrichtian) event (their "Late Gondwanan Phase"), and that it was triggered by the global warming that developed since the Cenomanian. Bertini et al. (1993) and Candeiro et al. (2006) noted the presence of a potentially therian mammal from the Turonian–Santonian (ca 85 Ma) Adamantina Formation of Brazil (1, Fig. 3.3), but this awaits further verification.

Table 3.1 Late Cretaceous-Early Eocene record of South American mammals, at the generic level. 1, presence; 0, absence. Abbreviations: Ala., Alamitian SALMA; Tiu., Tiupampian SALMA; Pel., Peligran SALMA; Car., Carodnia biozone; Itab., Itaboraian SALMA; Rio., Riochican SALMA; Sap., Paso del Sapo mammalian association. The GABI record

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
Superfamilial taxon	Family	Genus							
Multituberculata			1	0	0	0	0	0	0
“Symmetrodonta”	Bondesiidae	*Bondesius*	1	0	0	0	0	0	0
Dryolestoidea		*Paraungulatum*	1	0	0	0	0	0	0
		Austrotriconodon	1	0	0	0	0	0	0
	Dryolestidae	*Groeberitherium*	1	0	0	0	0	0	0
		Leonardus	1	0	0	0	0	0	0
	Mesungulatidae	*Mesungulatum*	1	0	0	0	0	0	0
		Coloniatherium	1	0	0	0	0	0	0
	Peligrotheriidae	*Peligrotherium*	0	0	1	0	0	0	0
	Regitheriidae	*Reigitherium*	1	0	0	0	0	0	0
	Brandoniidae	*Brandonia*	1	0	0	0	0	0	0
	Casamiguelidae	*Casamiguelia*	1	0	0	0	0	0	0
		Alamatherium	1	0	0	0	0	0	0
		Rougeritherium	1	0	0	0	0	0	0
	Barbereniidae	*Barberenia*	1	0	0	0	0	0	0
		Quirogatherium	1	0	0	0	0	0	0
Gondwanatheria	Sudamericidae	*Sudamerica*	0	0	1	0	0	0	0
		Gondwanatherum	1	0	0	0	0	0	0
	Ferugliotheriidae	*Ferugliotherium*	1	0	0	0	0	0	0
Gondwanatheria, Indet.		New genus	0	0	0	0	0	0	1
Monotremata	Ornithorhynchidae	*Monotrematum*	0	0	1	0	0	0	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
Metatheria									
“Ameridelphia”	Pediomyidae	*Khasia*	0	1	0	0	0	0	0
	Pucadelphyidae	*Pucadelphys*	0	1	0	0	0	0	0
		Andinodelphys	0	1	0	0	0	0	0
		Mizquedelphys	0	1	0	0	0	0	0
	Jaskhadelphyidae	*Jaskhadelphys*	0	1	0	0	0	0	0
	Mayulestidae	*Mayulestes*	0	1	0	0	0	0	0
	Protodidelphidae	*Carolocoutoia*	0	0	0	0	1	0	0
		Guggenheimia	0	0	0	0	1	0	0
		Protodidelphis	0	0	0	0	1	0	1
		Periprotodidelphis	0	0	0	0	1	0	0
		Zeusdelphys	0	0	0	0	1	0	0
	Derorhynchidae	*Derorhynchus*	0	0	1	0	1	0	1
		Pauladelphys	0	0	0	0	0	0	1
	Sternbergiidae	*Carolopaulacoutoia*	0	0	0	0	1	0	0
		Itaboraidelphys	0	0	0	0	1	0	1
		Didelphopsis	0	0	1	0	1	0	0
	Family indeterminate	*Incadelphys*	0	1	0	0	0	0	0
		Tiulordia	0	1	0	0	0	0	0
		Szalinia	0	1	0	0	0	0	0
		Eobrasilia	0	0	0	0	1	0	0
		Marmosopsis	0	0	0	0	1	0	1
		Gaylordia	0	0	0	0	1	0	0
		Minusculodelphis	0	0	0	0	1	0	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Monodelphopsis	0	0	0	0	1	0	0
		Sternbergia	0	0	0	0	1	0	0
Sparassodonta	Basal Sparassodonts	*Allqokirus*	0	1	0	0	0	0	0
		Nemolestes	0	0	0	0	1	0	1
		Patene	0	0	0	0	1	1	0
Marsupialia									
Didelphimorphia	Peradectidae	New genus	0	0	0	0	0	0	1
		Peradectes	0	1	0	0	0	0	0
	Caroloameghiniidae	*Procaroloameghinia*	0	0	0	0	1	0	1
		New genus	0	0	0	0	0	0	1
Paucituberculata	Family indeterminate	*Riolestes*	0	0	0	0	1	0	0
		Bardalestes	0	0	0	0	0	0	1
Australidelphia									
Microbiotheria	Microbiotheriidae	*Eomicrobiotherium*	0	0	0	0	0	0	1
		Mirandatherium	0	0	0	0	1	0	0
Polydolopimorphia	Family indeterminate	New genus and species	0	0	1	0	0	0	0
		Bobbschaefferia	0	0	0	0	1	0	0
	Glasbiidae	*Palangania*	0	0	0	0	0	1	1
	Bonapartheriidae	New genus	0	0	1	0	0	0	0
		Epidolops	0	0	0	0	1	0	0
	Gashterniidae	*Gashternia*	0	0	0	0	1	1	1
	Family indeterminate	*Roberthoffstetteria*	0	1	0	0	0	0	0
	Polydolopidae	*Amphidolops*	0	0	0	1	0	0	1
		Archaeodolops	0	0	0	0	0	1	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Pliodolops	0	0	0	0	1	1	1
		New genus	0	0	0	0	1	0	1
Eutheria									
Cingulata	Dasypodidae	*Prostegotherium*	0	0	0	0	0	1	1
		Riostegotherium	0	0	0	0	1	0	1
		Astegotherium	0	0	0	0	0	0	1
		Stegosimpsonia	0	0	0	0	0	0	1
	Peltephilidae	New genus	0	0	0	0	0	1	0
Astrapotheria	Astrapotheriidae	*Eoastrapostylops*	0	0	0	0	1	0	0
		Shecenia	0	0	0	0	1	0	0
		Tetragonostylops	0	0	0	0	1	0	0
	Trigonostylopidae	*Trigonostylops*	0	0	0	0	0	1	1
“Condylarthra”	Mioclaenidae								
	Kollpaniinae	*Molinodus*	0	1	0	0	0	0	0
		Tiuclaenus	0	1	0	0	0	0	0
		Pucanodus	0	1	0	0	0	0	0
		Silmoclaenus	0	1	0	0	0	0	0
		Andinodus	0	1	0	0	0	0	0
	Didolodontidae	New genus	0	0	0	0	0	0	1
		New genus	0	0	0	0	0	0	1
		Escribania	0	0	1	0	0	0	0
		Raulvaccia	0	0	1	0	0	0	0
		Ernestokokenia	0	0	0	0	1	1	0
		Lamegoia	0	0	0	0	1	0	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Paulacoutoia	0	0	0	0	1	0	0
		Umayodus	0	0	0	0	1	0	0
Pantodonta	Alcidedorbignyidae	*Alcidorbignia*	0	1	0	0	0	0	0
Litopterna	Protolipternidae	*Miguelsoria*	0	0	0	0	1	0	0
		Protolipterna	0	0	0	0	1	0	0
		Asmithwoodwardia	0	0	0	0	1	0	1
	Anisolabdidae	*Wainka*	0	0	0	1	0	0	0
		Anisolambda	0	0	0	0	1	1	0
	Notonychopidae	*Notonychops*	0	0	0	0	1	0	0
		Requisia	0	0	1	0	0	0	0
	Sparnotheriodontidae	*Victorlemoinea*	0	0	0	0	1	1	1
Notoungulata		*Satshatemnus*	0	0	0	0	1	0	0
	Perutheriidae	*Perutherium*	0	0	0	0	1	0	0
	Archaeopithecidae	*Archaeopithecus*	0	0	0	0	0	1	1
		Acropithecus	0	0	0	0	0	1	1
	Henricosborniidae	Genus indet.	0	1	0	0	0	0	0
		Henricosbornia	0	0	0	0	1	1	1
		Othnielmarshia	0	0	0	0	0	1	1
		Peripantostylops	0	0	0	0	1	0	0
		Simpsonotus	0	0	0	0	1	0	0
	Interatheriidae	*Notopithecus*	0	0	0	0	0	1	0
	Isotemnidae	*Isotemnus*	0	0	0	0	1	1	1
	Notostylopidae	*Brandmayria*	0	0	0	0	0	1	0
		Edvardotrouessartia	0	0	0	0	0	0	1

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Homalostylops	0	0	0	0	0	0	1
		Notostylops	0	0	0	0	0	1	1
		notostylopid indet.	0	0	0	0	1	0	0
	Oldfieldthomasiidae	*Colbertia*	0	0	0	0	1	0	0
		Itaboraitherium	0	0	0	0	1	0	0
		Kibenikhoria	0	0	0	0	1	0	0
		Maxschlosseria	0	0	0	0	0	1	0
		Oldfieldthomasia	0	0	0	0	0	1	0
Xenungulata	Carodniidae	*Carodnia*	0	0	0	1	1	0	0
		Notoetayoa	0	0	0	1	0	0	0
		Etayoa	0	0	0	0	1	0	0
Total number of genera			17	19	10	4	51	21	34
Number of FADs			17	19	10	4	48	13	12
Number of LADs			17	19	8	3	31	2	16
Through going			0	0	0	0	1	8	13
Number of taxa		Total	17	19	10	4	51	21	34
		FADs	17	19	10	4	48	13	12
			0	0	0	0	0	0	0
		LADs	−17	−19	−8	−3	−31	−2	−16
		Through going	0	0	0	0	1	8	13
Percent of taxa		FADs	100	100	100	100	94	62	35
			0	0	0	0	0	0	0
		LADs	−100	−100	−80	−75	−61	−10	−47
		Through going	0	0	0	0	2	38	38

The Alamitan mammal genera are basically unique to South America (Woodburne et al. 2014). Some of their higher-level groups indicate a Gondwanan influence and, with the possible exception of the multituberculate, none are clearly of North American origin. As discussed below, however, the Paleocene mammalian evidence favors a Late Cretaceous dispersal to South America. The conundrum may be partly alleviated by noting that Alamitan faunas do not extend into the late Maastrichtian (LA, Fig. 3.2), and it is to be hoped that mammals of this age will be discovered.

Pindell and Kennan (2001: Figs. 11, 13; 2009: Figs. 11, 12) reconstructed the Caribbean region to show that the Aves Ridge and adjacent areas of the Caribbean Arc experienced both volcanic and plutonic activity in the Campanian and early Maastrichtian. As shown in Figs. 3.4 and 3.5, this activity is considered here to have provided a pathway compatible with the above dispersals. In addition, Crawford and Smith (2005) performed a nuclear gene phylogenetic analysis of leptodactylid frogs that point to a northward dispersal of the subgenus *Craugastor* from South America to Central America (Costa Rica) in the Late Cretaceous or early Paleogene (77–63 Ma, contra Heinicke et al. 2007). These reconstructions are consistent with the proposed dispersal to South America of polydolopimorphian (Goin et al. 2006) as well as other metatherians (Woodburne and Case 1996; Case et al. 2005) to account for their early Paleocene diversity in South America.

3.2.3 Mammalian Immigrations

Woodburne et al. (2014) reviewed the Late Cretaceous to early Paleocene immigration of marsupial and placental mammals to South America, from which the following is paraphrased and updated. The earliest therian mammal is represented by the early Paleocene *Cocatherium*, from the pre-Tiupampan, earliest Paleocene, Grenier Farm fauna (GF, Fig. 3.2; 5, Fig. 3.3; Grenier Farm, Fig. 3.6) and is considered (Goin et al. 2006) to be a polydolopimorphian. Goin et al. (2009) suggested that polydolopimorphians are members of the Australidelphia clade (Szalay 1982, 1994), as are the microbiotheria (Nilsson et al. 2010). Along with the Tiupampan polydolopimorphian, *Roberthoffstetteria*, the clear early Paleocene presence of this relatively derived group contributes to the evidence in favor of there having been a Late Cretaceous entry and evolution of metatherians in South America. Whether or not Paleogene South American polydolopimorphians and microbiotheria have affinities with Australian taxa (see Chap. 5), the likely Late Cretaceous presence of these australidelphians in South America would provide a potential early biotic link between the two continents (Muizon 1991; Muizon and Brito 1993; Woodburne and Case 1996; Nilsson et al. 2010; Beck 2012). As discussed further below, this link also may be reflected by the early Paleocene presence of monotremes (Pascual et al. 1992) in the Punta Peligro fauna (6, Fig. 3.3; Peligran SALMA, Fig. 3.6) of Patagonia (Table 3.1).

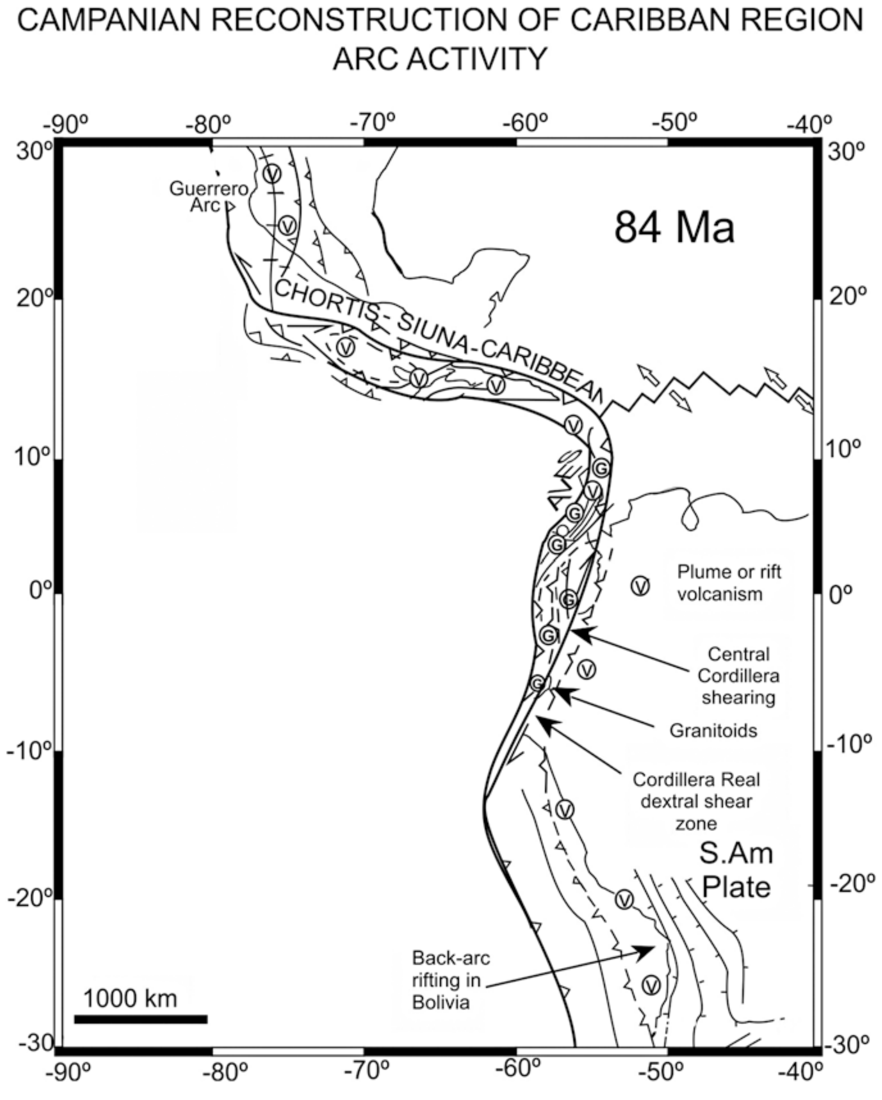


Fig. 3.4 Campanian reconstruction of Caribbean region arc activity. Modified from Pindell and Kennan (2009: Fig. 11)

The great metatherian diversity in the Tiupampan (7, Fig. 3.3) supports the inference of there having been a strong prior endemic radiation of the group. In Table 3.1, a majority of the 'ameridelphians' is considered to reflect this South American radiation (three pucadelphyids, a jaskhadelphyid, and a mayulestid). *Mayulestes* was once regarded as the earliest, and basal-most, sparassodontan (Muizon 1991, 1998), whereas it now is considered as a basal taxon to other South

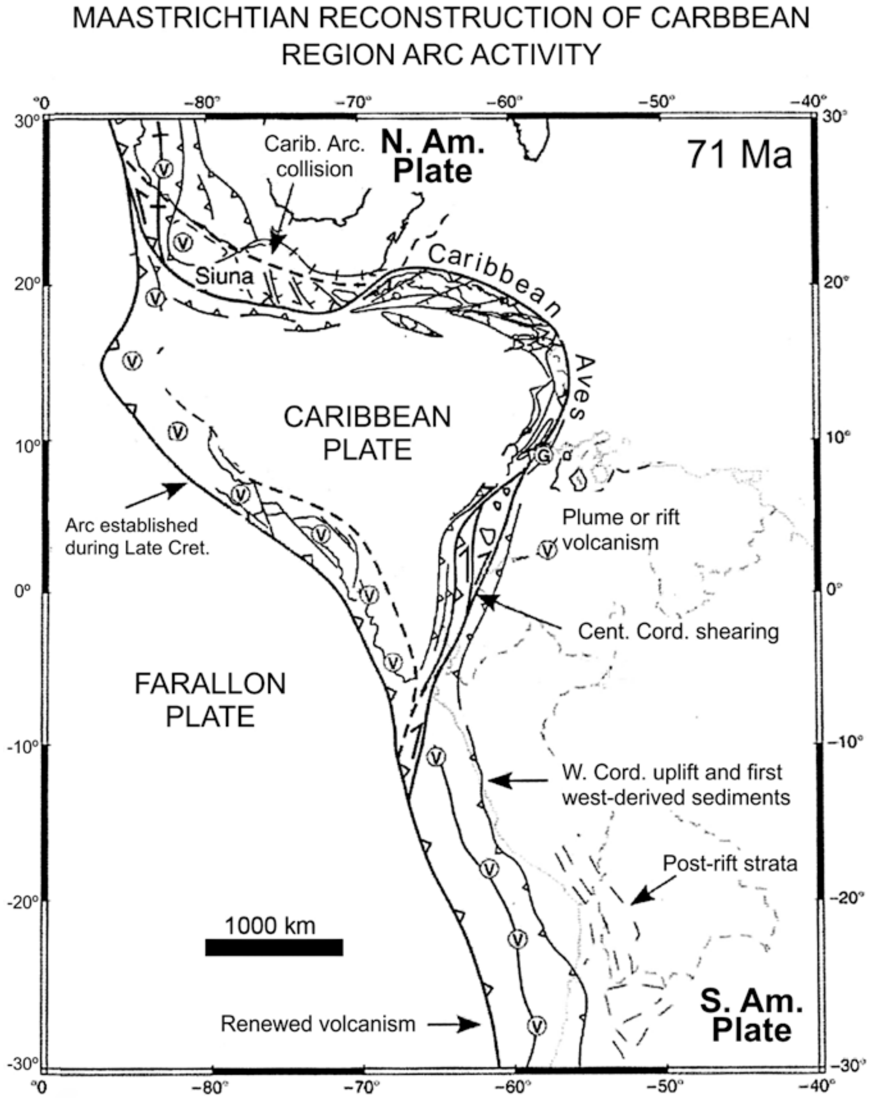


Fig. 3.5 Maastrichtian reconstruction of Caribbean region arc activity. Modified from Pindell and Kennan (2009: Fig. 13)

American metatherians (e.g., Forasiepi 2009). The other, indeterminate ‘ameridelphians,’ *Incadelphys*, *Tiulordia*, and *Szalinia*, further broaden the endemic Tiupampan diversity, as does the sparassodontan *Allqokirus* (Table 3.1) all of which points to a pre-Tiupampan radiation of the group. The ‘ameridelphian’ *Khasia* is an enigmatic taxon whose precise affiliations are still to be proven (see Chap. 5).

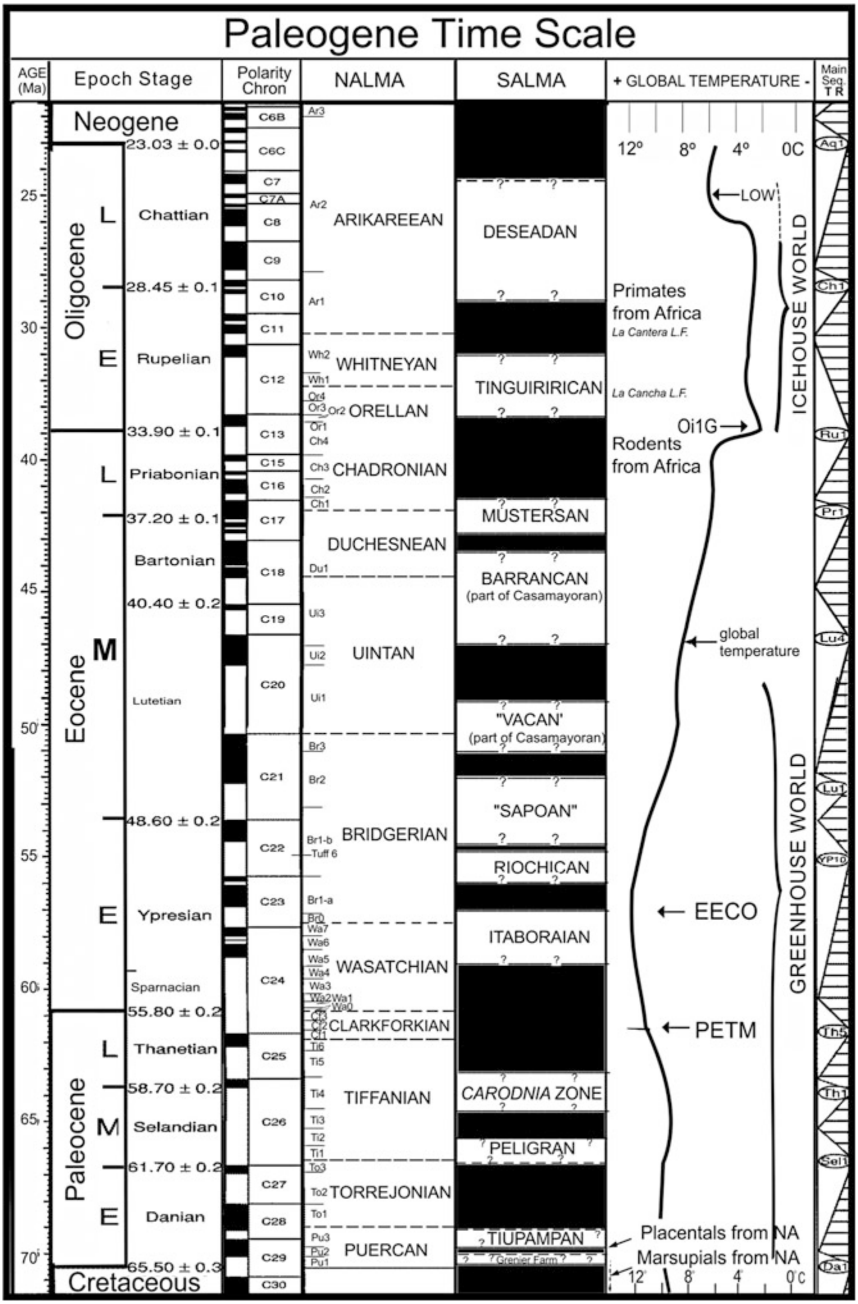


Fig. 3.6 Paleocene and Eocene time scale showing North American and South American mammalian biochronologic units. After Woodburne et al. (2014: Fig. 1). Age, Epoch, Stage and Polarity Chrons follow Luterbacher et al. (2004). Global Temperature curve is after Zachos et al. (2001)

Originally regarded as a microbiothere (Muizon 1991), more recently it has been argued to have pediomyid affinities (Goin et al. 2013, Woodburne et al. 2014: Table 1; see Chap. 5). If the latter is the case, it would also argue in favor of close affinities between South American and North American early metatherians (Case et al. 2005). The didelphimorphian *Peradectes* (Horovitz et al. 2009) is the last element of that archaic marsupial clade from North America (but see Goin and Abello 2013). Pediomyids are not known from younger deposits in South America. In summary, the basic ancestry of South American metatherians lies in North America. The early Paleocene South American diversity of the group suggests its Late Cretaceous entry.

Regarding placental mammals, *Molinodus* and four other taxa (Table 3.1) provide not only a major, but also nearly final, diversity of kollpaniine 'condylarths,' which have a lingering presence in the "Barrancan" (*Pascualodus*). The archaic placental group, Pantodonta, is last represented in South America by the Tiupampan *Alcidedorbignia*. Muizon and Cifelli (2000) noted the basic similarity between Puercan-aged North American 'condylarths' and those of South America, and suggested a close temporal link between them. Williamson and Carr (2007) reviewed the mioclaenid condylarths from North America, concluded that the group is monophyletic, endemic to western North America, and gave no support for a specific relationship with South American ungulates. They concluded that the mioclaenids are basically known only from New Mexico, but provided no suggestions as to the origin of South American 'mioclaenids.' The point taken here is that regardless of not being related to North American Mioclaenidae, the South American 'condylarths' unequivocally still had a North American ancestry, most likely from Puercan (Fig. 3.6) taxa (Williamson and Carr 2007: Fig. 12-1; compare taxa with ages in McKenna and Bell 2002), so the dispersal signal they contain still is relevant and pertinent. The Tiupampan henricosborniid signals the beginning of the notoungulates, a conspicuous group in Itaboraian (Fig. 3.6) and later Paleogene faunas (Table 3.1), as well as continuing into the Pleistocene (McKenna and Bell 2002).

Further suggestion in favor of a Paleocene overland dispersal is provided by the record of the menispermaceaean podocarp, *Palaeoluna*, from the Cerrejón flora of Colombia (9, Fig. 3.3). *Palaeoluna* also is found in ~60 Ma Paleocene sites in Wyoming, and thus is considered to reflect trans-Caribbean Paleocene connections between those places (Herrera et al. 2011). In addition, the Cerrejón genus, *Stephania*, is a possible precursor of modern Australian members (Herrera et al. 2011), but this dispersal scenario is hindered by the lack of information regarding fossil occurrences of the group in India and southeastern Asia, as well as Australia.

In contrast to Rage (1978), Rage (2005) proposed no snake genus as having dispersed northward from South America in the Late Cretaceous or early Tertiary, so the current vertebrate record favors north to south dispersal at those times. On the other hand, based on nuclear gene phylogenetic analysis, Crawford and Smith (2005) recently inferred a northward dispersal of the an ancestor of the leptodactylid subgenus *Craugastor* from South America across the Caribbean region to Central America (Costa Rica) in the Late Cretaceous or early Paleocene (77–63 Ma), perhaps facilitated by low sea levels at that time. Consistent with this hypothesis, *Craugastor* is considered to have begun a rapid diversification in the Chortis Block (present day Guatemala) at about the Paleocene–Eocene transition.

Overall, the Tiupampan fauna appears to have been dominated by metatherian insectivorous–omnivorous taxa of minute to small size. All insectivores are below 50 g in body mass, and a very small taxon of 5 g (*Jaskhadelphys*) occurs in this trophic category (Zimicz 2012). The carnivore niche is also filled by metatherians, the small sparassodontan (*Allqokirus*), and the medium-sized 'ameridelphians' *Mayulestes* and *Andinodelphys*. Other small-sized metatherians occupy the mixed insectivory–frugivory niche (e.g., *Roberthoffstetteria*). The remainder of the fauna appears to have been adapted to largely browsing herbivory. The Bolivian Tiupampa fauna (7, Fig. 3.3) occurs far to the north of Argentina, but a review of its distribution and paleoecology (Woodburne et al. 2014) suggests that its climate would have been tropical to subtropical and similar to that of the Palacio de los Loros flora of Argentina (8, Fig. 3.3), or the Cerrejón flora of Colombia (9, Fig. 3.3).

None of the 19 Tiupampan genera is related to any genus or higher taxonomic category of Alamitan age (Gelfo et al. 2009; Table 3.1). The totally new fauna can only have been derived by immigration from North America in the latest Cretaceous or earliest Paleocene (as discussed above). A similar statement applies to the basal polydolopimorphian, *Cocatherium*, from the earlier Paleocene Grenier Farm Local Fauna (GF, Fig. 3.2, Lefipán Formation of Chubut Province, Argentina and 5, Fig. 3.3; Case et al. 2005; Goin et al. 2006). As a likely derived, rather than stem, metatherian, its early Paleocene age supports the interpretation that 'ameridelphian' and other stem-group metatherians, as well as their more derived lineages now found in the Tiupampa fauna, reflect a Late Cretaceous dispersal from North to South America. The 'condylarths' support an early Paleocene dispersal from North America as well. Except for the possible therian from the Adamantina Formation of Brazil (see above) relevant mammals have not been found in South American Late Cretaceous faunas as currently known, so the matter remains undocumented, at least.

Taking all of the above into consideration, the present record provides a growing list of taxa that seem most compatible with an overland dispersal pathway between North and South America that is better established than a "sweepstakes" model, but not as fully developed as a "corridor." The Caribbean-Aves Ridge arc volcanism (Figs. 3.4 and 3.5) apparently produced a succession of relatively closely spaced, but probably not completely interconnected, terranes suitable for land animal dispersal during an interval of about 20 m.y. The GABI (Great American Biotic Interchange) occurred over a comparable (although shorter) interval in the Neogene with better documentation of dispersal episodes (Woodburne 2010) than now possible for the Late Cretaceous. The GABI record may be instructive as to there having been a Late Cretaceous pattern of dispersal intervals, as well.

3.2.4 Xenarthran Problem

The oldest Xenarthra in South America is of early Eocene age (Itaboraian; Bergqvist et al. 2004; Woodburne et al. 2014), but the group is considered to be ancient and fundamentally a sister-taxon to virtually all other placental mammals (Magnorder Xenarthra; McKenna and Bell 2002; comparable to O'Leary et al. 2013). In that context, it has been advocated that the group is fundamentally related to the Afrotheria and thus an association with the Gondwana continent of Africa, and its South American occurrence likely represents an association prior to the time of final separation of those continents at ca 106 Ma (Lawver et al. 2013). In addition, some South American notoungulates have been proposed as having Afrotherian affinities (Agnolin and Chimento 2011; O'Leary et al. 2013), but this has been soundly discounted by López et al. (in press).

Stanhope et al. (1998) defined the new mammalian superorder, Afrotheria, based on an analysis of nuclear and mitochondrial genes. Afrotheria includes Proboscidea, Sirenia, Hyracoidea, aardvark (Tubulidentata), elephant shrews (Macroscelidea), tenrecs (Tenrecidae), and golden moles (Chrysochloridae), and Stanhope et al. (1998) suggested that the group originated in Africa in the mid-Cretaceous (105–90 Ma). This was followed by a number of articles in support of the concept (Springer et al. 1997, 1999; Tabuce et al. 2007, 2008), and others suggested a phylogenetic relationship with Xenarthra (Amrine-Madsen et al. 2003; Hallström et al. 2007).

Whereas the major input was derived from molecular analyses, Sánchez-Villagra et al. 2007) found that Afrotheria can be characterized as having 23 or more thoracolumbar vertebrae (TLV), which is an increase from the 19 seen in marsupials as well as many placental groups. Using the placental mammal phylogeny proposed by Amrine-Madsen et al. (2003), Sánchez-Villagra et al. (2007) recorded that within Afrotheria, only Macroscelidea (20) and Tubulidentata (21) had fewer than 23 TLV. Interestingly the Xenarthra, considered to be the next-closest clade to Afrotheria, also has a range of 14–29 TLV. Comparably high numbers for other placental mammals are achieved only in Primates (15–24) and Perissodactyla (22–24), groups otherwise not considered phyletically near afrotheres. Asher and Lehmann (2008) also determined that afrotherians share a retarded eruption of the permanent dentition and Seiffert (2007) noted unifying features of the ankle bones. See O'Leary et al. (2013) for additional discussion of Afrotherian morphological characters.

As reviewed by Tabuce et al. (2008) the best known fossil record for Afrotheria is represented by early Eocene Hyracoidea and Proboscidea in Africa which (at 56 Ma; Vandenberghe et al. 2012, and extended to about 60 Ma for proboscideans by Gheerbrant 2009) is compatible with older molecular clock-based proposals for its origin (>80–80 Ma; Bininda-Emonds et al. 2007; Springer and Murphy 2007; Springer et al. 1997; Hällstrom et al. 2007). If Afrotherians are related to xenarthrans (Atlantogenata of Waddell et al. 1999; Amrine-Madsen et al. 2003; Murphy et al. 2007; Hällstrom et al. 2007; Churakov et al. 2009; dos Reis et al. 2012), then their phyletic separation most likely was prior to the ca 106 Ma separation of Africa and South America (Lawver et al. 2013). If so, their distribution apparently was a vicariant, rather than dispersal , event.

The phyletic and geographic portrayals of Nishihara et al. (2009) considered the African-South American connection having been severed shortly after 120 Ma. The timing is illustrated in greater detail by Jacobs et al. (2011) who indicated initial separation of coastal South America and Africa [Sergipe(SA)-Gabon (AF) and Campos (SA)-Kwanza (AF) basins] began about 115 Ma and was completed (deep water facies) by 90 Ma. This is generally compatible with the geophysical separation of the continents at about 106 Ma (Lawver et al. 2013). Nishihara et al. (2009) considered that the three major placental groups, Boreoeutheria, Afrotheria, and Xenarthra also were present by about 120 Ma. Whereas this has not been borne out by other work (above paragraph), the 106 Ma separation of Africa and South America requires that at least the ancestors of Xenarthra were present in Africa prior to that time, especially if they are considered as basal placental mammals. Meredith et al. (2011: Fig. 1) illustrated the basal node (Atlantogenata, but not named) for Xenarthra and Afrotheria as having been about 100 Ma old, arguably compatible with the 106 Ma Africa–South America separation, as could be the 98 Ma Atlantogenata age of Hallström et al. (2007). Other estimates for a younger Afrotheria age (see Tabuce et al. 2008; O'Leary et al. 2013) would require post-separation dispersals across the widening Atlantic Ocean which are here considered unlikely or at least not supported by other evidence. Inclusion of North American Paleocene leptictids in the Afrotheria (O'Leary et al. 2013) is the latest of a number of proposals (Asher et al. 2003; Zack et al. 2005; Penkrot et al. 2008) for including non-Gondwanan taxa in that group. In view of the strong Gondwanan integrity of the Afrotheria, such proposals seem best explained by homoplasy in both morphological and molecular data (e.g., Springer et al. 2013; characters in *Leptictis*; O'Leary et al. 2013; Supplemental Information, p. 31), and are not followed here.

3.2.5 Summary

The late Campanian to late Maastrichtian record of hadrosaurian dinosaurs in Patagonia and the Antarctic Peninsula suggests dispersal from North America within that interval. Such a dispersal is compatible with the early Paleocene diversity of metatherians, also of purported northern origin, and the northward dispersal of leptodactylid frogs. Plate tectonic reconstructions of the Caribbean region suggest that volcanism and related tectonic episodes provided an array of volcanic arcs sufficient to support those dispersals. The pathway apparently still was functional in the early Paleocene as implied by the North American origin of placental mammals to account for their Tiupampan record in South America, and the presence of the menispermaceaean podocarp, *Palaeoluna*, in Wyoming and Colombia at ~60 Ma.

3.3 Dispersal Between South America, Antarctica, and Australia

3.3.1 Geological Overview

Woodburne and Case (1996) reviewed the plate tectonic evidence relative to the separation of Antarctica and Australia and concluded that such dispersal would have been increasingly unlikely from about 64 Ma when the South Tasman Rise was considered flooded. This is reviewed and updated, beginning with a summary of the tectonics and stratigraphy of main sedimentary basins along the southeastern margin of Australia.

Exon et al. (2004) indicated that sea floor spreading in the Late Cretaceous resulted in Australian moving northward relative to Antarctica such that the Australo-Antarctic Gulf (AAG) developed and extended eastward over time to finally cross the southern end of the South Tasman Rise (STR) by the beginning of the Oligocene. Lawver et al. (2011) noted that if not actually originating at about 95 Ma (Cenomanian), then sea floor spreading in the Great Australian Bight was well underway by that time.

As indicated in Fig. 3.7, the main basins from west to east are Otway (and Sorell), Bass, and Gippsland. Norvick (2000: Fig. 7) showed that crustal thinning developed during the late Jurassic (Tithonian, 145 Ma) along the line of the future Australian Bight through the Duntroon , Otway and Gippsland active rift basins, with the Otway, Bass, and Gippsland basins (Fig. 3.7) contiguous in the Aptian (110 Ma; Norvick 2000: Fig. 10). At this time, and into the Albian, the Gippsland Basin (Fig. 3.8) was filled by the nonmarine volcaniclastic sandstones of the Strzelecki Group (Norvik et al. 2001), apparently associated with volcanic centers to the east. The Otway and Gippsland basins are portrayed as possibly interconnected active sag basins receiving nonmarine and volcaniclastic sediment by Norvick (2000, enclosures 5, 6, 13, 14), a condition which continued to the late Albian (100 Ma). Cummings et al. (2004: Fig. 3) show a similar condition for the Bass Basin (Crayfish and Otway Sequences, comparable to those of the Otway; Figs. 3.9 and 3.10).

A Cenomanian hiatus (ca 95 Ma) saw the Otway and Gippsland basins (Figs. 3.8 and 3.10) experience uplift and inversion (Hofford et al. 2011) with reorganization of the Otway and Bass basins, and a hiatus is present at this time in the Bass Basin, as well (Cummings et al. 2004; Fig. 3.9). Turonian sedimentation then produced a succession of nonmarine and lacustrine coal-bearing deposits in the Gippsland Basin (Kipper Shale), with the Bass and Otway basins being active as well (Figs. 3.8, 3.9 and 3.10; Norvick et al. 2001: Fig. 6). At this time, the Otway Basin was aligned with other active basins that extended southeastward along the western border of Tasmania (e.g., Sorell Basin; Exon et al. 2004), a pattern that continued into the Santonian (ca 85 Ma). During these intervals, active basins also were present from southern and southeastern Tasmania to the northeast along the weakening crust of the Lord Howe Rise along the eastern coast of Australia, as the Tasman Sea began to open (Norvick 2000: Fig. 15).

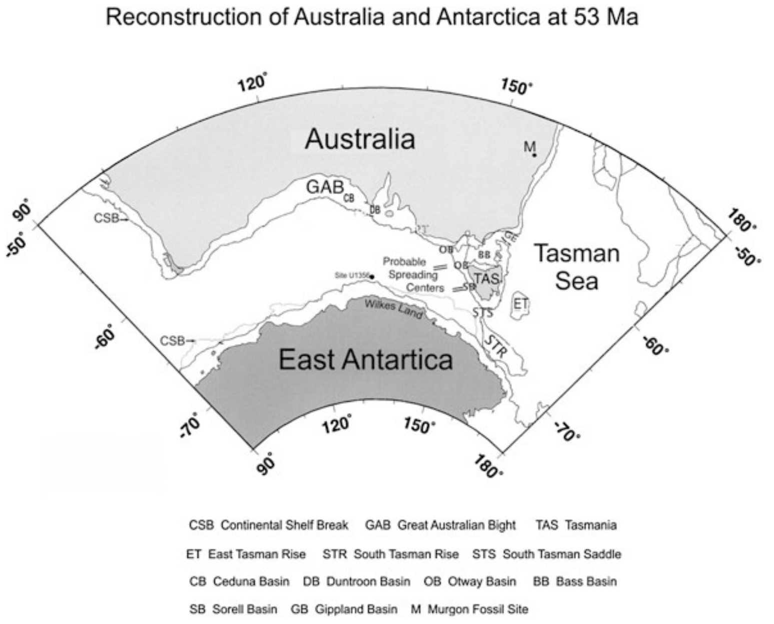


Fig. 3.7 Reconstruction of Australia and Antarctica at 53 Ma. After Lawver et al. (2011: Fig. 5). Shows opened seaway between Australia and Antarctica, with a connection to the Tasman Sea across the South Tasman Rise (STR). The Gippsland Basin is shown in a dashed line to indicate that whereas it opened at that time to the Tasman Sea on the east, there was no connection between the Gippsland and other basins to the west

Crustal thinning was occurring from the Australian Bight region (Ceduna Basin, Fig. 3.7) eastward through the above-named districts with active basins (Norvick 2000: Figs. 15, 16, enclosures 17–19) from the Turonian through Campanian (90–75 Ma), during which time the Tasman Sea opened by rifting along the eastern margins of Australia, Tasmania, and Antarctica. In the Coniacian and Turonian, the sequences begin with a marine unit, but these typically are followed by deltaic to regressive alluvial sequences.

Norvick (2000, enclosures 5 and 6) shows substantial marine sedimentation in the west-facing Ceduna and east-facing Gippsland basins from the Campanian through the Eocene which coincides with the progressive eastward transgression of the Southern Ocean on the one hand, and opening of the Tasman Sea on the other. Marine sedimentation in the Otway Basin was largely restricted to the early part of the sequence, again followed by deltaic regressive stratigraphically higher units. In fact, the Shipwreck through Sherbrook megasequences of Fig. 3.10 are considered to have been derived from both Australia and Antarctica at that time.

In the Paleocene, the Otway basin shelf mudstones and slope turbidites of the Wangerrip Group (Fig. 3.10) show northwestward progradation as marine conditions become more prevalent stratigraphically upward. By the middle Eocene, rapid marine transgression is recorded in the Nirranda megasequence (Fig. 3.10).

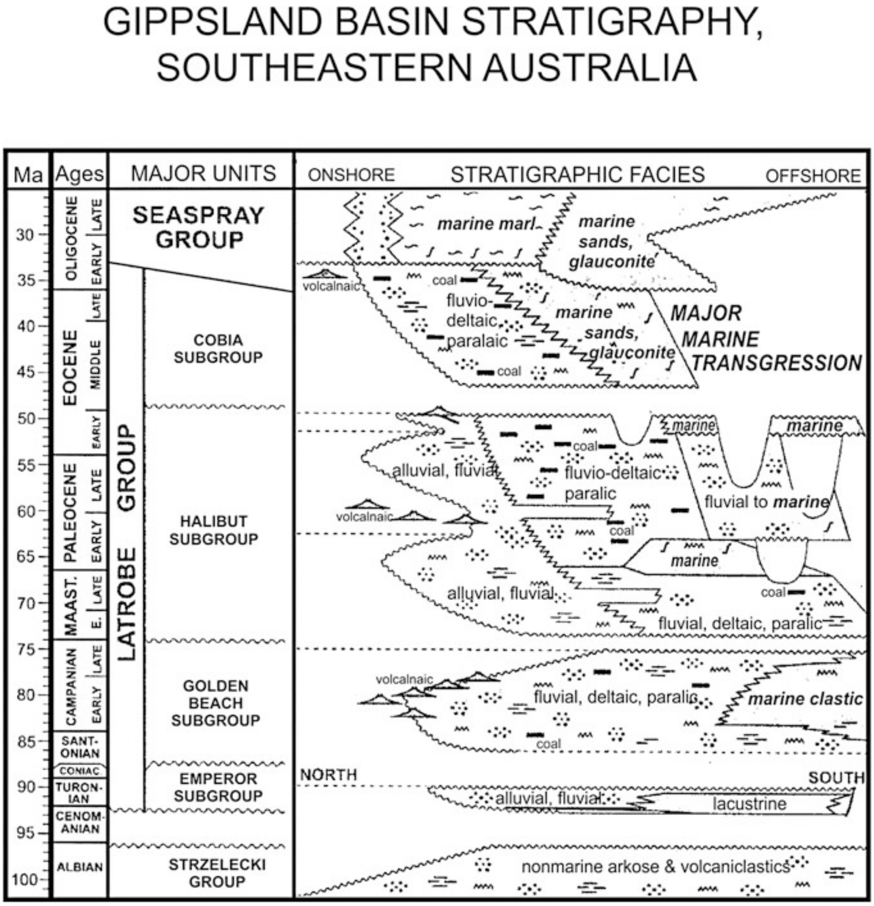
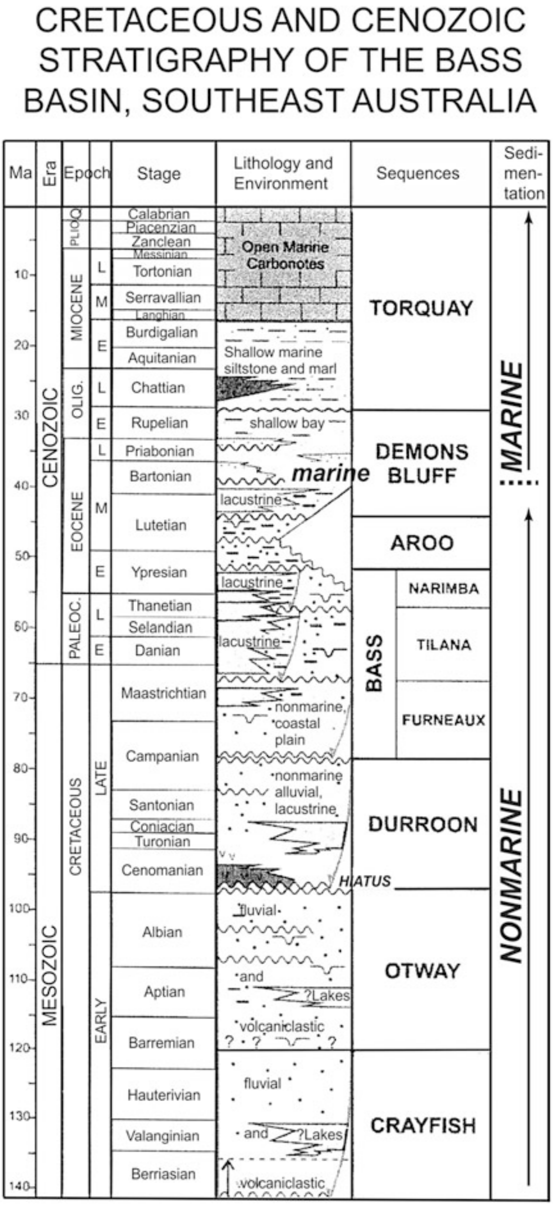


Fig. 3.8 Cretaceous and Paleogene stratigraphy of the Gippsland Basin, Australia. After Bernecker and Partridge (2001: Fig. 2)

During Campanian to Eocene, the Otway (and Bass) and Gippsland basins record the progressive separation of Australia and Antarctica along the Tasmanian-Antarctic shear zone, with final breaching of the South Tasman Rise by about 37 Ma (Exon et al. 2004). Certainly any overland dispersal of land animals between Antarctica and Tasmania (Australia) was severed from that time onward. The marine record on either side of the South Tasman Rise suggests that such may have begun by about the beginning of the Eocene, however.

