Chapter 4
Platyrrhine Ecophylogenetics in Space and Time

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4.1 Introduction

We are far from developing an informed synthesis regarding the evolution of New World Monkeys – probably decades away. For even with the important strides made over the past 30–40 years regarding platyrrhine ecology and behavior, there are large gaps in our knowledge of the evolutionary and historical context. The scarceness of fossils is but one factor. Equally critical is our incomplete knowledge of large-scale changes to the continent of South America (SAM), pertinent to the evolution of its fauna. An objective of this paper is to review some of this information as a basis for interpreting the platyrrhines from an ecophylogenetic point of view in space and time. Our goal is to integrate information on living and extinct forms in order to identify community or regional patterns of platyrrhine evolution, rather than examining the moderns and fossils as distinct entities or evolutionary problems. In keeping with the South American emphasis of this volume, we do not consider the primate fauna of the Middle American mainland but have elected to examine the Caribbean subfossil monkeys for reasons that will become clear below.

We suggest that the casual way of thinking about New World Monkeys (NWM) as a monolithic radiation inhabiting a rainforest wonderland – South America – is a model that needs to be changed. The continent is about 2.5 times the size of today's Amazonian rainforest in area, it contains diverse landscapes and habitats, and the Amazonian region changed vastly during the Cenozoic (e.g., Bigarella and Ferreira 1985). At present, more of the continent is grassland than rainforest (Fig. 4.1a), and the grasslands have been flourishing for 20–30 million years (*see* below). The first primates to arrive did not encounter the Amazonia we know, for it may have begun to take on its present character only about 15 Ma (Campbell et al. 2006). Thus, even though the NWM have a monophyletic, unitary origin, their

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Fig. 4.1a Grasslands of South America. *See* Color Insert.

evolution on the large landmass of SAM probably did not occur as a stately *in situ* unfolding.

Another adjustment in our thinking is bound up with the contrasts we tend to draw between Old and New World primates. We tend to see the platyrrhines as living in the largest, richest rain forest habitat in the world where the ecological dichotomies so evident among Old World anthropoids and strepsirhines – terrestriality and arboreality, diurnality and nocturnality, expansion of arid and humid habitats – seem like unnecessary evolutionary strategies. But it may be too facile to assume that a one-dimensional model of NWM evolving in an Edenic

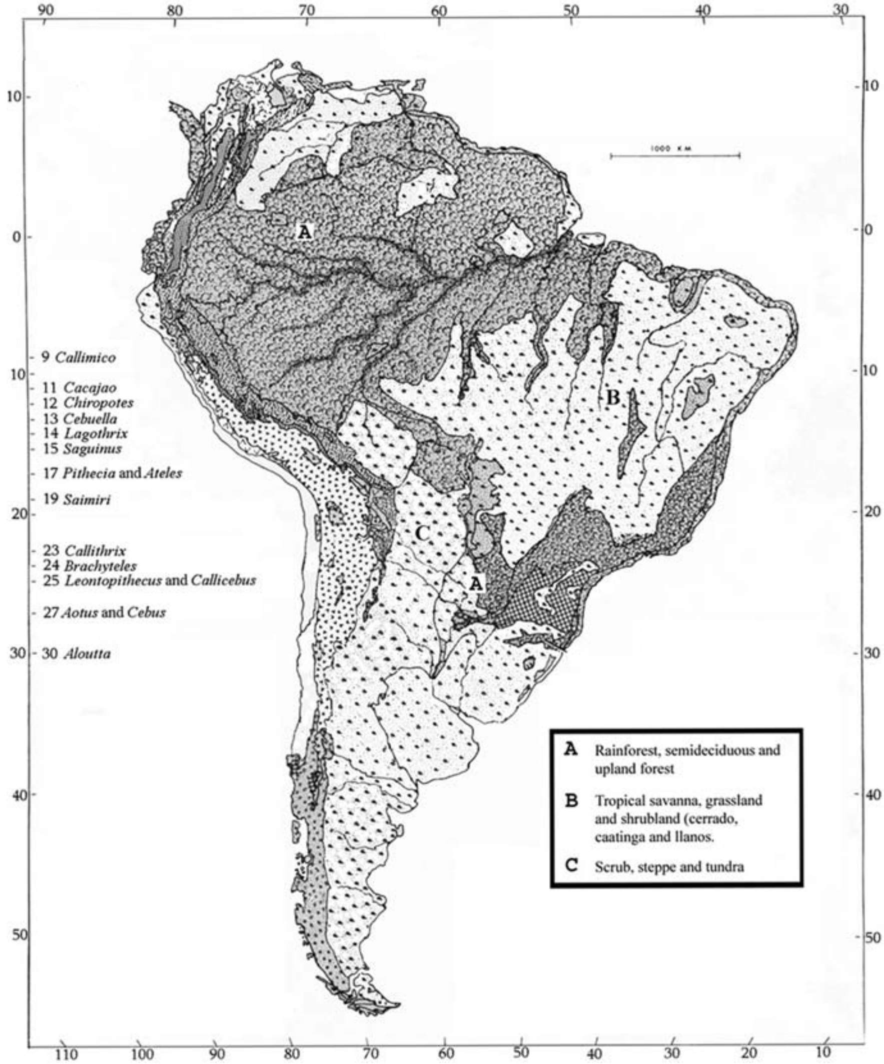

Fig. 4.1b Current distribution of tropical and subtropical forests, in South America (modified from Hershkovitz 1977). Approximate lowest latitudes of the distributions of living genera are shown on the left, compiled from Hershkovitz (1977), Kinzey (1997) and the BDGEOPRIM project, University Federal do Minas Gerais