The Bass Basin (Fig. 3.9) contains a stratigraphic record that extends from the Early Cretaceous (Berriasian) to the present (Cummings et al. 2004). From the Early Cretaceous to mid-Eocene (Lutetian), the sedimentary input is mostly non-marine clastic, volcaniclastic, and alluvial to lacustrine facies, including lakes and

Fig. 3.9 Cretaceous and Cenozoic stratigraphy of the Bass Basin, Australia. After Cummings et al. (2004: Fig. 3)



lacustrine coal beds. The Demons Bluff Megasequence [Mid-Eocene (mid-Lutetian) to early Oligocene (Rupelian), 44–30 Ma] records progressive drowning from west to east by a marine incursion that also affected the Otway and Sorell basins as well as western Tasmania, the South Tasman Saddle and South

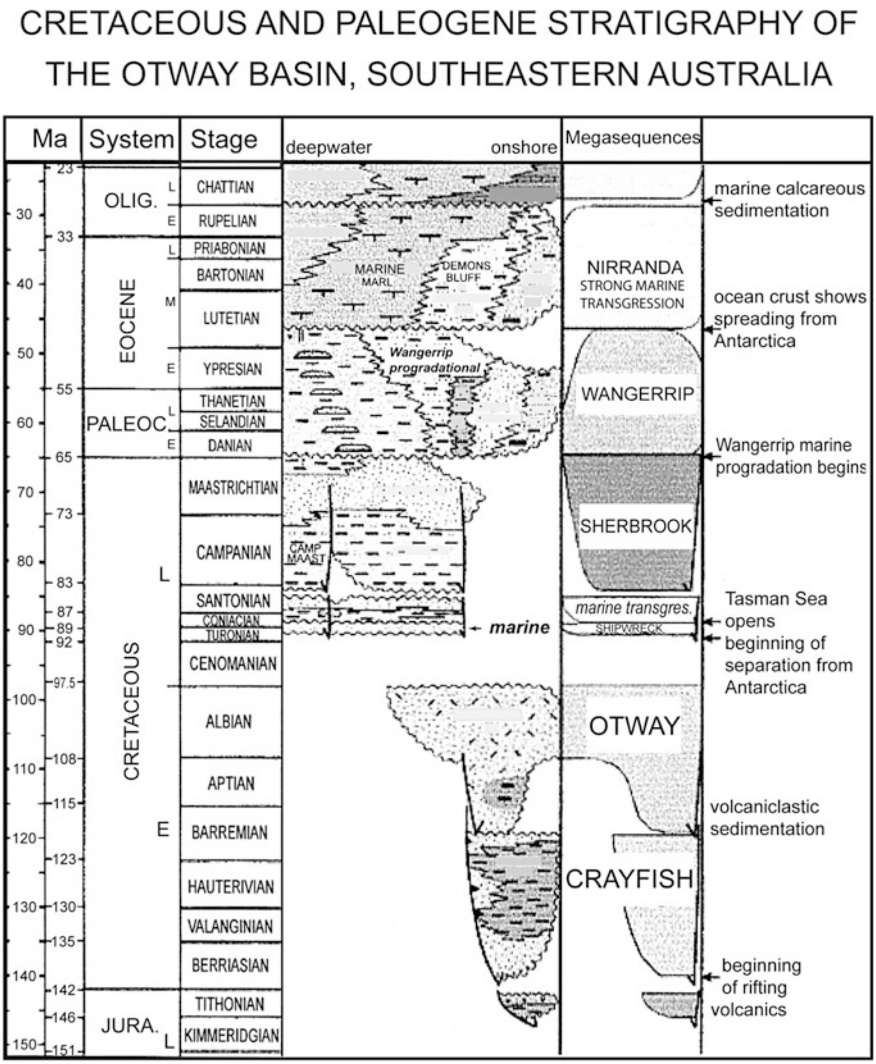


Fig. 3.10 Cretaceous and Paleogene stratigraphy of the Otway Basin, Australia. After Norvic (2000: enclosure 7)

Tasman Rise (Exon et al. 2004: Fig. F7A; Fig. 3.11). Apparently, the Durroon sub-basin of the southern Bass Basin made no connection to the opening Tasman Sea. The Demons Bluff is followed by the late Oligocene to Recent Torquay sequence of increasingly deeper marine conditions (Fig. 3.9).

Norvick et al. (2001) indicated that marine conditions prevailed in the offshore district of the Gippsland Basin from the Late Cretaceous well into the Neogene, compatible with a connection to the developing Tasman Sea. According to Michael Hall (personal communication To M.O. Woodburne in 2013), the Gippsland Basin developed a marine seaway connection to the Bass Basin in the late Middle Eocene, so that in conjunction with the connection between the Bass, Sorell and Otway basins a marine barrier to overland mammal dispersal was present along the southeastern coast of Australia from about 45 Ma (Fig. 3.11). Blevin et al. (2005) indicated that such conditions deepened and persisted into the Oligocene in the Bass Basin, by which time Australia and Antarctica were well separated.

As suggested above, the region between Tasmania and Antarctica did support a marine barrier to overland dispersal from the early Eocene, if not earlier. Lawver et al. (2011) noted that the South Tasman Saddle (STS, Fig. 3.7) developed during

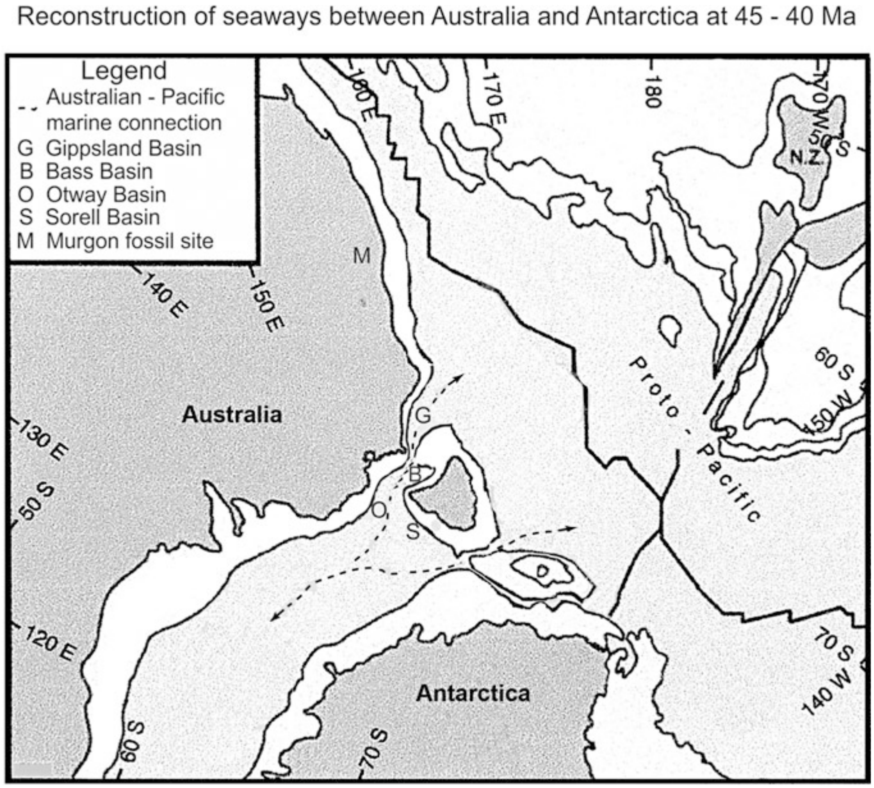


Fig. 3.11 Reconstruction of seaways between Australia and Antarctica at ca 45–40 Ma. Modified from Exon et al. (2004: Fig. F7A). Addition of Otway (O), Sorell (S), Bass (B) and Gippsland (G) basins after Norvick et al. (2001: Fig. 1). M = Murgon, southeast Queensland, after Godthelp et al. (1992). Shows separation of Tasmania from the South Tasman Rise and restricted land access between the Gippsland and Bass basins, southeastern Australia. AAG is Australo-Antarctic Gulf; EAC is Eastern Australian Current

the Campanian and Maastrichtian, and the spreading center passed west of the Sorell Basin by 53 Ma (Fig. 3.7).

White (2004) addressed the Eocene deposits recorded in ODP (Ocean Drilling Program) cores on the west, south, and east of Tasmania (sites 1168, 1170–1172, Fig. 3.12). He reported that not only did marine conditions prevail in all four drill sites but also that early to middle Eocene glacioeustacy may have affected the Australo-Antarctic Seaway between Antarctica and Tasmania. It is apparent, as well, that the Tasmanian sections were interconnected with those of the Otway Basin to the northwest and, through them, to those of the Ceduna and other basins along the Great Australian Bight on the one hand, to the Ross Sea on the other. As indicated in Fig. 3.12, site 1172 is on the east margin of Tasmania and records events in the Eocene Pacific Ocean. Sites 1171 (farthest south) and 1170 occur on the western margin of the South Tasman Rise (the so-called Tasmanian Land Bridge), and site 1168 is located on the western margin of Tasmania. These three sites are part of the Australo-Antarctic seaway. White (2004, p. 13) observed that whatever processes were operational in the Pacific Ocean basin also seem to have affected the Australo-Antarctic seaway.

This includes a marine flooding surface interpreted to be present at the Paleocene/Eocene boundary at sites 1171 and 1172 (White 2004). Numerous flooding surfaces are present, with peaks at 55, 50, 39, and 36 Ma. According to White (2004), these peaks were caused by glacioeustasy, but it also means at least intermittent marine separation of Australia from Tasmania during this time, beginning at least by 55 Ma. This is compatible with mid-Eocene (ca 43 Ma) sea floor spreading that led to the separation of the South Tasman Rise from Antarctica along the Tasman Fracture Zone (Hill and Exon 2004) and the initiation of subsidence from about 52 Ma that led to the development of a westbound Antarctic Counter Current across the southern Tasmanian Gateway at 49–50 Ma (Bijl et al. 2013). From these data, it seems probable that overland dispersal between Antarctica and Australia was rendered very unlikely from at least 50 Ma, and possibly as early as 55 Ma (Fig. 3.11; Exon et al. 2004: Fig. F7A). Recall also that Lawver et al. (2011) noted that sea floor spreading in the South Tasman Saddle may have been active from 74–66 Ma, so the sea floor there at the beginning of the Eocene would have been at least 1000 m deep. In summary, the body of evidence indicates the presence of a marine barrier across the South Tasman Saddle by at least the late early Eocene.

Figure 3.7 also reconstructs the presence of marine embayments of mid-Eocene and later age north of Tasmania, at the South Tasman Saddle. Figure 3.11 is based on Fig. F7A of Exon et al. (2004), with addition of coastlines relative to the Otway, Bass, Sorell, and Gippsland from Norvick et al. (2001: Fig. 1). The Tingamarra Local Fauna, of Murgon, Australia (M, Fig. 3.7) is the only early Paleogene (55 Ma; Godthelp et al. 1992) mammal fauna of Australia. As discussed below, it is most likely that the taxa of that fauna likely reflect the results of a prior overland dispersal to Australia of Paleocene age.

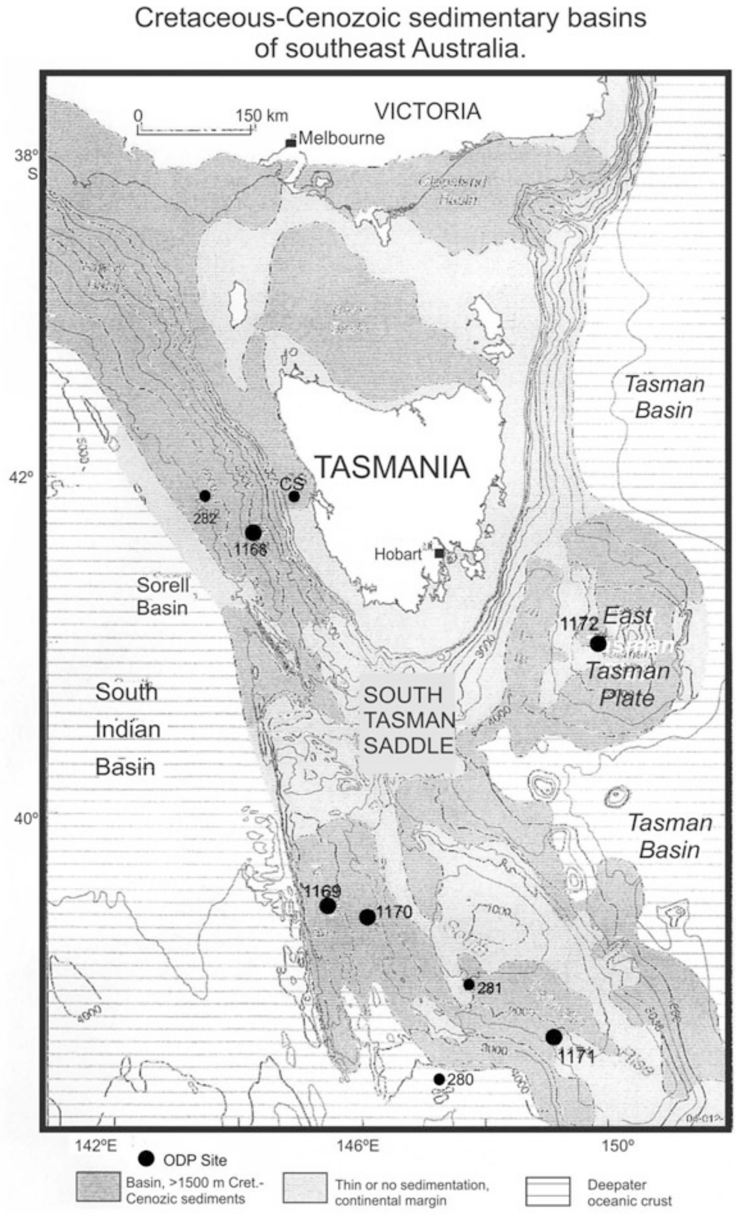


Fig. 3.12 Cretaceous-Cenozoic sedimentary basins of southeast Australia. After Exon et al. (2004: Fig. F1)

3.3.2 Tingamarra Local Fauna

As regards its geology and age, Godthelp et al. (1992) initiated the reports on the Tingamarra Local Fauna from Murgon, southeastern Queensland (Fig. 3.7). The fossils occur in greenish claystones considered to be part of the Oakdale Sandstone which crops out in an area of 36 km north of Murgon, about 140 km northwest of Brisbane (Murphy et al. 1976). The Oakdale Sandstone is about 100 m thick, unconformably overlies Permian and Triassic rocks and "may be overlain by Tertiary volcanics" (p. 57). The unit consists of poorly consolidated sandstone, mudstone, and conglomerate. Sandstone is buff colored, medium to coarse grained, quartzofeldspathic and quartzose, poorly bedded, and massive. Clasts are dominantly angular to subrounded granules of quartz. The matrix of both the conglomerate and sandstone is kaolinitic. Mudstone is light colored and grades into siltstone. Most outcrops are deeply lateritized.

Gaffney and Bartholomai (1979) reported fossil trionychid turtle material from a locality near Boat Mountain (152°E. longitude, 26°S. latitude), about 11 km NNE of Murgon. This also is the site of the Tingamarra Local Fauna, which includes the mammals, *Tingamarra porterorum* and *Thylacotinga bartholomaii* (Godthelp et al. 1992; Archer et al. 1993) as well as other taxa (below).

Regarding the age of the unit, note that Gaffney and Bartholomai (1979) pointed out the unlateritized nature of the fossil-bearing green clay beds at Boat Mountain and suggested on that basis that the beds might be Pliocene in age rather than the early Tertiary age they accepted, with reservation. Godthelp et al. (1992) reported an age of 54.6 ± 0.05 m.y. for the green clay beds, apparently the same as those reported by Gaffney and Bartholomai (1979). The radioisotopic age is derived from a single K-Ar date on illite and its analytical parameters have not been published. As noted by Woodburne and Case (1996), multiple samples of illite need to be analyzed in order to determine whether it is authigenic or detrital. Such samples have never been reported. Godthelp et al. (1992) noted that the basalts that apparently overlie the fossil beds at Boat Mountain are considered to be 29 Ma old.

The Undifferentiated Tertiary Volcanics that "may" overlie the Oakdale Sandstone are not dated. Murphy et al. (1976) chose the term, may, due to the fact that both the sediments and the volcanic rocks in the Murgon area are heavily lateritized and the contact between the two units is nowhere preserved. Based on the outcrop pattern presented on the geologic map in Murphy et al. (1976), it is reasonable that the volcanic rocks post-date the Oakdale Sandstone.

In summary, the geologic evidence appears to be potentially compatible with the isotopic age determined for the beds that produced the Tingamarra mammal fauna. Whether or not this can be clarified, the composition of the fauna appears compatible with an age earlier than Oligocene, at least. With that caveat, the approximately 55 Ma age for the Tingamarra Local Fauna is retained in the present discussion.

As regards the Tingamarra metatherians, the initial description of *Tingamarra* by Godthelp et al. (1992) was followed to include an 'ameridelphian' based on a calcaneus (Beck 2012), the australidelphians *Djarthia* (Godthelp et al. 1999; Beck et al. 2008), and *Thylacotinga* (Archer et al. 1993; Sigé et al. 2009). *Tingamarra* was initially regarded as a possible condylarth eutherian mammal (Godthelp et al. 1992), but this was called into question by Woodburne and Case (1996), who considered the single lower molar to be a metatherian, with some resemblance to the plesiomorphic metatherian, *Kokopellia*. Wroe and Archer (2006) noted that more material is needed before the actual affinities of the taxon can be determined.

Djarthia was originally based (Godthelp et al. 1999) on dentary and maxillary fragments with a dentition represented by lower p2-m4 and upper C1, P1 or P2, and P3-M4. Informal character analysis suggested it to be a plesiomorphic taxon with some derived characters that posed possible affinity with both ameridelphians and australidelphians. Beck et al. (2008) assigned cranial and postcranial materials to the genus and proposed that it was an australidelphian, with a chief character in that regard being the distinctive features of the ankle bones. Assessment of all its characters resulted in a hypothesis that *Djarthia* was a relatively plesiomorphic australidelphian and positioned on a phylogenetic tree (Beck et al. 2008: Fig. 3B) prior to the origin of extant Australian groups. In that illustration, *Djarthia* was closely associated with the living South American microbiotheriid, *Dromiciops*, as shown in Fig. 3.13. If accurate, this relationship suggested that *Dromiciops* not only was an australidelphian—as then understood—but also could represent (along with the mid-Miocene *Microbiotherium*) a post-*Djarthia* dispersal to South America, under the concept that all Australia's marsupials ultimately were derived from a taxon that had originally dispersed to Australia from South America.

Goin et al. (2006) reported on the early Paleocene polydolopimorphian marsupial *Cocatherium* from Argentina and suggested affinity with the Australidelphia and an alliance with the Tiupampan (later early Paleocene) genus *Roberthoffstetteria*. If australidelphians, these taxa pre-date *Djarthia* on the one hand and are part of a strong diversity of South American metatherians on the other. As part of that diversity, Goin et al. (2010) allied the Itaboraian *Mirandatherium*, which is approximately contemporaneous with *Djarthia,* with the Australidelphia. At this time, it appears that *Djarthia* may not be the oldest australidelphian, but is still a very plesiomorphic taxon.

In that context, the Tiupampan (early Paleocene of Bolivia) genus *Khasia* has been taken as a South American australidelphian, and to document the early presence of the group. Beck et al. (2008) and Woodburne et al. (2014) noted, however, that *Khasia* is an enigmatic form, the precise affiliations of which are still to be proven. Originally regarded as a microbiothere (Muizon 1991), more recently it has been argued to have pediomyid affinities (see Chap. 5 and Woodburne et al. 2014: Table 1). If the latter is the case, it would also argue in favor of close affinities between South American and North American early metatherians (Case et al. 2005). If *Khasia* has South American affinities, analysis of the timing and context of that relationship is still limited by the lack of other Eocene or older mammal faunas in Australia.

Thylacotinga was based on a broken LM2 or M3, to which a broken Lm2 (with damaged metaconid), RM4 or 5, and a fragmentary LM2 or 3 was assigned (Archer et al. 1993). It was considered to differ from Australian bunodont

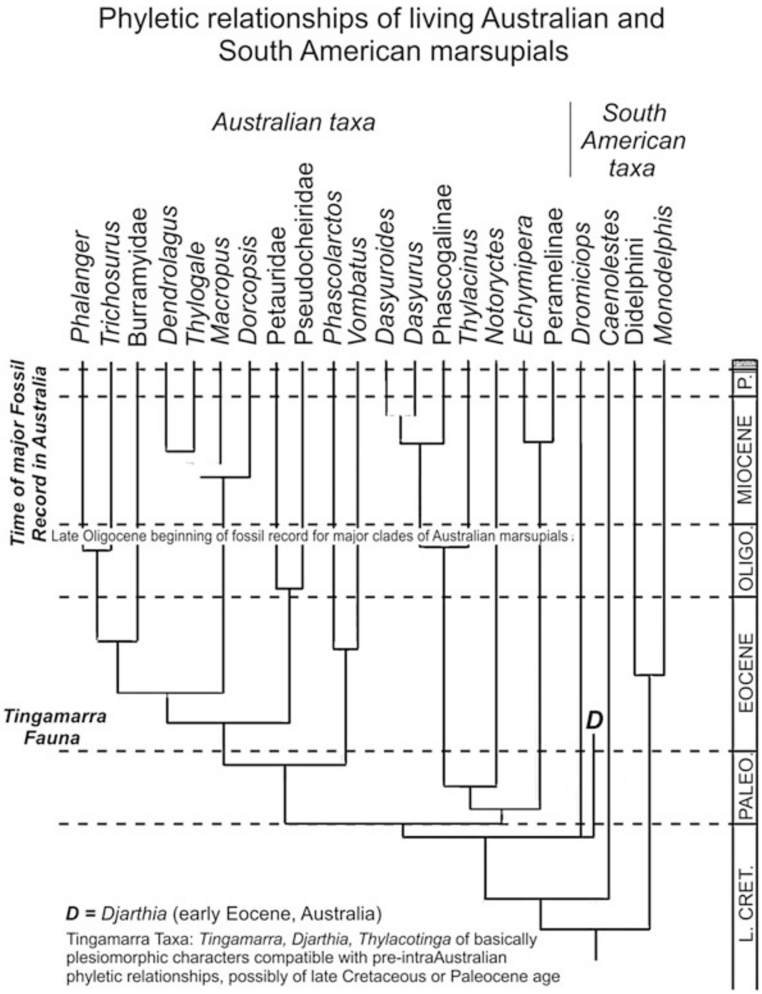


Fig. 3.13 Phyletic relationships of living Australian and South American marsupials and origination ages of taxon clades after Beck et al. (2008: Fig. 4). *Djarthia* added after Beck et al. (2008: Fig. 3b), coeval with the age of the Tingamarra Fauna. Whereas the fossils record of all other Australian marsupials begins in the late Oligocene, the timing of major groups is interpreted to have occurred prior to that time, in the Eocene and Paleocene. The Tingamarra Local Fauna is the only pre-Oligocene fauna in Australia and its genera, *Tingamarra, Djarthia, and Thylacotinga* are basically plesiomorphic taxa that show no relationship to intra-Australian taxa, but rather suggest affinities to South American groups. In that context it is possible that the Tingamarra Fauna is older than currently interpreted

metatherians and to share features found in South American forms. Sigé et al. (2009) described ten more specimens of *Thylacotinga* as well as a Tingamarra species of *Chulpasia*, *C. jimthorselli*, based on an isolated LM1 or 2. *Chulpasia* was previously known from Laguna Umayo, Peru (10, Fig. 3.3), considered to be of late Paleocene or possibly early Eocene age (Sigé et al. 2004). On this basis Sigé et al. (2009) considered the genus *Chulpasia* to record an effectively instantaneous early Eocene dispersal from Perú to Australia. The Paleogene mammal record of South America is not yet complete. Nevertheless, Woodburne et al. (2014) recognized no South American elements referable to *Chulpasia* or to the new subfamily, Chulpasiinae, to which is has been assigned. The limited material upon which its Australian occurrence is based, as well as the lack of an empirical character analysis to support assignment of the specimens to which the two species are based to the same genus, leads to the present appraisal that this paleogeographic inference is at best a very weakly supported hypothesis.

Finally, Beck (2013) described *Archaeonothos* as a faunivorous Metatheria *incertae sedis* based on a single-upper molar. The specimen shares similarities to both South American and Tunisian genera, but not with any indigenous Australian taxa.

In summary, the Tingamarra metatherians discussed above represent the only fauna of pre-late Oligocene age in Australia (Megirian et al. 2010; Black et al. 2012) and thus provide a remarkable, but singular, glimpse into the evolutionary status of Australian marsupials. As currently presented, it is clear that the Tingamarra metatherians are of generally plesiomorphic status, compatible with their early Eocene age. On the other hand, it also is clear that none of them show any suggestion of relationship to the diverse clades of Australian marsupials recognized from the late Oligocene (Fig. 3.13). Based on examples from South America, the nearest southern Hemisphere continent with a relatively well-developed mammal fauna (Woodburne et al. 2014), it is reasonable to propose that a great diversity of Paleogene mammals is to be expected to have lived in Australia as well, and that even with dispersal from Antarctica having been impeded from the early Eocene (50 Ma), if not earlier, it can be suggested that Australia potentially could have received input of a diverse assemblage of marsupials from South America and Antarctica. The extremely important Tingamarra Local Fauna yet displays only a minor glimpse of this potential diversity.

3.4 Antarctic Dispersals to and from South America

Based on the available fossil record which may yet mask a prior occurrence, monotremes apparently dispersed from Antarctica (at least) to South America in the early Paleocene (Pascual et al. 1992). The Punta Peligro site (PP, Fig. 3.2; 6, Fig. 3.3) is now indicated as about 63 Ma (Clyde et al. 2014) and the Peligran SALMA that contains it is so correlated in Fig. 3.6. Subsequently, the middle Eocene La Meseta Fauna of Seymour Island (Fig. 3.3) of the Antarctic Peninsula gives the only other glimpse of Paleogene Antarctic mammals. The La Meseta Fauna (Reguero et al. 2002; Chornogubsky et al. 2009; Reguero and Marenssi 2010; Bond et al. 2011) is composed of mammals of South American, rather than Australian, affinity. The bulk of the fauna ranges in age from about 47–45 Ma, but the distinctive, large litoptern *Notiolofos*, is recorded from about 51.5 Ma. Whereas some of the La Meseta mammals appear to reflect endemism (among microbiotheriid and prepidolopid metatherians and a sudamericid gondwanatheia) others, including the placentals *Notiolofos*, the astrapothere *Antarctodon*as well as the metatherian microbiotheriids *Marambiotherium* and *Woodburnodon*, and three derorhynchids, suggest derivation from early Eocene faunas of South America (Itaboraian, ca 53 Ma; Woodburne et al. 2014, which includes the initial diversity of astrapotheres, litopterns, and notoungulates; the "Sapoan" component includes taxa from the La Meseta fauna).

Overall, the La Meseta mammals represent derived elements of the groups to which they pertain, with those groups also being derived components of the South American mammal fauna. To the extent that it is representative, the La Meseta Fauna likely was characteristic of the contemporaneous land mammal fauna of the Antarctic continent, were it open to dispersal in the early Eocene. The lack of such a derived marsupial and placental mammal fauna in Australia can be laid in part to the sundering of the Tasmanian Gateway by about 50 Ma (Bijl et al. 2013), but the current absence of any input from derived South American mammals suggests that the dispersal window was closed prior to the Eocene, at least.

Based not only on the above, but also the diversity of metatherian, but not placental mammals, in the Paleocene of South America (Woodburne et al. 2014), the data further suggest that a dispersal to Australia was most likely to have occurred in that interval. As summarized above, metatherians are known in South America in the early Paleocene and, especially as recorded in the Tiupampan and Peligran SALMAs, were very diverse. This is shown (Table 3.1) by 12 genera distributed in eight Tiupampan families of largely insectivorous "Ameridelphians," a carnivorous sparassodontan, as well as a perhaps more omnivorous didelphimorphian and a polydolopimorphian australidelphian (*Roberthoffstetteria*). This diversity compares with five mioclaenid 'condylarths,' and a pantodont in the Tiupampan, and with two 'condylarths,' and a litoptern in the Peligran. The number of "Carodnian" taxa is too small to be significant here.

The above pattern is changed markedly in the Itaboraian. Whereas marsupials are still numerous (23 genera), some of their original diversity has been lost (four families, Table 3.1), partly compensated by a caroloameghiniid and a microbiothere (*Mirandatherium*; Goin et al. 2010). In strong contrast to Paleocene faunas, the Itaboraian shows a major placental diversification, ranging from cingulates on the one hand to the first astrapotheres, notoungulates, and a major increase of litopterns on the other. Whereas the Itaboraian fauna is well suited to a relation with the La Meseta Fauna, it has effectively no similarity with any Australian clade. The australidelphian microbiothere *Mirandatherium* is a relatively derived taxon and the polydolopimorphians pertain to indigenous South American genera (*Bobbschaefferia*, *Epidolops*, and *Gashternia*). The Itaboraian cingulate, astrapotheres, 'condylarths,' litopterns and notoungulates are typical endemic South American placental taxa (Woodburne et al. 2014). Based on these particulars, it appears that the most likely interval of faunal dispersal to Australia is from the Late Cretaceous to early Paleocene (Fig. 3.14), in part contemporaneous with the Antarctic connection recorded by the apparently Peligran dispersal of a monotreme

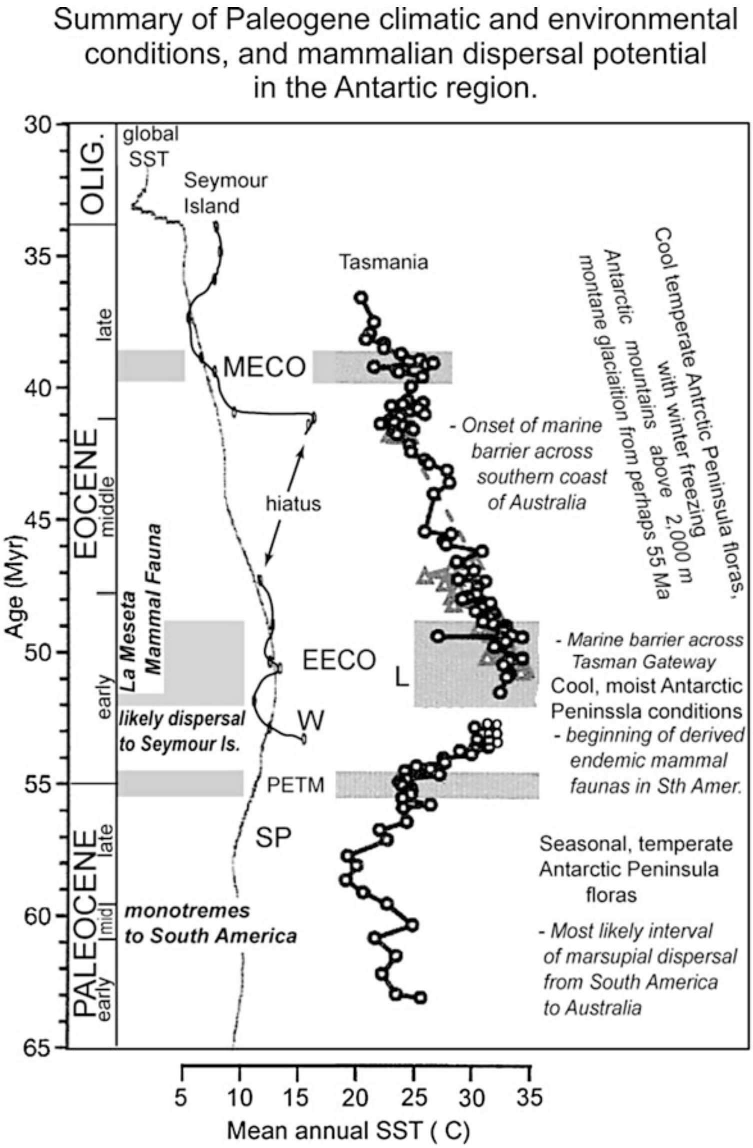


Fig. 3.14 Summary of temperatures, climatic events and mammal dispersals to South America and the Antarctic Peninsula. Tasmanian record after Bijl et al. (2009). Seymour Island record after Ivany et al. (2008). Global SST after Zachos et al. (2001). L = Leona Road, Tasmania, continental climate after Carpenter et al. (2012). W = Wilkes Land continental climates after Pross et al. (2012). SP = Seymour plants after Francis et al. (2008). PETM = Paleocene Eocene Thermal Maximum. EECO = Early Eocene Climatic Optimum. MECO = Middle Eocene Climatic Optimum La Meseta Mammal Fauna likely dispersed to Seymour Island about 53 M. Monotremes dispersed to South America from Antarctica at about 62 Ma. Antarctic glacio-eustatic activity possibly seen from 55 Ma in Tasmanian record (White 2004). See text

to Argentina (Pascual et al. 1992). If this is reasonable, it appears here that the Tingamarra Local Fauna most likely post-dates any dispersal from South America.

Additional context, derived from the Paleogene record of mammalian evolution and diversity in North and South America (Woodburne et al. 2009a, b, 2014), indicates that a comparably representative record in Australia would display strong diversity in its mammalian fauna, with numerous lineages representing a myriad of character states, potential homoplasies, and a general complexity that would include the evolution of the lineages that produced the Tingamarra metatherians on the one hand, and the extremely diverse and derived indigenous faunas of late Oligocene and later age (Fig. 3.13) on the other. In fact, Fig. 3.13 is overly simplified in that it stresses living taxa. It was not intended to include known fossil groups that do not survive to the present time, and which likely also would show ties to prior phyletic radiations, if patterns shown in other regions are a guide. Note that Black et al. (2012: Tables 1, 3) identified as many as 17 Australian mammal lineages that do not continue to the Recent. In this context, the resultant early mammal character matrix would be much more representative of Australian mammal evolution than now derivable from Tingamarra taxa alone, and questions of relationships both within and beyond Australia would be placed on a much firmer footing than now possible. The Tingamarra metatherians provide an extremely important, but still very limited glimpse of what must have been a much greater diversity of character development and evolution in Australia’s metatherian fauna. It is to be hoped that the Tingamarra Local Fauna will become one of a number of Paleocene and Eocene mammalian faunas of Australia.

One way to perhaps reconcile, the Tingamarra taxa with their singular unity and separation from the Oligocene and younger Australian mammals would be to suggest that they actually are older than currently interpreted (also Black et al. 2012). The proposed phyletic pattern (Fig. 3.13) for the evolutionary steps leading to the Oligocene and later marsupials in Australia as proposed by Beck et al. (2008) could be accomplished in spite of the Tingamarra character conflict were that fauna of early Paleocene or even Late Cretaceous age. Assessments of the non-marsupial taxa from Tingamarra [placental chiropteran (Hand et al. 1994), anseriform birds (Elzanowski and Boles 2012), crocodiles (Willis et al. 1993; Stein et al. 2012) and snakes (Scanlon 2005)] apparently would be compatible with such an age. Whether a detailed lithostratigraphic-magnetostratigraphic analysis of the Tingamarra succession would result in a substantial revision of its age remains to be determined.

3.5 Antarctic Climate

The Late Cretaceous to late Eocene climate and paleoecology of Antarctica formed the context in which mammal dispersals took place between South America and Antarctica, and to Australia. Bijl et al. (2009) addressed the paleoclimatic regime of the southwestern Pacific Ocean and adjacent areas, based on ODP Leg 189 site 1172, adjacent to the East Tasman Plateau (Fig. 3.7), in a section that ranges in age from 64 to 36 Ma. The data show that the SST (Sea Surface Temperature) was ~25 °C at about 63 Ma, and fell to ~20 °C at 58 Ma. Absent any pulse at the time of the PETM (55 Ma), the temperatures rose to about 34 °C during the EECO, 53–49 Ma, apparently about 10 °C higher than the continental climate in the same area (Carpenter et al. 2012; L, Fig. 3.14). The SST values declined thereafter to ~23 °C at about 42 Ma, and then rose briefly during the MECO (Middle Eocene Climatic Optimum) at ~40 Ma to ~27 °C. Subsequently SST declined to ~21 by 37 Ma. As indicated below there is some difference not only in continental temperatures during the Paleogene, but also SST values to the west.

With regard to the east Antarctic region, Carpenter et al. (2012) investigated foliar and pollen data from 53 to 50 Ma tidal channel deposits exposed along Lowana Road, Maquarie Harbour, in western Tasmania (near B in SB, Fig. 3.7). The results suggest that continental mean annual temperatures in southern Tasmania at that time were on the order of 24 °C, with warm temperatures indicated by dominance of entire-margined, probably evergreen, dicotyledonous leaves, and the presence of warm-water cysts of the dinoflagellate subfamily Wetzelielloideae. The presence of *Nypa*, cycads, and mangroves at the site also indicates winter temperatures above freezing. Epiphyllous fungal structures also reflect humid-rainforest conditions comparable to the subtropics and tropics, and pollen with warm-climate indications include *Alchornea*, Arecaceae, Cupanieae, *Diospyros ,and Ilex*. In fact, MAT may have been greater than 24 °C because the largest leaves were under represented.

Farther west, Pross et al. (2012) proposed a MAT of 16 ± 5 °C for the climate of continental Wilkes Land (Fig. 3.7; W, Fig. 3.14) for the 54–52 Ma interval based on materials recovered from ODP 318 site U1356 which is dominated by paratropical and tropical rainforest plants. These include dominant ferns, tree ferns and palms, with less frequent members of the Bombacoideae, including Malvaceae (cotton, hollyhock; shrubs) Strasburgeriaceae; Olacaceae (hog plum, African walnut), and Araceae (duckweed). The bombacoid group is insect-pollinated which is considered to reflect an areally interconnected forest. Winter temperatures were well above freezing. The presence of montane sporomorphs also indicates that a temperate rainforest inhabited more inland parts of Wilkes Land. The difference in Tasman SST and continental values versus those of Wilkes Land may reflect, in part, a local warm center in the Tasman—New Zealand region (Hollis et al. 2009).

The relatively cooler conditions shown by the Wilkes Land rainforest relative to that from Tasmania is continued farther west, to Seymour Island (Fig. 3.3) of the Antarctic Peninsula. The La Meseta Formation sampled for this study was assessed to range in age from 55 to 35 Ma. Based on $\delta^{18}O$ and $\delta^{13}C$ from aragonite in shells of two bivalve genera, Ivany et al. (2008: Fig. 10) documented a change from an early Eocene SST of ~15 °C at 53 Ma, likely reflective of the global EECO. The temperature then underwent a drop during 53–51 Ma to ~10 °C, recorded a short rise ~12 °C shortly after 51 Ma, and fell back to ~10 °C at about 48 Ma. After a 2 Ma hiatus, the temperature had risen again to ~15 °C by 42 Ma, likely coincident with the MECO. This pattern is also seen in the Southern Ocean on the Maud Rise and Kerguelen Plateau (Bohaty and Zachos 2003). Thereafter, sea temperature underwent a sharp drop to ~8 °C at about 41 Ma, and then fell further to ~5 °C at 37.3 Ma during the global Middle Eocene Cooling interval. As another local example, mountain glaciation on the nearby South Shetland Islands occurred from 45 to 41 Ma (Birkenmajer et al. 2005; Francis et al. 2008). Subsequently, the SST rose slightly again to ~7 °C from 36 to 34 Ma.

Paleofloras from the Antarctic Peninsula as represented by fossil wood, leaf, and pollen from the South Shetland Islands and James Ross Basin of the northern Antarctic Peninsula (Fig. 3.3) provide an indication of terrestrial climates of the region (Poole et al. 2005). Winter darkness is a pervasive factor affecting plant and animal life in high latitudes, but the plant community appears to have accommodated this overall. Growth-ring patterns reflecting winter darkness are found mostly in mid-Cretaceous conifer samples, whereas the pattern morphology of Paleocene and Eocene taxa appears to have resulted from seasonal variations in water availability, compatible with a change from warmer overall mid to Late Cretaceous climate to cooler conditions in the Paleogene.

The Coniacian–Campanian climate was warm and equable, during the Cretaceous Thermal Maximum (CTA; 100–80 Ma; Francis et al. 2008), more so than in the late Early Eocene. A MAP of 600 cm in the Campanian fell to 500 cm in the early Paleocene, and to 250 cm in the late Paleocene as conditions became drier and cooler. MAP increased to 400 cm in the early middle Eocene, but by the late middle Eocene had decreased to 100 cm. These data are based on fossil wood analyses and may be overestimated (Poole et al. 2005), although the overall trend is realistic. Comparable numbers based on leaf physiognomy are about 90 cm for Campanian to early Paleocene, 70–100 cm in the mid-Eocene (Poole et al. 2005: Fig. 2). Overall increased aridity through time was accompanied by a decrease in precipitation. MAT interpretations suggest that the Coniacian–Campanian reached 13.5 °C, cooled to 11 °C in the late Maastrichtian, ranged from 10 °C in the early Paleocene to about 15 °C in the late Paleocene (SP, Fig. 3.14), with cooling again in the Eocene (11–12 °C). The plant record contains a hiatus at the time of the EECO (50–53 Ma).

Together, the data indicate relatively warm and wet conditions in the Late Cretaceous, with higher rainfall during the growing season consistent with tropical to subtropical climates that lacked winter freezing. Angiosperm plants diversified strongly in the Santonian within the CTA (Francis et al. 2008). Conditions became much cooler and drier at the end of the Maastrichtian, and into the Paleocene. Dry conditions continued into the mid-Paleocene, becoming cooler but also wetter in the Eocene (Fig. 3.14).

A Late Paleocene flora of Seymour Island is represented by 36 angiosperms and two ferns, along with podocarp and araucarian conifers. The angiosperms are represented by Nothofagaceae (*Nothofagus*), Lauraceae (laurels) and Proteaceae, as well as by Myrtaceae (*Eucalyptus* family), Elaeocarpaceae (crinodendrons), Winteraceae (Winter's Bark), Moraceae (hemp), Cunoniaceae and Monimiaceae, collectively indicative of cool-warm temperatures and a mixed conifer-broad leaf evergreen and deciduous forest, dominated by large trees of *Nothofagus* and araucarian and podocarp conifers. Other angiosperms grew in the mid-canopy and as understorey shrubs. A MAT of about 14 °C is indicated (SP, Fig. 3.14) with a strongly seasonal climate, winter cold still above freezing, and MAP of about 210 cm. The MAT is comparable to that for the Palacio de los Loros flora from Patagonia (Woodburne et al. 2014: Fig. 8), but the MAP is much higher (210 vs. 115 cm.).

Early Eocene plants on Seymour Island included araucarian conifers and angiosperms (Francis et al. 2008), with the latter being similar to living Lauraceae, Myricaceae, Myrtaceae, and Proteaceae. The conifers suggest a cool and moist climate (Fig. 3.14), with MAT of about 8–13 °C, comparable to the SST of 12 °C (Ivany et al. 2008).

Later, the mid-Eocene flora is reduced in diversity by 47 %, with 19 leaf morphotypes. *Nothofagus* is dominant, and the flora is comparable to those of cool-temperate conditions (Fig. 3.14). Substantial cooling over the interval is indicated thereby. A MAT is given as about 11 °C, freezing conditions in winter, and a MAP of 150 cm (Francis et al. 2008). Thus, as also indicated by Poole et al. (2005), Francis et al. (2008) concluded that late Paleocene floras of the Antarctic Peninsula were relatively warm and ice-free in winter. By the middle Eocene (47–44 Ma), conditions were much cooler, and winter ice was likely (Fig. 3.14).

Poole et al. (2005) suggest that the Antarctic Peninsula supported a central mountain range likely 2000–3000 m in elevation, with a probable rain shadow to the east. Due to the high paleolatitude (ca 60°S) and relatively high atmospheric CO_2, vegetation would have experienced at least a month-long dormant phase due to reduced light intensity. In spite of the maritime influence, it is possible that winter frost might have been a factor in the growth cycle. Wilson and Luyendyk (2009) restored the paleotopography of West Antarctica in the late Eocene and early Oligocene and posited a reconstruction compatible with the elevation of the Antarctic Peninsula ranges. They also proposed that such elevations would have been present in the earlier Eocene, at least, and would have included much of East Antarctica having been at about 1000–2000 m (Queen Maud Land and adjacent parts of Wilkes Land as well as the Transantarctic Mountains). Lowland and coastal regions persisted in any case.

The cool mid to late Eocene climates derived from floral analysis is compatible with the presence of at least mountain glaciation on Antarctica including the Antarctic Peninsula (Birkenmajer et al. 2005), and White (2004) suggested a glacio-eustatic record at 55–50 Ma in Eocene ODP cores adjacent to Tasmania.

3.6 Summary

Based on SST and continental evidence, Late Cretaceous climatic conditions across the Antarctic region were warm and supported subtropical to tropical vegetation. As climate began to cool in the Paleocene, at least the Antarctic Peninsula records the persistence of cooler temperatures and a mixed conifer-broad leaf evergreen and deciduous forest that still lacked conditions of winter freezing, with no evidence of mountain glaciation. Early Eocene plants suggest a cool and moist climate, with MAT of about 8–13 °C, comparable to a SST value of 12 °C. Dispersal of a derived component of mammals from South America to Seymour Island from about 53 Ma apparently took place under such conditions (Fig. 3.14). Later in the Eocene, the development of yet cooler conditions, winter freezing, and mountain glaciation likely present at higher elevations across the entire Antarctic continent, would pose increasing difficulties to mammalian dispersal from South America to Australia, although coastal and lowland routes still would have been available. The 50 Ma sundering of the Tasmanian Gateway (with earlier potential interruptions from about 55 Ma) would have made a major impact on overland dispersals of animals with that, in conjunction with the 45 Ma marine barrier across the entire southern coast of Australia, essentially terminating any potential for dispersal.