arboreal milieu can aptly describe their full evolutionary history. To emphasize this point, consider the potential climatic implications of the important series of fossil platyrrhines from the Miocene of Patagonia. One locality in Southern Argentina, Killik Aike Norte, at about 51°S is situated more than 15° nearer to the South Pole than the southern edge of Africa. The Killik Aike Norte primates lived at the lowest latitude of any primates ever known.

The habitats occupied by today's platyrrhines are also less uniform than aerial views of Amazonia's monotonous canopy cover suggests. They are spread across a variety of biomes in Central and SAM (Hershkovitz 1977; *see* Fig. 4.1b). Calling NWM "neotropical" is something of a misnomer for while the geography of many NWM is bounded by the Tropics of Cancer and Capricorn, not all of this terrain consists of hot humid forest. Modern monkeys flourish in their own fashion as inhabitants of the extra-Amazonian, semi-deciduous domain of the Atlantic Coastal Forest (Mata Atlantica) of southeastern Brazil, for example. They also occur with success and regularity, but absent taxonomic diversity, in drier, sparsely treed, savannah-like habitats situated between the distant margins of Amazonia and the Mata Atlantica. These are tropical savannas, grasslands and shrubland habitats that comprise a large fraction of the landscape in Brazil and Venezuela. These species-poor primate communities in areas such as the Cerrado, Caatinga and Llanos regions (Fig. 4.1a), which are just as mature as rich, wet, tall-forest communities, also have a special importance for interpreting the NWM fossil record for, historically, the southern fossil NWM were anything but geographically tropical.

4.1.1 An Ecophylegenetic Approach

Why ecophylogenetic? As the foundational ideas of NWM systematics began to gel around phylogenetics (*see* Rosenberger 2002), evolutionary models have come to fuse phylogenetic and adaptational thinking (Rosenberger 1980, 1992). The result is a deeper appreciation of coherence, that platyrrhines diversified as interlinked arrays of taxa sharing unique patterns of behavior and ecology as much as they share cladogenic branches. There is a patterned structure to the platyrrhine ecological radiation that is its phylogeny. As a consequence, there are today four major guilds which we feel represent monophyletic groups, each occupying different adaptive zones. And, within each of these monophyletic groups, sublineages or genera have differentiated by evolving adaptive variations or alternative avenues of resource exploitation. To summarize, the four groups in general terms:

Callitrichines – Small-bodied predaceous frugivores specialized for locomotion and posture below the canopy of giant, large-crowned trees as well as within the fine terminal branches. They mostly exploit arthropods and insects as protein sources unless specially adapted via body size (and positional or dental specialization) for seizing large prey items (*Leontopithecus*, some *Saguinus*) or gums (especially *Callithrix, Cebuella*). Callitrichines are mostly Amazonian, but genera with derived character complexes related to specialized feeding patterns, *Leontopithecus* and *Callithrix*, are able to live successfully outside of Amazonia.

Cebines – Small-and medium-sized predaceous frugivores (*Saimiri*) and *bona fide* non-herbivorous, but also variously specialized omnivores (*Cebus*) who use the canopy as a resource base for exploiting arthropods and insects, which frequently may be embedded. *Saimiri* is decidedly Amazonian. *Cebus*, one of the order's champion generalists, is hardly limited geographically. The craniodentally specialized

C. apella group, adapted for destructive foraging, is highly successful outside of Amazonia even in the most sparse forest types.

Pitheciines – Small- and medium-sized hard-fruit and unripe-fruit eaters who live in the canopy and rely on a variety of protein sources, such as seeds (*Pithecia, Chiropotes, Cacajao*), insects (*Aotus*) and insects and leaves (*Callicebus*). Specializations on food types cluster pitheciin seed-predators such as *Chiropotes* and *Cacajao* in habitats near the Rio Amazonas, while the capacity to use low-value leaves and immature fruit allows *Callicebus* to be the most successful SAM pitheciine living at great distance from the Amazon basin, in the Mata Atlantica of Brazil and in the Chaco of western Paraguay. [We acknowledge that many researchers do not include *Aotus* in this group, but remain unconvinced that the molecular evidence outweighs a strong suite of derived morphological features shared exclusively by *Callicebus* and *Aotus* (Rosenberger and Tejedor, in press).]