The dominance of diverse marsupials in the early Paleocene of South America and the presence of monotremes in South America by about 63 Ma combine to highlight the early to middle Paleocene as the most likely time for mammalian dispersal to Australia (Fig. 3.14). If the Tingamarra Local Fauna proves to be of Paleocene, rather than early Eocene, age, the regional affiliations of its taxa would be most compatible with dispersal at that time.

3.7 Conclusions

The early Paleocene diversity of metatherians in Tiupampan faunas of South America and the pre-Tiupampan record of the polydolopimorphian *Cocatherium* speak in favor of a Late Cretaceous or earliest Paleocene dispersal of metatherians from North America. Whereas no Late Cretaceous metatherians have been recovered to date in South America, the late Campanian to Maastrichtian presence of hadrosaurine dinosaurs in Argentina as well as the late Maastrichtian of the Antarctic Peninsula is evidence of a biotic connection to North America at that time, also compatible with a concurrent northward dispersal of leptodactylid frogs. Placental ‘condylarths’ in the Tiupampan may have been related to, and dispersed southward relative to, Puercan taxa in North America and perhaps reflect a somewhat later event in comparison to metatherians, also attested to by the presence of the menispermaceaean podocarp, *Palaeoluna* in Wyoming and Colombia at ~60 Ma.

Other than hadrosaurine dinosaurs, Late Cretaceous vertebrates of South America are basically Gondwanan in affinities and reflect (and survived) the pre-106 Ma connection between South America, Africa, and Antarctica. The potential for a Late Cretaceous dispersal of metatherians would be compatible with a continued dispersal to Australia at that time, also supported by plate tectonic relationships, the basically endemic coeval dinosaurian Australian dinosaur fauna notwithstanding, and with the proviso that a late Maastrichtian Australian record of dinosaurian and other land vertebrates is effectively nonexistent. An early Paleocene connection between at least Antarctica and South America is suggested by the presence of a monotreme in the fauna at Punta Peligro, Patagonia. This, coupled with the fact that post-Peligran mammal faunas in South America and the Antarctic Peninsula (from at least 52 Ma in that location) are composed of derived metatherian as well as placental mammals, suggests that the dispersal of metatherians to Australia had been achieved prior to the Eocene. This is compatible with the still plesiomorphic level of Australian metatherians from the early Eocene Tingamarra fauna of Australia, the only pre-late Oligocene mammal fauna of that continent. The sundering of the Tasman Gate by marine waters at about 50 Ma and the development of a continuously marine southern coastline of Australia by about 45 Ma, effectively foreclosed overland mammal as well as other vertebrate dispersal to Australia from then on. If a relationship between South American xenarthrans and the Afrotheria is sustained, it would appear to reflect a vicariant separation of the groups when South America and Africa separated at about 106 Ma regardless of certain studies that imply a younger age for the two groups.

References

Agnolin FL, Chimento NR (2011) Afrotherian affinities for endemic South American "ungulates". Mamm Biol 76:101–108

Agnolin FL, Ezcurra MD, Pais DF, Salisbury SW (2010) A reappraisal of the Cretaceous non-avian dinosaur fauna from Australia and New Zealand: evidence for their Gondwanan affinities. J Syst Palaeontol 8(2):257–300

Amrine-Madsen H, Keopfli K-P, Wayne RK, Springer MS (2003) A new phylogenetic marker, apoliprotein B, provides compelling evidence for eutherian relationships. Mol Phylogenetics Evol 28:225–240

Andreis RR, Mazzoni MM, Spalletti LS (1975) Estudio estratigráfico y paleoambiental de las sedimentitas teriarias entre Pico Salamanca y Bahía Bustamante, Provincia de Chubut, República Argentina. Rev Asoc Geol Arg 30:85–103

Archer M, Godthelp H, Hand S (1993) Early Eocene marsupial from Australia. Kaupia 3:193–200

Asher R, Lehmann T (2008) Dental eruption in afrotherian mammals. BMC Biol 6:14. doi:10.1186/1741-7007-6-14

Asher RJ, Novacek MJ, Geisler JH (2003) Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. J Mamm Evol 10:131–194

Beck RMD (2012) An 'ameridelphian' marsupial from the early Eocene of Australia supports a complex model of Southern Hemisphere marsupial biogeography. Naturwissenschaften 99:715–729

Beck RMD (2013) A peculiar faunivorous metatherian from the early Eocene of Australia. Acta Palaeontol Pol. doi:http://dx.doi.org/10.4202/app.2013.0011

Beck RMD, Godthelp H, Weisbecker V, Archer M, Hand SJ (2008) Australia's oldest marsupial fossils and their biogeographical implications. PLoS One 3:e1858. doi:10.137

Bergqvist LP, Powell JE, Avilla LS (2004) A new xenungulate from the Río Loro Formation (Paleocene) from Tucumán province (Argentina). Ameghiniana Supl 41(4):36R

Bernecker T, Partridge AD (2001) Emperor and golden beach subgroups: the onset of late cretaceous sedimentation in the gippsland basin, SE Australia. PESA Eastern Australasian Basins symposium, pp 391–402

Bertini RJ, Marshall LG, Brito P (1993) Vertebrate faunas from the Adamantina and Marilia formations (Upper Bauru Group, late Cretaceous, Brazil) in their stratigraphic and paleobiogeographic context. N Jb Geol Paläont Abh 188(1):71–101

Bijl PK, Schouten S, Sluijs A, Reichart G-J, Zachos JC, Brinkhuis H (2009) Early Paleogene temperature evolution of the southwest Pacific Ocean. Nature 461:776–779

Bijl PK, Bendie JAP, Bohaty SM, Pross J, Schouten S, Tauxe L, Stickley CE, McKay RM, Röhl U, Olney M, Sluijs A, Escutia C, Brinkhuis H, Expedition 318 Scientists (2013) Eocene cooling linked to early flow across the Tasmanian Gateway. PNAS Early Ed. doi:10.1073/pnas.1220872110

Bininda-Emonds ORP, Cardillo J, Jones KE, MacPhee RDE, Beck RMD, Greyner F et al (2007) The delayed rise of present-day mammals. Nature 446:507–512

Birkenmajer K, Gaździcki A, Krajweski KP, Przybycin A, Solecki A, Tatur A, Yoon HI (2005) First Cenozoic glaciers in West Antarctica. Polish Polar Res 26(1):3–12

Black KH, Archer M, Hand S, Godthelp H (2012) The rise of Australian marsupials: a synopsis of biostratigraphic, phylogenetic, palaeoecologic and palaeobiogeographic understanding. In: Talent JA (ed) Earth and life, international year of planet earth. doi 10.1007/978-481-3429-1_35

Blevin JE, Trig KR, Partridge AD, Boreham CJ, Lang SC (2005) Tectonostratigraphy and potential source rocks of the Bass Basin. APPEA J 45:601–621

Bohaty SM, Zachos JC (2003) Significant Southern Ocean warming event in the late middle Eocene. Geology 31:1017–1020

Bonaparte JF (1987) The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Rev Mus Arg Cs Nat "B. Rivadavia" Paleont 3(3):103–178

Bond M, Kramarz A, MacPhee RDE, Reguero MA (2011) A new astrapothere (Mammalia, Meridungulata) from La Meseta Formation, Seymour (Marambio) Island, and a reassessment of previous records of Antarctic species. Amer Mus Novitates 3718:1–16

Candeiro CRA, Rich T (2010) Overview of the Late Cretaceous biota of the western São Paulo State, Brazil, Bauru Group. J South Amer Earth Sci 29:346–353

Candeiro CRA, Abranches CT, Abrantes EA, Avilla LS, Martins VC, Moreira AL, Torres SR, Bergqvist LP (2004) Dinosaurs remains from western São Paulo state, Brazil (Baru Basin, Adamantina Formation, Upper Cretaceous. J South Amer Earth Sci 18:1–10

Candeiro CRA, Martinelli AG, Avila LS, Rich TH (2006) Tetrapods from the upper Cretaceous (Turonian—Maastrichtian Baru group of Brazil: a reappraisal. Cretac Res 27:923–946

Candeiro CRA, Santos AR, Bergqvist LP, Ribeiro LCB, Apestgeuía S (2008) The Late Cretaceous fauna and flora of the Uberaba area (Minas Gerais State, Brazil). J South Amer Earth Sci 25:203–216

Carpenter RJ, Jordan GJ, Macphail MK, Hill RS (2012) Near-tropical early Eocene terrestrial temperatures at the Australo-Antarctic margin, western Tasmania. Geology 40(3):267–270

Case JA, Martin JE, Chaney DS, Reguero M, Marenssi SA, Santillana SM, Woodburne MO (2000) The first duck-billed dinosaur (Family Hadrosauridae) from Antarctica. J Vert Paleontol 20(3):612–614

Case JA, Goin FJ, Woodburne MO (2005) "South American" marsupials from the Late Cretaceous of North America and the origin of marsupial cohorts. J Mamm Evol 12(3/4):461–494

Case JA, Martin JE, Reguero M (2007) A dromaeosaur from the Maastrichtian of James Ross Island and the Late Cretaceous Antarctic dinosaur fauna. US Geol Surv Nat Acad USGS OF-2007-1047, Short Res Paper 083. doi:10.3133/of2007-1047.srp083

Chornogubsky L, Goin FJ, Reguero M (2009) A reassessment of Antarctic polydolopid marsupials (Middle Eocene, La Meseta Formation). Antarct Sci 21(3):285–297

Churakov G, Kriegs JO, Baertsch R, Zemann A, Brosius J, Schmitz J (2009) Mosaic retroposon insertion patterns in placental mammals. Genome Res 19:868–875

Clyde WC, Wilf P, Iglesias A, Slingerland RL, Barnum T, Bijl PK, Bralower TJ, Brinkhuis H, Comer EE, Huber BT, Ibañez-Mejia M, Jicha BR, Krause JM, Schueth JD, Singer BS, Raigemborn MS, Schmitz MD, Sluijs A, Zamaloa M del C (2014) New age constraints for the Salamanca Formation and lower Rio Chico Group in the western San Jorge Basin, Patagonia, Argentina: implications for K/Pg extinction recovery and land mammal age correlations. Geol Soc Amer Bull 126(3/4):289–306

Crawford A, Smith EN (2005) Cenozoic biogeography and evolution in direct-developing frogs of Central America (Leptodactylidae: *Eleuterodactylus*) as inferred from a phylogenetic analysis of nuclear and mitochondrial genes. Mol Phylogenetics Evol 35:536–555

Cummings AM, Hillis RR, Tingate PR (2004) New perspectives on the structural evolution of the Bass Basin: implications for petroleum prospectivity. In: PESA Eastern Australasian Symposium II, pp 133–149

de la Fuente M, Salgado L, Albino A, Báez AM, Bonaparte JF, Calvo JO, Chiappe LM, Codorniú LS, Coria RA, Gasparini Z, González Riga BJ, Novas FE, Pol D (2007) Tetrápodos continentales del Cretácico de la Argentina: una síntesis actualizada. Asoc Paleont Arg Publ Esp 11:137–153

de Muizon C (1991) La fauna de mamiferos de Tiupampa (Paleoceno inferior, Formación Santa Lucia), Bolivia. In: Suarez-Soruco R (ed) Fósiles y Facies de Bolivia, vol 1 (Vertebrados). Rev Tecn YPFB 3/4:575–624

de Muizon C (1998) *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Paleocene of Bolivia. Phylogenetic and paleobiologic implications. Geodiversitas 20(1):19–142

de Muizon C, Brito IM (1993) Le bassin calciaire de Sáo José de Itaboraí (Rio de Janeiro, Brésil): ses relacions fauniques avec le site de Tiupampa (Cochambamba, Bolivie). Annal Palaeontol 79:233–269

de Muizon C, Cifelli RL (2000) The ‘condylarths’ (archaic Ungulata, Mammalia) from the early Palaeocene Tiupampa (Bolivia): implications on the origin of the South American ungulates. Geodiversitas 22(1):47–150

dos Reis M, Inoue J, Haseqawa M, Asher RJ, Donoghue PCJ, Yang Z (2012) Phylogenetic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. Proc R Soc B 279(1742):3491–3500

Elzanowski A, Boles WE (2012) Australia’s oldest anseriform fossil: a quadrate from the early Eocene Tingamarra Local Fauna. Palaeontology 55(4):903–911

Exon NF, Kennett JP, Malone MJ (2004) 1 Leg 189 synthesis: Cretaceous—Holocene history of the Tasmanian Gateway. In: Exon NF, Kennett JP, Malone MJ (eds) Proceeding of the ocean drilling program, scientific results, vol 189, pp 1–37

Figueirido B, Janis CM, De Renzi M, Palmqvist P (2012) Cenozoic climate change influences mammalian evolutionary dynamics. PNAS 109(3):722–727

Forasiepi AM (2009) Osteology of Arctodictis sinclairi (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. Monogr Mus Arg Cs Nat NS 6:1–174

Francis JE, Ashworth A, Cantrill DJ, Crame JA, Howe J, Stephens R, Tosolini A-M, Thorn V (2008) 100 million years of Antarctic climate evolution: evidence from fossil plants. In: Cooper AK, Barrett PJ, Stagg H, Storey B, Stump E (eds) Antarctica: a keystone in a changing world, W Wise and the 10th ISAES editorial team. Proceedings of the 10 international symposium Antarctic Earth Sciences. The National Academies Press, Washington

Gaffney ES, Bartholomai A (1979) Fossil trionychids from Australia. J Palaeontol 53(6):1354–1360

Gayet M, Marshall LG, Sempere T, Meunier FJ, Cappetta H, Rage J-C (2001) Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. Palaeogeogr Palaeoclimatol Palaeoecol 169:39–68

Gelfo JN, Goin FJ, Woodburne MO, de Muizon C (2009) Biochronological relationships of the earliest South American Paleogene mammalian faunas. Palaeontology 52(1):251–269

Gheerbrant E (2009) Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. PNAS 106(26):10717–10721

Godthelp H, Archer M, Cifelli R, Hand S, Gilkeson CF (1992) Earliest known Australian Tertiary mammal fauna. Nature 356:514–516

Godthelp H, Wroe S, Archer M (1999) A new marsupial from the Early Eocene Tingamarra Local Fauna of Murgon, southeastern Queensland: a prototypical Australian marsupial? J Mamm Evol 6:289–313

Goin FJ, Abello MA (2013) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, Edad-mamífero Colhuehuapense). Parte 2: Microbiotheria y Polydolopimorphia. Ameghiniana 50(1):51–78

Goin FJ, Pascual R, Tejedor M, Gelfo JN, Woodburne MO, Case JA, Reguero MA, Bond M, López GM, Cione AL, Sauthier DU, Ballarino L, Scasso RA, Medina FA, Ubaldón MC (2006) The earliest Tertiary therian mammal from South America. J Vert Paleontol 26(2):505–510

Goin FJ, Candela AM, Abello A, Oliveira EO (2009) Earliest South American paucituberculatans and their significance in understanding of "pseudodiprotodont" marsupial radiations. Zool J Linn Soc 155:867–884

Goin FJ, Abello MA, Chornogubsky L (2010) Middle Tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America's *Grand Coupure*. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The Paleontology of Gran Barranca. Cambridge University Press, Cambridge

Goin FJ, Gelfo JN, Chornogubsky L, Woodburne MO, Martin T (2012a) Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: an 80-million year history of recent Neotropical mammals. University of Chicago Press, Chicago

Goin FJ, Tejedor MF, Chornogubsky L, López GM, Gelfo JN, Bond M, Woodburne MO, Gurovich Y, Reguero M (2012b) Persistence of a Mesozoic, non-therian mammalian lineage (Gondwanatheria) in the mid-Paleogene of Patagonia. Naturwissenschaften 99:449–463

Goin FJ, Zimicz N, Forasiepi AM, Chornogubsky LC, Abello MA (2013) The rise and fall of South American metatherians: contexts, adaptations, radiations, and extinctions. In: Rosenberger AL, Tejedor MF (eds) Origins and evolution of Cenozoic South American mammals. Springer, New York

Gurovich Y, Beck R (2009) The phylogenetic affinities of the enigmatic mammalian clade Gondwanatheria. J Mamm Evol 16:25–49

Hahn G, Hahn R (2003) New multituberculate teeth from the Early Cretaceous of Morocco. Acta Palaeontol Pol 48:349–356

Hahn G, Hahn R (2006) Evolutionary tendencies and systematic arrangement in the Haramyida (Mammalia). Geol Palaeontol 40:173–193

Hallström BM, Kullberg M, Nilsson MA, Janke A (2007) Phylogenomic data analyses provide evidence that Xenarthra and Afrotheria are sister groups. Mol Biol Evol 24(9):2059–2068

Hand S, Novacek M, Godthelp H, Archer M (1994) First Eocene bat from Australia. J Vert Paleontol 14(3):375–381

Heinicke MP, Duellman WE, Hedges SB (2007) Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. PNAS 104(24):10092–10097

Herrera F, Manchester SR, Hoot SB, Wefferling KM, Carvalho MR, Jaramillo C (2011) Phytogeographic implications of fossil endocarps of Menispermaceae from the Paleocene of Colombia. Amer J Bot 98(12):2004–2017

Hill PJ, Exon NF (2004) Tectonics and basin development of the offshore Tasmania area incorporating the results from deep ocean drilling. The Cenozoic Southern Ocean: tectonics, sedimentation and climate change between Australia and Antarctica. Amer Geophys Union, Geophysical Monogr Ser 151:19–42

Hofford SP, Hillis RR, Duddy IR, Green PF, Stoker MS, Tuitt AK, Backé G, Tassone DR, MacDonald JD (2011) Cenozoic post-breakup compressional deformation and exhumation of the southern Australian margin. APPEA J 51:618–638

Hollis CJ, Handley L, Crouch EM, Morgans HEG, Baker JA, Creech J, Collins KS, Gibbs SJ, Huber M, Schouten S, Zachos JC, Pancost RD (2009) Tropical sea temperatures in the high-latitude South Pacific. Geology 37:99–110

Horovitz I, Martin T, Bloch J, Ladevèze S, Kurz C, Sánchez-Villagra M (2009) Cranial anatomy of the earliest marsupials and the origin of opossums. PLoS ONE 4(12):e8278. doi:10.1371/journal.pone.0008278

Iglesias A, Wilf P, Johnson KR, Zamuner AB, Cuńeo NR, Matheos SD (2007) A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. Geology 35(10):947–950

Ivany LC, Lohmann KC, Hasiuk F, Blake DB, Glass A, Aronson RB, Moody RM (2008) Eocene climate record of a high southern latitude continental shelf: Seymour Island. Antarctica Geol Soc Amer Bull 120(5/6):659–678

Jacobs LL, Strganac C, Scotese C (2011) Plate motions, Gondwana dinosaurs, Noah's arks, beached Viking funeral ships, Ghost ships, and landspans. An Acad Bras Cs 83(1):3–22

Juárez Valieri RD, Haro JA, Fiorelli LE, Calvo JO (2010) A new hadrosaurid (Dinosauria: Ornithopoda) from the Allen Formation (Late Cretaceous) of Patagonia, Argentina. Rev Mus Arg Cs Nat NS 12(2):217–231

Kielan-Jaworowska Z, Ortiz-Jaureguizar E, Vieytes C, Pascual R, Goin FJ (2007) First ? cimolodontan multituberculate mammal from South America. Acta Palaeontol Pol 52(2):257–262

Lawver LA, Gahagan LM, Dalziel IWD (2011) A different look at gateways: Drake Passage and Australia/Antarctica. In: Anderson JB, Wellner JS (eds) Tectonic, climate, and cryospheric evolution of the Antarctic Peninsula. The Amer Geophys Union Sp Publications, vol 63, pp 5–33

Lawver LA, Dalziel IWE, Gahagan LM, Norton IO (2013) Intercontinental dispersal routes for South American land mammals: paleogeographic constraints. In: Rosenberger AL, Tejedor MF (eds) Origins and evolution of Cenozoic South American mammals. Springer, New York

Leanza HA, Apesteguía S, Novas FE, de la Fuente MS (2004) Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. Cretac Res 25:61–87

López G, Gelfo JN, Bond M, Lorente M, Reguero MA (in press) Towards the origin of South American native ungulates and their Paleocene and Eocene diversity. In: Rosenberger AL, Tejedor MF (eds) Origins and evolution of Cenozoic South American mammals. Springer, New York

Luterbacher HP, Ali JR, Brinkhuis H, Gradstein FM, Hooker JJ, Monechi S, Ogg JG, Powell J, Röhl U, Sanfilippo A, Schmitz B (2004) Paleogene. In: Gradstein F, Ogg J, Smith A (eds) A geologic time scale. Cambridge University Press, Cambridge

Marshall LG, Hoffstetter R, Pascual R (1983) Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. Palaeovertebrata Mem Extraord, 1–93

Massabie AE (1995) Estratigrafía del límite Cretácico-Terciario de la región del Río Colorado, según el perfil de Casa de Piedra, provincia de La Pampa. 12 Congr Geol Arg 2 Congr Expl Hidrocarb Mendoza Actas 2:124–131

McInerney FA, Wing SL (2011) The Paleocene-Eocene Thermal Maximum; a perturbation of carbon cycle, climate, and biosphere with implications for the future. Ann Rev Earth Planet Sci 39:489–516

McKenna MC, Bell SJ (2002) Classification of mammals above the species level. Columbia University Press, New York

Megirian D, Prideaux GJ, Murray PF, Smit N (2010) An Australian land mammal age biochronological scheme. Paleobiology 36(4):658–671

Meredith RW, Janecka JE, Gatesy J (2011) Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334(521):521–524

Murphy PR, Schwarzbock H, Cranfield LC, Withnall IW, Murray CG (1976) Geology of the Gympie 1:250,000 Sheet Area. Geol Surv Queensland Rep 96:1–157

Murphy WJ, Pringle TH, Crider TA, Springer MS, Miller W (2007) Using genomic data to unravel the root of the placental mammal phylogeny. Genome Res 17:413–421

Murphy BH, Farley KA, Zachos JC (2010) An extraterrestrial 3He-based timescale for the Paleocene-Eocene Thermal Maximum (PETM) from Walvis Ridge, IODP site 1266. Geochem Cosmochem Acta 74:5098–5108

Nilsson MA, Churakov G, Sommer M, Tran NV, Zemann A, Brosius J, Schmitz J (2010) Tracking marsupial evolution using archaic genomic retroposon insertions. PLoS Biol 8(7):1–9

Nishihara H, Maruyama S, Okada N (2009) Retroposon analysis and recent geological data suggest near-simultaneous divergence of the three superorders of mammals. PNAS 106 (13):5235–5240

Norvik MS (2000) Plate tectonic reconstructions of Australia's southern margins. Geosci Aust Rec 2005(07):1–107

Norvik MS, Smith MA, Power MR (2001) The plate tectonic evolution of eastern Australia guided by the stratigraphy of the Gippsland Basin. In: PSEA Eastern Australasian Basins symposium, pp 15–23

O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Gaillombardo A, Giannini NP, Goldberg SL, Kraatz BP, Luo Z-X, Meng J, Ni X, Novacek MJ, Perini FA, Randall ZS, Rougier GW, Sargis EJ, Silcox MT, Simmons NB, Spaulding M, Velazco PM, Weksler M, Wible JR, Cirranello AR (2013) The placental mammal ancestor and the post-K-Pg radiation of placentals. Science 339:662–667

Pascual R, Ortiz-Jaureguizar E (2007) The Gondwanan and South American episodes: two major and unrelated moments in the history of the South American mammals. J Mamm Evol 14:75–137

Pascual R, Ortega Hinojosa EJ, Gondar D, Tonni E (1965) Las edades del Cenozóico mamalifero de la Argentina, con especial atención a aquellas del territorio bonarense. Anales Comisión Invest Cient Buenos Aires 6:165–193

Pascual R, Archer M, Ortiz-Jaureguizar E, Prado JL, Godthelp H, Hand SJ (1992) First discovery of monotremes in South America. Nature 356:704–705

Pascual R, Goin FJ, González P, Ardolino A, Puerta PF (2000) A highly derived docodont from the Patagonian Late Cretaceous: evolutionary implications for Gondwanan mammals. Geodiversitas 22(3):395–414

Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast AE, Erk FC, Glass B (eds) Evolution, mammals, and southern continents. State University New York Press, Albany

Penkrot TA, Zack SP, Rose KD, Bloch DI (2008) Postcranial morphology of *Apheliscus* and *Haplomylus* (Condylarthra, Apheliscidae): evidence for a Paleocene Holarctic origin of Macroscelidea. In: Sargis EJ, Dagosto M (eds) Mammalian evolutionary morphology: a tribute to Frederick S. Szalay. Springer, New York

Pindell JL, Kennan LJG (2001) Kinematic evolution of the Gulf of Mexico and the Caribbean. In: Fillon R (ed) Transactions, 21st Bob Perkins GCSSEPM research conference

Pindell J, Kennan L (2009) Tectonic evolution of the Gulf of Mexico, Caribbean and northern South America in the mantle reference frame: an update. In the origin and evolution of the Caribbean Plate. Geol Soc London Sp Publ 328:1–55

Poole I, Cantrill D, Utescher T (2005) A multi-proxy approach to determine Antarctic terrestrial palaeoclimate during the Late Cretaceous and Early Tertiary. Palaeogeogr Palaeoclimat Palaeoecol 222:95–121

Powell JE (1987) Hallazgo de un dinosaurio hadrosaurido (Ornithischia, Ornithopoda) en la Formación Allen (Cretácico Superior) de Salitral Moreno, Provincia de Río Negro, Argentina. Actas 10 Congr Geol Arg 3:149–152

Pross J, Contreras L, Bijl PK, Greenwood DR, Bohaty SM, Schouten S, Bendle JA, Röhl U. Tauxe L, Raine JI, Huck CE, van de Flierdt T, Jamieson SSR, Stickley CE, van de Schootbrugge B, Escutia C, Brinkhuis H, and Integrated Ocean Drilling Program Expedition 318 Scientists (2012) Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. Nature 488:73–77

Rage J-C (1978) Une connexion continentale entre Amérique du Nord et Amérique du Sud au Crétacé superieur? L'exemple des vertébrés continentaux. Compt Rendu somm Sc Soc Géol France 6:281–285

Rage J-C (2005) Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part III. Ungaliophiinae, booids, *incertae sedis*, and Caenophidia. Summary, update, and discussion of the snake fauna from the locality. Palaeovertebrata 36(1–4):37–73

Reguero MA, Marenssi SA (2010) Paleogene climatic and biotic events in the terrestrial record of the Antarctic Peninsula: an overview. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The Paleontology of Gran Barranca. Cambridge University Press, Cambridge

Reguero MA, Marenssi SA, Santillana SN (2002) Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. Palaeogeogr Palaeoclimatol Palaeoecol 179:189–210

Rich TH, Rich PV, Flannery TF, Kear BP, Cantrill D, Komarower P, Kool L, Pickering D, Trusler P, Morton S, van Klaveren N, Fitzgzerald MG (2009) An Australian multituberculate and its paleobiogeographic implications. Acta Palaeontol Polonica 54(1):1-6

Rougier GW, Chornogubsky L, Casadio S, Arango NP, Gaillombardo A (2009a) Mammals from the Allen Formation, Late Cretaceous, Argentina. Cretac Res 30:223–238

Rougier GW, Forasiepi AM, Hill RV, Novacek MJ (2009b) New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia. Argentina Acta Palaeont Pol 54(2):195–212

Rougier GW, Apesteguía S, Gaetano LS (2011) Highly specialized mammalian skulls from the Late Cretaceous of South America. Nature 479:98–102

Ruiz LE (2006) Estudio sedimetológico y estratigráfico de las formaciones Paso del Sapo y Lefipán en el valle medio del Río Chubut. Master thesis, University of Buenos Aires

Salgado L, Gasparini Z (2006) Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). Geodiversitas 28(1):119–135

Sánchez-Villagra M, Narita Y, Kuratani S (2007) Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Syst Biodiv 5(1):1–7

Scanlon JD (2005) Australia's oldest known snakes: *Patagoniophis, Alamitophis*, and cf. *Madtsoia* (Squamata: Madstoiidae) from the Eocene of Queensland. Mem Queensland Mus 51(1):215–235

Seiffert ER (2007) A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. BMC Evol Biol 7. doi:10.1186/1471-2148-7-224

Sigé B, Sempere T, Butler RF, Marshall LG, Crochet JY (2004) Age and stratigraphic reassessment of the fossil-bearing Laguna Umayo red mudstone unit, SE Peru, from regional stratigraphy, fossil record, and paleomagnetism. Geobios 37:771–794

Sigé B, Archer M, Crochet J-Y, Godthelp H, Hand S, Beck RMD (2009) *Chulpasia* and *Thylacotinga*, late Paleocene-earliest Eocene trans-Antarctic Gondwanan bunodont marsupials: new data from Australia. Geobios 42:813–823

Sigogneau-Russell D (1991) First evidence of Multituberculata (Mammalia) in the Mesozoic of Africa. N Jb Pälaont Abh 2:119–125

Simpson GG (1971) The evolution of marsupials in South America. Ann Acad Bras Ciénc 43:103–119

Spalletti LA, Matheos SD, Merodio JC (1999) Sedimentitas carbonaticas Cretacico-Terciaris de la platforma norpatagonica. Actas 12 Congr Geol Arg, 2 Congr Expl Hidrocarburos 1:249–257

Springer MS, Murphy WJ (2007) Mammalian evolution and biomedicine: new views from phylogeny. Biol Rev 82:375–392

Springer MS, Cleven GC, Madsen O, de Jong WW, Waddell VG, Amrine HM, Stanhope MJ (1997) Endemic African mammals shake the phylogenetic tree. Nature 388:61–64

Springer MS, Amrine HM, Burk A, Stanhope MJ (1999) Additional support for Afrotheria and Paenungulata, the performance of mitochondrial versus nuclear genes, and the impact of data partitions with heterogeneous base composition. Syst Zool 48(1):65–75

Springer MS, Meredith RW, Teeling EC, Murphy WJ (2013) Technical comment on the placental mammal ancestor and the post–K-Pg radiation of placentals. Science 341:613

Stanhope MJ, Madsen O, Waddell VG, Cleven GC, de Jong WW, Springer MS (1998) Highly congruent molecular support for a diverse superordinal clade of endemic African mammals. Mol Phylogenetics Evol 9(3):501–508

Stein M, Salisbury SW, Hand SJ, Archer M, Godthelp H (2012) Humeral morphology of the early Eocene mekosuchine crocodylian *Kambara* from the Tingamarra Local Fauna southeastern Queensland. Aust Alcheringa 36(4):1–15

Szalay FS (1982) Phylogenetic relationships of the marsupials. Geobios Mém Spéc 6:177–190

Szalay FS (1994) Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge University Press, New York

Tabuce R, Marivaux L, Adaci M, Bensalah M, Hartenbarger J-L, Mahboubi M, Mebrouk F, Tafforeau P, Jaeger J-J (2007) Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. Proc R Soc B 274:1159–1166

Tabuce R, Asher RJ, Lehmann T (2008) Afrotherian mammals: a review of current data. Mammalia 72:2–14

Tsuki K, Clyde WC (2012) Fine-tuning the caslibration of the early to meddle Eocene geomagnetic polarity time scale: Paleomagnetism of radioisotopically dated tuffs from Laramide foreland basins. Geol Soc Amer Bull 124(5/6):870–885

Vandenberghe N, Hilgen FJ, Speijer RP (2012) The Paleogene Period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (eds) The geologic time scale 2012. Elsevier, Amsterdam

Waddell PJ, Cao Y, Hasegawa M, Mindell DP (1999) Assessing the Cretaceous superordinal divergence times within birds and placental mammals using whole mitochrondrial protein sequences and an extended statistical framework. Syst Biol 48(1):119–137

Westerhold T, Röhl U, Donner B, McCarren H, Zachos J (2009) Latest on the absolute age of the Paleocene-Eocene Thermal Maximum (PETM): new insights from exact stratigraphic position of key ash layers +19 and -17. Earth Planet Sci Let 287:412–419

White TS (2004) A chemostratigraphic and geochemical facies analysis of strata deposited in an Eocene Australo-Antarctic Seaway: is cyclicity evidence for glacioeustacy? Amer Geophys Union Monogr Ser 148, Climate Evolution in the Southern Ocean 153–172

Williamson TE, Carr TD (2007) *Bomburia* and *Ellipsodon* (Mammalia: Mioclaenidae) from the early Paleocene of New Mexico. J Paleontol 81(5):966–985

Willis PMA, Molnar RE, Scanlon JD (1993) An early Eocene crocodilian from Murgon, southeastern Queensland. Kaupia 3:27–33

Wilson DS, Luyendyk BP (2009) West Antarctic paleotopography estimated at the Eocene-Oligocene climate transition. Geophys Res Let 36. doi:10.1029/2009GL039297

Wolfe JA (1978) A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. Amer Scient 66:694–703

Woodburne MO (2004) Definition. In: Woodburne MO (ed) Late Cretaceous and Cenozoic Mammals of North America: biostratigraphy and geochronology. Columbia University Press, New York

Woodburne MO (2010) The Great American Biotic Interchange; dispersals, tectonics, climate, sea level and holding pens. J Mamm Evol 17:245–264

Woodburne MO, Case JA (1996) Dispersal, vicariance and the late Cretaceous to early Tertiary land mammal biogeography from South America to Australia. J Mamm Evol 3(2):121–161

Woodburne MO, Gunnell GF, Stucky RK (2009a) Climate directly influences Eocene mammal faunal dynamics in North America. PNAS 106(32):13399–13403

Woodburne MO, Gunnell GF, Stucky RK (2009b) Land mammal faunas of North America rise and fall during the Early Eocene Climatic Optimum. Denver Mus Nat Sci Ann 1:1–75

Woodburne MO, Goin FJ, Bond M, Carlini A A, Gelfo JN, López GM, Iglesias A, Zimicz, AN (2014) Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. J Mamm Evol. doi 10.1007/s10914-012-9222-1

Wroe S, Archer M (2006) Origins and early radiations of marsupials. In: Merrick J, Archer M, Hickey GM, Lee MSY (eds) Evolution and Biogeography of Australasian Vertebrates. Australian Scientific Publishing, Sydney

Zachos J, Pagani M, Sloan L, Thomas E, Billip K (2001) Trends, rhythms, and aberrations in global climate, 65 Ma to present. Science 292(5517):686–693

Zachos JC, Dickens GR, Zeebe RE (2008) An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 45:279–283

Zack SP, Penkrot TA, Bloch JI, Rose KD (2005) Affinities of ‘hyopsodontids’ to elephant shrews and a Holarctic origin of Afrotheria. Nature 434:497–501

Zimicz AN (2012) Ecomorfología de los marsupiales paleógenos de América del Sur. Unpublished PhD. thesis, Universidad Nacional La Plata

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

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8_4

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.

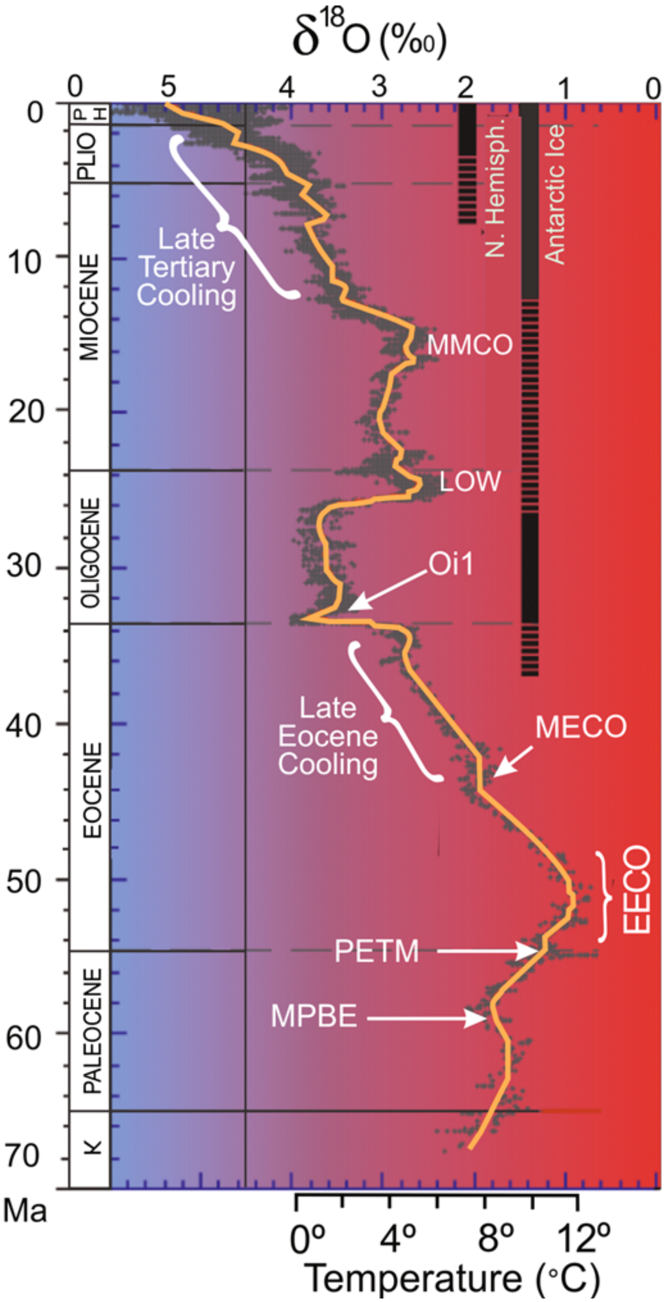
4.1 Climate

During the Cenozoic Era global climates shifted from Grenhouse 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 Gallager 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


δ18O (‰)
0
5
4
3
2
1
0
0
10
20
30
40
50
60
70
Ma
P
H
PLIO
MIOCENE
OLIGOCENE
EOCENE
PALEOCENE
K
Late Tertiary Cooling
N. Hemisph.
Antarctic Ice
MMCO
LOW
Oi1
Late Eocene Cooling
MECO
EECO
PETM
MPBE
0°
4°
8°
12°
Temperature (°C)

◀ **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). $\Delta^{18}O$ 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 pÃ¡ramo. 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

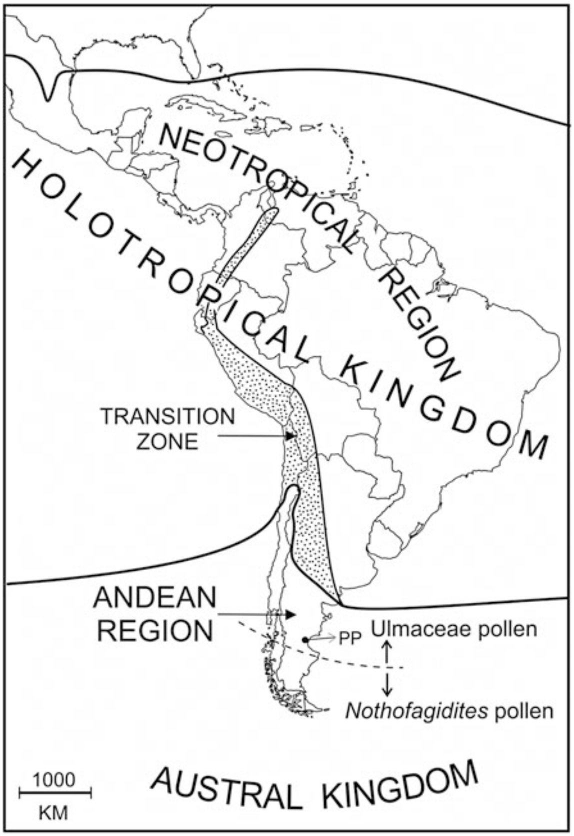


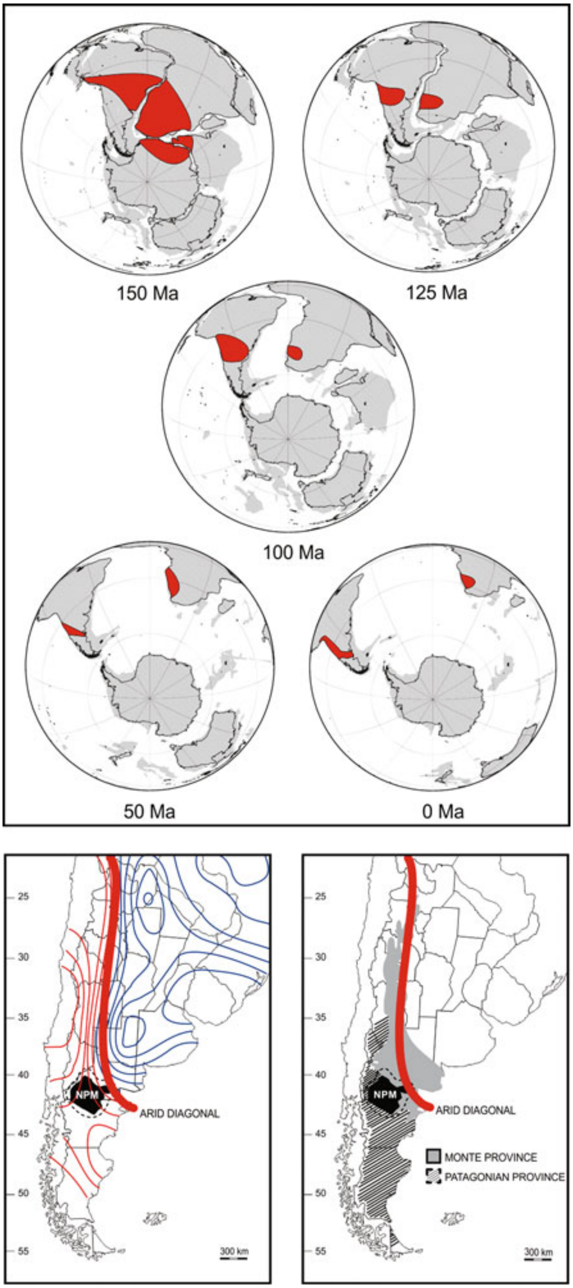
Fig. 4.2 Central and South American biogeography. The map shows the biogeographic boundary between the Andean Region of the Austral Kingdom (south), and the Neotropical Region of the Holotropical Kingdom (north). The dotted area represents the Transition Zone sensu Morrone (2006). The dashed line in 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 Afrotemperate Region), eastern and southern Australia (Australotemperate 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 Karroo 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.


150 Ma
125 Ma
100 Ma
50 Ma
0 Ma
25
30
35
40
45
50
55
NPM
ARID DIAGONAL
300 km
25
30
35
40
45
50
55
NPM
ARID DIAGONAL
MONTE PROVINCE
PATAGONIAN PROVINCE
300 km

◀ **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, rougly 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 southeastern 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., Ringuelet 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 ingressions 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-Nágera 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 Fueguian 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 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).

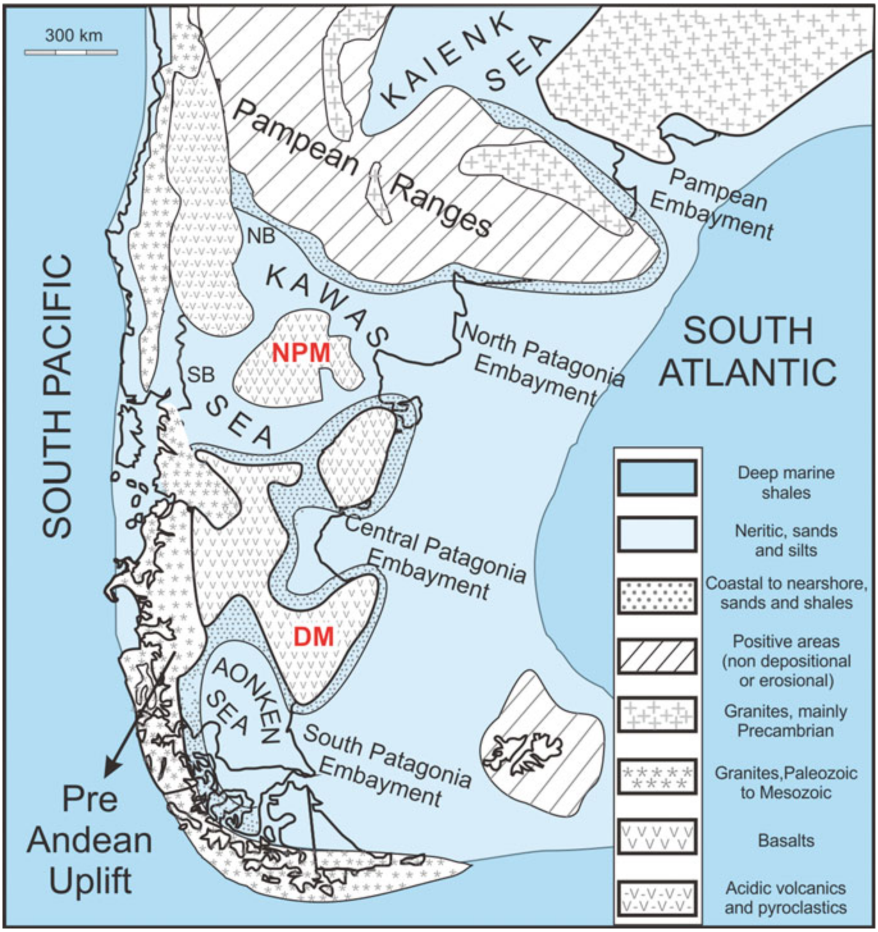


Fig. 4.4 Paleogeography of southern South America during the Late Cretaceous (Maastrichtian) – early Paleocene (Danian). *Abbreviations* DM, Deseado Massif; NB, northern branch; NPM, North Patagonian Massif; SB, southern branch. The name of Kawas Sea follows Casamiquela (1979); names of the Kaienk and 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., mesungulatids, 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 Alamitan 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 (Tiupampan, 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.

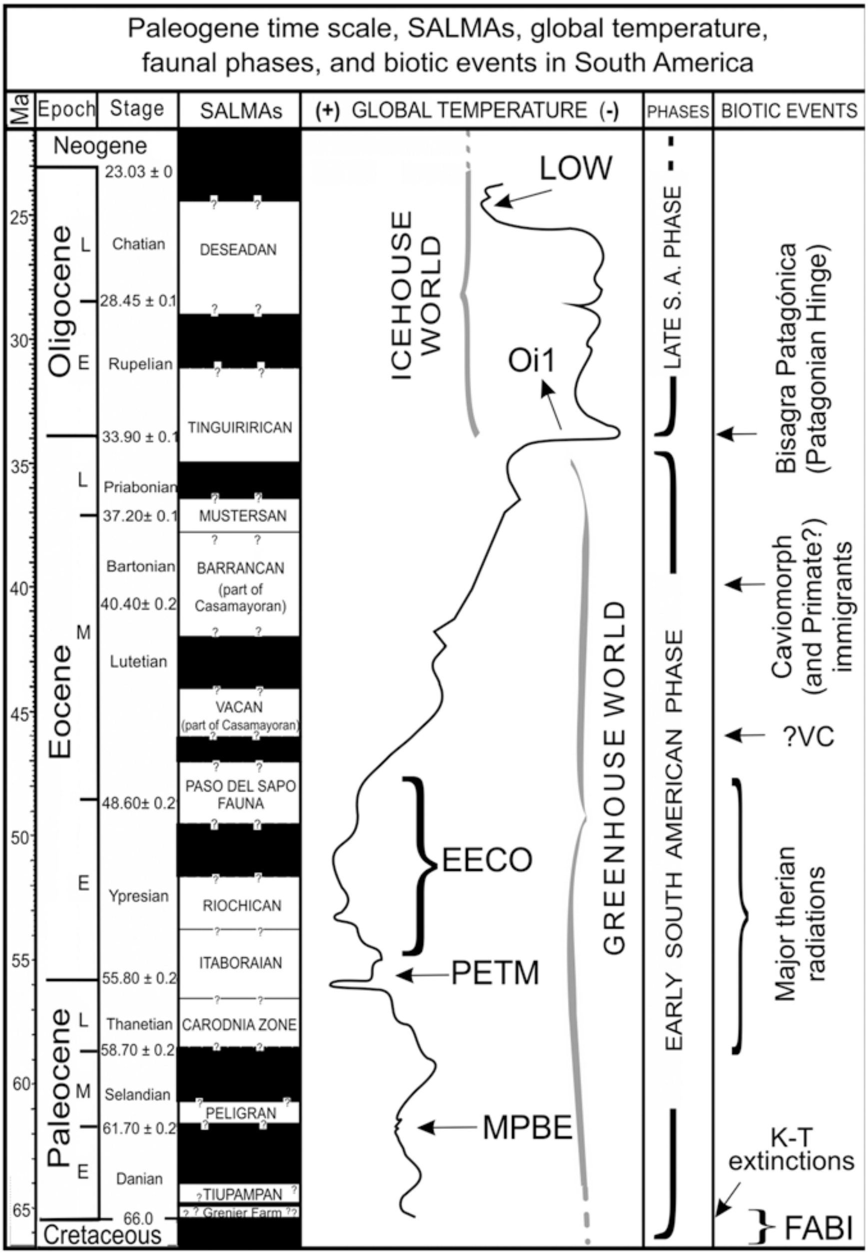


Fig. 4.5 Paleogene time scale, South American land-mammal ages (SALMAs), global temperatures, and biotic events. For most abbreviations, see legend to Fig. 4.1. Other *abbreviations* FABI, First American Biotic Interchange; K-T, Cretaceous-Tertiary; Ma, Megannum; ?VC, "Vacan Crash?" (see Chap. 7)

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 Palaeothentoid 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:

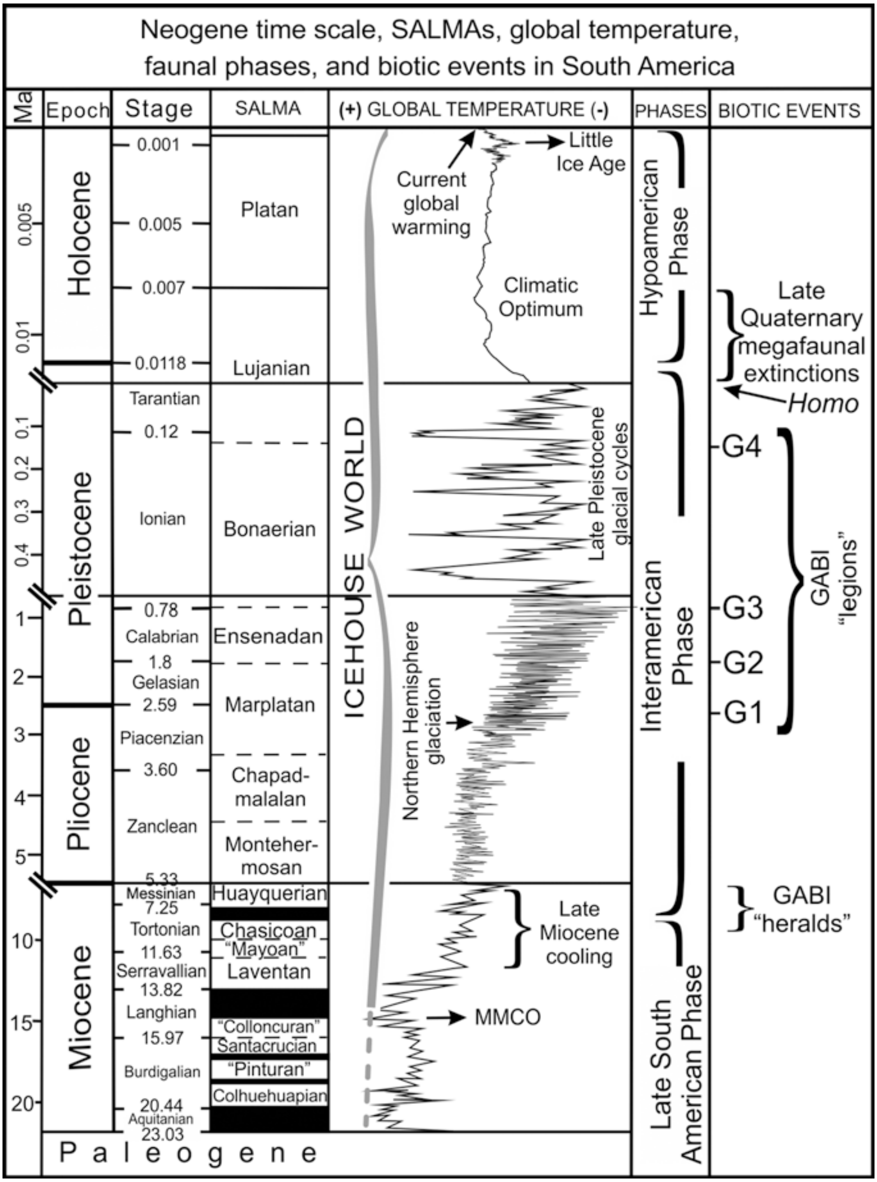


Fig. 4.6 Neogene time scale, South American land-mammal ages (SALMAs), global temperatures, and biotic events. For most abbreviations, see legend to Fig. 4.1. Other *abbreviations* GABI, Great American Biotic Interchange; G1, G2, G3, G4, mayor dispersal events within GABI (see Woodburne 2010); Ma, Meganumm. 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	*Lestodelphys halli*	*Thylamys* sp.	*Monodelphis* sp.	*Monodelphis dimidiata*	*Lutreolina crassicaudata*	*Didelphis* 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 referrable to the living species *T. pallidior*. Modified after Goin (2006: Table 6)

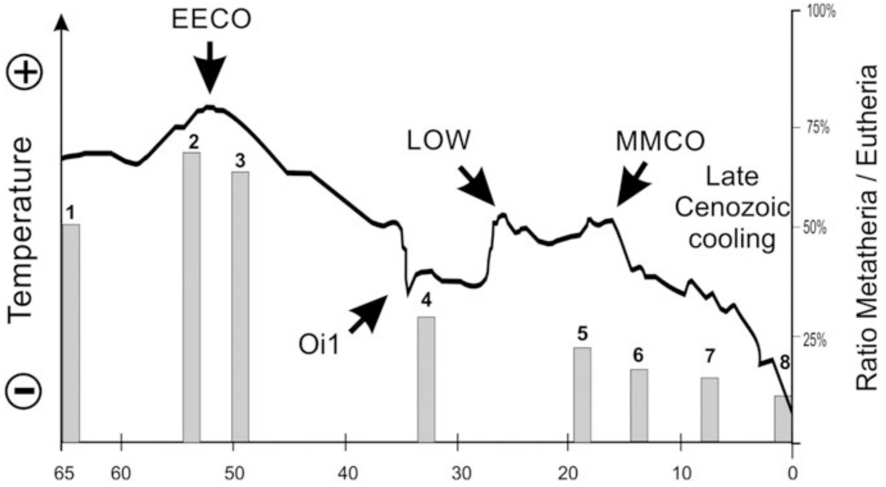


Fig. 4.7 Relative diversity of the South American metatherians throughout the Cenozoic. Columns represent the percentage of metatherian species in relation to the whole terrestrial mammalian faunas in selected SALMAs/faunas. The curve (from Zachos et al. 2001) indicates global surface temperatures for 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 Tinguiririćan and into the Deseadan . That is, the group peaks subsequent to the EECO, and continues in diversity until the Tinguiririćan. 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 (Oi1 event). Among many South American mammals, this event is clearly exposed in Tinguiririćan 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 *Grand 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).

References

Antoine P-O, Marivaux L, Croft DA, Billet G, Ganerød M, Jaramillo C, Martin T, Orliac MJ, Tejada J, Altamirano AJ, Duranthon F, Fanjat G, Rousse S, Salas Gismondi R (2011) Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. Proc R Soc B 279:1319–1326

Aragón E, Goin FJ, Aguilera YE, Woodburne MO, Carlini AA, Roggiero MF (2011) Paleogeography and paleoenvironments of northern Patagonia from the late cretaceous to the miocene: the paleogene andean gap and the rise of the Northern Patagonian High Plateau (NPHP). Biol J Linn Soc 103:305–315

Artabe AE, Morel EM, Spaletti LA (2003) Caracterización de las provincias fitogeográficas triásicas del Gondwana extratropical. Ameghiniana 40(3):387–406

Barreda V, Palazzesi L (2007) Patagonian vegetation turnovers during the Paleocene-Early Neogene: origin of arid-adapted floras. Bot Rev 73(1):31–50

Barros V (2008) Tendencias y cambio climático en la Argentina. APRESID, Rosario, 8 pp (Unpublished report)

Barros V, Clarke R, Silva Dias P (eds) (2006) El cambio climático en la Cuenca del Plata. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires

Bartoli G, Sarnthein M, Weinelt M, Erlenkeuser H, Garbe-Schönberg D, Lea DW (2005) Final closure of Panama and the onset of Northern hemisphere glaciation. Earth Planet Sci Let 237:33–44

Bernaola G, Baceta JI, Orue-Etxebarria X, Alegret L, Martín-Rubio M, Arosteguji J, Dinarès-Turell J (2007) Evidence of an abrupt environmental disruption during the mid-Paleocene biotic event (Zumaia section, western Pyrenees). Bull Geol Soc Amer 119 (7/8):785–795

Campbell KE Jr, Prothero DR, Romero-Pittman L, Hertel F, Rivera N (2010) Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. J South Amer Earth Sci 26:619–626

Casamiquela RM (1961) Sobre la presencia de un mamífero en el primer elenco (icnológico) de vertebrados de Latinoamérica (Noticia). Physis 22(63):225–233

Casamiquela RM (1979) La zona litoral de la transgresión maastrichtense en el norte de la Patagonia. Aspectos ecológicos. Ameghiniana 15:137–148

Case JA, Goin FJ, Woodburne MO (2005) “South American” marsupials from the late cretaceous of North America and the origin of marsupial cohorts. J Mammal Evol 12:461–494

Cione AL, Tonni EP, Soibelzon LH (2003) The broken zig-zag: late Cenozoic large mammal and turtle extinction in South America. Rev Mus Arg Cs Nat B Rivadavia 5:1–19

Cione Al, Tonni EP, Soibelzon L (2009) Did humans cause the Late Pleistocene-Early holocene mammalian extinctions in South America in a context of shrinking open areas? In: Haynes G (ed) American Megafaunal extinctions at the end of the Pleistocene. Springer, Dordrecht

Condie KC (1982) Plate tectonics and crustal evolution. Pergamon Press, New York

Cox CB (2001) The biogeographic regions reconsidered. J Biogeogr 28:511–523

Croft DA (2012) Punctuated isolation: the making and mixing of South America’s mammals. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: an 80-million year history of recent neotropical mammals. Univ Chicago Press, Chicago

Crowley CW (2012) An atlas of cenozoic climate zones. PhD thesis, University of Texas

de Oliveira FP, Cassola Molina E, Marroig G (2009) Paleogeography of the South Atlantic: a route for primates and rodents into the new world? In: Garber P et al (eds) South American primates. Springer, Dordretch

de Saint Pierre M, Bravi CM, Motti JMB, Fuku N, Tanaka M et al (2012) An alternative model for the early peopling of southern south america revealed by analyses of three mitochondrial DNA haplogroups. PLoS ONE 7(9):e43486. doi:10.1371/journal.pone.0043486

De Valais S (2009) “Ichnotaxonomic revision of Ameghinichnus, a mammalian Ichnogenus from the Middle Jurassic La Matilde Formation, Santa Cruz Province, Argentina. Zootaxa 2203:1–21

Ezcurra E, Mellink E, Wehncke E, González C, Morrison S, Warren A, Dent D, Driessen P (2006) Natural history and evolution of the world's deserts. In: Ezcurra E (ed) Global deserts outlook. United Nations Environment Programme (UNEP), Nairobi

Flynn JJ, Wyss AR, Croft DA, Charrier R (2003) The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal 'Age'. Palaeogeogr Palaeoclimatol Palaeoecol 195:229–259

Forasiepi AM (2009) Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. Monogr Mus Arg Cs Nat B Rivadavia NS 6:1–174

Gallagher SJ, Wagstaff BE, Baird JG, Wallace MW, Li CL (2008) Southern high latitude climate variability in the late cretaceous greenhouse world. Global Planet Change 60:351–364

Goin FJ (1997) New clues for understanding Neogene Marsupial radiations. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) A history of the neotropical fauna. Vertebrate paleobiology of the miocene in Colombia. Smithsonian Institution Press, Washington

Goin FJ (2001) Marsupiales (Didelphidae: Marmosinae & Didelphinae). In Mazzanti D, Quintana C (eds) Cueva Tixi: Cazadores y recolectores de las Sierras de Tandilia Oriental. 1: Geología, Paleontología y Zooarqueología. Lab Arqueol, Univ Nac Mar del Plata, Publ Esp 1, Mar del Plata

Goin FJ (2006) A review of the Caroloameghiniidae, Paleogene South American "primate-like" marsupials (?Didelphimorphia, Peradectoidea). In: Kalthoff D, Martin T, Möors T (eds) Festband für Herrn Professor Wighart v. Koenigswald anlässlich seines 65. Palaeontographica Abteilung A, vol 278. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp 57–67

Goin FJ, Abello MA (2013) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, edad mamífero Colhuehuapense): Microbiotheria y Polydolopimorphia. Ameghiniana 50(1):51–78

Goin FJ, Pardiñas U (1996) Revisión de las especies del Género *Hyperdidelphys* Ameghino, 1904 (Mammalia, Marsupialia, Didelphidae). Su significación filogenética, estratigráfica y adaptativa en el Neógeno del Cono Sur Sudamericano. Est Geol 52:327–359

Goin FJ, Montalvo C, Visconti G (2000) Los Marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (Provincia de La Pampa, Argentina). Rev Esp Geol 56:101–126

Goin FJ, Abello MA, Bellosi E, Kay RF, Madden R, Carlini AA (2007) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, Edad-mamífero Colhuehuapense). Parte 1: Introducción, Didelphimorphia y Sparassodonta. Ameghiniana 44 (1):29–71

Goin FJ, Abello MA, Chornogubsky L (2010) Middle tertiary marsupials from central patagonia (early Oligocene of Gran Barranca): understanding South America's Grande Coupure. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The Paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York

Goin FJ, Gelfo NF, Chornogubsky L, Woodburne MO, Martin T (2012a) Origins, radiations, and distribution of South American Mammals: from greenhouse to icehouse worlds. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: an 80-million year history of Recent Neotropical mammals. University of Chicago Press, Chicago

Goin FJ, Tejedor MF, Chornogubsky L, López GM, Gelfo JN, Bond M, Woodburne MO, Gurovich Y, Reguero M (2012b) Persistence of a Mesozoic, non-therian mammalian lineage (Gondwanatheria) in the mid-Paleogene of Patagonia. Naturwissenschaften 99:449–463

Goin FJ, Zimicz AN, Forasiepi AM, Chornogubsky LC, Abello MA (in press) The rise and fall of South American Metatherians: contexts, adaptations, radiations, and extinctions. In: Rosenberger AL and Tejedor MF (eds) Origins and evolution of Cenozoic South American Mammals. Springer, Berlin

Graham A (2011) The age and diversification of terrestrial new world ecosystems through cretaceous and cenozoic time. Am J Bot 98(3):336–351

Gregory-Wodzick KM (2000) Uplift history of the Central and Northern Andes: a review. Bull Geol Soc Am 112(7):1091–1105

Heimhofer U, Hochuli PA, Burla S, Dinis JML, Weissert H (2005) Timing of Early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change. Geology 33 (2):141–144

Iglesias A, Wilf P, Johnson KR, Zamuner AB, Cúneo NR et al (2007) A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. Geology 35(10):947–950

Iglesias A, Artabe AE, Morel EM (2011) The evolution of Patagonian climate and vegetation from the Mesozoic to the present. Biol J Linn Soc 103:409–422

IPCC (International Panel on Climate Change) (2008) Cambio climático 2007: informe de síntesis. IPCC, Geneva

Jaramillo C, Rueda MJ, Mora G (2006) Cenozoic Plant Diversity in the Neotropics. Science 311 (5769):1893–1896

Kalin-Arroyo MT, Squeo F, Armesto JJ, Villagrán C (1988) Effects of aridity on plant diversity in the northern chilean Andes: results of a natural experiment. Ann Missouri Bot Garden 75 (1):55–78

Lawver LA, Gahagan LM (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeogr Palaeoclimatol Palaeoecol 198:11–37

Livermore R, Nankivell A, Eagles G, Morris P (2005) Paleogene opening of drake passage. Earth and Planet Sci Lett 236:459–470

Lopretto EC, Menni RC (2003) Raúl Ringuelet: La zoogeografía como síntesis. In Morrone JJ, Llorente Bousquets J (eds) Una perspectiva latinoamericana de la biogeografía, Ed. Las Prensas de Ciencias, UNAM, México

Malumián N, Náñez C (2011) The Late Cretaceous–Cenozoic transgressions in Patagonia and the Fuegian Andes: foraminifera, palaeoecology, and palaeogeography. Biol J Linnean Soc 103:269–288

Marquet PA, Bozinovic F, Bradshaw GA, Cornelius C, Gonzalez H, Gutierrez JR, Hajek ER, Lagos JA, López-Cortés F, Nuñez L, Rosello EF, Santoro C, Samaniego H, Standen VG, Torres-Mura JC, Jaksic FM (1998) Los ecosistemas del desierto de Atacama y área andina adyacente en el norte de Chile. Rev Chilena Hist Nat 71:593–617

Mazzanti D, Quintana C (eds) (2001) Cueva Tixi: Cazadores y recolectores de las Sierras de Tandilia Oriental. 1: Geología, Paleontología y Zooarqueología. Lab Arqueol, Univ Nac Mar del Plata, Publ Esp 1, Mar del Plata

Meng J, McKenna MC (1998) Faunal turnovers of Paleogene mammals from the Mongolian Plateau. Nature 394:364–367

Menni RC (2004) Peces y ambientes en la Argentina continental. Monogr Mus Arg Cs Nat B Rivadavia 5:1–316

Monge-Nájera J (1996) Jurassic-Pliocene biogeography: testing a model with velvet worm (Onychophora) vicariance. Revista de Biología Tropical 44(1):159–175

Moreira-Muñoz A (2007) The Austral floristic realm revisited. J Biogeogr 34:1649–1660

Morgan GR (2008) Vertebrate fauna and geochronology of the Great American Biotic Interchange in North America. In: Lucas SG, Mogan GS, Spielmann JA, Prothero DR (eds) Neogene mammals: Bulletin, vol 44. New Mexico Museum of Natural History and Science ,pp 93–140

Morrone JJ (2002) Biogeographical regions under track and cladistic scrutiny. J Biogeogr 29: 149–152

Morrone JJ (2004a) Panbiogeografía, componentes bióticos y zonas de transición. Rev Bras Entomol 48(2):149–162

Morrone JJ (2004b) La Zona de Transición sudamericana: caracterización y relevancia evolutiva. Rev Entomol Chilena 28(1):41–50

Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. Ann Rev Entomol 51:467–494

Oliveira EV (1998) Taxonomia, filogenia e paleobiogeografia de marsupiais “poliprotodontes” do Mesopaleoceno da Bacia de Itaboraí, Rio de Janeiro, Brasil. Ph.D. thesis, Univ Fed Rio Grande do Sul

Oliveira EV, Goin FJ (2011) A reassesment of bunodont metatherians from the Paleogene of Itaboraí (Brazil): systematics and age of the Itaboraian SALMA. Rev Bras Paleontol 14 (2):105–136

Parrish JT (1993) Climate of the supercontinent Pangea. J Geol 101:215–233

Pascual R (2006) Evolution and geography: the biogeographic history of South American land mammals. Ann Missouri Bot Garden 93(2):209–230

Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast A, Erk FC, Glass B (eds) Evolution of mammals and Southern Continents. State Univ New York Press, Albany

Poux C, Chevret P, Huchon D, De Jong WW, Douzery EJP (2006) Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. Syst Biol 55(2):228–244

Quattrocchio ME (2006) Palynology and palaeocommunities of the Paleogene of Argentina. Rev Bras Paleontol 9:101–108

Quattrocchio ME (2009) Paleogene dinoflagellate cysts from Punta Prat, southern Chile. Palynology 33:141–156

Quattrocchio ME, Volkheimer W (2000) Danian microfloral provinces in Argentina. Rev Esp Paleontol 15(1):3–11

Quattrocchio ME, Sarjeant WAS, Volkheimer W (1996) Marine and terrestrial jurassic microfloras of the Neuquén Basin (Argentina): palynological zoonation. Geo Research Forum 1–2:167–178

Quattrocchio ME, Volkheimer W, Marquillas RA, Salfity JA (2005) Palynostratigraphic, palaeobiogeographic and evolutionary significance of the Late Senonian and Early Paleogene floras of northern Argentina”. Rev Esp Micropaleontol 37:259–272

Quattrocchio ME, Volkheimer W, Borromei AM, Martínez MA (2011) Changes of the palynobiotas in the Mesozoic and Cenozoic of Patagonia: a review. Biol J Linn Soc 103:380–396

Quiroga MP (2010) Comparación entre el bosque templado austral y el bosque tucumano-boliviano considerando géneros con especies de hábito arbóreo. Gayana Bot 67 (2):176–187

Rees PM, Ziegler AM, Valdes PJ (2000) Jurassic phytogeography and climates: new data and model comparisons. In: Huber BT, MacLeod KG, Wing SL (eds) Warm climates in earth history. Cambridge Univ Press, Cambridge

Ringuelet RA (1955) Vinculaciones faunísticas de la zona boscosa del Nahuel Huapi y el dominio zoogeográfico Australcordillerano. Notas Mus La Plata 18(160):21–121

Ringuelet RA (1961) Rasgos fundamentales de la zoogeografía de la Argentina. Physis 22:151–170

Roig FA, Roig-Juñent S, Corbalán V (2009) Biogeography of the monte desert. J Arid Envir 73:164–172

Ruban DA (2012) Mesozoic mass extinctions and angiosperm radiation: does the molecular clock tell something new? Geology 18(1):37–42

Ruiz LE (2006) Estudio sedimetológico y estratigráfico de las formaciones Paso del Sapo y Lefipán en el valle medio del Río Chubut. Lic. Thesis, Univ Buenos Aires

Scotese CR, Boucot AJ, McKerrow MS (1999) Gondwanan palaeogeography and palaeoclimatology. J Afr Earth Sci 28:99–114

Sluijs A, Brinkhuis H, Crouch EM, John CM, Handley L, Munsterman D, Bohaty SM, Zachos JC, Reichart G-J, Schouten S, Pancost RD, Sinninghe Damsté JS, Welters NLD, Lotter AF, Dickens GR (2008) Eustatic variations during the Paleocene-Eocene greenhouse world. Paleoceanograph 23 PA4216. doi:10.1029/2008PA001615

Sluijs A, Bijl PK, Schouten S, Röhl U, Reichart J-G, Brinkhuis H (2011) Southern ocean warming, sea level and hydrological change during the Paleocene-Eocene thermal máximum. Clim Past 7:47–61

Stehlin HG (1909) Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Basin de Paris. Bull Soc Géol France 9:488–520

Tapponnier P, Zhiqin X, Roger F, Meyer B, Arnaud N, Wittlinger G, Jingsui Y (2001) Oblique stepwise rise and growth of the tibet plateau. Science 294:1671–1677

Uliana MA, Biddle KT (1988) Mesozoic-Cenozoic paleogeographic and geodynamic evolution of southern South America. Rev Bras Geociencias 18:172–190

Urien CM, Zambrano JJ, Yrigoyen MR (1995) Petroleum basins of southern South America: an overview. In: Tankard AJ, Suárez SR, Welsink HJ (eds). Petroleum basins of South America, vol 62. American Association of Petroleum Geologists Memorial, pp 63–77

Vargas G, Ortlieb L (1998) Patrones de variaciones climáticas durante el Cuaternario tardío en la costa de la región de Antofagasta Chile. Bull Inst Francais d'Etudes Andines 27(3):385–394

Villagrán C, Armesto JJ (2005) Fitogeografía histórica de la Cordillera de la Costa de Chile. In: Smith-Ramírez C, J Armesto y C Valdovinos (eds) Historia, biodiversidad y ecología de los bosques costeros de Chile. Ed. Universitaria, Santiago

Villagrán C, Hinojosa LF (2005) Esquema Biogeográfico de Chile. In: Llorente Bousquets J, Morrone JJ (eds) Regionalización Biogeográfica en Iberoamérica y tópicos afines. Eds UNAM, Jiménez Editores, México

Webb SD (1976) Mammalian faunal dynamicso f the Great American Interchange. Palaeobiol 2:216–234

Webb SD (1985) Late Cenozoic mammal dispersals between the Americas. In: Stehli FD, Webb SD (eds) The great American biotic interchange, topics in geobiology, vol 4. Plenum Press, New York

Webb SD (2006) The great American biotic interchange: patterns and processes. Ann Missouri Bot Garden 93:245–257

Wilf P, Cúneo NR, Johnson KR, Hicks JF, Wing SL, Obradovich JD (2003) High plant diversity in Eocene South America: evidence from Patagonia. Science 300:122–125

Wilf P, Johnson KR, Cúneo NR, Smith ME, Singer BS, Gandolfo MA (2005) Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. Amer Nat 165 (6):634–650

Wilf P, Cúneo R, Escapa I, Pol D, Woodburne MO (2013) Splendid and Seldom Isolated: the paleobiogeography of Patagonia. Ann Rev Earth and Planetary Sci 41:561–603

Wilson GP, Arens N (2001) The evolutionary impact of an epeiric seaway on Late Cretaceous and paleocene palynofloras of South America. In: 7th International Symposium on Mesozoic Terrestrial Ecosystems. Special Publ 7, Asociación Paleontológica Argentina, Buenos Aires

Woodburne MO (2010) The great American biotic interchange: dispersals, tectonics, climate, sea level and holding pens. J Mammal Evol 17:245–264

Woodburne MO, Cione AL, Tonni EP (2006) Central American provincialism and the Great American Biotic Interchange. In: Carranza-Castañeda O, Lindsay EH (eds) Advances in late tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange, vol 4. Inst de Geol y Centro de Geociencias, UNAM, Publ Esp, pp 73–101

Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN et al (2014) Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. J Mammal Evol 21:1–73

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292(5517):686–693

Chapter 5
Phylogeny and Diversity of South American Metatherians

Abstract The Metatheria include not only marsupials but all therians more related to Marsupialia than to the Eutheria. Marsupialia is considered as a metatherian crown group including all extant marsupials, their common ancestor and all of their descendants. "Ameridelphia" is not a natural group. Australidelphia includes the Microbiotheria and all Australasian marsupials. Several authors also argue that the Polydolopimorphia are Australidelphians as well. Relationships of Sparassodonta with other Metatheria are a matter of discussion. To several authors, they are more closely related to South American and Australian groups than to basal North American and/or Asian metatherians. Our concept of Didelphimorphia includes the Peradectoidea (Peradectidae and Caroloameghiniidae) and the Didelphoidea (Didelphidae and Sparassocynidae). In several analyses, the Paucituberculata appear as more closely related to the Australidelphia than to the Didelphimorphia. The relationships of the Microbiotheria within the Australidelphia have been subject of much discussion. They have been considered either as sister-taxa of all other Australidelphia, at the base of Diprotodontia, as a sister-taxon of Dasyuromorpha, as a sister-taxon of Phalangeriformes + Diprotodontia, or even related with part of the former.

Keywords Metatheria · Marsupialia · Ameridelphia · Australidelphia · Sparassodonta · Didelphimorphia · Paucituberculata · Microbiotheria · Polydolopimorphia

5.1 Metatherian Phylogenetic Analyses

After its first recognition as a group (Illiger 1811), relationships among living marsupials and their extinct relatives have been largely discussed based on different structures, such as bones (e.g., Szalay 1982), bones and teeth (e.g., Marshall et al. 1990), blood serum (e.g., Kirsch 1977), and genes (e.g., Nilsson et al. 2004, 2010), among other sources. Since Rowe (1988), Marsupialia is conventionally considered

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8_5

a crown group including all extant marsupials, their common ancestor and all of their descendants. Following Rowe, Rougier et al. (1998) defined Metatheria as the group including not only Marsupialia but therians more related to Marsupialia than to Eutheria (Rougier et al. 1998), having Metatheria and Eutheria a sister-group relationship (Kielan-Jaworowska et al. 2004). In the last decades, phylogenetic cladistic analyses have progressively become dominant in elucidating metatherian affiliations and classification, being the earlier studies those carried out by the late seventies and early eighties of the last century (e.g., Marshall 1977a; Archer 1982; Sharman 1982).

Among phylogenetic analyses, a broad division can be made between morphological and molecular analyses. Morphological studies have been carried out using craneodentary (e.g., Rougier et al. 1998), dentary (e.g., Goin et al. 2009; Oliveira and Goin 2011; Vullo et al. 2009; Williamson et al. 2012), basicranial (e.g., Ladevèze 2004, 2007), postcranial (Flores 2009), or complete osteological characters (e.g., Sánchez-Villagra 2001; Luo et al. 2003; Horovitz and Sánchez-Villagra 2003; Horovitz et al. 2009; Beck 2008, 2012; Forasiepi 2009). Some specific sets of morphological characters (e.g., the internal nasal skeleton; Macrini 2012) have been used in the testing of previous phylogenetic hypotheses. Molecular phylogenetic analyses use either nuclear (e.g., IRBP, BRCA1, APOb, RAG1, Vwf genes; Amrine-Madsen et al. 2003; Protamine P1, Retief et al. 1995) or mitochondrial DNA (e.g., 12S rRNA, 16S rRNA, tRNA valine; Burk et al. 1999; complete mitochondrial DNA, Nilsson et al. 2003), although some combine the two types of DNA (e.g., Phillips et al. 2006). Some analyses include both morphological and molecular data (e.g., Voss and Jansa 2003, 2009; Jansa and Voss 2005; Flores 2009). Cardillo et al. (2004) state that 158 phylogenetic studies have been published since 1980, which include all or some metatherian lineages.

5.1.1 Relationships Among South American Metatherians

Even though the eutherian-metatherian divergence can be traced back to the Late Jurassic (Luo et al. 2011), the oldest record of a metatherian corresponds to early Cretaceous times: *Sinodelphys szalayi*, from the Barremian of China (Luo et al. 2003). Additional, Cretaceous metatherians have been only recovered from northern continents, mainly from Asia and North America (e.g., Rougier et al. 1998; Luo et al. 2003; Williamson et al. 2012; but see Vullo et al. 2009). Metatherians from the Cretaceous of Asia usually appear either as a distinct group (e.g., Rougier et al. 1998; Beck 2008) or as part of the stem Metatheria (Luo et al. 2003; Horovitz et al. 2009; Beck 2012) along with most North American taxa (e.g., *Holoclemensia, Atokatheridium, Turgidodon, Didelphodon* ; Luo et al. 2003). However, some Cretaceous metatherians from North America, like *Pediomys*, *Glasbius*, and *Ectocentrocristus* have been related to a number of South American groups (e.g., Reig et al. 1985, 1987; Goin et al. 2009; Ladevèze and Muizon 2010; see a more recent review in Williamson et al. 2012, 2014).

When he first recognized the group Australidelphia, Szalay (1982) also acknowledged the "**Ameridelphia**". This group included North and South American metatherians (excluding *Dromiciops*). Subsequent analyses have demonstrated that this is not a natural group (e.g., Rougier et al. 1998; Forasiepi 2009; Ladevèze and Muizon 2010). Other conflictive ordinal group is the Didelphimorphia , which has variously included a number of different lineages of American metatherians, such as didelphids and sparassodonts (e.g., Kirsch 1977) or "… generalized metatherians with a didelphid-like dentition , which form a paraphyletic assemblage stem to the Australidelphia lineage (i.e., pucadelphyids, protodidelphids, didelphids, Types I, III, IV, VI, VII, *Derorhynchus* , *Carolopaulacoutoia*, and *Gaylordia*)." (Ladevèze and Muizon 2010: 759). Horovitz et al. (2009) defined the Didelphimorphia as the natural group comprising the Peradectidae and the Didelphidae . However, more recently the monophyly of the Peradectidae has been put into question (Williamson et al. 2012).

The most ancient South American "ameridelphians" are recorded from the Tiupampa locality (early Paleocene, Bolivia). Even though several species were recognized from this locality, only three are well represented by craniodental remains: *Pucadelphys andinus, Andinodelphys cochabambensis,* and *Mayulestes ferox* (Fig. 5.1). These species have been included in several analyses and they are usually stem to the marsupial radiation (e.g., Luo et al. 2003). In most analyses, *Andinodelphys* and *Pucadelphys* appear as sister-taxa (the Pucadelphyidae; Ladevèze and Muizon 2010; but see Rougier et al. 1998). *Mayulestes* is often recovered at the base of the cladogram. Even though *Mayulestes* was originally interpreted as related to the Sparassodonta (e.g., Muizon 1998) in more recent analyses it has been related to the pucadelphyids (e.g., Horovitz and Sánchez-Villagra 2003; Horovitz et al. 2009; Forasiepi 2009; Ladevèze and Muizon 2007).

Even though they have been matter of discussion for decades, other (non-Tiupampian) Paleogene marsupials from southern South America do not usually form part of phylogenetic analyses, mainly because they are represented by scarce materials. Only a few analyses included several Itaboraian taxa from Brazil (Ladevèze and Muizon 2010; Oliveira and Goin 2011) and a few taxa from Argentina (Goin et al. 2009). Due to differences in taxa selection, these analyses are difficult to compare and offer quite dissimilar results. Ladevèze and Muizon (2010) included some Asian, Australian, and American taxa (the latter particularly from Bolivia and Brazil). They found that metatherians from Itaboraí are represented by different monophyletic clades: (1) *Epidolops*, *Gaylordia*, *Carolopaulacoutoia*, and *Derorhynchus* are part of the stem Australidelphia; (2) Protodidelphidae is the sister-taxon of Didelphidae; (3) *Guggenheimia* + *Mirandatherium* is the sister-clade of Marsupialia; (4) Pucadelphidae is the sister-taxon of all the clade represented in (3); (5) Boreometatheria is represented by *Bobbschaefferia*, *Pediomys*, *Didelphodon* , and *Eobrasilia* and they are related to the former. On the other hand, Oliveira and Goin (2011), in an analysis were they include almost exclusively Itaboraian taxa, found different relationships: (1) *Mirandatherium* + *Microbiotherium* + *Khasia* form a monophyletic group; (2) the group in (1) is the sister of Polydolopimorphia

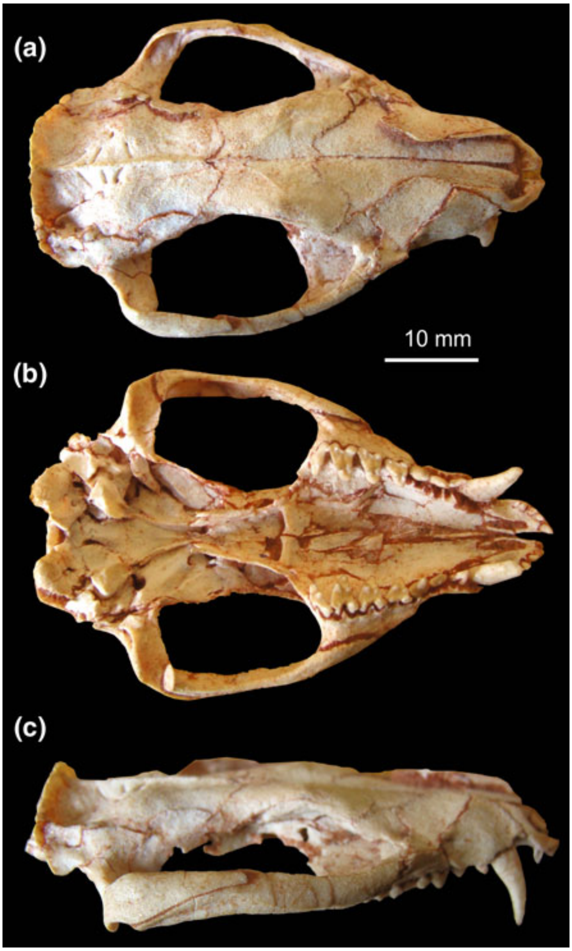


Fig. 5.1 *Mayulestes ferox* ("Ameridelphia," Mayulestidae); specimen MHNC (Museo de Historia Natural de Cochabamba, Bolivia) n° 1249 (type), almost complete skull in dorsal **a**, palatal **b** and lateral (**c** right side) views. (Specimen MHNC 1249 also includes both dentaries and a fairly complete postcranial skeleton). Scale: 10 mm. Total skull length is around 53 mm (see Muizon 1998). Early Paleocene (Tiupampian SALMA). Photographs by Laura Chornogubsky

(in this case *Epidolops* + *Gashternia* + *Roberthoffstetteria* + *Bobbschaefferia*); (3) Protodidelphidae is the sister-taxon from Didelphidae + remaining marsupials of Itaboraí. Finally, Goin et al. (2009) analyzed the relationship among several South American "pseudodiprotodont" taxa and they found two major groups: (1) Polydolopimorphia + *Glasbius* + *Microbiotherium*; and (2) Paucituberculata + *Derorhynchus* + *Pucadelphys*. Among polydolopimorphians, the Bonapartheriiformes includes the Argyrolagidae (*Proargyrolagus* + *Klohnia* in that analysis) *contra* Sánchez-Villagra (2001) who had previously regarded *Argyrolagus* as belonging to the Paucituberculata. Goin et al. (2009) suggested that Polydolopimorphia could be regarded as part of the Australidelphia.

Sparassodonta has been recovered as a natural group in many phylogenetic analyses (e.g., Forasiepi 2009; Forasiepi et al. 2014, among the most recent ones). Their relationships with other Metatheria are, however, a matter of discussion. To several authors, they are more closely related to South American and Australian groups than to basal North American and Asian metatherians (Rougier et al. 1998). In several analyses, Sparassodonta is either placed basally as part of the stem Metatheria, being *Pucadelphys* and *Andinodelphys* most closely related to Marsupialia (represented by *Patene* in Ladevèze and Muizon 2010), or as a sister-taxon of Herpethoteriids + Marsupialia (Forasiepi 2009). Muizon (1999) considered *Mayulestes* as basal to the Borhyaenoidea radiation, a hypothesis not followed subsequently.

Our concept of **Didelphimorphia** includes the Peradectoidea (Peradectidae and Caroloameghiniidae; see Horovitz et al. 2009; Goin 2006) and the Didelphoidea (Didelphidae and Sparassocynidae; Forasiepi et al. 2009 and literature cited). In the last years, a series of broad analyses have been carried out including living didelphids, some of them including molecular plus osteological structures (e.g., Flores 2009) or molecular, osteological and soft tissue structures (Jansa and Voss 2000, 2005; Voss and Jansa 2003, 2009; Jansa et al. 2006). All these works agree on the relationships among the four didelphid subfamilies (Didelphinae, Hyladelphinae, Caluromyinae, and Glironiinae): Didelphinae is the sister-taxon of Hyladelphinae; this clade is more related to the Caluromyinae, while Glironiinae is related to the latter (Voss and Jansa 2009; Flores 2009). Differences in the inferred relationships exist however among the tribes of Didelphinae. Voss and Jansa (2009) included the Didelphini , Marmosini, Metachirini, and Thylamini, an arrangement followed here (Table 5.1).

One South American group that has been variously related with the Australasian radiation is the **Paucituberculata**. The relationships of Paucituberculata, represented in most phylogenetic analyses by the living South American marsupial *Caenolestes* (but see Goin et al. 2009; Abello 2013, for a more complete representation of the group), is also variable, although in several analyses the group appear as more closely related to the Australidelphia (including *Dromiciops*; e.g., Nilsson et al. 2004, 2010; Ladevèze 2004; Ladevèze and Muizon 2007) than to the Didelphimorphia (Burk et al. 1999). Recent phylogenetic analyses support the existence of two main groups within the Paucituberculata: Caenolestoidea (including Caenolestidae) and Palaeothentoidea (including Pichipilidae, Palaeothentidae, and Abderitidae; Abello 2007, 2013; Goin et al. 2009).

Microbiotheria. Szalay's (1982) initial hypothesis of *Dromiciops* (and, consequently, all the Microbiotheria) being more closely related to Australian marsupials than to South American lineages has been repeatedly confirmed by a variety of phylogenetic analyses (see Reig et al. 1987 for a different point of view). Many studies have considered and/or tested the position of Microbiotheria either as sister-group of all other australidelphians or as a group nested within them (see, e.g., Aplin and Archer 1987; Reig et al. 1987; Marshall 1987; Marshall et al. 1990;

Kirsch et al. 1991, 1997; Luckett 1994; Szalay 1994; Springer et al. 1998; Burk et al. 1999; Colgan 1999; Palma and Spotorno 1999; Szalay and Sargis 2001; Phillips et al. 2001, 2006; Amrine-Madsen et al. 2003; Luo et al. 2003; Horovitz and Sánchez-Villagra 2003; Nilsson et al. 2003, 2004, 2010; Asher et al. 2004; Munemasa et al. 2006; Ladevèze 2007; Ladevèze and Muizon 2007, 2010; Meredith et al. 2008; Beck 2008, 2012; Beck et al. 2008; Horovitz

Table 5.1 Classification of Cenozoic South American metatherians

- Class MAMMALIA Linnaeus (1758)
  - Infraclass METATHERIA Huxley (1880)
    - Cohort "AMERIDELPHIA" Szalay (1982)
      - "AMERIDELPHIA" *incertae sedis*
        - Family PEDIOMYIDAE Simpson (1927)
          - *Khasia*
        - Family PUCADELPHYIDAE Muizon (1998)
          - *Andinodelphys*
          - *Mizquedelphys*
          - *Pucadelphys*
        - Family JASKHADELPHYIDAE Muizon (1991)
          - *Jaskhadelphys*
          - *Minusculodelphis*
        - Family MAYULESTIDAE Muizon (1994)
          - *Mayulestes*
        - Family PROTODIDELPHIDAE Marshall (1987)
          - *Carolocoutoia*
          - *Guggenheimia*
          - *Periprotodidelphis*
          - *Protodidelphis*
          - *Zeusdelphys*
        - Family DERORHYNCHIDAE Marshall (1987)
          - *Derorhynchus*
          - *Pauladelphys*
        - Family STERNBERGIIDAE Szalay (1994)
          - *Carolopaulaoutoia*
          - *Didelphopsis*
          - *Itaboraidelphys*
        - Family HERPETOTHERIIDAE Trouessart (1879)
        - Family indet.
          - *Eobrasilia*
          - *Incadelphys*
          - *Gaylordia*
          - *Marmosopsis*
          - *Monodelphopsis*

(continued)

Table 5.1 (continued)

Szalinia
Tiulordia
Order SPARASSODONTA Ameghino (1884)
Allqokirus
Nemolestes
Patene
Family HONDADELPHIDAE Marshall et al. (1990)
Family HATHLIACYNIDAE Ameghino (1894)
Superfamily BORHYAENOIDEA Ameghino (1894)
Lycopsis
Pharsophorus
Plesiofelis
Prothylacynus
Family BORHYAENIDAE Ameghino (1894)
Arctodictis
Australohyaena
Borhyaena
Family PROBORHYAENIDAE Ameghino (1897)
Arminiheringia
Callistoe
Paraborhyaena
Proborhyaena
Family THYLACOSMILIDAE Riggs (1933)
Anachlysictis
Patagosmilus
Thylacosmilus
Supercohort MARSUPIALIA Gill (1872)
Order DIDELPHIMORPHIA Gill (1872)
Superfamily PERADECTOIDEA Marshall et al. (1990)
Family PERADECTIDAE Crochet (1979)
Peradectes
Family CAROLOAMEGHINIIDAE Ameghino (1901)
Caroloameghinia
Procaroloameghinia
Superfamily DIDELPHOIDEA Gray (1821)
Family **DIDELPHIDAE** Gray (1821)
Subfamily GLIRONIINAE Voss and Jansa (2009)
Glironia
Subfamily CALUROMYINAE Kirsch (1977)
Caluromys
Caluromysiops
Subfamily HYLADELPHINAE Voss and Jansa (2009)
Hyladelphys
Subfamily DIDELPHINAE Gray (1821)
Tribe MARMOSINI Hershkovitz (1992)
Marmosa

(continued)

Table 5.1 (continued)

          - *Micoureus*
          - *Monodelphis*
        - Tribe METACHIRINI Hershkovitz (1992)
          - *Metachirus*
        - Tribe DIDELPHINI Gray (1821)
          - *Chironectes*
          - *Didelphis*
          - *Hyperdidelphys*
          - *Lutreolina*
          - *Philander*
        - Tribe THYLAMYINI Hershkovitz (1992)
          - *Chacodelphys*
          - *Cryptonanus*
          - *Gracilinanus*
          - *Lestodelphys*
          - *Marmosops*
          - *Thylamys*
      - Family SPARASSOCYNIDAE Reig (1958)
  - Order PAUCITUBERCULATA Ameghino (1894)
          - *Bardalestes*
          - *Evolestes*
          - *Riolestes*
    - Superfamily CAENOLESTOIDEA Trouessart (1898)
      - Family **CAENOLESTIDAE** Trouessart (1898)
          - *Caenolestes*
          - *Lestoros*
          - *Rhyncholestes*
    - Superfamily PALAEOTHENTOIDEA Sinclair (1906)
          - *Perulestes*
          - *Pilchenia*
          - *Sasawatsu*
      - Family PICHIPILIDAE Marshall (1980)
      - Family PALAEOTHENTIDAE Sinclair (1906)
          - *Carlothentes*
          - *Palaeothentes*
      - Family ABDERITIDAE Ameghino (1889)
          - *Abderites*
          - *Parabderites*
- Cohort AUSTRALIDELPHIA Szalay (1982)
  - Order MICROBIOTHERIA Ameghino (1887)
      - Family WOODBURNODONTIDAE Goin et al. (2007a, b)
          - *Woodburnodon*
      - Family **MICROBIOTHERIIDAE** Ameghino (1887)
          - *Kirutherium*
          - *Marambiotherium*

(continued)

Table 5.1 (continued)

- Subfamily MICROBIOTHERIINAE Simpson (1929)
  - *Dromiciops*
  - *Microbiotherium*
- Subfamily PACHYBIOTHERIINAE Goin et al. (in press)
  - *Clenia*
  - *Eomicrobiotherium*
  - *Pachybiotherium*
- MICROBIOTHERIA or POLYDOLOPIMORPHIA
  - Family indet.
    - *Mirandatherium*
- Order POLYDOLOPIMORPHIA Archer (1984)
  - Family GLASBIIDAE Clemens (1966)
    - *Bobbschaefferia*
    - *Chulpasia*
    - *Palangania*
  - Suborder BONAPARTHERIIFORMES Pascual (1980)
    - Superfamily BONAPARTHERIOIDEA Pascual (1980)
      - Family PREPIDOLOPIDAE Pascual (1980)
        - *Incadolops*
        - *Prepidolops*
        - *Punadolops*
      - Family BONAPARTHERIIDAE Pascual (1980)
        - Subfamily BONAPARTHERIINAE Pascual (1980)
          - *Bonapartherium*
        - Subfamily EPIDOLOPINAE Pascual and Bond (1981)
          - *Epidolops*
      - Family GASHTERNIIDAE Marshall (1987)
        - *Gashternia*
      - Family ROSENDOLOPIDAE Goin et al. (2010)
        - *Rosendolops*
        - *Hondonadia*
    - Superfamily ARGYROLAGOIDEA Ameghino (1904)
      - *Praedens*
      - Family GROEBERIIDAE Patterson (1952)
        - *Groeberia*
      - Family PATAGONIIDAE Pascual and Carlini (1987)
        - *Patagonia*
      - Family ARGYROLAGIDAE Ameghino (1904)
        - *Argyrolagus*
  - Suborder POLYDOLOPIFORMES Kinman (1994)
    - *Cocatherium*
    - Family SILLUSTANIIDAE Crochet and Sigé (1996)

(continued)

Table 5.1 (continued)

  - *Roberthoffstetteria*
  - *Sillustania*
- Family POLYDOLOPIDAE Ameghino (1897)
  - *Amphidolops*
  - *Archaeodolpos*
  - *Kramadolops*
  - *Pliodolops*
  - *Polydolops*
  - *Pseudolops*

We include all South American metatherian genera, living or extinct, mentioned in this volume. Families with living representatives are marked in bold. “Ameridelphia” is regarded as paraphyletic (see text). Pediomyidae is included among the South American “ameridelphians” because of *Khasia tiupampina*, here allocated within this family (see text). Classification of Sparassodonta follows Forasiepi (2009; see also Forasiepi et al. 2014), with the addition of *Allqokirus* as a basal member of the order (Muizon 1991). Classification of Didelphimorphia partially follows Horovitz et al. (2009; but see Williamson et al. 2012), with the inclusion of Caroloameghiniidae in Peradectoidea (Goin 2006). Classification within the Didelphidae follows Voss and Jansa (2009). Classification of Paucituberculata follows Abello (2007, 2013; see also Goin et al. 2009). Classification of Microbiotheria follows Goin and Abello (2013) and Goin et al. (in press). Classification of Polydolopimorphia follows Goin et al. (2009 and in press). After Chornogubsky and Goin (2015) we include the basal polydolopiformes *Sillustania* and *Roberthoffstetteria* in the family Sillustaniidae Crochet and Sigé (1996). Classification within the Polydolopidae follows Chornogubsky (2010)

et al. 2008, 2009; May-Collado et al. 2015). In several of these analyses, *Dromiciops* appears as the sister-group of all the extant Australian marsupial radiation (Australidelphia sensu Szalay 1982), being some examples those studies carried out by Amrine-Madsen et al. (2003), and Palma and Spotorno (1999) for molecular phylogenies, and Beck (2012) for an analysis based on morphological data (but using molecular constraints). The relationship between *Dromiciops* and other Australidelphia vary from the one described before (i.e., sister-taxa of all other Australidelphia), at the base of Diprotodontia (e.g., Horovitz and Sánchez-Villagra 2003; Beck 2008; Nilsson et al. 2010), as a sister-taxon of Dasyuromorpha (e.g., Wible et al. 2001; Ladevèze and Muizon 2007), as a sister-taxon of Phalangeriformes + Diprotodontia (Luo et al. 2003), or even related with part of the former (see e.g., Nilsson et al. 2004; Ladevèze and Muizon 2010). Asher et al. (2004) performed both morphological and molecular phylogenetic analyses proving different results (*Dromiciops* as sister-group of Diprotodontia in the former and as sister-taxon of Peramelemorphia in the latter).

Polydolopimorphia. The dental pattern of all polydolopimorphians can be easily derived from a microbiotherian one; this argues in favor of regarding the latter as part of the Australidelphian radiation (see also Goin et al. 2009). Examples of basal polydolopimorphians are the Glasbiidae, represented since the Late Cretaceous of North America (the Lancian *Glasbius*) to mid-Paleogene times in South America (e.g., the Riochican *Palangania*; see Table 5.1).

Bonapartheriiformes are one of two major lineages of polydolopimorphians. They were abundant in Paleogene times, though one of its most derived lineages (the Argyrolagidae) evolved since the early Oligocene up to the late Pliocene. Polydolopimorphians successfully occupied frugivorous and omnivorous niches (Bonapartherioidea), as well as more stictly herbivorous ones (Argyrolagoidea).

Even though it was originally considered as a caroloameghinid "opossum-like" marsupial (Marshall et al. 1983), more recent analyses suggest that *Roberthoffstetteria nationalgeographica* belongs with the Polydolopimorphia (Goin et al. 2003), as a basal clade of the Polydolopiformes (sensu Goin et al. 2009; see Table 5.1). More recently Chornogubsky and Goin (2015) have argued in favor of the affinities between *Roberthoffstetteria* and *Sillustania*, the latter from the early Paleogene of Laguna Umayo, Perú. In consequence, they included both genera in the Sillustanidae, a family of Polydolopiformes previously recognized by Crochet and Sigé (1996). In turn, the most derived group of Polydolopiformes (and of all Metatheria, probably) are grouped in the Polydolopidae. They constitute a strictly southern group, restricted to Patagonia and the Antarctic Peninsula (see Woodburne and Zinsmeister 1982, 1984; Chornogubsky 2010; Chornogubsky et al. 2009).

The phylogenetic relationships of all metatherians, and especially of North and South American metatherians, will continue to be the subject of intense scrutiny in the next years. New findings, character sources, and methodological approaches will probably shed additional light; much research is still to be done on the basal "Ameridelphia," for instance. In the following section we offer a brief description of the salient morphological features of South American's major lineages of metatherians (see also Table 5.1). As mentioned previously, the "Ameridelphia" is not regarded here as a natural group.

5.2 Diversity of South American, Cenozoic Metatherians

5.2.1 "Ameridelphia" Incertae Sedis

We provisionally regard as "Ameridelphia" *incertae sedis* a series of (probably, non-marsupial) metatherian lineages whose affinities are still far from clear (cf, e.g., Forasiepi 2009; Ladevèze and Muizon 2010; Oliveira and Goin 2011). Part of the problem lies in the fragmentary nature of many of their representatives (but not all;

among mayulestids and pucadelphyids there are fairly complete specimens; Muizon 1991, 1998). Another problem is the lack of comprehensive phylogenetic analyses that include both North and South American taxa from the late Cretaceous-Cenozoic. A preliminary, welcome study in this regard is the analysis recently performed by Williamson et al. (2012, 2014), including representatives of most North American extinct genera of Metatheria, as well as a few Paleocene South American ones: *Roberthoffstetteria*, *Szalinia*, and *Pucadelphys*. A relevant result of this study is the inclusion of these South American taxa within a group (their Node 19; see Williamson et al. 2014: Fig. 6) that also includes Herpetotheriids, Pediomyids, and "Peradectidae"

Representatives of these "ameridelphian" lineages show, already in the early Paleogene of South America (early Paleocene to early Eocene) many distinctive features that account for their taxonomic and adaptive diversities. A series of phylogenetic analyses are currently being performed on these groups by some of us, so we will refrain from advancing further hypotheses on their relationships until these analyses are made. A few considerations on the morphological diversity and inferred paleobiological aspects of these forms are mentioned in Chap. 6 of this volume.

5.2.2 Sparassodonta

All sparassodonts share some features in the overall morphology of the skull: with very few exceptions (e.g., *Lycopsis longirostrus*) the snout is short to very short; the nasals extend posteriorly overpassing the anterior line of the orbits; a naso-lacrimal contact is common; the orbital process is generally subtle and the orbits are open (except in thylacosmilids); the zygomatic arch is strong; the occipital region is backwardly expanded and the nuchal crest is strong in all taxa. Almost invariably, the palate is posteriorly divergent and incisive and maxillary foramina are present. Several modifications to this overall pattern occur mostly as an adaptive response to diet ; for instance, in most hathliacynids the snout is longer than in the remaining sparassodonts. The sagittal crest is strong; the postorbital constriction is pronounced; the postorbital processes are developed but does not close the orbit; the lateral outline of the skull is flattened; the zygomatic arch is lower; the dentary is dorsoventrally and consistently shallow and the symphysis is ligamentous.

In many borhyaenoids (e.g., *Borhyaena*, *Prothylacynus*, *Lycopsis*), the snout is short; the postorbital constriction is weaker than in hathliacyniids; there is no postorbital bar and the postorbital processes are weak or absent; the sagittal and frontal crests are variably developed; the zygomatic arch is high and strong; the dentary is dorsoventrally deeper and massive; the symphysis may be ankylosed and variably fussed in the adults.

In some borhyaenids (*Arctodictis* (Fig. 5.2), *Australohyaena*) and the majority of proborhyaenids (*Arminiheringia*, *Callistoe*, *Paraborhyaena*), the snout is short; the

Fig. 5.2 *Arctodicts sinclairi* (Sparassodonta, Borhyaenidae); specimen MLP (División Paleontología Vertebrados, Museo de La Plata, Argentina) n° 85-VII-3-1, an almost complete skull in lateral right) view. Many other parts of the postcranial skeleton have also been preserved. Total skull length is 240 mm (see Forasiepi 2009). Early Miocene (Colhuehuapian SALMA). Drawing by Martín Barrios

sagittal crest is weak; the lateral outline of the skull is dome-shaped; the postorbital constriction is weak; there is no postorbital bar; the dentary is dorsoventrally deep and massive; and the fussed symphysis generally extends to the posterior root of p3 or the anterior root of m1.

In the sabre-toothed Thylacosmilidae (Fig. 5.3), the snout is extremely short; the hypertrophied upper canines are implanted dorsally at the posterior border of the orbit; the lateral outline of the skull is dome-shaped; the postorbital bar is complete (*Thylacosmilus*) or nearly complete (*Patagosmilus*); the sagittal crest is strong; the zygomatic arch is high and robust; the back of the skull is high and the nuchal crest is very strong; the dentary is massive, with a conspicuous flange that allocates the hypertrophied upper canines (see Riggs 1934; Marshall 1976, 1977b, 1978, 1979, 1981; Goin and Pascual 1987; Babot et al. 2002; Forasiepi 2009; Forasiepi and Carlini 2010; Forasiepi et al. 2014).

The basic adaptations of the sparassodont molar pattern are related to their faunivorous (e.g., small Hathliacynidae) to hypercarnivorous (e.g., Borhyaenidae) diets. Upper molars have reduced protocones; small paracones which are basally fused to the (much larger) metacones; the postmetacrista is large to very large; the stylar shelf is reduced to absent, and stylar cusps are absent in almost all members

Fig. 5.3 *Thylacosmilus atrox* (Sparassodonta, Thylacosmilidae); specimen MMP (Museo Municipal de Mar del Plata, Argentina) n° 1443; an almost complete skull and jaws in lateral (left) view. Total skull length is 210 mm (Goin and Pascual 1987). Late Pliocene (Chapadmalalan SALMA). Drawing by Martín Barrio. Reproduced from Goin and Pascual (1987: plate1) with permission of the Academia Argentina de Ciencias Exactas, Físicas y Naturales (Buenos Aires)

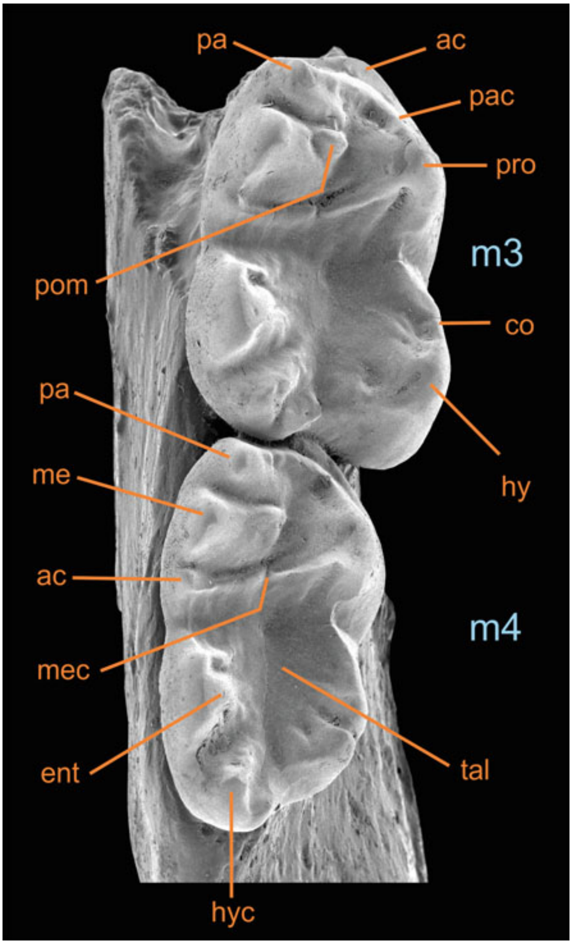


Fig. 5.4 *Caroloameghinia mater* (Didelphimorphia, Peradectoidea; Caroloameghiniidae; see Goin 2006); specimen MLP n° 83-III-1-170b, a fragment of right dentary with m3-4 in occlusal view. Length of m3: 4.13 mm. Late Eocene (Barrancan subage of Casamayoran SALMA). *Abbreviations* ac, anterior cingulum (in m3) and accessory cuspule (in m4); co, cristidobliqua; ent, entoconid; hy, hypoconid; hyc, hypoconulid; me, metaconid; mec, metacristid; pa, paraconid; pac, paracristid; pom, postmetacristid; pro, protoconid

of the order. In turn, lower molars have large to very large paracristids and reduced to absent metaconids in the trigonids, while the talonids are reduced to absent. Summarizing, the crushing structures are reduced to absent, while the cutting ones are well developed. Masticatoy movements were predominantly orthal (vertical; Zimicz 2012) (Fig. 5.4).

5.2.3 *Didelphimorphia*

The skull of living didelphids is anteroposteriorly elongated; the braincase and the rostrum are equally developed, with the nasals extending posteriorly between the

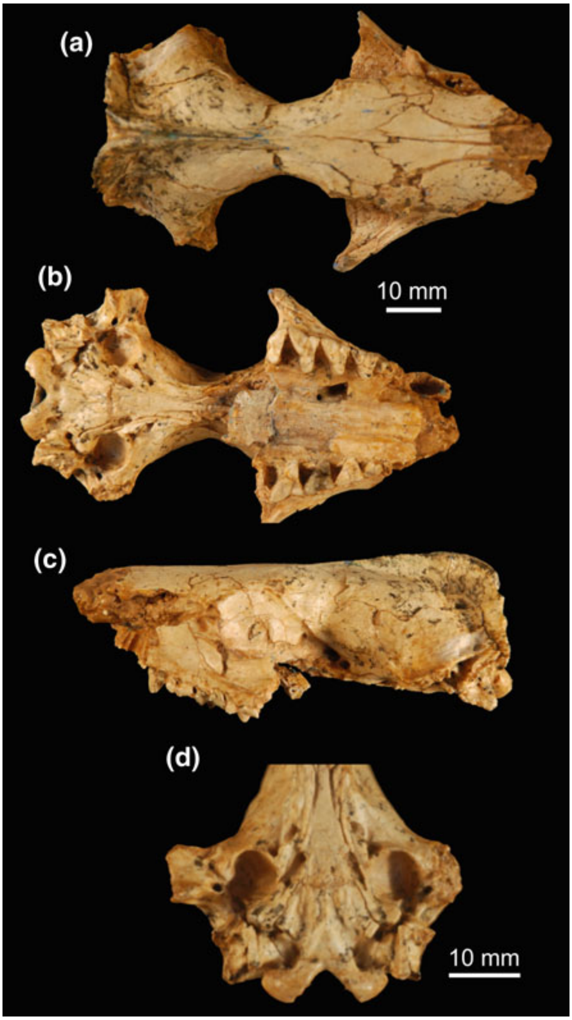


Fig. 5.5 *Hyperdidelphys dimartinoi* (Didelphimorphia, Didelphidae); specimen MBB (Museo Municipal de Bahía Blanca, Argentina) n° 11.248 (type); almost complete skull lacking both jaws, the tip of the snout and the zygomatic archs, in dorsal **a**, palatal **b** and lateral (left, **c**) views. **d** Detail of basicranial region. Skull length is 79 mm (Goin and Pardiñas 1996). Scale: 10 mm. Late Pliocene (Chapadmalalan SALMA). Photograph by Bruno Pianzola

lacrimals—they are wider posteriorly than anteriorly. The only vacuity present in the rostrum is the prominent infraorbitary foramen; the zygomatic arch is variably robust and invariably includes a jugal process. The lacrimals have a facial process and two or more foramina; the orbital margin formed by the lacrimal is smoothly rounded. The interparietal bone is fused to the supraoccipital one; the occiput is not projected backwardly and the nuchal crest is moderated; the sagittal and frontal crests reach different degrees of development, from absent to strong (a strong sagittal crest is well developed in the carnivorous *Hyperdidelphys*; see Fig. 5.5). The palate is perforated by several openings; the incisive foramina are surrounded by the premaxillary–maxillary suture; the maxillopalatine fenestrae are present (except in *Caluromys* and *Caluromysiops*) and never extend posteriorly to the molar row; palatal foramina are absent; the palatine fenestrae are sometimes present; the dentary consists of an anteroposteriorly elongate horizontal ramus, an ascending ramus with well-developed coronoid and condylar processes, and a posteroventral angular process; the mandibular symphysis is never fused; the retromolar space is either imperforate or pierced by tiny nutrient foramina; the masseteric fossa is always imperforate, and its posteroventral border is bounded by a distinct shelf; the articular condyle is transversely elongate and more or less semicylindrical (see Voss and Jansa 2009).

The molar pattern in didelphimorphians does not differ strikingly from that of basal "ameridelphians," one clear difference among the upper molars being the reduced stylar shelf (though usually not the stylar cusps). In the Caroloameghiniidae (Peradectoidea) molars are bunodont and a series of wrinkles on the enamel surface. Other difference is the reduction and/or absence of conules (paraconule and metaconule) at the distal end of the pre- and posprotocristae. In the lower molars, it is noticeable the reduction of the hypoconulid among the Didelphoidea (Didelphidae and Sparassocynidae) . As recently reviewed by Goin (2006), the dental pattern of the Caroloameghiniidae include quite derived features, as the presence of accessory neocusps in the lower molars (see Fig. 5.4). As inferred from paleobiological analyses, the masticatory movements in the Didelphimorphia were predominantly orthal (Zimicz 2012).

5.2.4 Paucituberculata

The cranial anatomy of paucituberculatans is mostly known from representatives of the living genera *Caenolestes*, *Ryncholestes,* and *Lestoros*). The skull is elongated and laterally compressed; the orbits are small; the zygomatic arch is somewhat reduced and laterally expanded; the interorbital zone is wide; the braincase is bulbous, being the largest component of the skull; finally, there are two large vacuities above the infraorbital foramen, anterior to the orbits; the dentary is slender with the ventral border straight; the symphysis is long and weak; the coronoid process is large and broad with the anterior border curved; the masseteric fossa is broad with a tiny foramen in the lower edge; the angular process is moderately inflected.

The most noticeable features of the Paucituberculatan dentition are the proportionally enormous, procumbent lower incisors (see Osgood 1921). The molar pattern is characterized by the gradual acquisition of a quadrangular profile in occlusal view, by means of the expansion of the metaconule. The paracone and metacone basally coalesce, and merge, at the bases of the very large stylar cusps B (at the anterolabial edge of the molar), and C + D (at the posterolabial edge), respectively (Figs. 5.6 and 5.7). Lower molars, except the first one (m1) progressively show a tendence to fuse the paraconid and metaconid, and frequently have

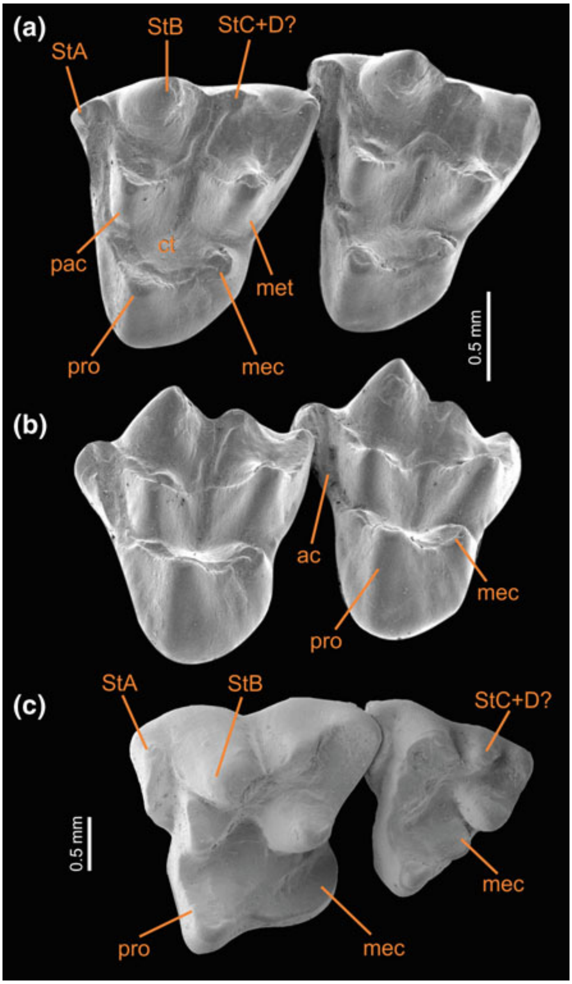


Fig. 5.6 **a**, **b** *Bardalestes hunco* (Paucituberculata, family indet.); specimen LIEB-PV (Laboratorio de Investigaciones en Evolución y Biodiversidad, Esquel, Argentina) n° 1135 (type), left upper molars M2-3, in occlusal (**a**) and occlusal–lingual (**b**) views (Goin et al. 2009). Paso del Sapo Fauna, Early Eocene. **c** *Evolestes hadrommatos* (Paucituberculata, family indet.); specimen MNHN-Bol (Museo Nacional de Historia Natural, La Paz, Bolivia) n° 96-400 (type); detail of left M2-3 in occlusal view (the specimen is a fragmentary skull preserving part of the rostrum, palate, skull roof and a few upper teeth; see Goin et al. 2007a). Salla Beds, Late Oligocene. Scale: 0.5 mm. *Abbreviations* ac, anterior cingulum; ct, trigon basin; mec, metaconule; met, metacone; pac, paracone; pro, protocone; St, stylar cusp

sharp, well-developed crests anterior (and sometimes posterior) to the entoconid. The last upper and lower molars are usually reduced to very reduced. Masticatory movements were inferred as predominantly orthal (Zimicz 2012; Fig. 5.7).

5.2.5 Microbiotheria

The cranial morphology of Microbiotheria is mostly known from the living microbiotheriid *Dromiciops gliroides*. The skull is oval in dorsal view; the snout is relatively short; the nasals do not overpass the orbital line; there is not postorbital

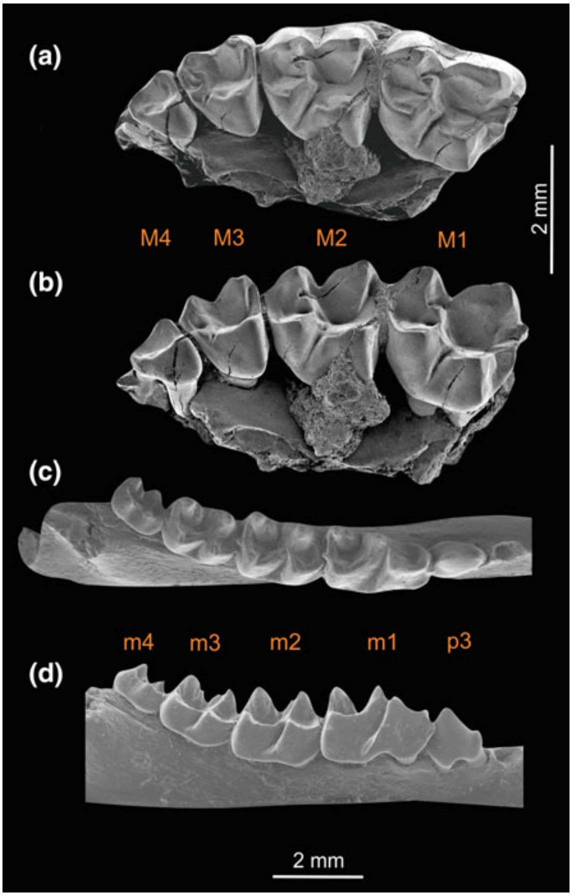


Fig. 5.7 *Palaeothentes minutus* (Paucituberculata, Palaeothentidae). **a**, **b** Specimen MACN (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina) n° 3286, a right maxillary with M1-4 in occlusal (**a**) and lingual (**b**) views. **c**, **d** Specimen MACN n° 8464 (type), a right dentary with incisors (not shown here) and p3-m4, in occlusal (**c**) and labial (**d**) views. Early middle Miocene (Santacrucian SALMA) (Abello 2007, 2013). Scale: 2 mm. *Abbreviations* M1, M2, M3, M4: upper molars; m1, m2, m3, m4, lower molars; p3, posteriormost lower premolar. We thank Alejandra Abello for facilitating the scanning micrographs of the specimens

process; the orbits are large and open; the zygomatic arch is gracile and strongly inflected at the maxillary–jugal suture; the tympanic bullae are very large, inflated, as well as the brain case; the sphenoid crest is present; the palate is backwardly divergent, the incisive foramens are large; the maxillary foramens are large and occupy the half part of the posterior palate; the dentary is slender, with the ventral inflection weakly defined (see Giannini et al. 2004; Marshall 1982).

A remarkable aspect of the microbiotherian dentition is, among the lower incisors, the lack of a buttressed (“staggered”) i3 (Hershkovitz 1995). The molar pattern is characterized, in the upper molars, by the strong and wide protocones and a reduced stylar shelf, with almost absent stylar cusps; the paracone and the metacone are subequal in size and height, while the centrocrista is straight. Among the most generalized microbiotherians, the Woodburnodontidae, stylar cusps can still be distinguished (Fig. 5.8). In the lower molars the paraconid is reduced, the talonid is wide, and, in the first two molars, the hypoconulid tends to locate quite centrally on the posthypocristid. Masticatory movements were predominantly orthal.

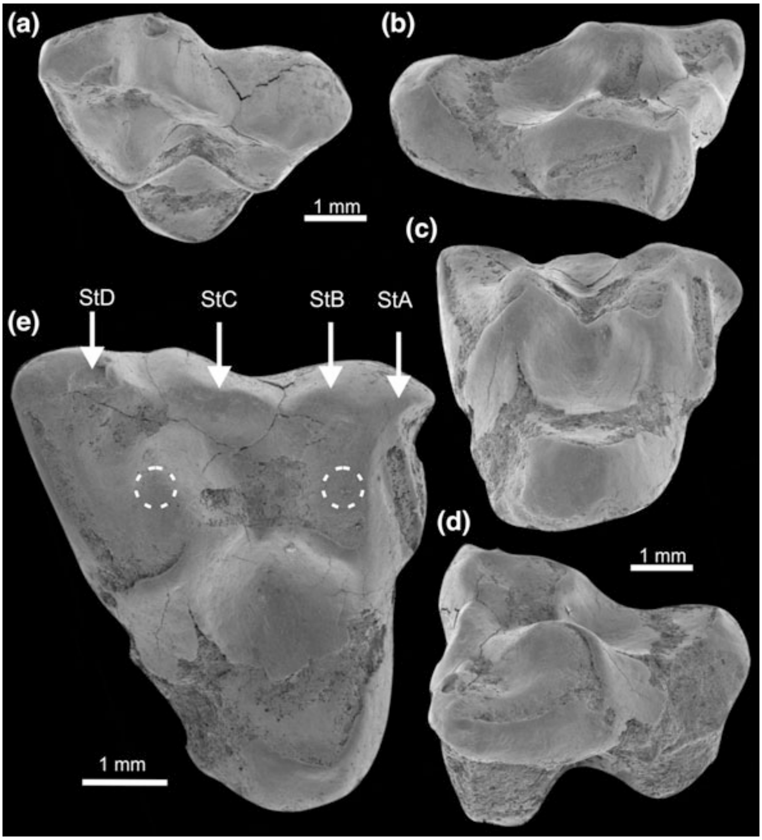


Fig. 5.8 *Woodburnodon casei* (Microbiotheria, Woodburnodontidae); specimen MLP n° 04-III-1-2 (type); upper-right molar (M2 or M3) in labial **a**, anterior **b**, lingual **c**, posterior **d** and occlusal (**e**) views (see Goin et al. 2007b). In (**e**), circles drawn in white dashed lines indicate the inferred location of the (very worn) paracone and metacone cusps (Goin et al. 2007b). Early Eocene (La Meseta Fm). Scale: 1 mm. *Abbreviations* St, stylar cusp. Reproduced from Goin et al. (2007b: Fig. 1) with permission of the Asociación Geológica Argentina (Buenos Aires)

5.2.6 Polydolopimorphia

All known polydolopimorphians share some characteristics in the skull morphology: the braincase is globular, a character most evident in those types with narrows snouts; the nasals are posteriorly expanded to the level of the orbits; the zygomatic arch is strong; the palate widens at the molar row level; the incisive foramina are always present in different sizes and maxillary and palatal foramina are also present. Deviations from this pattern can be observed among representatives of various lineages.

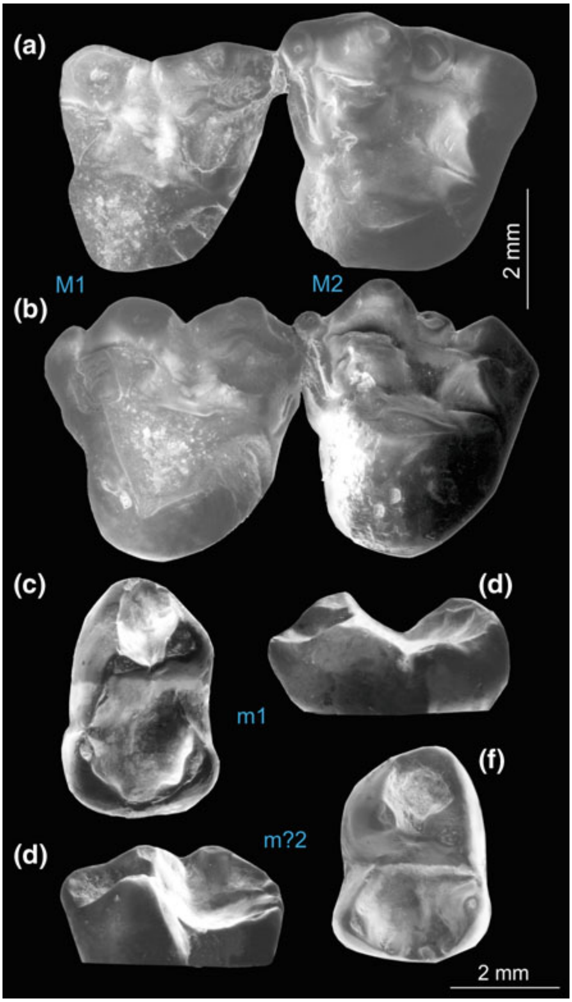


Fig. 5.9 *Palangania brandmayri* (Polydolopimorphia, Glasbiidae; see Goin et al. 1998). **a**, **b** Specimen UNSJB-PV (Vertebrate paleontology Collection, Universidad Nacional de la Patagonia, C. Rivadavia, Argentina) n° 114 (type), left M1-2 in occlusal (**a**) and lingual (**b**) views. **c**, **d** Specimen MLP n° 40-VI-20-19, right m1 in occlusal (**c**) and lingual (**d**) views. **e**, **f** Specimen MLP n° 79-I-17-6, left m?2 in labial (**e**) and occlusal (**f**) views. Early Eocene (Riochican SALMA). Scale: 2 mm

Basal Polydolopimorphians are represented by glasbiids (e.g., *Chulpasia*, *Palangania*) which have a relatively generalized molar pattern (Fig. 5.9). In the Bonapartheriiformes Bonapartheroidea (i.e., *Bonapartherium* and *Epidolops*), the snout is short and wide; the zygomatic arch is lower; the postorbital processes are subtle or absent; the orbit is completely open; the postorbital constriction is moderate; the palate is suboval or diamond-shaped; the incisive foramina are minute and the maxillary fenestrae are apparently large; the dentary is strong and short; the deep masseteric fossa is anteriorly bordered by a strong crest on the anterior border of the high and wide coronoid process; the masseteric crest is well developed and posteriorly wider; the condyle is strong and slightly elevated above the dental level; the angular process is strong and inwardly inflected, with its posterior tip pointing

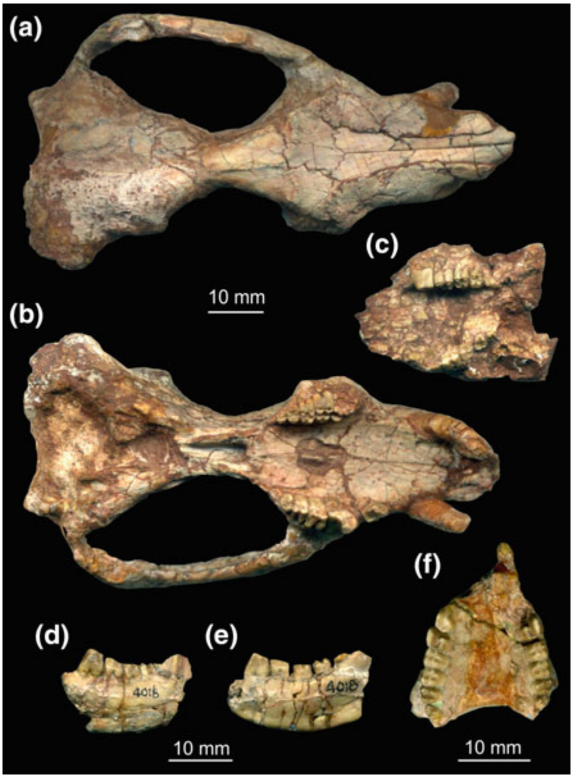


Fig. 5.10 *Bonapartherium hinakusijum* (Polydolopimorphia, Bonapartheriiformes, Bonapartheriidae). **a**, **b** Specimen MMP n° 1408, a partial skull in dorsal (**a**) and palatal (**b**) views. **c** PZVL (Colección Paleozoología Vertebrados, Fundación Miguel Lillo, Tucumán, Argentina) n° 4191, a fragmentary skull in palatal view; **d**–**f** PVL 4018 (type), a partial skull and both jaws; **d** left jaw in labial view; **e** right jaw in lingual view; **f** skull in palatal view (Pascual 1980, 1981). Middle to late Eocene (Lumbrera Fm). Scale: 10 mm. Photographs by Bruno Pianzola

upwards; the symphyseal region is thin and narrow before p2; the maximum height of the bone is below the sectorial complex p3-m1 (see Pascual 1980, 1981; Paula Couto 1952 (Fig. 5.10).

In the Bonapartheriiformes Argyrolagoidea (i.e., *Argyrolagus scagliai*), the snout is narrow with the nasal cavity protruding upon the incisive line; the zygomatic arch is lower and has a prominent jugal process; the infraorbital foramen is large; the orbits are anteriorly closed and backwardly opened with a noticeable orbital border; the temporal region is reduced; the palate is oval with large incisive foramens; the auditive bulla is proportionally enormous and inflated; the dentary is relatively gracile, with very large lower incisors implanted at the level of m3 (Simpson 1970 (Fig. 5.11).

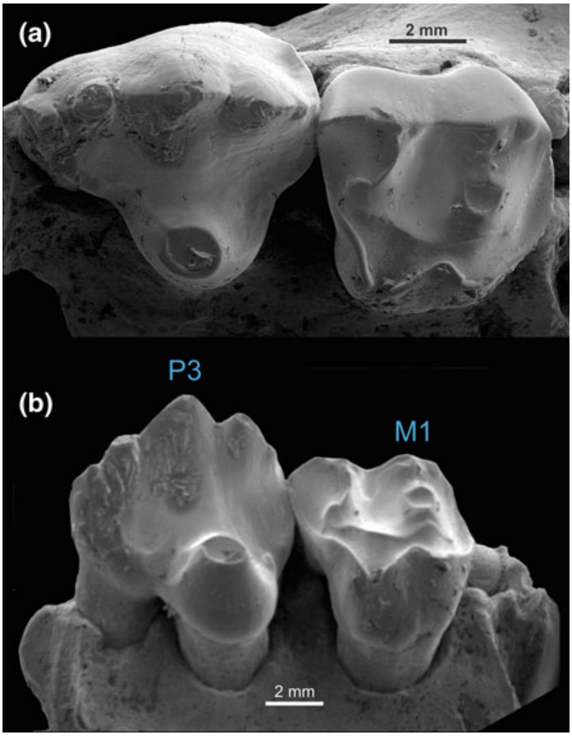


Fig. 5.11 *Gashternia carioca* (Polydolopimorphia, Bonapartheriiformes, Gashterniidae; see Goin and Oliveira 2007); specimen MCN-PV (Museu de CiénciasNaturais, FundacaoZoobotánica do Rio Grande do Sul, Porto Alegre, Brazil) n° 1801 (type); left maxillary with P3-M1 in occlusal (**a**) and lingual (**b**) views. Early Eocene (Itaboraian SALMA). Scale: 1 mm

In the Polydolopiformes (i.e., *Kramadolops mckennai*: the only known skull partially preserved), the snout is elongate and narrow; the palate widens across the molar row reaching the maximum width near the anterior base of the zygomatic arches and the braincase is fairly expanded and globular as in other polydolopimorphians (Flynn and Wyss 2004).

The generalized molar pattern of polydolopimorphians is quadrangular, as in the Paucituberculata; however, its evolution followed a different pathway. In the upper molars, the paracone and metacone ere twinned with the similarly sized StB and StD respectively (see, e.g., Fig. 5.11)—in paucituberculatans, the stylar cusps are proportionally enormous (Fig. 5.7 a-b). At the lingual edge, the expanded metaconule forms the posterolingual corner of the tooth; different from Paucituberculatans, it is leveled with the protocone and the trigon basin. In the lower molars, the paraconid and metaconid are somewhat reduced and close to each other; the hypocone is large though not salient as in most paucituberculatans. Several variants can be observed from this basic pattern; for instance, that of Argyrolagoids (Goin et al. 2010; Goin and Abello 2013) or of the Polydolopiformes (Goin et al. 2003; Chornogubsky et al. 2009; see Fig. 5.12). Ectental, oblique, and propalinal movements have been inferred for several lineages of this order (Zimicz 2011, 2012, 2014).

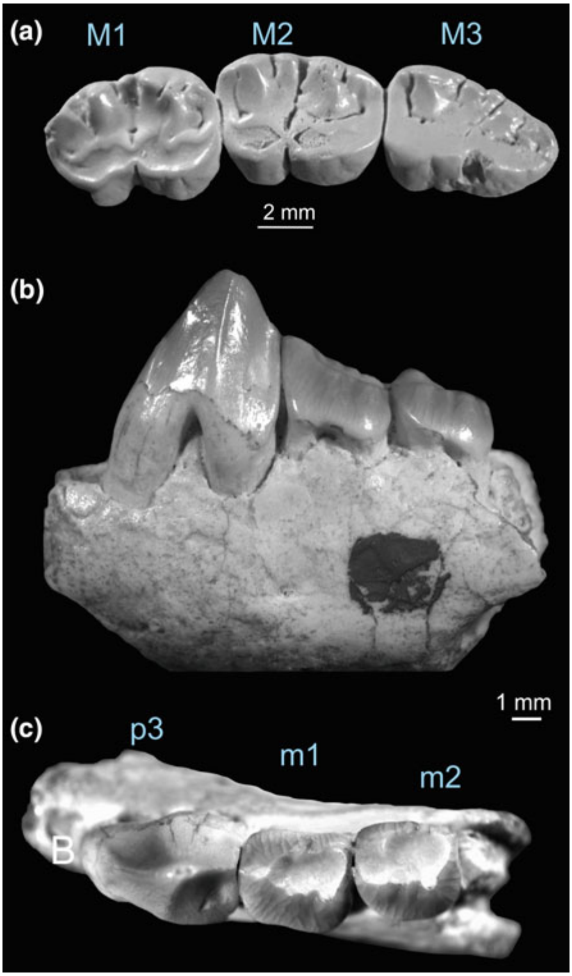


Fig. 5.12 **a** *Kramadolops hernandezi* (Polydolopimorphia, Polydolopiformes, Polydolopidae); cast of specimen AMNH (American Museum of Natural History, New York, USA) n° 28,932 (type); a left maxillary with M1-3. Late Eocene (BarrancanSubage of the Casamayoran SALMA). Scale: 2 mm. **b**, **c** *Pliodolops rothi* (Polydolopimorphia, Polydolopidae); specimen MLP 11-122 (type), a fragment of left dentary with p3-m2 in labial (**b**) and occlusal (**c**) views. Early to middle Eocene. Scales: **a** 2 mm; **b**, **c** 1 mm. For recent reviews on the taxonomy of the Polydolopidae, see Chornogubsky (2010). *Abbreviations* M1, M2, M3, upper molars; m1, m2, lower molars; p3, posteriormost lower premolar

References

Abello MA (2007) Sistemática y bioestratigrafía de los Paucituberculata (Mammalia, Marsupialia) del Cenozoico de América del Sur. Unpublished thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, p 381

Abello MA (2013) Analysis of dental homologies and phylogeny of Paucitu-berculata (Mammalia: Marsupialia). Biol J Linn Soc 2013(109):441–465

Amrine-Madsen H, Scally M, Westerman M, Stanhope MJ, Krajewski C, Springer MS (2003) Nuclear gene sequence provides evidence for the monophyly of australidelphian marsupials. Mol Phylogenet Evol 28:186–196

Aplin KP, Archer M (1987) Recent advances in marsupial systematics with a new syncretic classification. In: Archer M (ed), Possums and opossums–studies in evolution, vol 1. Surrey Beatty and Sons, Sydney, pp xv–lxxii

Archer M (1982) Review of the Dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. In: Archer M (ed) Carnivorous marsupials. Royal Zoological Society of New South Wales, Sydney, pp 397–443

Asher RJ, Horovitz I, Sánchez-Villagra MR (2004) First combined cladistic analysis of marsupial mammal interrelationships. Mol Phylogenet Evol 33:240–250

Babot MJ, Powell JE, Muizon C (2002) *Callistoe vincei*, a new Proborhyaenidae (Borhyaenoidea, Metatheria, Mammalia) from the early Eocene of Argentina. Geobios 35:615–629

Beck RMD (2008) A dated phylogeny of marsupials using a molecular supermatrix and multiple fossil constraints. J Mammal 89:175–189

Beck RMD (2012) An 'ameridelphian' marsupial from the early Eocene of Australia supports a complex model of southern hemisphere marsupial biogeography. Naturwissenschaften 99: 715–729

Beck RMD, Godthelp H, Weisbecker V, Archer M, Hand SJ (2008) Australia's oldest marsupial fossils and their biogeographical implications. PLoS One 3(3):e18–e58. doi:10.1371/journal.pone.0001858

Burk B, Westerman M, Kao DJ, Kavanagh JR, Springer MS (1999) An analysis of marsupial inter ordinal relationships based on 12S rRNA, tRNA Valine, 16S rRNA, and cytochrome b sequences. J Mamm Evol 6(4):317–334

Cardillo M, Bininda-Emonds ORP, Boakes E, Purvis A (2004) A species-level phylogenetic supertree of marsupials. J Zool 264:11–31

Chornogubsky L (2010) Sistemática de la familia Polydolopidae (Mammalia, Marsupialia, Polydolopimorphia) de América del Sur y la Antártica. Unpublished PhD thesis, Universidad de Buenos Aires, p 352

Chornogubsky L, Goin FJ (2015) A review of the molar morphology and phylogenetic affinities of *Sillustania quechuense* (Metatheria, Polydolopimorphia, Sillustaniidae), from the early paleogene of Laguna Umayo, southeastern Perú. J Vertebr Paleontol

Chornogubsky L, Goin FJ, Reguero M (2009) A reassessment of Antarctic polydolopid marsupials (middle Eocene, La Meseta formation). Antarct Sci 21(3):285–298

Colgan DJ (1999) Phylogenetic studies of marsupials based on phosphoglycerate kinase DNA sequences. Mol Phylogenet Evol 11:13–26

Crochet JY, Sigé B (1996) Un marsupial ancien (transition Crétacé–Tertiaire) à denture évoluée en Amérique du Sud (Chulpas, Formation Umayo, Pérou). Neues Jarhbuch für Geologie und Paläontologie 10:622–634

de Muizon C (1998) *Mayulestes ferox*, a boryaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. Geodiversitas 20:19–142

de Muizon C (1999) Marsupial skulls from the Deseadan (Late Oligocene) of Bolivia and phylogenetic analysis of the Borhyaenoidea (Marsupialia, Mammalia). Geobios 32:483–509

de Paula Couto C (1952) Fossil Marsupials from the beginning of the Cenozoic in Brazil. Marsupialia: Polydolopidae and Borhyaenidae. Am Mus Novitates 1559:1–27

Flores DA (2009) Phylogenetic analyses of postcranial skeletal morphology in didelphid marsupials. Bull Am Mus Nat Hist 320:1–81

Flynn JJ, Wyss AR (2004) A polydolopine marsupial skull from the Cachapoal Valley, Andean main range, Chile. Bull Am Mus Nat Hist 285:80–92

Forasiepi AM (2009) Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. Monografías del Museo Argentino de Ciencias Naturales 6:1–174

Forasiepi AM, Carlini AA (2010) New thylacosmilid (Mammalia, Metatheria, Sparassodonta) from the Miocene of Patagonia, Argentina. Zootaxa 2552:55–68

Forasiepi AM, Babot J, Zimicz N (2014) *Australohyaena antiqua* (Mammalia, Metatheria, Sparassodonta), a large predator from the late Oligocene of Patagonia. J Syst Paleontol. doi:10.1080/14772019.2014.926403

Giannini NP, Abdala F, Flores y DA (2004) Comparative postnatal ontogeny of the skull in *Dromiciops gliroides* (Marsupialia: Microbiotheriidae). Am Mus Novitates 3460:1–17

Goin FJ (2006) A review of the Caroloameghiniidae, Paleogene South American “primate-like” marsupials (Didelphimorphia, Peradectoidea). In: D. Kalthoff T, Martin T, Möors T (eds.), Palaeontographica Abteilung A, 278:57–67

Goin FJ, Oliveira EV (2007) A new species of *Gashternia* (Marsupialia) from Itaboraí (Brazil). Neues Jahrbuch für Geologie and Paläontologie, Stuttgart 245(3):309–313

Goin FJ, Pardiñas U (1996) Revisión de las especies del Género *Hyperdidelphys* Ameghino, 1904 (Mammalia, Marsupialia, Didelphidae). Su significación filogenética, estratigráfica y adaptativa en el Neógeno del Cono Sur Sudamericano. Estud Geol 52:327–359

Goin FJ, Pascual R (1987) News on the biology and taxonomy of the marsupials Thylacosmilidae (late tertiary of Argentina). Anales de la Academia Nacional de Ciencias Exactas Físicas y Naturales de Buenos Aires 39:219–246

Goin FJ, Abello MA (2013) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, edad mamífero Colhuehuapense): Microbiotheria y Polydolopimorphia. Ameghiniana 50:51–78

Goin FJ, Candela AM, de Muizon C (2003) The affinities of *Roberthoffstetteria nationalgeographica* (Marsupialia) and the origin of the polydolopine molar pattern. J Vertebr Paleontol 23:869–876

Goin FJ, Candela AM, Bond M, Pascual R, Escribano V (1998) Una nueva “comadreja” (Mammalia, Marsupialia) del Paleoceno de Patagonia. In: Casadío S (ed), Paleógeno de América del Sur y de la Península Antártica, vol 5, Asociación Paleontológica Argentina, Buenos Aires, pp 71–78

Goin FJ, Candela AM, Abello A, Oliveira EO (2009) Earliest South American paucituberculatans and their significance in the understanding of “pseudodiprotodont” marsupial radiations. Zool J Linn Soc 155:867–884

Goin FJ, Abello MA, Chornogubsky L (2010) Middle tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America’s *Grande Coupure*. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The Paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York, pp 71–107

Goin FJ, Sánchez-Villagra MR, Abello MA, Candela AM (2007a) A new generalized paucituberculatan marsupial from the Oligocene of Bolivia, and the origin of ‘shrew-like’ opossums. Palaeontology 50(5):1267–1276

Goin FJ, Zimicz N, Reguero M, Santillana S, Marenssi SS, Moly JJ (2007b) New mammal from the Eocene of Antarctica, and the origins of the Microbiotheria. Revista de la Asociación Geológica Argentina 62(4):597–603

Hershkovitz P (1995) The staggered marsupial third lower incisor: hallmark of cohort Didelphimorphia, and description of a new genus and species with staggered i3 from the Albian (lower Cretaceous) of Texas. Bonner Zoologische Beitrage 45:153–169

Horovitz I, Sánchez-Villagra MR (2003) A morphological analysis of marsupial mammal higher-level phylogenetic relationships. Cladistics 19:181–212

Horovitz I, Ladèveze S, Argot C, Macrini TE, Martin T, Hooker JJ et al (2008) The anatomy of *Herpetotherium* cf. *fugax* Cope, 1873, a metatherian from the Oligocene of North America. Palaeontogr Abt A 284:109–141

Horovitz I, Martin T, Bloch J, Ladevèze S, Kurz C, Sánchez-Villagra MR (2009) Cranial anatomy of the earliest marsupials and the origin of opossums. PLoS One, p e8278, doi:10.1371/journal.pone.0008278

Illiger C (1811) Prodromus systematis mammalian et avium additus terminus zoographicis utriudque classis. C. Salfeld, Berlin

Jansa SA, Forsman JF, Voss RS (2006) Different patterns of selection on the nuclear genes IRBP and DMP-1 affect the efficiency but not the outcome of phylogeny estimation for didelphid marsupials. Mol Phylogenet Evol 38:363–380

Jansa SA, Voss RS (2000) Phylogenetic studies on didelphid marsupials I. Introduction and preliminary results from nuclear IRBP gene sequences. J Mamm Evol 7:43–77

Jansa SA, Voss RS (2005) Phylogenetic relationships of the marsupial genus Hyladelphys based on nuclear gene sequences and morphology. J Mamm 86:853–865

Kielan-Jaworowska Z, Cifelli RL, Luo ZX (2004) Mammals from the age of dinosaurs: origin, evolution, and structure. Columbia University Press, New York

Kirsch JAW (1977) The comparative serology of Marsupialia, and a classification of marsupials. Aust J Zool 52:1–152

Kirsch JAW, Dickerman AW, Reig OA, Springer MS (1991) DNA hybridization evidence for the Australian affinity of the American marsupial *Dromiciops australis*. Proc Natl Acad Sci 88:10465–10469

Kirsch JAW, Lapointe FJ, Springer MS (1997) DNA-hybridisation studies of marsupials and their implications for metatherian classification. Aust J Zool 45:211–280

Ladevèze S (2004) Metatherian petrosals from the late Paleocene of Itaboraí (Brazil), and their phylogenetic implications. J Vertbr Paleontol 24:202–213

Ladevèze S (2007) Petrosal bones of metatherian mammals from the late Paleocene of Itaboraí (Brazil), and a cladistic analysis of petrosal features in metatherians. Zool J Linn Soc 150:85–115

Ladevèze S, de Muizon C (2007) The auditory region of early Paleocene Pucadelphydae (Mammalia, Metatheria) from Tiupampa, Bolivia, with phylogenetic implications. Palaeontology 50:1123–1154

Ladevèze S, de Muizon C (2010) Evidence of early evolution of Australidelphia (Metatheria, Mammalia) in South America: phylogenetic relationships of the metatherians from the late Palaeocene of Itaboraí (Brazil) based on teeth and petrosal bones. Zool J Linn Soc 159:746–784

Luckett WP (1994) Suprafamiliar relationships within Marsupialia: resolution and discordance from multidisciplinary data. J Mammal Evol 2:255–283

Luo Z-X, Ji Q, Wible JR, Yuan CX (2003) An early Cretaceous tribosphenic mammal and metatherian evolution. Science 302:1934–1940

Luo ZX, Yuan CX, Meng QJ, Ji Q (2011) A Jurassic eutherian mammal and divergence of marsupials and placentals. Nature 476:442–445

Macrini TE (2012) Comparative morphology of the internal nasal skeleton of adult marsupials based on X-ray computed tomography. Bull Am Mus Nat Hist 365:1–91

Marshall LG (1976) Evolution of the Thylacosmilidae, extinct saber—tooth marsupials of South America. PaleoBios 23:1–30

Marshall LG (1977a) Cladistic analysis of borhyaenoid, dasyuroid, didelphoid, and thylacinid (Marsupialia, Mammalia) affinity. Syst Zool 26:410–425

Marshall LG (1977b) Evolution of the carnivorous adaptative zone in South America. In: Hecht MK, Goody PC, Hecht BM (eds) Major patterns in vertebrate evolution. Plenum Press, New York, pp 709–722

Marshall LG (1978) Evolution of the Borhyaenidae, extinct South American predaceous marsupials. Univ California Publ Geol Sciences 117:1–89

Marshall LG (1979) Review of the Prothylacyninae, an extinct subfamily of South American “dog-like” marsupials. Fieldiana Geology, n s 3:1–50

Marshall LG (1981) Review of the Hathlyacyninae, an extinct subfamily of South American “dog-like” marsupials. Fieldiana Geology, n s 7:1–120

Marshall LG (1982) Systematics of the extinct South American marsupial family Polydolopidae. Fieldiana Geology, n s 12:1–109

Marshall LG (1987) Systematics of Itaboraian (middle Paleocene) age “opossum-like” marsupials from the limestone quarry at São José de Itaboraí, Brazil. In: Archer M (ed) Possums and opossums—studies in evolution, vol 1. Surrey Beatty and Sons, Sydney, pp 91–160

Marshall LG, Case JA, Woodburne MO (1990) Phylogenetic relationships of the families of marsupials. In: Genoways HH (ed) Current mammalogy. Plenum Press, New York, pp 433–505

Marshall LG, de Muizon C, Sigé B (1983) Late Cretaceous mammals (Marsupialia) from Bolivia. Geobios 16:739–745

May-Collado LJ, Kilpatrick CW, Agnarsson I (2015) Mammals from ‘down under’: a multi-gene species-level phylogeny of marsupial mammals (Mammalia, Metatheria). PeerJ 3:e805. doi:10.7717/peerj.805

Meredith RW, Westerman M, Case JA, Springer MS (2008) A phylogeny and timescale for marsupial evolution based on sequences for five nuclear genes. J Mammal Evol 15:1–36

Muizon C de (1991) La fauna de mamíferos de Tiupampa (Paleoceno inferior, Formación Santa Lucía), Bolivia. In: Suárez-Soruco R (ed) Fósiles y Fácies de Bolivia, vol I, Vertebrados. Santa Cruz: Revista Técnica, Yacimientos Petrolíferos Fiscales Bolivianos, pp 575–624

Munemasa M, Nikaido M, Donnellan S, Austin CC, Okada N, Hasegawa M (2006) Phylogenetic analysis of diprotodontian marsupials based on complete mitochondrial genomes. Genes Genet Syst 81:181–191

Nilsson MA, Gullberg A, Spotorno AE, Arnason U, Janke A (2003) Radiation of extant marsupials after K/T boundary: evidence from complete mitochondrial genomes. J Mol Evol 57:3–12

Nilsson MA, Arnason U, Spencer PBS, Janke A (2004) Marsupial relationships and a timeline for marsupial radiation in South America. Gene 340:189–196

Nilsson MA, Churakov G, Sommer M, Van Tran N, Zemann A, Brosius J, Schmitz J (2010) Tracking Marsupial evolution Using archaic genomic retroposon insertions. PLoS Biol 8(7):1–9

Oliveira EV, Goin FJ (2011) A reassessment of bunodont metatherians from the Paleogene of Itaboraí (Brazil): systematics and Age of the Itaboraian SALMA. Rev Bras Paleontol 14 (2):105–136

Osgood WH (1921) A monographic study of the American marsupial *Caenolestes*. Field Mus Nat Hist, Zool Ser 16(1):1–162

Palma RE, Spotorno AE (1999) Molecular systematics of marsupials based on the rRNA 12S mitochondrial gene: the phylogeny of Didelphimorphia and of the living fossil microbiotheriid *Dromiciops gliroides* Thomas. Mol Phylogenet Evol 13:525–535

Pascual R (1980) Nuevos y singulares tipos ecológicos de Marsupiales extinguidos de América del Sur (Paleoceno Tardío o Eoceno Temprano) del Noroeste Argentino. 2º Congreso Argentino de Paleontología y Bioestratigrafía. Buenos Aires, Actas 2:151–173

Pascual R (1981) Adiciones al conocimiento de *Bonapartherium hinakusijum* (Marsupialia, Bonapartheriidae) del Eoceno temprano del Noroeste argentino. 2º Congreso Latino-americano de Paleontología, Porto Alegre, Anais, pp 507–520

Phillips MJ, Lin Y-H, Harrison G, Penny D (2001) Mitochondrial genomes of a bandicoot and a brushtail possum confirm the monophyly of australidelphian marsupials. Proc R Soc London B 268:1533–1538

Phillips MJ, McLenachan PA, Down C, Gibb GC, Penny D (2006) Combined mitochondrial and nuclear DNA sequences resolve the interrelations of the major Australasian marsupial radiations. Syst Biol 55:122–137

Reig OA, Kirsch JAW, Marshall LG (1985) New conclusions on the relationships of the opossum-like marsupials, with an annotated classification of the Didelphimorphia. Ameghiniana 21:335–343

Reig OA, Kirsch JAW, Marshall LG (1987) Systematic relationships of the living and Neocenozoic American “opossum-like” marsupials (suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In: Archer M (ed) Possums and opossums-studies in evolution. Surrey Beatty & Sons, Sydney, pp 1–89

Retief JD, Krajewski C, Westerman M, Winkfein RJ, Dixon GH (1995) P1 genes molecular phylogeny and evolution of marsupial protamine. Proc R Soc London 259:7–14

Riggs ES (1934) A new marsupial saber-tooth from the Pliocene of Argentina and its relationships to other South American predaceous marsupials. Trans Am Phil Soc n s 24:1–31

Rougier GW, Wible JR, Novacek MJ (1998) Implications of *Deltatheridium* specimens for early marsupial history. Nature 396:459–463

Rowe T (1988) Definition, diagnosis and origin of Mammalia. J Vertebr Paleontol 8:241–264

Sharman GB (1982) Karyotypic similarities between *Dromiciops australis* (Microbiotheriidae, Marsupialia) and some Australian marsupials. In: Archer M (ed) Carnivorous marsupials. Roy Zool Soc New South Wales, Sydney, pp 711–714

Sánchez-Villagra MR (2001) The phylogenetic relationships of Argyrolagid marsupials. Zool J Linn Soc 131:481–496

Simpson GG (1970) The Argyrolagidae, extinct South American marsupials. Bull Mus Comp Zool 139:1–86

Springer MS, Westerman M, Kavanagh JR, Burk A, Woodburne MO, Kao DJ (1998) The origin of the Australasian marsupial fauna and the phylogenetic affinities of the enigmatic *monito del monte* and marsupial mole. Proc Roy Soc London B 265:2381–2386

Szalay FS (1982) A new appraisal of marsupial phylogeny and classification. In: Archer M (ed) Carnivorous marsupials. Roy Zool Soc New South Wales, Sydney, pp 621–640

Szalay FS (1994) Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge University Press, Cambridge

Szalay FS, Sargis EJ (2001) Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria. Geodiversitas 23:139–302

Voss RS, Jansa SA (2003) Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. Bull Am Mus Nat Hist 276:1–82

Voss RS, Jansa SA (2009) Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. Bull Am Mus Nat Hist 322:1–177

Vullo R, Gheerbrant E, de Muizon C, Néraudeaub D (2009) The oldest modern therian mammal from Europe and its bearing on stem marsupial paleobiogeography. Proc Nat Acad Sci USA 106(47):19910–19915

Wible JR, Rougier GW, Novacek MJ, McKenna MC (2001) Earliest eutherian ear region: a petrosal referred to *Prokennalestes* from the early Cretaceous of Mongolia. Am Mus Novitates 3322:1–44

Williamson TE, Brusatte SL, Carr TD, Weil A, Standhardt BR (2012) The phylogeny and evolution of Cretaceous-Palaeogene metatherians: cladistic analysis and description of new early Palaeocene specimens from the Nacimiento formation New Mexico. J Syst Palaeontol 10 (4):625–651

Williamson TE, Brusatte SL, Wilson GP (2014) The origin and early evolution of metatherian mammals: the Cretaceous record. ZooKeys 465:1–76

Woodburne MO, Zinsmeister WJ (1982) Fossil land mammal from Antarctica. Antarct Sci 218:284–286

Woodburne MO, Zinsmeister WJ (1984) The first land mammal from Antarctica and its biogeographic implications. J Paleontol 58(4):913–948

Zimicz AN (2011) Patrones de desgaste y oclusión en el sistema masticatorio de los extintos Argyrolagoidea (Marsupialia, Polydolopimorphia, Bonapartheriiformes). Ameghiniana 48:605–620

Zimicz AN (2012) Ecomorfología de los marsupiales paleógenos de América del Sur. Unpublished Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, p 454

Zimicz AN (2014) Paleoecología de los Bonapartherioidea (Marsupialia, Polydolopimorphia, Bonapartheriiformes). Ameghiniana 51(2):106–128

Chapter 6
Paleobiology and Adaptations of Paleogene Metatherians

Abstract Diversity, dietary, and body mass analyses suggest that the early Eocene represents the major radiation event in South America metatherian evolutionary history. During this period, representatives of all orders typical of the Paleogene reached their greatest diversity (i.e., "basal ameridelphians"; Polydolopimorphia Polydolopiformes, and Bonapartheriiformes Bonapartherioidea); frugivory was the dominant trophic niche. By the middle late Eocene occurs a functional and taxonomic turnover. Among the Polydolopimorphia, frugivore types declined and were replaced by larger-sized frugivores/folivores (Polydolopiformes) and smaller-sized granivores (Bonapartheriiformes). The Sparassodonta showed a diversity increase and occupied the large-sized hypercarnivore niches. The Eocene–Oligocene boundary constitutes another extinction and turnover event marked by the disappearance of "basal ameridelphians", the Polydolopiformes and Bonapartheriiformes Bonapartherioidea. Lineages that survive into the Deseadan are the Sparassodonta, Paucituberculata, Microbiotheria, and Bonapartheriiformes Argyrolagoidea. Dominant trophic types were those of carnivores and granivores. Environmental factors probably modeled the Paleogene metatherian faunal dynamics in South America. Mean annual temperatures (MAT) and precipitations seem the main factors modeling the taxonomic and trophic diversity, respectively. The adaptive radiation of the early Eocene seems associated with the maximum thermal event of the late Paleocene-early Eocene. The turnover event of the late Eocene seems associated with a sharp drop in the rainfall regime. The extinction and turnover event of the Eocene–Oligocene boundary also seem associated with a strong drop in ambient temperatures. The diversity in evolution of Paleogene metatherians shows a pattern similar to that of living marsupials at the latitudinal level. For a given mean temperature, the number of species in extinct associations is very close to that of the living ones.

Keywords Metatheria · South America · Diversity · Adaptations · Diet · Mastication · Body mass · Paleoclimates

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8_6

6.1 Introduction

Most of our understanding about the paleobiology of South American metatherians is based on the information provided by molar morphology. Although several postcranial bones (and even complete skeletons) are known for a few species (Argot 2001, 2003, 2004; Abello and Candela 2010; Argot and Babot 2011), they are rare compared with the overwhelming record of metatherians based almost exclusively on dental remains. The use of molar morphology as a paleodietary indicator has a long tradition in mammalian paleobiology (Kay and Hylander 1978; Butler 1983, 1985; Sanson 1989, 1996). All aspects of tooth shape contain information about its function: the overall size and shape of the teeth, the form and topographic location of cusps and valleys, the relative development of crests, the enamel thickness, the development of notches along crests, or the differential arrays of crests or lophs, are all informative about the physical properties of food particles processed by the teeth under study (Lucas 1984, 1994; Lucas and Luke 1984; Hiiemae 2000; Lucas and Peters 2000; Lucas et al. 2000, 2002; Spears and Crompton 1995; Strait and Vincent 1998). Some authors have questioned the use of molar morphology as the single source for paleodietary reconstructions (e.g., Sanson 1996). These authors point out that the mastication is only the first stage in the digestive process and many animals compensate their dental adaptations with modifications of their soft digestive systems. Although this is evident, it has also been well demonstrated that the morphology of masticatory systems is responsible for the acquisition and mechanical processing of foods, while the soft digestive anatomy is mostly related with the chemical digestion process (see Chivers and Langer 1994; Hiiemae 2000). This is why the real diet of mammalian species is close to that one inferred from their molar morphology (see, e.g., Walker et al. 1978; Janis 1984, 1988; Solounias et al. 1988).

Traditionally, paleodietary reconstructions of South American metatherians have been based on the qualitative analysis of molar morphology and the masticatory apparatus. However, these inferences were made in a general context of taxonomical studies rather than in strictly paleobiological ones. Examples of this can be found in the literature for almost all taxonomic groups. The Sparassodonta, for instance, have been commonly categorized as carnivorous metatherians (Marshall 1977, 1978, 1980a; Bond and Pascual 1983; Babot et al. 2002, etc.); the Polydolopimorphia have been treated as frugivorous and insectivorous-frugivorous (Pascual 1980; Marshall 1982a; Goin and Candela 2004; Goin et al. 1999, 2010a, b, etc.); the Paucituberculata have been considered as insectivorous-frugivorous and sometimes folivorous (Marshall 1980b; Bown and Fleagle 1993; Dumont et al. 2000); the Microbiotheria have been included in the niche of insectivorous-frugivorous marsupials (Marshall 1982b; Goin 1997; Goin and Abello 2013; Goin et al. 2007, 2010a, b); the Didelphimorphia have been classified as omnivorous with a variable trend towards carnivory or insectivory (Goin 1991, Goin et al. 1992, 2009); finally, the several families included in the "Ameridelphia" (basal metatherians which do not comprise a natural group; see Chap. 5) have been referred to the carnivorous

(Mayulestidae and Herpethotheriidae; de Muizon 1998; Goin and Candela 2004), frugivorous (Protodidelphidae and Pucadelphidae; de Muizon 1998) and insectivorous niches (Jaskhadelphyidae and Derorhynchydae; de Muizon 1991; Goin et al. 1999).

A detailed analysis of the feeding ecology of Paleogene metatherians was recently carried out by Zimicz (2012), who applied the principles and methods of ecomorphology to reconstruct the paleodiet of 97 % species of Paleogene South American metatherians. Her study evaluated the dental morphology from both qualitative and quantitative perspectives, the functional morphology of molar teeth by means of the analysis of wear occlusal patterns and the body mass inferred from dental measurements. The dietary inferences emerged from the integration of the information provided by such different sources. Additionally, she analyzed the diversity patterns at different hierarchical levels, relating them with the evolution of main climatic parameters during Paleogene (MAT and MAP; see below). The present chapter summarizes Zimicz's (2012) results and main conclusions. It should be noted that the Paleogene period is crucial for the understanding of many biological parameters developed by mammals throughout the world. This is so because of the distinct climate phases that transpired during this time interval. Briefly, Paleogene times saw the climax of Cenozoic's Greenhouse World (the Early Eocene Climatic Optimum, or EECO), as well as the beginning of the Icehouse World (with the isotopic event known as "Oi1" by the Eocene–Oligocene boundary).

6.2 Metatherian Diversity and Climates During the Paleogene in South America

Metatherian diversity throughout the Paleogene shows a main radiation episode by the early Eocene, followed by a fall and stabilization periods in species richness (Fig. 6.1). The first event coincided with the LPTM (Late Paleocene Thermal Maximum) and EECO climatic events (Zachos et al. 2001). These warm episodes were characterized by mean annual temperatures (MAT) above 20 °C, and, in southern South America, by mean annual precipitations (MAP) higher than 200 cm (Hinojosa 2005). Extremely high values of species richness are recorded in this period: 56 species recovered from the Itaboraian localities of Las Flores (Patagonia) and Itaboraí (Brazil). This diversity is comprised within no less than six orders that include all Cenozoic lineages (Fig. 6.1). Diversity declines from the late early Eocene (Ypresian–Lutetian boundary) to the middle Eocene with 40 species recovered at the "Sapoan" localities of Paso del Sapo (Patagonia), and La Meseta (Antarctic Peninsula), concomitantly with a progressive fall in MAT values which were established around 17 °C (Wilf et al. 2005). For southern South America, this interval is regarded as one of the most humid of the entire Cenozoic Era, with an

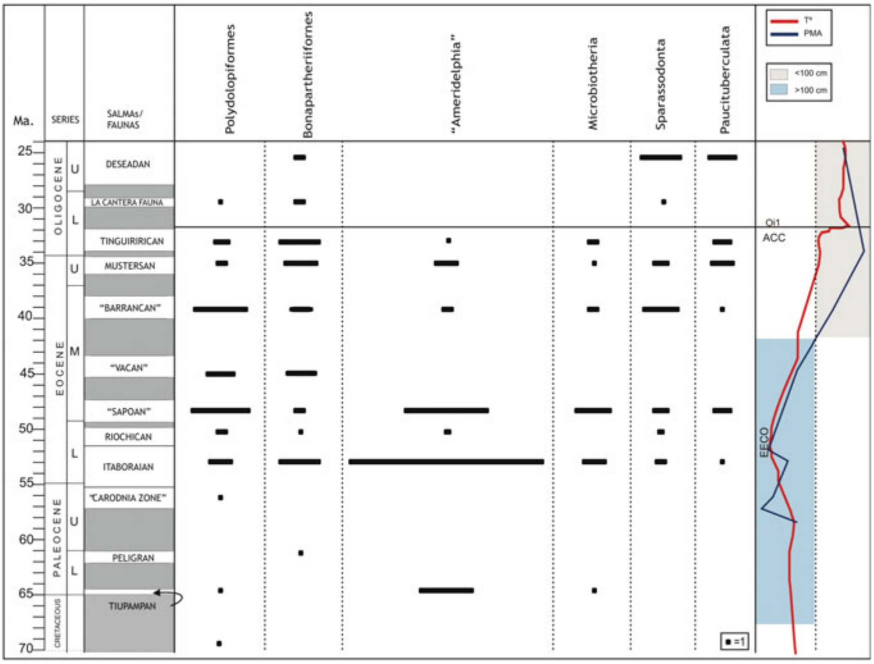


Fig. 6.1 Paleogene chronostratigraphic and biochronologic chart with the biochrons and relative diversity of each of South American metatherian lineages, and the evolution of climatic parameters. *References* T°, global temperatures (from Zachos et al. 2001); MAP, Mean Annual Precipitation (from Hinojosa 2005); SALMAs, South American Land-Mammal Ages

estimated MAP of 400 cm (Wilf et al. 2009). By the late middle Eocene diversity equilibrates to around 20 species (during the Barrancan Subage of the Casamayoran SALMA), and remains stable through the late Eocene–early Oligocene (Mustersan and Tinguiririca SALMAs). Climatic parameters by this interval attest, at least for Patagonia, to a strong reduction in MAP, down to 100 cm or less with relatively stable values of MAT around 17 °C (Fig. 6.2) both inferred from foliar physiognomy of the Río Turbio floral association (Hinojosa 2005). Later, the fossil record indicates a sharp reduction in species richness (only ten recorded species) by the early Oligocene La Cantera Patagonian local fauna (Fig. 6.2). From a paleoclimatic perspective, this fauna represents the span immediately after the Oi1 global cooling event (Zachos et al. 2001). Temperatures fall to lowest values of the Cenozoic with an estimated MAT of about 14.5 °C (Middle Ñirihuau Fm. Flora; Hinojosa 2005). This fall in global temperatures correlates with several oceanographic events that took place at the Eocene–Oligocene boundary, such as the strong drop in eustatic level (Haq et al. 1987), the opening of the Drake Passage, and the establishment of the Antarctic Circumpolar Current (ACC; Lagabrielle et al. 2009; see Chap. 3).

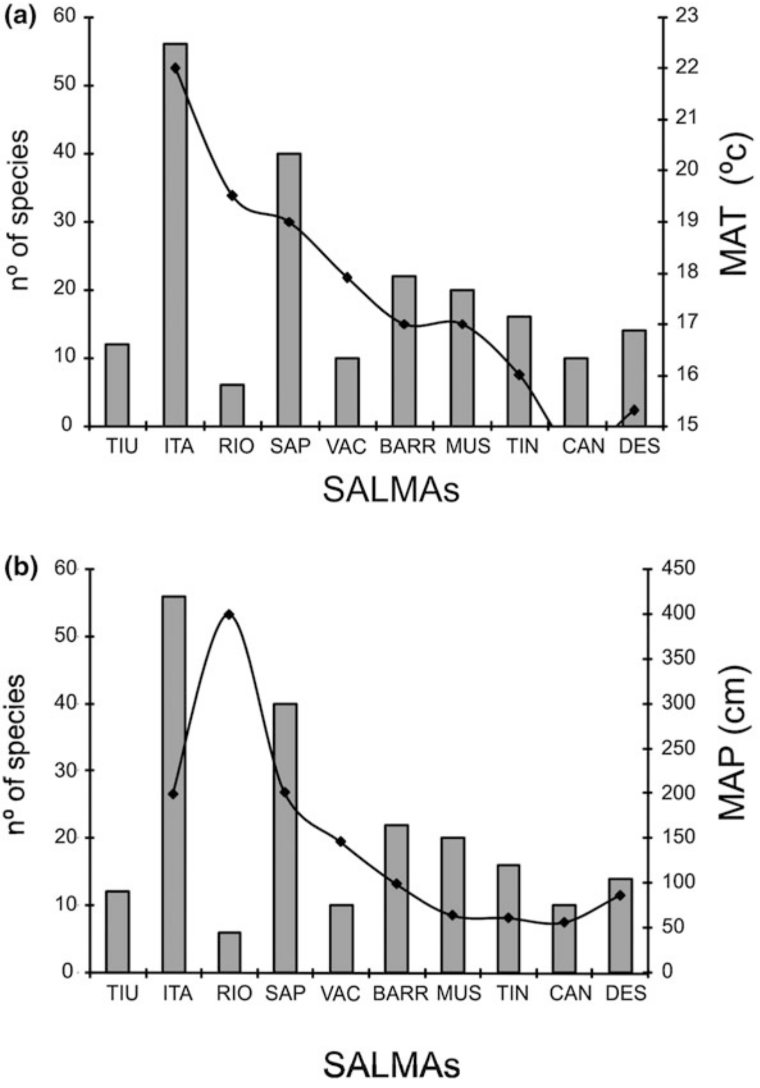


Fig. 6.2 Diversity and climatic parameters during the Paleogene for South American metatherians. Metatherian species richness is expressed as a function of **a** Mean Annual Temperatures (TMA; mainly from Hinojosa 2005), **b** Mean Annual Precipitation (MAP). *References* Bar, Barrancan Subage (Casamayoran SALMA); Can, La Cantera fauna; Des, Deseadan SALMA; Ita, Itaboraian SALMA; Mus, Mustersan SALMA; Rio, Riochican SALMA; Sap, Paso del Sapo fauna (also named as "Sapoan" in the text); Tin, Tinguiririican SALMA; Tiu, Tiupampan SALMA; Vac, Vacan Subage of the Casamayoran SALMA

The slight increase in the species richness recorded during the late Oligocene (Deseadan SALMA; 14 species; see Fig. 6.2) also correlates with a transient rise in global temperatures (an event known as Late Oligocene Warming, or LOW) and MAT (Hinojosa 2005).

The climatic evolution of South America during the Paleogene was accompanied by a succession of floristic assemblages strongly influenced by the evolution of MAT and MAP (Woodburne et al. 2013). During most of the Paleocene and early middle Eocene, megathermal forests dominate the South American landscapes. These forests were composed of Neotropical elements (Romero 1986; Hinojosa et al. 2005; Barreda and Palazzesi 2007). From the late middle Eocene (Barrancan Subage) to the early Oligocene (Tinguirirican SALMA) there was a remodeling in the floristic associations, which is evidenced by the presence of the austral microthermal genus *Nothofagus* and other meso- and micro-thermal angiosperms in Patagonian landscapes (Barreda and Palazzesi 2007). The development of savanna-like environments is supported by the record of paleosoils that attest to a transition from humid or subhumid to arid or semiarid conditions during the middle Eocene–early Oligocene (Bellosi and González 2010). Additionally, the late Eocene signals the disappearance from Patagonia of megathermal taxa, which were replaced by micro- and meso-thermal ones (Barreda and Palazzesi 2007). Finally, the Oligocene–Miocene transition in Patagonia verifies a new expansion of mega- and meso-thermal elements and a structural change in the landscapes that show a mixture of forests and grasslands biomes (Barreda and Palazzesi 2007).

It is noteworthy that metatherian diversity throughout the Paleogene shows clear similarities to that of extant South American marsupials when species richness is analyzed as a function of MAT. Birney and Monjeau (2003) concluded that the diversity of living South American marsupials is a function of the latitudinal gradient at a continental scale. For each latitudinal band they tabulated the MAT and MAP, plus other climatic variables. Comparing the species richness of fossil and living faunas of equivalent values of MAT, the result is surprisingly consistent: past diversity is quite similar to the present, both fitting well into a logarithmic curve (Fig. 6.3). Interestingly, fossil assemblages are richer than the living ones for each temperature value. Taking into account the extreme cases: the species richness of the tropical Las Flores association (Itaboraian SALMA) is 36 while any of its living, Neotropical equivalents (latitudinal bands between 10°N and 20°S) have maximum values of 30 species (Zimicz 2012). On the contrary, the cooler La Cantera Patagonian local fauna includes 10 metatherian species, while their living Patagonian equivalent that occurs between 35°S and 40°S has 7 species. This pattern is verified at virtually each latitudinal band and well-known fossil faunas, thus suggesting that the strong influence of temperatures on metatherian biology can be traced to the origin of the group, at least in South America (Zimicz 2012; see also Chap. 2).

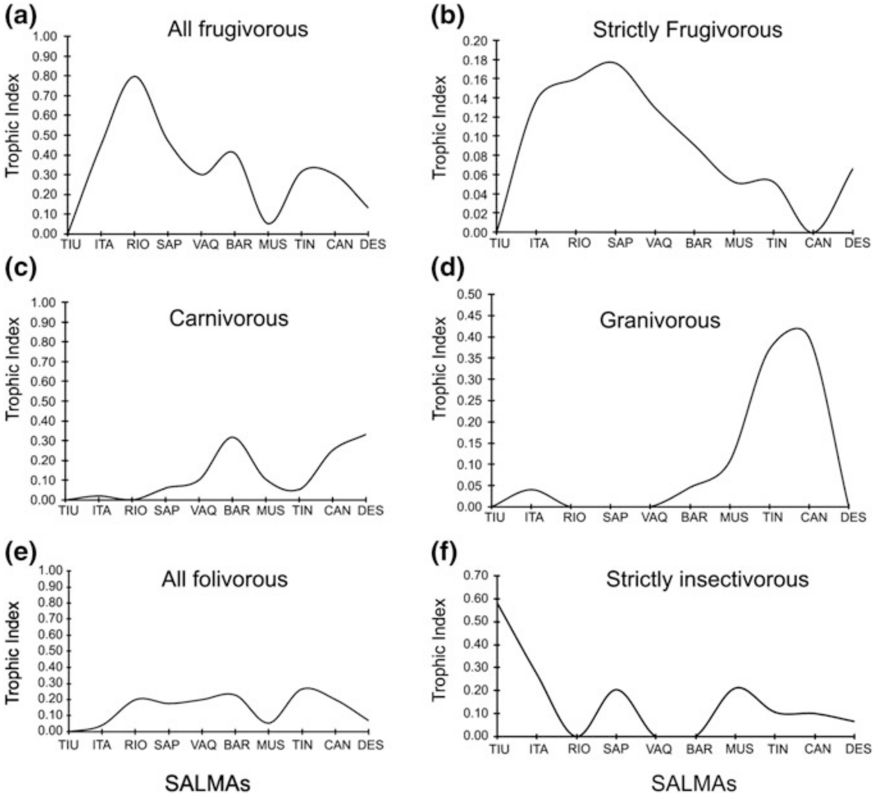


Fig. 6.3 Evolution of several trophic indexes during the Paleogene among South American metatherians. **a** All Patagonian frugivores, **b** only Patagonian strict frugivores, **c** all Patagonian carnivores, **d** all Patagonian granivores, **e** all South American folivores, **f** all South American strict insectivores

6.3 Feeding Ecology

6.3.1 *Insectivory*

Mammals that feed on invertebrate prey are regarded as insectivorous (Feldhamer et al. 2004). Invertebrates are a resource rich in high digestible nutrients such as fats and proteins, in addition to their proportionally high water contents (Hume 1999). Many invertebrates have gregarious habits; this minimizes the energy expenditure that a predator must invest in locating them. However, some restrictions exist in the feeding on invertebrate prey, restrictions which are mostly related to body mass and the input/output energy rate (Schmidt-Nielsen 1975). A medium- or large-sized mammal would require a large amount of invertebrates for satisfying its high-energy requirements, something that implies the investment of many active hours in searching for food. This would obviously unbalance the metabolic equation for a large mammal. On the contrary, a small mammal can exploit advantageously the invertebrate resource because it satisfies its requirements while exclusively feeding on one patch.

From a mechanical perspective, invertebrates are highly variable in their physical properties (Evans 2003). Taking into account exclusively the hardness of the exoskeleton, invertebrates can be subdivided into five categories, from soft to hard (Freeman 1981). This variability in the mechanical food properties has a correlate in the tooth morphology of the predator. In this sense, insectivorous mammals show a great diversity in crown morphology that follows some morphofunctional principles (Lucas 1994). The relative development of trigon and talonid basins and the roundness of cusps and crests reflect the relative hardness of the processed material. The crushing activity needed to comminute hard particles takes place on the molar basins; in turn, soft insect materials do not require large amount of crushing, but instead shearing activity prevails. The relief between the molar trigonid and talonid is also variable, depending of the hardness of the food particle: low relief is indicative of hard invertebrate processing because it is able to generate large crushing stresses (Dewar 2003). On the contrary, high relief is suggestive of soft invertebrate comminution because of the resulting shearing stress needed to reduce them.

Living marsupials that exploit the insectivorous niche in any of their multiple combinations are numerous; some examples are the caenolestids *Lestoros*, *Ryncholestes* and *Caenolestes*; the microbioterid *Dromiciops gliroides*, as well as several didelphids as *Thylamys*, *Marmosa*, *Monodelphis*, and *Lestodelphys* (Hume 1999; Gardner 2007; see Chap. 2). Extinct metatherians that have an inferred insectivorous diet can be found in many different lineages. Almost all Paleogene orders include at least some insectivorous taxa. Among the “Ameridelphia”, main exponents of insectivorous feeding habits are the Derorhynchidae and Jaskhadelphidae, which probably fed strictly on invertebrate resources. Several combinations of insectivory with other dietary categories are exemplified by the Peradectidae, Sternbergiidae and Pucadelphyidae. Among the Polydolopimorphia, only one Bonapartheriiformes (*Praedens aberrans*) was strictly insectivorous; nevertheless, insectivorous habits were widespread when combined with other feeding categories such as frugivory or granivory (e.g., Glasbiidae, Polydolopidae, Bonapartheriidae, and Prepidolopidae). Extinct Paucituberculata had several strictly insectivorous members (e.g., *Bardalestes*, *Evolestes*), as well as many insectivorous-frugivorous types (e.g., *Pilchenia*, *Parabderites*, *Carlothentes*). Microbiotherians exploited the insectivory niche, mostly related with frugivory through their entire biochron; some examples are *Microbiotherium*, *Kirutherium*, and *Mirandatherium*. Finally, Paleogene Didelphimorphia exploited insectivory in a strict sense (e.g., *Peradectes*), as well as combined with frugivory (e.g., *Caroloameghinia*, *Procaroloameghinia*).

6.3.2 Carnivory

The term refers to the intake of animal tissue as the principal dietary item (Feldhamer et al. 2004). Some authors (Chivers and Langer 1994) used the word "faunivorous" to refer those animals that feed on other animals. Here, the term "carnivory" is exclusively employed for those animals that feed exclusively on vertebrate tissues. Although vertebrate meat is a material with highly digestible nutrients, prey acquisition usually involves a great amount of energy expenditure by means of active hunting. This entails some metabolic constraints that are reflected in the body mass of the carnivorous species, which have normally intermediate sizes between the (smaller) insectivorous, granivorous, or frugivorous types on the one hand, and the (larger) herbivorous grazers on the other hand. However, the size range occupied by them is quite large, and size classification requires a particular scale. Consequently, *small* species are regarded as those weighing less than 2 kg; *medium* species are those whose body mass range from 2 to 10 kg, while *large* species are those weighing more than 10 kg.

Carnivorous mammals display a set of unique morphological specializations in the dentition for vertebrate meat comminution, in such a way that they can be studied as a separate guild with respect to the remaining dietary categories. The functional classification used here follows that of Van Valkenburgh (1988) in which *hypercarnivore* species are those whose diet is exclusively composed by vertebrate meat or bones; *mesocarnivore* species are those that eat mainly vertebrate meat but can include other items as invertebrates; finally, the *hypocarnivore* species are those whose diet is mainly composed of nonvertebrate prey such as invertebrates and fruits. Each of the above categories has a morphological correlate that can be measured by a set of morphometric parameters (Van Valkenburgh 1991). Five variables were used for discriminating between the three carnivory subcategories. The relative grinding area (RGA) is the most powerful of them and allows comparison of the relative development of the talonid—which is null in hypercarnivore species and large in hypocarnivore ones. The relative shape of the largest lower premolar (RPS) indicates the use of this tooth as a crushing or shearing tool, being a sharp crest in hypercarnivore species (except for bone eaters) and a crushing tool in the remaining subcategories. The relative size of the largest lower premolar (PS), indicates the potential use of the same as the principal element that supports the main forces during the power stroke. The relative height of the dentary or jaw depth (JD), below the carnassial tooth, is a measure of the load that the shearing complex can support during power stroke; it varies across the subcategories. The shape of the talonid is a qualitative variable that describes the relative development of this structure as well as the number of cusps carried by it. Hypercarnivore species have no talonid in their lower molars; mesocarnivore species have a moderate talonid with one cusp; hypocarnivore species have large talonids with two cusps.

Among living marsupials, only the reddish opossum, *Lutreolina crassicaudata* (Fig. 2.2b) can be regarded as a mesocarnivore species, while the remaining large didelphids are either hypocarnivore or omnivore species (e.g., *Didelphis*, *Chironectes*, *Philander*; see Fig. 2.2c–e, respectively). In sharp contrast, Paleogene metatherians show a great diversity of carnivorous species, most of which are referable to the Sparassodonta; a few other Paleogene lineages also exploited the carnivory niche to some extent (e.g., Herpetotheriidae, Mayulestidae). Most carnivorous taxa were hypercarnivores and, to a lesser degree, mesocarnivore. Among the Sparassodonta (undoubtedly, the most carnivorous of all metatherian lineages) the mesocarnivory niche was filled by the basal genus *Patene*. Hypercarnivory was largely occupied by sparassodonts of medium (e.g., *Nemolestes*) to large size (e.g., Proborhyaenidae, basal Borhyaenoidea, and Borhyaenidae; although the latter were almost exclusively of Neogene times). Among the wide variety of hypercarnivores, can be mentioned the large predaceous *Arminiheringia* (middle to late Eocene; Barrancan Subage) and the large predaceous *Pharsophorus* and *Plesiofelis*. A special mention is deserved by the giant proborhyaenids *Proborhyaena gigantea* and *Paraborhyaena boliviana*; the large sizes reached by these metatherians (93 and 76 kg each) were comparable to the largest Australasian predaceous marsupials, the Thylacoleonidae (Wroe 2003, 2004). Particularly interesting is the feeding ecology inferred for *P. gigantea*, whose morphometric indexes suggest hypercarnivorous as well as scavenger habits. Although the large size of *P. gigantea* prevented the use of bone as a food resource, at least in the context of the Optimal Foraging Theory (Charnov 1976), the widely documented co-existence with large predaceous birds of the family Phorusrhacidae, suggests a positive interaction between both, being birds responsible for the capture and killing of the prey, consuming only meat tissues, while the large proborhyaenids could have taken advantage of the carcasses. This type of interaction is well documented in living and extinct faunas (Palmqvist et al. 2011).

6.3.3 Frugivory

Mammals that feed on reproductive structures of plants are considered frugivorous (Feldhamer et al. 2004). Fruits are variable in their consistency as well as in their chemical composition. The diversity of fruits is reflected in the wide variety of morphotypes among frugivorous mammals. From a mechanical perspective, fruits can be classified as soft and juicy or hard and brittle (see Crompton and Hiiemae 1985; Lucas et al. 2002; Lucas and Peters 2000). Here, hard and brittle fruits are included in the granivory category because they share most physical properties with seeds. Soft fruits do not offer a great amount of resistance to comminution and this is reflected in the tooth morphology of frugivorous mammals. Mainly due to the fact that only lower compressive forces are required for dividing a fruit, frugivorous molars exhibit lower crowns, wide and shallow basins (which are the more prominent character of the molars), lower and rounded cups and crests, and low or null relief between talonids and trigonids in the lower molars. Sometimes, enamel crenulations are visible on the basin of the frugivorous molars.

Living South American marsupials that feed mainly on fruits are the species of the genus *Caluromys*, *Glironia*, and *Metachirus* (see Fig. 2.2a, f). Among the extinct taxa, with the single exception of the Sparassodonta, all remaining lineages of Paleogene metatherians had at least one frugivorous taxon referable to them. Among the "Ameridelphia" the most frugivorous trend was observed in the Protodidelphidae, which exhibited a wide range of body masses, from medium to large. The Polydolopimorphia exploited intensively the frugivory strategy in all combinations. The Glasbiidae (basal Polydolopimorphia) has been identified as frugivorous-insectivorous (e.g. *Palangania*, *Bobbschaefferia*). Among Polydolopidae polydolopiforms there have been recorded some strictly frugivorous types (*Pliodolops*), several frugivorous-insectivorous (e.g., *Archaeodolops*, *Polydolops*, *Pseudolops*) as well as several frugivorous-folivorous types (e.g., *Kramadolops*, *Amphidolops*). The Bonapartheriidae bonapartheriiforms shows some of its members feeding on fruits and insect resources (i.e., *Bonapartherium*, *Incadolops*). Paucituberculata was a lineage that exploited extensively the strict frugivory (e.g., *Pilchenia*, *Sasawatsu*, *Perulestes*) as well as combined with insectivory (e.g., *Carlothentes*, *Parabderites*). The Microbiotheria exploited strict frugivorous habits in their medium to large-sized members (i.e., Woodburnodontidae), as well as the frugivorous-insectivorous niche in small- and medium-sized forms (i.e., Microbiotheriidae, as *Microbiotherium* and *Clenia*).

6.3.4 Granivory

Animals that feed mainly on seeds and nuts are named granivorous (Feldhamer et al. 2004). Seeds have a high nutritional value because of their proportionally large fat contents. Fats are the principal energy reserve in mammals because they provide twice the energy of carbohydrates per weight unit (Randall et al. 1997) and are a food resource widely used by small mammals. From a mechanical point of view, seeds and nuts are hard and brittle materials (see Crompton and Hiiemae 1985; Lucas et al. 2002; Lucas and Peters 2000) that require great compressive loads in order to fracture them. Molars adapted to the processing of seeds and nuts have low crowns, low relief between talonids and trigonids, thick enamel layers, and short, rounded crests. Additionally, other dental elements (incisors and premolars) commonly show some specializations to granivory, such as their differential enamel distribution or the development of striated crests (Lucas and Peters 2000; Krause 1982).

Paleogene metatherians widely exploited the granivory niche in diverse combinations and with a variety of molar morphologies, always associated to small body masses. Among the Polydolopimorphia, the Bonapartheriiformes developed a variety of granivorous morphotypes. The Prepidolopidae includes several granivorous-insectivorous species (i.e., *Prepidolops*, *Punadolops*). The Rosendolopidae strongly exploited seed resources, all being members of the family strictly granivorous (i.e., *Rosendolops*, *Hondonadia*). All Argyrolagoidea show a trend towards granivory, mostly associated with folivory except for a single insectivorous species (*Praedens aberrans*). Both the Groeberiidae and the Argyrolagidae, as well as basal argyrolagoids, display an extraordinary combination of morphological characters that allowed them to exploit alternatively seeds as well as foliage resources.

6.3.5 Folivory

Mammals that feed on leaves and stems of dicot plants are named folivorous (Feldhamer et al. 2004). The foliage consumption requires several digestive adaptations for the processing of a food item characterized by its low digestibility and nutritional content. This requires that the folivorous mammal must devote much time to food intake, develop highly specialized digestive modifications in order to maximize the energy extraction, or both. Living Australasian folivorous marsupials (e.g., *Phascolarctos*, *Pseudocheirus*) use the digestive strategy of hindgut fermenters, in which the caecum and sometimes the proximal colon are strongly enlarged and modified for the digestion of leaves (Chivers and Langer 1994). However, the digestion in the gut is maximized by the reduction of the food particle that is carried out by molars during mastication (Hume 1999). The highly specialized molar teeth of koalas are subselenodont in structure and are composed of a series of curved blades and additionally accessory crests that provide extra cutting edges. Koalas are oblique-chewers, their main chewing activity taking place along all crests, and there is a continuous contact between opposing blades, so that mastication occurs in the horizontal plane (Hume 1999). Paleogene Bonapartheriiformes of the family Gashterniidae display a quite similar pattern, although more simple, than that of Australian folivorous marsupials. Bonapartheriiform molars are composed of a series of curved blades that suggest an oblique movement of the mandible during the power stroke. Molar enamel shows relicts of several crenulations directed at the same angle that the main molar crests. The wear pattern of gashterniids is quite similar to that of *Phascolarctos* and *Pseudocheirus* in the relative development of Phase I and Phase II facets during mastication (Zimicz 2012). The strong morphological similarities mentioned above suggest that gashterniids were the most obvious South American folivorous marsupials; their inferred body mass, although much smaller than that of a koala, for instance, lies within the range of folivorous mammals (see Zimicz 2012).

6.4 Trophic Index and Paleogene Climates

The trophic index is a rate that quantifies the relative proportion of some trophic category over the whole fauna or taxonomic association (Zimicz 2012).The frugivory index, for example, measured in an assemblage referable to a particular time

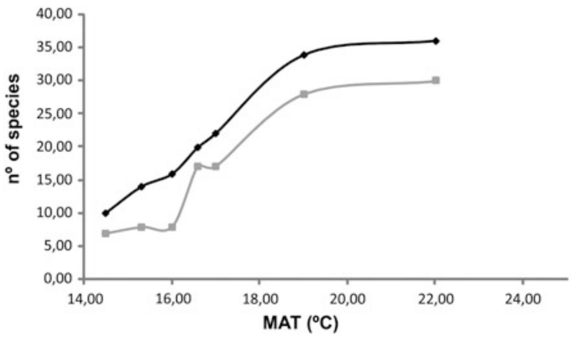


Fig. 6.4 A comparison between species richness of fossil (black line) and living (gray line) South American metatherian assemblages as a function of the mean annual temperatures (MAT)

span, is the number of frugivorous species over the total species number for that age. Throughout the Paleogene, two trophic indexes show a strong relation with climatic variables among South American metatherian associations: the *frugivory* and *carnivory* indexes.

The frugivory index shows a positive correlation with MAT (Zimicz 2012) which is particularly evident during the middle Eocene, when temperatures began to decrease (Fig. 6.4a, b). Frugivorous types dominate the late Paleocene-early Eocene tropical associations; their decline is closely correlated with the fall in average temperatures. On the contrary, the carnivory index shows a negative correlation with MAT (Zimicz 2012). It increases while MAT falls from the middle Eocene to the middle Oligocene (Fig. 6.4c). This association between frugivorous and carnivorous types with MAT also occurs in living faunas of South American marsupials (Birney and Monjeau 2003). The granivory index, although does not show a linear correlation with MAT, is particularly informative because it increases by the middle Eocene, when MAP falls around or below 100 cm (Fig. 6.4d). From the middle Eocene to the late Oligocene, granivorous types dominate the Patagonian metatherian associations together with carnivorous types (Zimicz 2012). Other trophic indexes, such as the insectivorous and folivorous ones, are not correlated with specific climatic variables, and show similar values during most of the Paleogene, independently of MAT or MAP fluctuations (Fig. 6.4e, f).

6.5 Body Mass

Body size is a measure of the spatial dimension of an organism and is the most important attribute of a biological entity (Damuth and McFadden 1990). It is traditionally measured by mean body mass, a physical quantity whose unit is the kilogram (kg), and it can be inferred for extinct mammals. Traditionally, body size of extinct mammals was inferred from the linear measurement of dental elements, which are highly correlated with body mass (Damuth and McFadden 1990). The information on body mass of extinct species is of great utility in order to understand their ecological role, as well as for the comprehension of evolutionary events that have affected different lineages. This is why the study of the evolution of body mass has a long tradition virtually in all branches of the tree of life (McNab 1971; Stanley 1973; McKinney 1990a, b). Two main theories (rules) about changes in body mass have focused researchers' attention during most of the last six decades: Cope's Rule and Bergman's Rule.

Cope's Rule describes the widespread trend of animal groups to evolve toward larger physical sizes (Cope 1887). Even though this rule was derived primarily from mammalian studies, other animal groups have been shown as examples of size increase within lineages (Stanley 1973). Although the validity of Cope's concept has been reputed several times because of its numerous exceptions, its recognition as a rule acknowledges the great number of confirmed cases of evolution towards larger sizes. Several advantages of evolutionary size increases are recognized, the most salient being: improved capacity to capture prey or ward off predators; increased home range and, consequently, a larger availability of foods resources; extended longevity; reduced mortality; greater reproductive success; finally, an increased heat retention per volume unit (Stanley 1973). However, as pointed by Stanley, the intrinsic advantage is a largely oversimplified concept. Small animals are well adapted to their own conditions as are larger ones, and the selective factors that influence the size direction are mostly related to the ancestral size and the limits that the lineage can reach—which are mainly determined by body design as well as phylogenetic or environmental constraints (Mckinney 1990a). The generalized trend to size increase in mammals is, then, the result of a probabilistic process, because small animals are much more common than larger ones (McKinney 1990b). Therefore, the ancestral size of any clade is more probably smaller than larger, in such a way that the only possible trend is to increase or keep stable the body mass. Gould (1988) named this pattern as "asymmetrical expansion of variance around founding lineages." The asymmetrical nature of this pattern is caused by the placing of the ancestral size near the lower limit of size variation. The same logic is applied to the inverse pattern in which the ancestral size is near the upper limit of size variation, so that the expansion of variance occurs toward smaller sizes (McKinney 1990a).

The geographic variation of body mass within animal groups sometimes follows a pattern toward an increase in size with latitude. This pattern was originally described at the species level (Mayr 1963) and was named as the Bergman's Rule. Briefly, this rule states that "the races from cooler climates tend to be larger than the same races living at warm climates" (Mayr 1963), at least for warm-blooded vertebrates. The basic assumption of this rule is that the increase in body mass has an energetic advantage in cold environments because the surface/volume ratio is lower in larger animals than in smaller ones (McNab 1971). A consequence of this is that the cost of thermoregulation that depends on the thermal gradient between the animal and the environment diminishes with size increase. Like Cope's, Bergman's

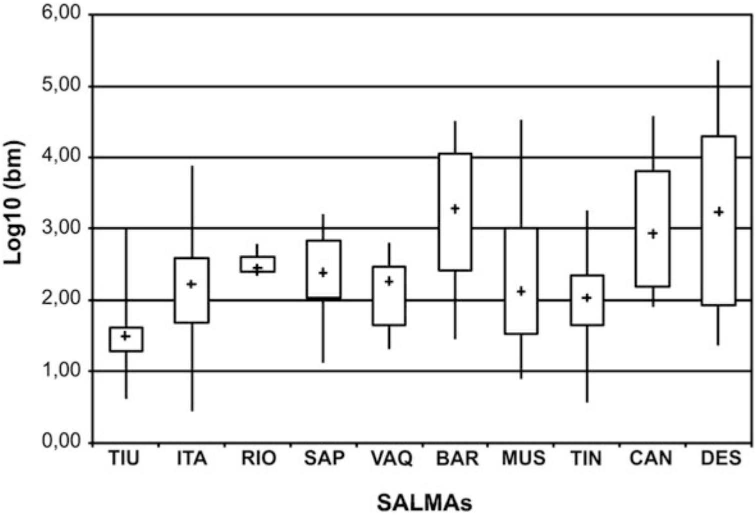


Fig. 6.5 Evolution of South American metatherians body mass throughout the Paleogene. Boxes represents 50 % of the species in each category; the plus sign (+) represents the value of the median; bars represents the variation range. *Reference* bm, body mass, estimated from molar measurements using the least square regression equations of Gordon (2003) and Zimicz (2004)

Rule cannot apply to all animal groups and is mostly restricted to some groups of homeothermic animals, marsupials among them.

The evolution of metatherian body mass during the Paleogene shows that most of the lineages had a body mass below 1000 g; however, during some time intervals this barrier was widely overcome (Fig. 6.5). The early Eocene Itaboraian SALMA constitutes the first episode of a size range expansion toward larger sizes. The large frugivorous Protodidelphidae and the large folivorous Gashterniidae are responsible for this range variation. During the middle to the late Eocene (up to the Barrancan Subage) there is a new size expansion toward larger sizes, this time staged by the hypercarnivorous Sparassodonta which are also involved in the late Oligocene (Deseadan SALMA) range expansion. In general, throughout the Paleogene, larger sizes were associated to frugivory, folivory, and carnivory, with other dietary categories mostly restricted to sizes below 1 kg. During the Paleogene, the Cope's Rule is verified at different hierarchical levels among the Polydolopiformes. The same pattern occurs at the family and genus level (i.e., *Kramadolops*). Polydolopiformes occupied a range from small to large sizes. An inverse pattern to Cope's Rule is verified in the Microbiotheria and bonapartheriiform polydolopimorphians. The first shows a general trend towards size decrease, which is independent of temperatures (Zimicz in prep.). Microbiotheres were confined mostly to the smaller size ranges (<100 g) but some members reached the medium (100–1000 g) and large (>1000 g) sizes (e.g. *Pachybiotherium* and Woodburnodontidae). Most bonapartheriiforms were confined to the smaller size ranges below 100 g

(Zimicz 2012) and only some Bonapartheriidae and Gashterniidae reached medium (100–1000 g) and large (>1000 g) sizes respectively.

Paleogene metatherians verify Bergman's Rule, Cope's Rule and in several cases a pattern of inverse trends to these. The Polydolopiformes polydolopimorphians and the Paucituberculata show several cases of adjustment to Bergman's Rule at different hierarchical levels. Among the Polydolopiformes, size increase as a function of temperature drop is a process verified at the subordinal, as well as at the family and genus (*Kramadolops* and *Amphidolops*) levels. Different families of Paucituberculata show clinal increases in body mass as a consequence of temperature drops (Abderitidae and Palaeothentidae; Zimicz 2004). Woodburnodontid microbiotherians shows an increase in body mass according to temperature fall, an opposite trend to that of the whole order, in which the average body mass diminishes through time (Zimicz 2004). At the subfamily level, both bonapartheriiform polydolopimorphians and the Sparassodonta show an apparent adjustment to Bergman's Rule in some Lazarous genus or species (*Gashternia* and *Pharsophorus*, respectively). However, in the case of Bonapartheriiformes, although the pattern is latitudinal, it doesn't correlate with any fall in temperatures because, by the early Eocene, a strong latitudinal gradient in temperatures was not yet established. In the case of the Sparassodonta, the size increase seems to be associated with the evolution of hypercarnivory. By the late Oligocene occurs the giant proborhyanid *Proborhyaena gigantea*, of about 93 kg (Zimicz 2012). The total size range within the Sparassodonta extends from small (<2 kg) to large (>10 kg) sizes; the largest amplitude of this range was reached between the late Oligocene and the middle Miocene (Zimicz, in preparation).

6.6 Paleogene Macroevolutionary Events

Throughout the Paleogene, overall diversity patterns in all lineages of metatherians exhibit some critical intervals that characterize major biotic events:

Basal ameridelphians were especially abundant during the early Eocene (Itaboraian SALMA). They filled the niches of medium- to large-sized frugivorous, small-sized insectivorous, and small mesocarnivorous types. After the early middle Eocene ("Sapoan"), "ameridelphians" show a strong reduction in their species richness and continue to decline until their extinction in late Eocene.

Polydolopiform polydolopimorphians exhibit a radiation process during the early Eocene (Itaboraian SALMA) reaching their acme during the early middle Eocene ("Sapoan" age). By this time, the ecological niches filled by the group were mainly frugivorous and insectivorus of small and medium sizes. The middle Eocene is a span of stable diversity for Polydolopiformes; by the late Eocene their species richness begins to decline. Finally, the last record of a representative of this suborder occurs at the La Cantera local fauna in Patagonia. This final interval (from the Barrancan Subage to the La Cantera times) is ecologically characterized by the dominance of large-sized frugivorous-folivorous types and the virtually absence of small- and medium-sized frugivorous ones.

Among the bonapartheriiform polydolopimorphians, the Bonapartherioidea shows a similar pattern: a strong radiation process during the early Eocene (Itaboraian SALMA) followed by a stable interval during the middle to late Eocene (Barrancan Subage to Tinguiririan SALMA). The last record for bonapartheriids transpired at the La Cantera local fauna. The Bonapartheriidae of the early Eocene was large-sized folivorous and medium-sized insectivorous-frugivorous forms. After the middle late Eocene (Barrancan Subage) a strong change towards small-sized granivorous types was recorded for most Bonapartherioidea (Zimicz 2012). The Argyrolagoidea have their first record during the middle Eocene (Vacan Subage) and continues at low diversity values (3–4 species) during the remaining Paleogene and Neogene times. They were mainly specialized in the small-sized granivorous and folivorous niches. Their last-known record occurs by the late Pliocene (Marplatan Subage).

Microbiotherians are first recorded by the early Eocene (Itaboraian SALMA; *Khasia* is regarded here as a probable pedyiomiid; consequently, it is excluded from the Microbiotheria; see Chap. 5). Microbiothere diversity was relatively stable and low, during Paleogene times; by the early Miocene they reached their acme (Goin and Abello 2013) and their record continues through the Neogene up to the recent. By the early middle Eocene, two families of microbiotheres, with different ecological roles, are recorded: Woodburnodontidae (medium- and large-sized frugivorous) and Microbiotheriidae (small-sized insectivorous-frugivorous types). Thereafter, a size constraint toward small sizes occurs with a few exceptions (i.e., *Pachybiotherium*) during the Neogene.

Sparassodonta diversity is low until the middle late Eocene (Barrancan Subage) when several medium- and large-sized hypercanivore types make their appearance. A decline in species richness occurs after the middle Eocene, while a new increase followed by the acme of the group took place during the late Oligocene–early Miocene (from the Deseadan SALMA to the Santacrucian SALMA).

The Paucituberculata shows a low diversity during the Paleogene. The order is recorded since the early Eocene (Itaboraian SALMA); it remained scarce throughout the whole Paleogene. In sharp contrast, the acme of the group took place by the beginning of the Neogene, during the early Miocene (Colhuehuapian and Santacrucian SALMAs). From an ecological perspective, the niches filled by them during the Paleogene were those of small- to large-sized insectivorous and frugivorous.

The above summary led us to identify three main Paleogene episodes in the evolution of metatherians in South America. The late Paleocene-early Eocene constitutes the main radiation event of the Paleogene and, moreover, of the entire Cenozoic. All Cenozoic lineages of South American metatherians were already present from the early Eocene (Itaboraian SALMA); the main ecological niche filled by them was that of the various frugivorous types. This diversity peak and the domain of frugivorous types indicated by the trophic index correlates with the hyperthermal events LPTM and EECO (Zachos et al. 2001) and the high precipitation regime that configured South America's tropical landscapes. After the early Eocene, global temperatures experienced a progressive drop only interrupted by the transient warming event of the middle Eocene (MECO).

The most conspicuous environmental change that took place in southern South America during the early middle Eocene was the abrupt fall in precipitation evidenced in the MAP variation from 400 cm (Laguna del Hunco Flora; Wilf et al. 2009) to 150 cm (Río Turbio Flora; Hinojosa 2005). Metatherian assemblages went with this climatic deterioration declining in species richness; they also experienced several functional and taxonomic turnovers. This biotic event is particularly evident, within the Polydolopidae, in the replacement of small- and medium-sized insectivorous-frugivorous types by the large frugivorous-folivorous ones. The replacement of folivorous and frugivorous bonapartheriids by their granivorous counterparts, as well as the advent of the large- and medium-sized hypercarnivore sparassodonts, constitute additional evidence in favor of the existence of more open (less forested) environments. The Barrancan Subage not only marks the initial radiation of open landscape indicators but also shows the declining and subsequent extinction of groups that could not adapt to the changing conditions (e.g., "basal ameridelphians"). This relatively warm but arid interval extends from the early late Eocene (Barrancan Subage) to the Tinguirirican SALMA.

The most abrupt, drastic episode in Cenozoic metatherian evolution is the Eocene–Oligocene transition which is recorded as a sudden drop in species richness accompanied by the extinction of several lineages and functional turnovers in many of the survivor lineages. This extinction event was global in its impact and has been variously termed in different regions and continents: *Grande Coupure* in Europe (Sthelin 1910), Terminal Eocene Event in North America (Prothero 1994) or Mongolian Remodeling in Asia (Meng and McKenna 1998). In the context of South American mammals, the extinction event of the Eocene–Oligocene boundary was named the Patagonian Hinge (*Bisagra Patagónica*; Goin et al. 2010a, b). From a taxonomic perspective, the early Oligocene La Cantera local fauna verifies the last record of Polydolopiformes and Bonapartheriiformes Bonapartheriioidea, as well as that of "basal ameridelphians." From an ecological perspective, this brief interval attests to several adjustments to Bergman's Rule (i.e., Sparassodonta, Polydolopiformes, Microbiotheria), the radiation of carnivorous and granivorous types, and the virtual absence of frugivorous species. This event was crucial for the future development of metatherian associations. The Sparassodonta, Paucituberculata, Bonapartheriiformes Argyrolagoidea, Didelphimorphia, and Microbiotheria were the only survivors to this "hinge," and they characterized a new, quite different history of metatherian mammals in South America during the Neogene.

All Paleogene biotic events that affected metatherian faunas in South America can be included in a model of Turnover-pulses (Vrba 1985) or Court Jester hypothesis (Barnosky 2001) in which the climatic factors are the main regulators of the successive mammalian associations. In the case of South American metatherians, both temperatures (global and MAT) and rainfall (MAP) were the factors that mostly influenced their evolutionary history throughout these times—and, quite probably, during the whole Cenozoic.

6.7 Thermal Biology: Key for the Understanding of Metatherian Evolution

Traditionally, ambient temperatures have been considered the main factor that regulates the distribution, diversity and other variables of the life history of living marsupials. The underlying reason for this is the high cost of thermoregulation that prevents marsupials from inhabiting cold environments (McNab 2005). Marsupials have a low ability to survive in cold regions because they allocate virtually all energy to maintain their body temperature; this process depends on the temperature gradient between the individual and its environment (McNab 1986, 2005; see also Chap. 2). Consequently, the energy needed to maintain homeostasis is high, and marsupials must employ diverse strategies for surviving in cold areas. Some of these strategies are the caudal fat storage and hibernation or daily torpor capacity (Geiser 2001; Birney and Monjeau 2003; Bozinovic et al. 2005). Although the effects of temperature on the biology of marsupials are widely known, the impact of precipitation was poorly considered. Fisher et al. (2001) pointed out that the rainfall regime has not influenced the life history variables of marsupials. However, other authors have provided information about the effect of rainfall on many variables of marsupial life strategies (see a review in Lee and Cockburn 1985). Among the most important life history parameters, lactation has a strong impact on the survivorship of the breeding marsupial, a fact that is highly correlated with the seasonal variation in rainfall (Green 1997). It is important to note that the gestation period in marsupials is short, and the youngones are born in a completely altricial condition (Tyndale-Biscoe 1987). Marsupial females perform the highest energy expenditure of the reproductive process during lactation to ensure the complete development of their altricial young (Lee and Cockburn 1985). The lactation period is strongly synchronized with water and food availability (Shaw 2006; see Chap. 2).

The impact of precipitation on the geographic distribution of living South American marsupials has been documented by Birney and Monjeau (2003) and Martin (2008). Other authors have argued that hibernation is triggered by a sustained scarcity of food and water availability in the South American microbiotherian *Dromiciops gliroides* (Bozinovic et al. 2004; Körtner and Geiser 1998) and other small Australian marsupials (Geiser 2001; Geiser and Ferguson 2001). Food availability is directly linked with rainfall, especially for herbivorous mammals. The successive frugivory indexes emerging from metatherian associations throughout the Paleogene strongly support this assertion. MAP had an impact on Paleogene mammal communities because of the restructuring of landscapes as well as its impact in food availability at the lowest levels of the food web. The result can be observed in the evolution of ecological and taxonomic diversity which, in metatherians, is reflected as biotic events of different intensity.

As summarized above, temperatures as well as precipitation were the most important factors that regulated the life history of Paleogene metatherians. Temperatures are the main regulator of taxonomical diversity; precipitations constitute a complementary factor whose additive effects impact on the ecological configuration of faunas, promoting functional turnovers at different scales.

References

Abello MA, Candela AM (2010) Postcranial skeleton of the Miocene marsupial *Palaeothentes* (Paucituberculata, Palaeothentidae): paleobiology and phylogeny. J Vert Paleontol 5:1515–1527

Argot C (2001) Functional-adaptive anatomy of the forelimb in the didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 247(1):51–79

Argot C (2003) Functional adaptations of the postcranial skeleton of two Miocene borhyaenoids (Mammalia, Metatheria) *Borhyaena* and *Prothylacynus*, from South America. Palaeontol 46:1213–1267

Argot C (2004) Evolution of South American mammalian predators (Borhyaenoidea): anatomical and palaeobiological implications. Zool J Linn Soc 140:487–521

Argot C, Babot J (2011) Postcranial morphology, functional adaptations and paleobiology of *Callistoe vincei*, a predaceous metatherian from the Eocene of Salta, North-western Argentina. Paleontol 54(2):447–480

Babot MJ, Powell JE, de Muizon C (2002) *Callistoe vincei*, a new Proborhyaenidae (Borhyaenoidea, Metatheria, Mammalia) from the Early Eocene of Argentina. Geobios 35:615–629

Barnosky AD (2001) Distinguishing the effects of the red queen and court jester on Miocene mammal evolution in the northern Rocky Mountains. J Vertebr Paleontol 21:172–185

Barreda V, Palazzesi I (2007) Patagonian vegetation turnovers during the Paleogene-early Neogene: origin of arid-adapted floras. Botan Rev 73:31–50

Bellosi ES, Gonzales P (2010) Paleosols of the middle Cenozoic Sarmiento Formation, central Patagonia. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York

Birney EC, Monjeau JA (2003) Latitudinal variation in South American marsupial biology. In: Menna J, Dickman C, Archer M (eds) Predators with pouches. The biology of carnivorous marsupials. Csiro Publishing, Colingwood

Bond M, Pascual R (1983) Nuevos y elocuentes restos craneanos de *Proborhyaena gigantea* Ameghino, 1897 (Marsupialia, Borhyaenidae, Proborhyaeninae) de la edad Deseadense. Un ejemplo de coevolución. Ameghiniana 10(1–2):47–60

Bozinovic F, Ruiz G, Rosenmann M (2004) Energetics and torpor of a South American living fossil, the microbiotheriid *Dromiciops gliroides*. J Comp Physiol B 174:293–297

Bozinovic F, Ruiz G, Cortés A, Rosenmann M (2005) Energetics, thermoregulation and torpor in the Chilean mouseopossum *Thylamys elegans* (Didelphidae). Rev Chilena Hist Nat 78:199–206

Bown TM, Fleagle JG (1993) Systematics, Biostratigraphy, and dental evolution of the Palaeothentidae, later Oligocene to earlymiddle Miocene (Deseadan-Santacrucian) caenolestoid marsupials of South America. Mem Paleont Soc 29:1–76

Butler PM (1983) Molar wear facets of early tertiary North American primates. In: Symposium of the 4 international congress of primatology, vol 3, pp 1–27

Butler PM (1985) Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. In: Luckett WP, Hartenberger J-L (eds) Evolutionary relationships among rodents. A multidisciplinary analysis. Plenum Press, New York

Charnov EL (1976) Optimal foraging: attack strategy of a mantid. Am Nat 110(971):141–151

Chivers DJ, Langer P (1994) The digestive system in mammals. Cambridge University Press, Cambridge

Cope ED (1887) The origin of the fittest. D. Appleton & Co, New York

Damuth J, MacFadden BJ (1990) Body size in mammalian paleobiology: estimation and biological implications. Cambridge University Press, Cambridge

de Muizon C (1991) La fauna de mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucía) Bolivia. In: Suarez-Soruco R (ed) Fósiles y Facies de Bolivia, Vol. I: Vertebrados. Rev Técn Yacimientos Petrolíferos Fiscales de Bolivia 12:575–624

de Muizon C (1998) A new carnivorous marsupial from the Paleocene of Bolivia and the problem of the marsupial monophyly. Nature 370:208–211

Dewar EW (2003) Functional diversity within the Littleton fauna (early Paleocene) Colorado: evidence from body mass, tooth structure and tooth wear. Paleobios 23(1):1–19

Dumont ER, Strait SG, Friscia AR (2000) Abderitid marsupials from the Miocene of Patagonia: an assessment of form, function, and evolution. J Paleontol 74(6):1161–1172

Evans AR (2003) Functional dental morphology of insectivorous microchiropterans: spatial modelling and functional analysis of tooth form and the influence of tooth wear and dietary properties. PhD thesis, School of Biological Sciences, Monash University

Feldhamer GA (2004) Mammalogy: adaptation, diversity, and ecology. McGraw-Hill, San Francisco

Fisher DO, Owens IPF, Johnson C (2001) The ecological basis of life history variation in marsupials. Ecol 82(12):3531–3540

Freeman PW (1981) Correspondence of food habits and morphology in insectivorous bats. J Mammal 62(1):166–173

Gardner AL (2007) Mammals of South America, Volume 1: Marsupials, Xenarthrans, Shrews and bats. University of Chicago Press, Chicago

Geiser F (2001) Hibernation: endotherms. In: Enciclopedia of life sciences. Wiley, Chichester

Geiser F, Ferguson C (2001) Intraspecific differences in behaviour and physiology: effects of captive breeding on patterns of torpor in feathertail gliders. J Comp Physiol B 171:569–576

Goin FJ (1991) Los Didelphoidea (Mammalia, Marsupialia, Didelphimorphia) del Cenozoico tardío de la Región Pampeana. PhD thesis, Univ Nac La Plata

Goin FJ (1997) New clues for understanding Neogene marsupial radiation. In: Kay RF, Madden RH, Cifelli RL, Flynn JF (eds) Vertebrate paleontology in the neotropics. The Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, Washington

Goin FJ, Abello MA (2013) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano Edad Mamífero Colhuehuapense): Microbiotheria y Polydolopimorphia. Ameghiniana 50(I):51–78

Goin FJ, Candela A (2004) New Paleogene Marsupials from the Amazon Basin of Eastern Perú. In: Campbell KE Jr (ed) The Paleogene Mammalian Fauna of Santa Rosa, Amazonian Perú. Nat Hist Mus Los Angeles County, Science Series, vol 40, pp 15–60

Goin FJ, Velázquez C, Scaglia O (1992) Orientación de las crestas cortantes en el molar tribosfénico. Sus implicancias funcionales en didelfoideos (Marsupialia) fósiles y vivientes. Rev Mus La Plata, ns, Paleontol 9(57):183–198

Goin FJ, Woodburne MO, Case JA, Vizcaíno SF, Reguero MA (1999) New discoveries of "opossum-like" marsupials from Antartica (Seymour Island, Middle Eocene). J Mammal Evol 6(4):335–365

Goin FJ, Zimicz AN, Reguero MA, Santillana S, Marenssi SA, Moly JJ (2007) A new Mammal from the Eocene of Antarctica, and the origins of the microbiotheria. Rev Asoc Geol Arg 62 (4):597–603

Goin FJ, Candela AM, Abello MA, Oliveira EO (2009) Earliest South American Paucituberculatans and their significance in the understanding of “pseudodiprotodont” marsupial radiations. Zool J Linn Soc 155:867–884

Goin FJ, Abello MA, Chornogubsky L (2010a) Middle Tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America’s Grande Coupure. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York

Goin FJ, Tejedor MF, Abello MA, Martin GM (2010b) Un nuevo microbiotérido (Mammalia, Marsupialia, Microbiotheria) de la Formación Pinturas (Mioceno temprano) de la provincia de Santa Cruz. Ameghiniana 47(1):117–122

Goin FJ, Zimicz AN, Forasiepi AM, Chornogubsky L, Abello MA (2013) The rise and fall of South American metatherians: contexts, adaptations, radiations, and extinctions. In: Rosenberger AL, Tejedor MF (eds) Origins and evolution of cenozoic South American Mammals. Vertebrate Paleobiology and Paleoanthropology Series. Springer, Berlin

Gould SJ (1988) Trends as changes in variances: a new slant on progress and directionality in evolution. J Paleontol 62:319–329

Gordon CL (2003) A first look at estimating body size in dentally conservative marsupials. J Mammal Evol 10(1/2):1–21

Green B (1997) Field energetics and water flux in marsupials. In: Saunders NR, Hinds LA (eds) Marsupial biology: recent research, new perspectives. University of New South Wales Press, Sydney

Haq BU, Handerbol J, Vail PR (1987) Chronology of fluctuating sea levels since the triassic. Science 235:1156–1167

Hiiemae KM (2000) Feeding in mammals. In: Schwenk K (ed) Feeding, form, function and evolution in tetrapod vertebrates. Academic Press, San Diego

Hiiemae K, Crompton AW (1985) Mastication, food transport and swallowing. In: Hildebrand M, Bramble B, Liem K, Wake D (eds) Functional vertebrate morphology. Belknapp Press-Harvard University Press, Cambridge

Hinojosa LF (2005) Cambios climáticos y vegetacionales inferidos a partir de paleofloras cenozoicas del sur de Sudamérica. Rev Chilena Hist Nat 32:95–115

Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge

Janis CM (1984) The use of fossil ungulate communities as indicators of climate and environment. In: Brenchley P (ed) Fossils and climate. Wiley, Chichester

Janis CM (1988) An estimation of tooth volume and hypsodonty indices in ungulate mammals; and the correlation of these factors with dietary preferences. In: Proceedings of the VIIth international symposium on dental morphology. Mem Mus nat Hist Nat 53:367–387

Kay RF, Hylander WL (1978) The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea (Marsupialia). In: Montgomery G (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington

Körtner G, Geiser F (1998) Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). Oecologia 113:170–178

Krause DW (1982) Jaw movement, dental function, and diet in the Paelocene multituberculate Ptilodus. Paleobiol 8:265–281

Lagabrielle Y, Godderis Y, Donnadieu Y, Mallabieille J, Suarez M (2009) The tectonic history of Drake Passage and its possible impacts on global climate. Earth Planet Sci Lett 279:197–211

Lee AK, Cockburn A (1985) Evolutionary ecology of marsupials. Cambridge University Press, Cambridge

Lucas PW (1994) Categorization to food items relevant to oral processing. In: Chivers DJ, Langer P (eds) The digestive system in mammals: food, form and function. Cambridge University Press, Cambridge

Lucas PW, Luke DA (1984) Chewing it over: basic principles of food breakdown. In: Chivers DJ, Wood BA, Bilsborough A (eds) Food acquisition and processing in primates. Plenum Press, New York

Lucas PW, Peters CR (2000) Function of postcanine tooth crown shape in mammals. In: Teadford MF, Smith MM, Ferguson MWJ (eds) Development, function and evolution of teeth. Cambridge University Press, Cambridge

Lucas PW, Prinz JF, Agrawal KR, Bruce IC (2002) Food physics and oral physiology. Food Qual Prefer 13:203–213

McKinney ML (1990a) Clasifying and analysing evolutionary trends. In: McNamara KJ (ed) Evolutionary trends. Belhaven Press, London

McKinney ML (1990b) Trends in body-size evolution. In: McNamara KJ (ed) Evolutionary trends. Belhaven Press, London

McNab BK (1971) On the ecological significance of Bergmann's rule. Ecology 52:845–854

McNab BK (1986) Food habits, energetics and the reproduction of marsupials. J Zool London A 208:595–614

McNab BK (2005) Uniformity in the basal metabolic rate of marsupials: its causes and consequences. Rev Chilena Hist Nat 78:183–198

Marshall LG (1977) A new species of *Lycopsis* (Borhyaenidae: Marsupialia) from the La Venta Fauna (Late Miocene) of Colombia, South America. J Paleontol 51(3):633–642

Marshall LG (1978) Evolution of the Borhyaenidae, extinct South American predaceous marsupials. Univ California Publ Geol Sci 117:1–89

Marshall LG (1980a) Review of the Hathlyacyninae, an extinct subfamily of South American "dog-like" marsupials. Fieldiana Geol NS 7:1–132

Marshall LG (1980b) Systematics of the South American marsupial family Caenolestidae. Fieldiana Geol NS 5:1–145

Marshall LG (1982a) Systematics of the South American marsupial family Microbiotheriidae. Fieldiana Geol NS 10:1–75

Marshall LG (1982b) Systematics of the extinct South American marsupial family Polydolopidae. Fieldiana Geol NS 12:1–109

Martin GM (2008) Sistemática, distribución y adaptaciones de los marsupiales patagónicos. PhD thesis, Univ Nac La Plata

Mayr E (1963) Animal species and evolution. Belknap Press, Cambridge

Meng J, Mckenna MC (1998) Faunal turnovers of Paleogene mammals from the Mongolian Plateau. Nature 394:364–367

Palmqvist P, Martínez-Navarro B, Pérez-Claros JA, Torregrosa V, Figuerido B, Jiménez Arenas JM, Patrocinio Espigares M, Ros-Montoya S, De Renzi M (2011) The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. Quatern Int 12:1–19

Pascual R (1980) Nuevos y singulares tipos ecológicos de marsupiales extinguidos de América del Sur (Paleoceno tardío o Eoceno temprano) del noroeste argentino. Actas 2 Congr Arg Paleontol Bioestrat 2:151–173

Prothero DR (1994) The late Eocene-Oligocene extinctions. Ann Rev Earth Planet Sci 22:145–165

Randall D, Burggren W, French K (1997) Eckert. Fisiología animal. Mecanismos y adaptaciones. McGraw-Hill Interamericana, Madrid

Romero EJ (1986) Paleogene Phytogeography and Climatology of South America. Ann Missouri Bot Gard 73(2):449–461

Sanson GD (1989) Morphological adaptations of theeth to diets and feeding in the Macropodoidea. In: Grigg G, Jarman P, Hume I (eds) Kangaroos, Wallabies and Rat-kangaroos. Surrey Beatty and Sons Pty. Limited, New South Wales

Sanson GD (1996) Predicting the diet of fossil mammals. In: Vickers-Rich P, Monaghan JM, Baird RF, Rich TH (eds) Vertebrate Palaeontology of Australasia. Monash University of Publishing Committee, Melbourne

Schmidt-Nielsen K (1975) Scaling in biology: the consequences of size. J Exp Zool 194:287–307

Shaw G (2006) Reproduction. In: Armati PJ, Dickman CRY, Hume ID (eds) Marsupials. Cambridge University Press, Cambridge

Solounias N, Teaford M, Walker A (1988) Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. Paleobiology 14(3):287–300

Spears RI, Crompton RH (1995) The mechanical significance of the occlusal geometry of great ape molars in food breakdown. J Human Evol 31:517–535

Stanley MS (1973) An explanation for Cope's rule. Evol 27(1):1–26

Stehlin HG (1910) Remarques sur les faunules de Mammifères des couches Éocènes et Oligocènes du Bassin de Paris. Bull Soc Géol France 9:488–520

Strait SG, Vincent JFV (1998) Primate Faunivores: physical properties of prey items. Int J Primatol 19(5):867–878

Tyndale-Biscoe CH, Renfree MB (1987) Reproductive physiology of Marsupials. Cambridge University Press, Cambridge

Van Valkenburgh B (1988) Diversity in past and present guilds of large predatory mammals. Paleobiology 14(2):155–173

Van Valkenburgh B (1991) Iterative evolution of hipercarnivory in canids (Mammalia, Carnivora): evolutionary interactions among sympatric predators. Paleobiology 17(4):340–362

Vrba ES (1985) Environment and evolution: alternative causes of the temporal distribution of evolutionary events. S Afr J Sci 81:229–236

Walker A, Hoeck HN, Pérez L (1978) Microwear of mammalian teeth as indicator of diet. Science 201(4359):908–910

Wilf P, Johnson KR, Cuneo R, Smith ME, Singer BS, Gandolfo MA (2005) Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. Am Nat 165(6):10–44

Wilf P, Little SA, Iglesias A, Zamaloa M, Gandolfo MA, Cúneo NR, Johnson KR (2009) *Papuacedrus* (Cupressaceae) in Eocene Patagonia: a new fossil link to Australasian rainforests. Am J Bot 96(11):2031–2047

Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN, López GM, Iglesias A, Zimicz AN (2013) Paleogene Land Mammal Faunas of South America; a response to global climatic changes and indigenous floral diversity. J Mamm Evol. doi:10.1007/s10914-012-9222-1

Wroe S, Myers T, Seebacher F, Kear B, Gillespie A, Crowther M, Salisbury S (2003) An alternative method for predicting body mass: the case of the Pleistocene marsupial lion. Palaeobiology 29(3):403–411

Wroe S, Argot C, Dickman C (2004) On the rarity of big fierce carnivores and primacy of isolation and area: tracking large mammalian carnivore diversity on two isolated continents. Proc R Soc London (B) 271:1203–1211

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693

Zimicz AN (2004) Paleoecología y extinción de los marsupiales con dentición plagiaulacoide de América del Sur: un estudio basado en los cambios en el tamaño corporal. Lic thesis, Univ Nac Patagonia S J Bosco

Zimicz AN (2012) Ecomorfología de los marsupiales paleógenos de América del Sur. PhD thesis, Univ Nac La Plata

Chapter 7
Summary: Milestones in the Evolution of South American Metatherians

Abstract We summarize the configuration of plates, geographical barriers, and possible dispersal events during the Late Cretaceous–Cenozoic between North and South America, the Caribbean, Antarctica, and Australia. The arrival of metatherians in South America was a Late Cretaceous event, and probably a Maastrichtian one. There are few doubts that the first metatherians in this continent arrived from North America. We suggest that not only eutherian mammals but also metatherians may have reached South America from the north in a series of successive dispersal waifs. This FABI (First American Biotic Interchange) may have replicated the successive waif dispersal mood of the late Cenozoic GABI (Great American Biotic Interchange). The initial radiation of basal South American metatherian lineages ("Ameridelphia") may have already occurred by Late Campanian-Maastrichtian times. We also suggest that a cooling pulse happening by the Latest Cretaceous (Late Maastrichtian, ca. 68–67 Ma) may have been involved in the origin of the Australidelphia, as part of the southern (Austral Kingdom) *Nothofagus* biota. Four out of six faunal phases were involved in the evolution of South American metatherians: (1) Early South American (Late Cretaceous to the Late Eocene), Late South American (Early Oligocene to late Miocene), Interamerican (Plio–Pleistocene), and Hypoamerican (Holocene). The first of these phases involved the arrival and expansion of many lineages and adaptive types. The global cooling by the Eocene–Oligocene Boundary implied the extinction of many (mostly tropical) lineages, as well as the diversification of several specialized ones. The third of these faunal phases transpired during a time lapse of ecological imbalance and global cooling, while the last phase saw already much impoverished metatherian associations throughout the continent.

Keywords Metatheria · Ameridelphia · Australidelphia evolution · Faunal phases · Paleogeography

We concluded last chapter (see Sect. 6.7) stating that ambient temperature is the main factor driving the distribution, diversity, and adaptations of metatherian mammals, living and extinct. As suggested by McNab (2005), the high cost of thermoregulation prevents living marsupials from inhabiting cold environments.

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8_7

The fossil record suggests that the same can be said of extinct metatherians (Goin et al. 2010). Also, previous studies (e.g., Martin 2008) concluded that precipitations constitute an important additional factor that regulates the life history and evolution of metatherians. While temperature triggers changes mostly in their taxonomic diversity, precipitation impacts on the ecological configuration of the faunas, promoting functional turnovers. A third major aspect, of specific impact on the origin and intercontinental affinities of South American therian mammals, is the tectonic setting of the South American Plate and that of its neighboring plates.

7.1 The Paleogeographic Context

Figure 7.1 summarizes the configuration of plates, geographical barriers, and possible dispersal events during the Late Cretaceous–Cenozoic between North and South America, the Caribbean, Antarctica, and Australia (see Chap. 3). As it happened since Late Jurassic times, the Late Cretaceous-Recent history of South American mammals can be regarded as “splendid and seldom isolated” (Wilf et al. 2013: 561). (1) Evidence at hand (see below) favors a Late Cretaceous dispersal of therian mammals from North to South America, as part of the FABI event (Goin et al. 2012); connections between the latter and Antarctica–Australia also favored dispersal events. Woodburne and Case (1996) and Case et al. (2005) suggested that the most likely dispersal of metatherians to Australia took place prior to 64 Ma when the South Tasman Rise was considered to be flooded. (2) By mid-late Paleocene, connections between North and South America were already severed, as well as, probably, between Antarctica and Australia by the end of the Paleocene (3). It is highly probable that connections between South America and Antarctica persisted throughout the Paleocene and ?early Eocene. (4) The setting of the Antarctic Circumpolar Current by the Eocene–Oligocene boundary prevented further connections between South America and Antarctica. For South America, the Oligocene and most of the Miocene was a period of strict geographic isolation. (5) By the late Miocene–Pliocene, the setting of the Panamanian isthmus reconnected the Americas, thus allowing the GABI dispersal event.

7.2 Origins of South American Metatherians

As mentioned, the most reasonable hypothesis up to date is that therian mammals are not native of South America but instead they arrived in this continent from North America by the Late Cretaceous. To Ortiz Jaureguizar and Pascual (2011 and literature cited), the arrival of therians into South America occurred during a critical, still unrecorded hiatus: the latest Cretaceous-earliest Paleocene. As suggested in Chap. 3, hadrosaur dispersal from North to South America may have been a late Campanian-early Maastrichtian event. Hadrosaurs are present in several vertebrate

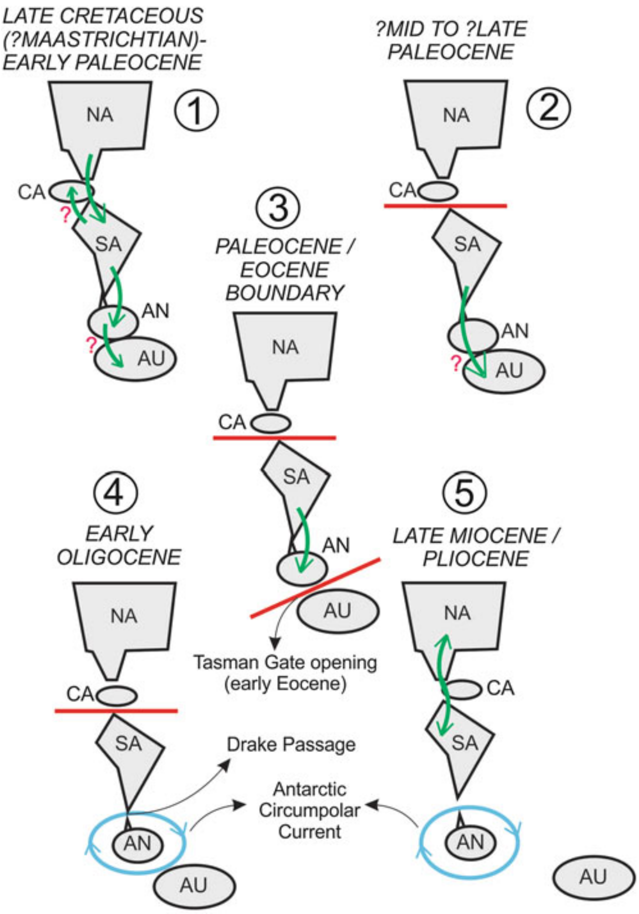


Fig. 7.1 Schematic representation of continental plates, geographical barriers for terrestrial vertebrates, and possible dispersal events during the Late Cretaceous–Cenozoic between North and South America, the Caribbean, Antarctica, and Australia. See text for an explanation

assemblages from Patagonia referred to this age (e.g., Allen Formation near Roca town; see Coria et al. 2012; Juárez Valieri et al. 2010). These assemblages have been assigned to the Late Cretaceous "Allenian tetrapod assemblage" (Leanza et al. 2004) or Alamitan Age (Bonaparte 1986; Fig. 7.1). Most important Patagonian localities of similar age and vertebrate assemblages, including mammals, are those of Los Alamitos, La Colonia, and Cerro Tortuga—though Rougier et al. (2009) have suggested that La Colonia may represent a slightly younger age than that of Los Alamitos. None of these localities (including the well-sampled Los Alamitos) has produced therian mammals up to now. The presence of a *Mesodma*-like, ?cimolodontan multituberculate from the La Colonia deposits, *Argentodites coloniensis* (Kielan-Jaworowska et al. 2007) could represent the late Cretaceous record of an immigrant non-therian mammal from North America (Ortiz-Jaureguizar 2009). Alternatively, it can be argued that the recently recorded multituberculate *Corriebaatar*, from the Early Cretaceous of Australia (Rich et al. 2009), could represent a much earlier, gondwanian lineage of allotherian mammals, to which it, as well as *Argentodites*, can be referred. Gayet et al. (2001) claimed that the younger, middle Maastrichtian levels of Pajcha Pata in Bolivia include a few therian mammals. However, further descriptions and comparisons of these scarce materials are still to be made. If their claims prove to be correct, they would represent the first arrival, in a (second?) immigrant wave from the north, of therians in South America (Ortiz Jaureguizar 2009). Finally, the North American-related South American "condylarths" of the early Paleocene of Tiupampa, Bolivia, are suggestive of an even younger, ?earliest Paleocene (Puercan equivalent) dispersal event (Gelfo et al. 2009). Thus, the First American Biotic Interchange (FABI; Fig. 7.1) may have replicated in part the complex, multi-waif dispersals of the late Neogene GABI, much better known in its timing and taxonomic content (see also Gayet et al. 1992). This also would argue in favor of the "sweepstakes" mode of dispersal of mammals from North to South America by the Late Cretaceous (see Chap. 3 and Woodburne and Case 1996). Notwithstanding, and based in the common occurrence of taxonomically related freshwater fishes from North and South America, some authors (Gayet et al. 1992) sustained a more stable, continuous connection between both continents by the late Cretaceous and early Paleocene.

Taking in account the derived nature of the earliest known South American therian mammal, the polydolopimorphian *Cocatherium lefipanum*, it is reasonable to infer that the arrival of metatherians in this continent was a Late Cretaceous event, and probably a Maastrichtian one. Muizon and Cifelli (2001) also argued that the high diversity of Tiupampian metatherians supports their Late Cretaceous dispersal into South America. It is a matter of debate whether this (these) waif(s) of dispersal(s) brought metatherian mammals to northern (Neotropical) South America much earlier, where they have not still been recorded, and that their arrival to the southern parts of the continent was done after the biogeographic barrier between Neotropical and Andean South America (i.e., the proto-arid diagonal or seasonal dry climate belt; see Chap. 4) was finally surpassed.

Case et al. (2005) hypothezised that there was not a single lineage entering South America during the Late Cretaceous, but instead several lineages already differentiated in North America. This adds a further layer of complexity to the question of metatherian arrivals in this continent. If polydolopimorphians are indeed australidelphians, a hypothesis advanced by Goin et al. (2009), it would seem to be the case that basal australidelphians were already present in North America by the Late Cretaceous (the Hatcheriiformes; Case et al. 2005, but see Williamson et al. 2012, 2014). A similar case was suggested for sparassodonts (Forasiepi 2009).

A final level of complexity results from considering whether some lineages of metatherians from the latest Cretaceous-earliest Paleocene of North America are actually immigrants *from* South America. An example of this is *Glasbius*, from the latest Cretaceous (uppermost Lance Formation, Lancian NALMA) of North

America (Clemens 1966). As mentioned, Case et al. (2005) suggested that several "South American" lineages, as the Polydolopimorphia, originated in North America. They argued that the late Campanian *Ectocentrocristus foxi* was basal to the polydolopiform radiation (but see Williamson et al. 2012), while *Hatcheritherium alpha*, as basal to the whole order. Within the Hatcheriformes, the latest Cretaceous, North American *Glasbius*, as well as the late Paleocene, South American *Palangania* (Goin et al. 1998), are currently included in the family Glasbiidae as basal polydolopimorphians. Interesting enough, *Palangania* shows several features which are more generalized than those of *Glasbius*. At least two additional, still undescribed glasbiids from the early Eocene of South America (Las Flores Formation in Patagonia) are also quite generalized as compared to the North American taxon. Because of their abundance and plesiomorphic appearance, it seems a plausible hypothesis that glasbiids had their origins in South America, by the Late Cretacous, and that they were part of a northward migration by the very end of that period. Coincidentally, Wilson (2005) suggested that *Glasbius* represents a warm-adapted species from southerly regions that expanded or shifted its geographic range northward during warming conditions near the end of the Cretaceous. Williamson et al. (2012: 646) added that "[T]he relative greater abundance of *Glasbius* in the more southerly San Juan Basin, New Mexico during the Lancian is consistent with this hypothesis." Contrary to Williamson et al. (2012) we suggest that the ultimate origin of *Glasbius* or its ancestor may have been, not southern North America, but instead South America.

7.3 Initial Radiations of Native "Ameridelphians"

When considering the diversity of the "opossum-like" metatherians from the early Paleocene of Tiupampa, Bolivia (see Muizon 1991 and literature cited), it appears that there is a mixture of relatively generalized taxa (e.g., *Pucadelphys*, *Mizquedelphys*) together with several specialized types (*Roberthoffstetteria*, *Tiulordia*, *Jaskhadelphys*). *Roberthoffstetteria's* molar pattern already anticipates that of the polydolopiform polydolopimorphians (Goin et al. 2003; Chornogubsky and Goin 2015). Besides its bunodont aspect, its upper molars have a lingually placed StC, well-developed preparaconular, and postmetaconular crista that perform high and wide anterior and posterior cinguli, and paraconule and metaconule that are shifted toward the lingual edge of the molar. All these features are even more developed in polydolopid Polydolopiformes (Goin et al. 2003). *Jaskhadelphys* shows derived features that anticipate those of the early Eocene (Itaboraian SALMA) *Minusculodelphis minimus*, an extremely derived, minutely sized "opossum-like" metatherian (3–7 g in body mass; N. Zimicz, unpublished data). For instance, its reduced, eccentric, anteroposteriorly compressed protocone seems to fit well in a quite reduced talonid structure, as that of *Minusculodelphis* (Muizon 1991; see also Oliveira 1998). Upper molars of *Tiulordia* are very compressed anteroposteriorly, with strong protocones and subparallel preparacrista and postmetacrista, while the lower dentition includes a proportionally large, swollen P3 and molars with reduced talonids and paraconids. All these features are even more derived in the Itaboraian *Gaylordia* (Oliveira 1998). An additional taxon, *Allqokirus*, shows derived features (upper molars with proportionally large postmetacrista, reduced paracone relative to the metacone, reduced and anteroposteriorly compressed protocone; lower molars with large paracristid and reduced, laterally compressed talonids) that warrants its inclusion within the Sparassodonta (Muizon 1991 and literature cited).

Marshall and Muizon (1988) and Muizon (1991) argued that the metatherian assemblage of Tiupampa was composed of structural ancestors to the early Eocene metatherians from Itaboraí. As mentioned above, several of the Tiupampian taxa can be regarded as basal to Polydolopiformes, Sparassodonta, or "Didelphimorphia". This is why Muizon (1991) and Muizon and Céspedes (in press) stated that, as a whole, the Tiupampian fauna shows few resemblances to North American Late Cretaceous and Paleocene metatherians. However, a few exceptions can be made. As it has already been suggested (see Chap. 5), molar morphology suggest affinities between the Late Cretaceous, North American *Iqualadelphys* (traditionally referred to the Pediomyidae; see alternative views in Davis 2007; Williamson et al. 2012, 2014) and the Tiupampian *Khasia* (the latter regarded as a microbiotherian marsupial by Muizon 1991). Regarding the origins of the Sparassodonta, they are still obscure (see a review on this topic in Forasiepi 2009 and literature cited). The evolution of a carnivorous diet usually involves similar (convergent) dental adaptations (the "functional complex" of Muizon and Lange-Badré 1997); therefore, phylogenetic analyses can be subject of noise derived from homoplasies. Muizon and Lange-Badré (1997) suggested that Sparassodont (their Borhyaenoidea) origins are related to early South American didelphimorphians "…rather than to Asiatic (deltatheroidan), North American (stagodontid), or Australian (dasyuroid) lineages (Muizon et al. 1997: 486). However, the term "Didelphimorphia" is so wide (see Horovitz et al. 2009, and counterarguments by Jansa et al. 2014) that, to some authors, many Late Cretaceous–Paleocene, North and South American taxa can be included. Summarizing, it is our view that the early Paleocene metatherian assemblage of Tiupampa is composed of a mixture of basal taxa indicative of North American affinities, as well as taxa suggestive of a native South American radiation. This reinforces our assumption that not eutherian mammals but also metatherians may have reached South America from the north in a series of successive dispersal waifs.

Williamson et al. (2012, 2014) recently reviewed many of the metatherians of the Late Cretaceous–Paleogene of North America. Their aim was to clarify the origin of Paleogene North American metatherians as well as the dynamics of metatherian survival after the K/Pg boundary. A major finding of this work is that the Pediomyidae (Pediomyoidea sensu Davis 2007), the "Peradectidae sensu lato," the Herpetotheriidae, and a few additional taxa as *Swaindelphys* or *Thylacodon*, comprise a major metatherian clade which is derived with respect to "alphadelphians" (see node 20 in Williamson et al. 2012: Fig. 3, and Online Supplementary

Material, Appendix 3). Derived molar features that support this clade are, in the upper molars: metacone taller than the paracone, and weakly developed or absent internal cristae en the upper molars; in the lower molars: cristid obliqua that meets the distal trigonid wall buccal to the protocristid notch, approximately below apex of the protoconid. Interestingly enough, such basal South American ameridelphians as *Szalinia* and *Pucadelphys* (the only “didelphimorphians” of this continent considered in the study) are within this clade (the paraphyletic “Peradectidae sensu lato” of Williamson et al. 2012), as well as Polydolopimorphians from North and South America (*Glasbius* and *Roberthoffstetteria*, respectively). Even though we are cautious with respect of some of their conclusions (especially, the inclusion of *Ectocentrocristus* in the Herpetotheriidae, and the exclusion of *Nortedelphys* from this clade), the study by Willliamson et al. (2012) is a significant step forward in the reconsideration of the origins of South American “basal ameridelphians.” Further hypotheses to be tested include: (1) the origins of the Microbiotheria (and, in consequence, the Australidelphia) from a pediomyoid stock (e.g., Forasiepi 2009: Fig. 54; but see below, Chap. 5, and Goin et al. 2007); (2) the origins of quite specialized lineages, like the primate-like Caroloameghiniidae (Didelphimorphia) from a peradectoid ancestor (hypothesis already advanced by Goin 2006), or (3) the origins of the Polydolopimorphia from an herpetotheriid-like ancestor (but see Case et al. 2005; Goin et al. 2009). In any case, the consideration of Williamson et al.’s (2012) results led to the conclusion that the origin of most of the major South American clades of Metatheria was a Late Cretaceous rather than a Paleocene event (Goin et al. 2006). Accordingly, several relaxed molecular clock methods suggest a Late Cretaceous common ancestor for Marsupialia (e.g., 84–78 Ma; see Meredith et al. 2008).

7.4 Origins of the Australidelphia

Assuming a Late Cretaceous origin of major South American metatherian clades (e.g., Sparassodonta, Marsupialia), it follows a consideration on the origins and initial radiation of the Australidelphia. If Goin et al.’s (2009) hypothesis on the belonging of Polydolopimorphia to the Australidelphia is confirmed, then either *Ectocentrocristus foxi* (late Campanian, North America), or *Hatcheritherium alpha* (late Maastrichtian, North America), could be regarded as the oldest known members of the Australidelphia (Case et al. 2005). It should be noted, however, that Williamson et al.’s (2012) phylogenetic analysis of late Cretaceous–Paleogene North American metatherians, led to reassign *Ectocentrocristus* to the Herpetotheriidae, while *Hatcheritherium* fell outside their node 20 (Herpetotheriidae, “Peradectidae”, and Pediomyidae) clade. *Glasbius*, the oldest polydolopimorphian considered by Williamson et al. (2012) is of latest Cretaceous (Late Maastrichtian) age.

Another approach to the problem of Australidelphian origins is to consider the Microbiotheria. Molecular and morphological features support the belonging of the

Microbiotheria to the Australidelphia (e.g., Szalay 1982, Meredith et al. 2008); an important question, therefore, concerns the origins of the microbiotherian clade. It has been previously argued (Marshall 1987; Marshall et al. 1990; Muizon 1991) on the origin of the Microbiotheria from a pediomyoid-like ancestor. Analyzing the early Paleocene, South American taxon *Khasia cordillerensis*, Muizon (1991) noted the similarities between it (regarded by him as a microbiotheriid) and the pediomyid basic molar structure, thus supporting a close phylogenetic relationship between pediomyids and microbiotherians. As mentioned in Chap. 5, however, here we consider that *Khasia* is more probably referrable to the Pediomyidae (sensu Williamson et al. 2012) than to the Microbiotheria. Particularly interesting are the similarities between *Khasia tiupampina* and *Iqualadelphis lactea*, included within the Pediomyidae by Williamson et al. (2012), even though Davis (2007) previously regarded it as an "Ameridelphian", family *incertae sedis*.

In their analysis of the basal microbiotherian *Woodburnodon casei* (Woodburnodontidae), Goin et al. (2007) suggested that, contrary to previous opinions, microbiotherians are more easily derivable from a peradectoid-like ancestor than from a pediomyid-like one. Woodburnodontids were first recognized from early to middle Eocene levels of the Antarctic Peninsula, probably equivalent in age to those of the "Sapoan" fauna of western Patagonia (Ypresian-Lutetian boundary; see Fig. 1.3). Newly discovered specimens referable to this family, coming from earlier (Itaboraian, early Eocene) deposits from central Patagonia, are currently being studied (F. Goin and A. Forasiepi, unpublished data). Notwithstanding, the origins of the Microbiotheria may largely predate the early Eocene. Goin et al. (2007) suggested that the origin, radiation, and dispersal of microbiotherians are probably related to the origin, radiation, and dispersal of the *Nothofagus* flora in the Austral biogeographic Kingdom by the late Cretaceous (see Zhang 2011 and literature cited). A series of cooling phases in the otherwise Greenhouse World of the Late Cretaceous may have triggered the radiation and expansion of the *Nothofagus* biota, including southernmost South American and Antarctic metatherians. Cooling events occurred in pulses, most probably triggering biotic responses; one of them occurred by the late Maastrichtian, ca. 68–67 Ma (GC in Fig. 7.2; Gallagher et al. 2008). Taking in account the overall metatherian fossil record, we suggest that this last cooling pulse, rather than an older one, may have been the one involved in the expansion and radiation of the *Nothofagus* biota as a whole, and of the Australidelphia as well. Meredith et al. (2008) argued that the basal split within the Australidelphia, between the Microbiotheria and the Eometatheria of Kirsch et al. (1997), occurred by 65–58 Ma, i.e., in Paleocene times. They regarded this basal split as "…compatible with the hypothesis of a single dispersal event from South America to Australia via Antarctica" (Meredith et al. 2008: 396). While we regard their suggestion as a quite plausible one, we think a stronger case to be made is that, disregarding the particular continent of their ultimate origins (South America, Antarctica, or Australia), the Australidelphian radiation was an Austral Kingdom event (Fig. 7.3).

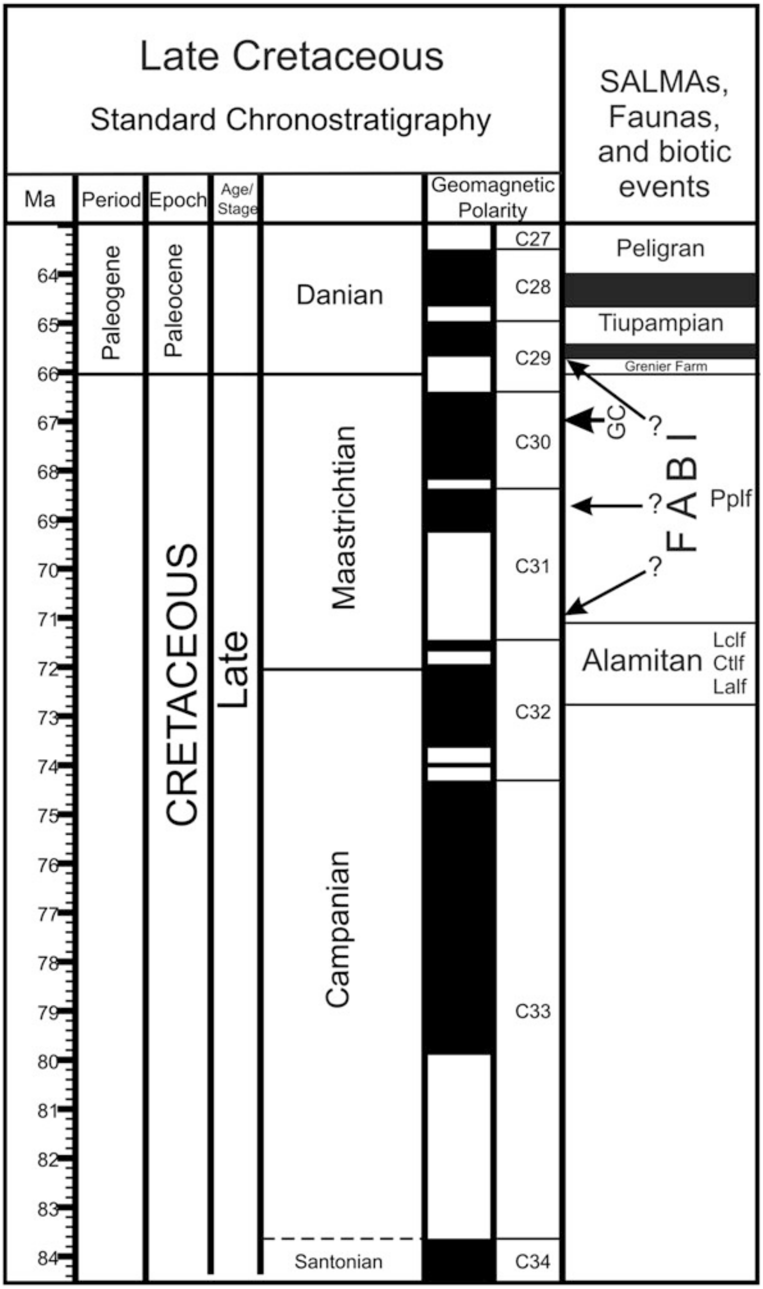


Fig. 7.2 Chronostratigraphy of the Late Cretaceous-Danian South American SALMAs, local faunas, and biotic events. For the age of the Peligran SALMA we follow Clyde et al. (2014). *References* Ctlf, Lalf, Lclf, and Pplf refer to Cerro Tortuga, Los Alamitos, La Colonia, and Pajcha Pata local faunas, respectively; FABI, First American Biotic Interchange (the arrows indicate possible dispersal events); GC, Global cooling, 67–66 Ma (see Gallagher et al. 2008 and literature cited)

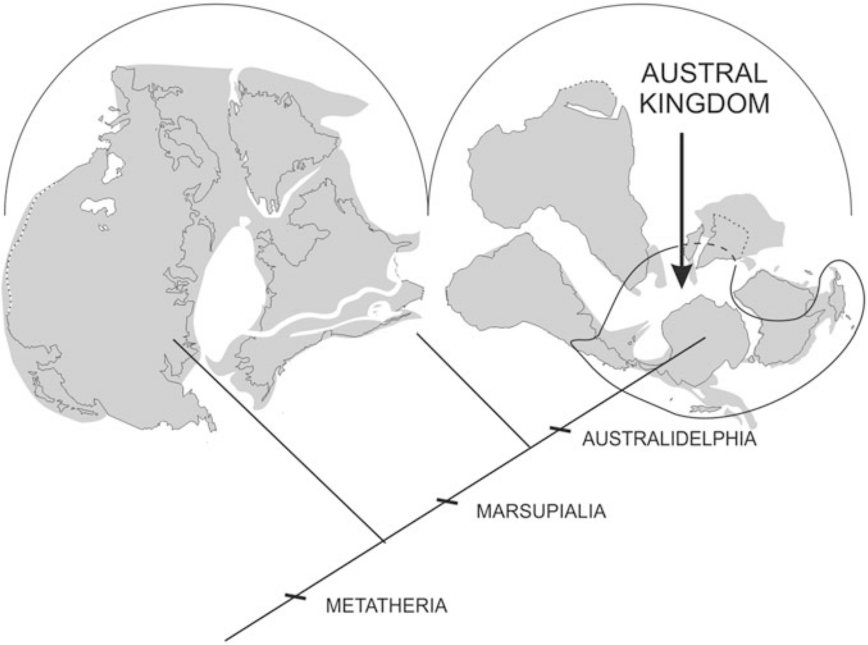


Fig. 7.3 Simplified representation of metatherian phylogenetic relationships (after, e.g., Luo et al. 2003), and the paleogeographical configurations of Northern (left) and Southern (right) hemispheres by the early Late Cretaceous. As implied here, the origins and radiation of the Australidelphia marsupials was a strictly Austral event; i.e., within the Austral (biogeographic) Kingdom. The latter includes southern South America, Antarctica, and Australasia. India, Africa, and Madagascar were far away (and isolated) from the remaining southern continents by the time of marsupial radiation

7.5 Successive Phases in the Evolution of South American Metatherians

Metatherian evolution in South America involved four out of six major phases previously described (Goin et al. 2012, in press; see Fig. 7.4). Briefly, they include:

7.5.1 Early South American Phase

This phase includes the arrival of the earliest metatherians into South America (most probably from North America), their initial diversification, their climax by the Early Eocene Climatic Optimum, and the extinction of many tropical types by the "Big Chill" that happened by the Eocene–Oligocene Boundary.

As mentioned above, the early Paleocene metatherian assemblage of Tiupampa shows several taxa that anticipate the much more derived lineages that would reach their climax by the early Eocene. Therefore, it would be expectable that, throughout the Paleocene, South American metatherians show a gradual specialization toward their more definite adaptive types of the Eocene (but see below). Unfortunately, Paleocene faunas in this continent are only poorly known. A promising fauna whose metatherians are currently under study is that of the early Paleocene (late Danian) association of Punta Peligro in eastern Patagonia (Bonaparte et al. 1993; Bond et al. 1995; Gelfo et al. 2009; see Woodburne et al. 2014: Table 1). Mammals from the biostratigraphic interval known as the *Carodnia* Zone (Simpson 1935; Peñas Coloradas Formation) are very scarce, though definite Polydolopidae marsupials are known from these levels (Marshall 1982). A recent work by Clyde et al. (2014) suggests that mammal-bearing levels of the *Carodnia* Zone could be latest Danian-early Selandian in age (see Fig. 1.3; Woodburne et al. 2014). There have been reports on the finding of mammals from the late Paleocene, vertebrate-bearing fauna of the Cerrejón Formation, in northeastern Colombia (Jaramillo et al. 2007; Cadena et al. 2012), though no study on them has yet been published.

The late Danian metatherians of Punta Peligro include a medium-sized sparassodont, a derorhynchid, a sternbergiid, a bonapartheriid polydolopimorphian, as well as a basal polydolopimorphia (see Woodburne et al. 2014: Table 1). All these taxa are clearly derived as compared to most of the Tiupampian metatherians, and compare well to Eocene taxa, even at the generic level (*Derorhynchus*, *Didelphopsis*). Probably the most derived South American metatherians (at least in molar morphology), the Polydolopidae, were already present in the latest Danian-early Selandian (Marshall 1982). This means that the radiation of major lineages in this continent was already achieved by mid-Paleocene times. Again, the early presence of derived lineages by these times suggest: (1) their probable origin in the Late Cretaceous, and (2) a long, post-Danian, pre-Vacan period of stability in the evolution of these lineages.

The great radiation of tropical forms and lineages of South American mammals has been recently described elsewhere (Woodburne et al. 2014; see also Goin et al. 2012 and in press for the Metatheria), as well as their decline by the global cooling of the Eocene–Oligocene boundary. This decline was abrupt, but probably had a series of previous steps following the gradual decline of global temperatures since the middle Eocene (Vacan subSALMA) onward.

7.5.2 *Late South American Phase*

This phase, from the early Oligocene to the Late Miocene, was characterized by the extinction of many metatherian lineages, the origin of others, and the radiation of several distinct, specialized adaptive types (e.g., granivorous, herbivorous, strictly carnivorous). In a paleogeographical sense, it was the only phase in which South

America was strictly isolated from other continents, as the Panamanian isthmic connection with North America was not yet established, and connections with Antarctica were already severed (see above and Fig. 7.1).

Two specialized lineages, the Argyrolagoidea (Polydolopimorphia) and the Borhyaenoidea (Sparassodonta) reach their climaxes and develop their most extreme adaptive types in this phase. Examples are the herbivorous, ricochetal *Argyrolagus* (Argyrolagidae), and the hypercarnivore, saber tooth *Thylacosmilus* (Thylacosmilidae). By the end of this phase, most polydolopimorphian and sparassodont lineages became extinct, and the few remaining ones were in steep decline.

7.5.3 Interamerican Phase

The faunal event (or, better, series of events) dominating this phase was the Great American Biotic Interchange or GABI, one of the most interesting biotic interchanges between two continents ever recorded. Metatherian evolution in this phase was probably marked by the adjustment to the new ecological conditions imposed by the global climatic cooling and the arrival of northern types of eutherian mammals. The last specialized types were extinct by this phase. However, and regardless of the apparently coincident timing, it is still debatable whether their extinction was a consequence of competitive displacements vis a vis eutherians. Forasiepi et al. (2007) argued there is a significant time gap between the extinction of several sparassodontan lineages and the arrival of their alleged ecological counterparts, the carnivorans. Borhyaenids have their last record in Huayquerian (late Miocene) times; Hathliacynids were extinct ca. 4 Ma; finally, Thylacosmilids have their last record during the Chapadmalalan SALMA (middle Pliocene). The last of the polydolopimorphians, the Argyrolagidae, also have their last record during the Chapadmalalan. Other lineages of specialized marsupials, such as palaeothentid and abderitid paucituberculatans, were already extinct by the late Miocene (Abello 2007). Only the generalized caenolestid paucituberculatans, together with didelphids (Didelphimorphia) and microbiotheriids (Microbiotheria), persisted until Recent times.

7.5.4 Hypoamerican Phase

The arrival of humans at the end of the Pleistocene, one of the last waves of the GABI, probably had no significant impact on metatherian populations in South America. However, marsupial diversity was already diminished, representing, in species number, less than 10 % of the mammalian associations. Of all metatherian

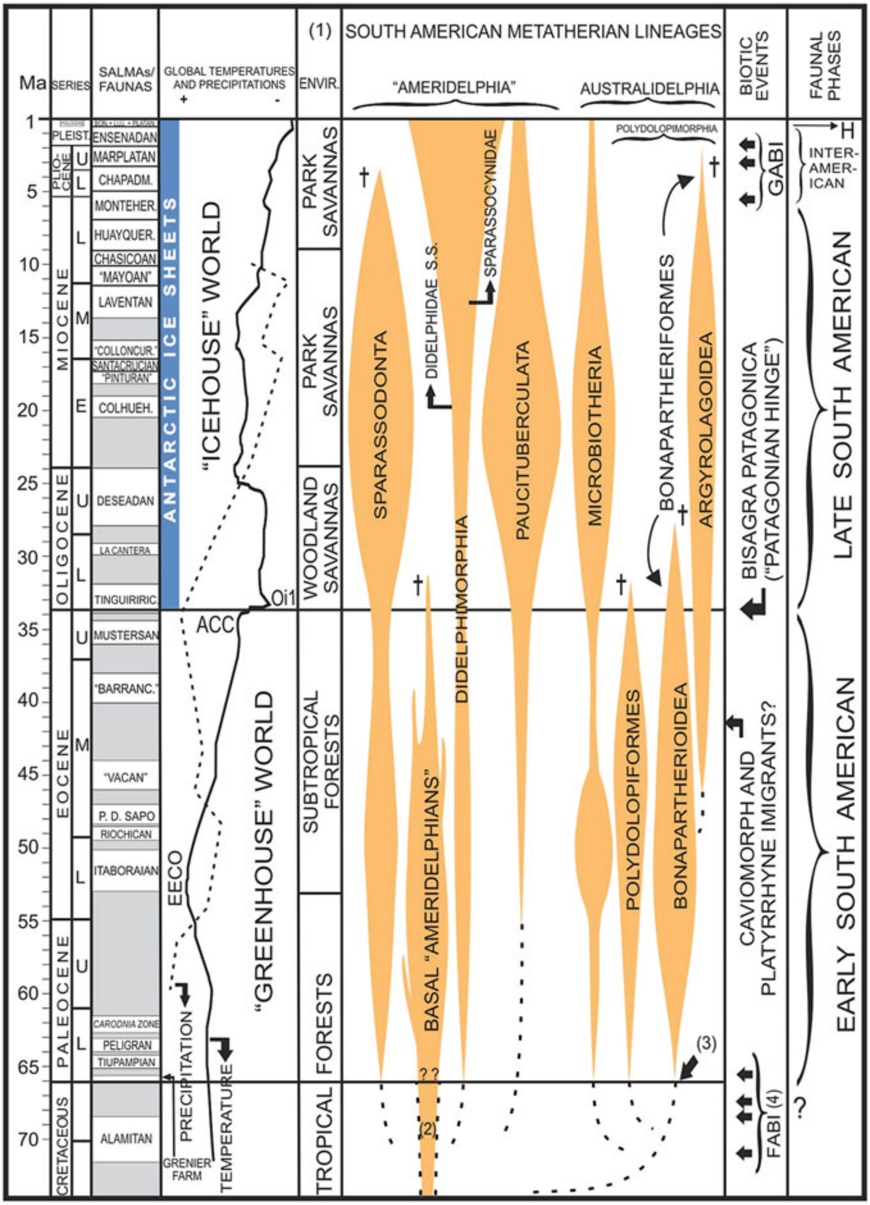


Fig. 7.4 Summary of metatherian evolution in South America throughout the Cenozoic Era. The representation includes the standard chronostratigraphic units for the last 70 m.y., SALMAs, abiotic patterns (global temperature and regional precipitations in southern South America), regional environments (Patagonia), the relative diversity of major lineages (orders) of South American metatherians, biotic events, and faunal phases. *References* (1) after Ortiz Jaureguizar and Cladera (2006); (2) there is yet no Late Cretaceous record of basal "Ameridelphians" in South America; (3) *Cocatherium lefipanum* (Goin et al. 2006) constitutes the oldest record of a Metatherian mammal known up to date

lineages once thriving in the Cenozoic of South America, representatives of only three families survived into Recent times: the pauperized Microbiotheriidae (with a single species), the Caenolestidae, and the Didelphidae.

References

Abello MA (2007) Sistemática y bioestratigrafía de los Paucituberculata (Mammalia, Marsupialia) del Cenozoico de América del Sur. Doctoral thesis, Universidad Nacional de La Plata

Bonaparte JF (1986) History of the terrestrial Cretaceous vertebrates of Gondwana. 4 Congr Arg Paleontol Bioestrat Mendoza, Actas 2:63–95

Bonaparte JF, Van Valen LM, Kramartz A (1993) La fauna local de Punta Peligro, Paleoceno Inferior, de la Provincia del Chubut, Patagonia, Argentina. Evol Monogr 14:1–61

Bond M, Carlini AA, Goin FJ, Legarreta L, Ortiz-Jaureguizar E, Pascual R, Uliana MA (1995) Episodes in South American land mammal evolution and sedimentation: testing their apparent concomitance in a Palaeocene succession from Central Patagonia. VI Congr Arg Paleontol Bioestrat Trelew, Actas 47–58

Cadena EA, Bloch JI, Jaramillo CA (2012) New bothremydid turtle (Testudines, Pleurodira) from the Paleocene of Northeastern Colombia. J Paleontol 86(4):689–699

Chornogubsky L, Goin FJ (2015) A review of the molar morphology and phylogenetic affinities of *Sillustania quechuense* (Metatheria, Polydolopimorphia, Sillustaniidae), from the early Paleogene of Laguna Umayo, southeastern Perú. J Vert Paleontol

Case JA, Goin FJ, Woodburne MO (2005) "South American" Marsupials from the Late Cretaceous of North America and the Origin of Marsupial Cohorts. J Mammal Evol 12 (3/4):461–494

Clyde WC, Wilf P, Iglesias A, Slingerland RL, Barnum T, Bijl PK, Bralower TJ, Brinkhuis H, Comer EE, Huber BT, Ibañez-Mejia M, Jicha BR, Krause JM, Schueth JD, Singer BS, Raigemborn MS, Schmitz MD, Sluijs A, Zamaloa M del C (2014) New age constraints for the Salamanca Formation and lower Río Chico Group in the western San Jorge Basin, Patagonia, Argentina: Implications for K/Pg extinction recovery and land mammal age correlations. Geol Soc Am Bull 3–4:289–306

Clemens WA (1966) Fossil mammals from the type Lance Formation, Wyoming. Part II. Univ Calif Publ Geol Sci 66:1–122

Coria RA, González Riga B, Casadío S (2012) Un nuevo hadrosáurido (Dinosauria, Ornithopoda) de la Formación Allen, Provincia de La Pampa, Argentina. Ameghiniana 49(4):552–572

Davis BM (2007) A revision of "pediomyid" marsupials from the Late Cretaceous of North America. Acta Palaeontol Pol 52(2):217–256

de Muizon C (1991) La fauna de mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucia), Bolivia. Rev Técn Yac Petrolíf Fiscales Bolivianos 12(3–4):575–624

de Muizon C, Céspedes R (in press) The beginning of the age of therian mammals in South America: Tiupampa, a transition between Northern and Southern worlds in the basal Paleocene. In: Rosenberger AL, Tejedor MF (eds) Origins and evolution of Cenozoic South American Mammals. Springer, New York

de Muizon C, Cifelli RL (2001) A new basal "Didelphoid" (Marsupialia, Mammalia) from the early Paleocene of Tiupampa (Bolivia). J Vertebr Paleontol 21(1):87–97

de Muizon C, Lange-Badré B (1997) Carnivorous dental adaptations in tribosphenic mammals and phylogenetic reconstruction. Lethaia 30:353–366

de Muizon C, Cifelli RL, Cespedes Paz R (1997) The origin of borhyaenoids, South American dog-like marsupials. Nature 389:486–489

Forasiepi AM (2009) Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. Monogr Mus Arg Cs Nat “B Rivadavia” NS 6:1–174

Forasiepi AM, Martinelli AG, Goin FJ (2007) Revisión taxonómica de *Parahyaenodon argentinus* Ameghino y sus implicancias en el conocimiento de los grandes mamíferos carnívoros del Mio-Plioceno de América de Sur. Ameghiniana 44(1):143–159

Gallagher SJ, Wagstaff BE, Baird JG, Wallace MW, Li CL (2008) Southern high latitude climate variability in the Late Cretaceous greenhouse world. Global Planet Change 60:351–364

Gayet M, Rage J-C, Sempere Th, Gagnier P-Y (1992) Modalités des échanges des vertébrés continentaux entre l’Amérique du Nord et l’Amérique du Sud au Crétacé supérieur et au Paléocène. Bull Soc géol France 163:781–791

Gayet M, Marshall LG, Sempere T, Meunier FJ, Cappetta H, Rage JC (2001) Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. Palaeogeogr Palaeoclimatol Palaeoecol 169:39–68

Gelfo JN, Goin FJ, Woodburne MO, de Muizon C (2009) Biochronological Relationships of the Earliest South American Paleogene Mammalian Faunas. Palaeontology 52(1):251–269

Goin FJ (2006) A review of the Caroloameghiniidae, Paleogene South American “primate-like” marsupials (PDidelphimorphia, Peradectoidea). In: Kalthoff D, Martin T, Möors T (eds) Festband für Herrn Professor Wighart v. Koenigswald anlässlich seines 65. Geburtstages. Palaeontographica Abt. A 278. Schweizerbart’sche Verlagsbuchhandlung, Stuttgart

Goin FJ, Candela AM, Bond M, Pascual R, Escribano V (1998) Una nueva “comadreja” (Mammalia, Marsupialia, Polydolopimorphia) del Paleoceno de Patagonia, Argentina. In: Paleógeno de América del Sur y de la Península Antártica. Spec Pub 5, Asociacion Paleontológica Argentina, Buenos Aires

Goin FJ, Candela AM, de Muizon C (2003) The affinities of *Roberthoffstetteria* nationalgeographica (Marsupialia) and the Origin of the Polydolopine Molar Pattern. J Vertebr Paleontol 23(4):869–876

Goin FJ, Pascual R, Tejedor MF, Gelfo JN, Woodburne MO, Case JA, Reguero M, Bond M, Cione AL, Udrizar Sauthier D, Balarino L, Scasso RA, Medina FA, Ubaldón MC (2006) The earliest Tertiary therian mammal from South America. J Vertebr Paleontol 26(2):505–510

Goin FJ, Zimicz AN, Reguero MA, Santillana S, Marenssi SA, Moly JJ (2007) New Mammal from the Eocene of Antarctica, and the origins of the Microbiotheria. Rev Asoc Geol Arg 62:597–603

Goin FJ, Candela AM, Abello MA, Oliveira EV (2009) Earliest South American Paucituberculatans and their significance in the understanding of “pseudodiprotodont” marsupial radiations. Zool J Linnean Soc 155:867–884

Goin FJ, Abello MA, Chornogubsky L (2010) Middle Tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America’s Grande Coupure. In: Madden RH, Carlini AA, Vucetich MG, Kay RF (eds) The Paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge University Press, New York

Goin FJ, Gelfo JN, Chornogubsky L, Woodburne MO, Martin T (2012) Origins, Radiations, and Distribution of South American Mammals: from Greenhouse to Icehouse Worlds. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: an 80-million year history of Recent Neotropical mammals Univ Chicago Press, Chicago

Goin FJ, Zimicz AN, Forasiepi AM, Chornogubsky L, Abello MA, Oliveira EV (in press) The rise and Fall of South American Metatherians: contexts, adaptations, radiations, and extinctions. In Rosenberger AL, Tejedor MF (eds), Origins and evolution of Cenozoic South American Mammals. Springer, Berlin

Horovitz T, Bloch MJ, Ladevèze S, Kurz C, Sánchez-Villagra MR (2009) Cranial anatomy of the earliest marsupials and the origin of opossums. PLoS ONE 4(12):e8278. doi:10.1371/journal.pone.0008278

Jansa SA, Barker FK, Voss RS (2014) The early diversification history of didelphid marsupials: a window into South America's "Splendid Isolation". Evolution 68:684–695

Jaramillo CA, Bayona G, Pardo-Trujillo A, Rueda M, Torres V, Harrington GJ, Mora G (2007) The palynology of the Cerrejón formation (Upper Paleocene) of Northern Colombia. Palynology 31:153–189

Juárez Valieri RD, Haro JH, Fiorelli LE, Calvo JO (2010) A new hadrosauroid (Dinosauria: Ornithopoda) from the Allen formation (Late Cretaceous) of Patagonia, Argentina. Rev Mus Arg Cs Nat "B Rivadavia" NS 12(2):217–231

Kielan-Jaworowska Z, Ortiz-Jaureguizar E, Vieytes MC, Pascual R, Goin FJ (2007) First? cimolodontan multituberculate mammal from South America. Acta Palaeontol Pol 52(2): 257–262

Kirsch JAW, Lapointe F-J, Springer MS (1997) DNA-hybridisation studies of marsupials and their implications for metatherian classification. Aust J Zool 45:211–280

Leanza HA, Apesteguía S, Novas FE, de la Fuente MS (2004) Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. Cretac Res 25:61–87

Luo ZX, Ji Q, Wible JR, Yuan CX (2003) An Early Cretaceous tribosphenic mammal and metatherian evolution. Science 302:1934–1940

Marshall LG (1982) Systematics of the extinct South American Marsupial Family Polydolopidae. Fieldiana NS 12:1–109

Marshall LG (1987) Systematics of Itaboraian (middle Paleocene) age "opossum-like" marsupials from the limestone quarry at São José de Itaboraí, Brazil. In: Archer M (ed) Possums and opossums: studies in evolution. R Zool Soc New South Wales, Surrey Beatty & Sons Pty Ltd, Chipping Norton

Marshall LG, de Muizon C (1988) The dawn of the age of mammals in South America. Nat Geogr Res 5(3):268–661

Marshall LG, Case JA, Woodburne MO (1990) Phylogenetic relationships of the families of marsupials. In: Genoways H (ed) Current mammalogy, vol 2. Plenum Press, New York

Martin GM (2008) Sistemática, Distribución y Adaptaciones de los Marsupiales Patagónicos. PhD thesis, Univ Nacional de La Plata

McNab BK (2005) Uniformity in the basal metabolic rate of marsupials: its causes and consequences. Rev Chilena Hist Nat 78:183–198

Meredith R, Westerman M, Case J, Springer M (2008) A phylogeny and timescale for marsupial evolution based on sequences for five nuclear genes. J Mammal Evol 15:1–36

Oliveira EV (1998) Taxonomia, filogenia e paleobiogeografia de marsupiais "poliprotodontes" do Mesopaleoceno da Bacia de Itaboraí, Rio de Janeiro, Brasil. PhD Thesis, Univ Fed Rio Grande do Sul, Porto Alegre

Ortiz-Jaureguizar E (2009) Evolución de la Fauna de Mamíferos de América del Sur: Evidencias, Interrogantes e Interpretaciones. In: Dopazo H, Navarro A (eds) Evolución y Adaptación. 150 años después del Origen de las Especies. Obrapropia Eds, Madrid

Ortiz-Jaureguizar E, Cladera GA (2006) Paleoenvironmental evolution of southern South America during the Cenozoic. J Arid Envir 66:498–532

Ortiz-Jaureguizar E, Pascual R (2011) The tectonic setting of the Caribbean region and the K/T turnover of the South American land-mammal fauna. Bol Geol Min 122:333–344

Rich TH, Vickers-Rich P, Flannery TF, Kear BP, Cantrill DJ, Komarower P, Kool L, Pickering D, Trusler P, Morton S, Klaveren N van, Fitzgerald EMG (2009) An Australian multituberculate and its palaeobiogeographic implications. Acta Palaeont Polonica 54:1–6

Rougier GW, Chornogubsky L, Casadio S, Páez Arango N, Giallombardo A (2009) Mammals from the Allen Formation, Late Cretaceous, Argentina. Cretac Res 30:223–238

Simpson GG (1935) Descriptions of the oldest known South American mammals, from the Río Chico Formation. Amer Mus Novit 793:1–25

Szalay FS (1982) A new appraisal of marsupial phylogeny and classification. In: Archer M (ed) Carnivorous Marsupials, vol 2. R Zool Soc New South Wales, Sydney

Wilf P, Cúneo NR, Escapa IH, Pol D, Woodburne MO (2013) Splendid and seldom isolated: the paleobiogeography of Patagonia. Ann Rev Earth Planet Sci 41:561–603

Williamson TE, Brusatte SL, Carr TD, Weil A, Standhardt BR (2012) The phylogeny and evolution of Cretaceous-Palaeogene metatherians: cladistic analysis and description of new early Palaeocene specimens from the Nacimiento Formation. New Mexico J Syst Palaeontol 10 (4):625–651

Williamson TE, Brusatte SL, Wilson GP (2014) The origin and early evolution of metatherian mammals: the Cretaceous record. ZooKeys 465:1–76. doi:10.3897/zookeys.465.8178

Wilson GP (2005) Mammalian faunal dynamics during the last 1.8 million years of the Cretaceous in Garfield County, Montana. J Mammal Evol 12(1–2):53–76

Woodburne MO, Case JA (1996) Dispersal, vicariance and the late Cretaceous to early Tertiary land mammal biogeography from South America to Australia. J Mamm Evol 3(2):121–161

Woodburne MO, Goin FJ, Bond M, Carlini AA, Gelfo JN, López GM, Iglesias A, Zimicz AN (2014) Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. J Mammal Evol. doi: 10.1007/s10914-012-9222-1

Zhang ML (2011) A cladistic scenario of Southern Pacific biogeographical history based on *Nothofagus* dispersal and vicariance analysis. J Arid Land 3(2):104–113

Index

F.J. Goin et al., *A Brief History of South American Metatherians*,
Springer Earth System Sciences, DOI 10.1007/978-94-017-7420-8