Atelines – Large-bodied frugivores and semi-folivores who rely on large trees to forage and exploit leaves for protein (*Alouatta, Lagothrix, Brachyteles*), or are able to subsist almost entirely on fruit (*Ateles*). The capacity to exploit leaves for extensive periods allows two convergently derived members, *Brachyteles* and *Alouatta*, to live in less diverse, less fertile, semi-deciduous forests in the Mata Atlantica. *Alouatta*, the most folivorous platyrrhine, like the omnivorous *Cebus*, is quite successful in living under riverine conditions in sparsely treed, woodland and savannah habitats far from humid rain forests.

An obvious rationale for adopting an ecophylogenetic approach relates to our focus on the fossil record, as paleontology is naturally given to the study of interrelationships. Unfortunately, only a few scattered locations on the continent of SAM and in the Caribbean have produced platyrrhine fossils thus far; nothing is known from Middle America. What these fossils offer to better understand the nature and histories of the living species as ecological communities is a question we address. And the reverse: What do the living communities teach us about the paleobiology of fossil taxa when they co-occur? Finally, we ask if the Long Lineage Hypothesis, namely the argument that much of NWM evolution has been shaped by an impressive number of genera and lineages that have deep phylogenetic origins and little changed adaptive histories (*see* Rosenberger 1979; Delson and Rosenberger 1984; Setoguchi and Rosenberger 1987) is a robust explanation of the platyrrhines?

Although our interests in this paper can be satisfactorily addressed by examining genera and lineages, we voice a note of caution regarding an underappreciated challenge to community thinking, the poor state of alpha-level platyrrhine systematics. Without knowing how many *real biological taxa* – species – exist in any one place or region, how are we to articulate scientific questions about them? As readers of this chapter will know, while the study of NWM, historically, has rarely given energy to problems of alpha taxonomy, there has been an unprecedented proliferation of NWM species names put into use during the past 10–15 years. Comparing taxonomic works such as Napier (1976) and Groves (2001) presents a profound, de-constructivist image of this radical phenomenon. Almost always, these recent judgments have been made in the absence of original empirical research, new data or strong justification. Rather, this trend appears to stem from a shift in philosophies, thinking about what a species is and how it can be studied, and about how upward counts of biodiversity can be used, in theory, to promote conservation. We lament this diversion of purpose in the use of taxonomic terms for it can destabilize systematics, the core of all forms of biological research.

4.2 Before Platyrrhines: Paleoecology of SAM

Euprimates were achieving a pinnacle of success during the Eocene on the northern continents as adapiforms and tarsiiforms became widespread and diverse (e.g., Simons 1972; Szalay and Delson 1979; Gebo 2002; Gunnell and Rose 2002). The ultimate cause for this is related to tectonic events, but global climate may be a more direct, proximate factor. Primates appear to have been very adept at dispersal during the Eocene, presumably riding a wave of humid forest habitat expansion during a period that has been described as a "greenhouse world." Global temperatures during the Eocene were elevated, making this the ideal time for tropical flora and fauna to spread. Since the Late Paleocene Thermal Maximum (LPTM) and during the Early Eocene Climatic Optimum (EECO), between 50 and 55 Ma (Zachos et al. 2001), wet, botanically diverse forests were even in place thousands of kilometers south of the equator, at latitudes of 47–48°S (Wilf et al. 2003) in Patagonian Argentina. Thus, primates appeared abruptly in North America at the Paleo-Eocene boundary, 55–57 Ma, amidst a succession of moves from Asia (Beard 2002), including the migration of *Teilhardina* from China through Europe and into North America, a trip which may have occurred in as little as 20,000 years (Smith, Rose and Gingerich 2006). For the southern continents, we know less about diversity and biogeography. There is no evidence of their presence during the LPTM and the EECO in SAM. However, in equatorial Africa, by the end of the Eocene anthropoids were prolific in the Fayum, Egypt. There are no near-equator localities with mammals known in the Eocene of SAM but there are many concentrated in the Patagonian region. None have yielded any primates so far.

The absence of primates from the Patagonian Eocene is an important issue, but the existence of abundant fossils from other orders informs us about the conditions primates would eventually meet on the continent. Before they arrived, more than 20 different families representing over 12 orders of mammals were already established, apart from the rodents. These have been called the first phase, or Stratum 1, of the history of mammals in SAM, and include forms that were all indigenous to the continent (Fig. 4.2). The second stratum is characterized by two features, primates and caviomorph rodents, who are generally believed to be co-immigrants coming from the same source continent, and native faunal turnover. This phase brackets the late Eocene and early Miocene, when the archaic Stratum 1 mammals were replaced by their more advanced relatives. Many of the archaics were herbivorous, and they were becoming more adapted to open-country herbivory over time (Patterson and Pascual 1972; Pascual and Ortíz Jaureguizar 1990; Pascual 2006). By the late Oligocene-earliest Miocene, most of the Stratum 1 mammals had disappeared. Few could be found in the localities that have produced primates during the Early

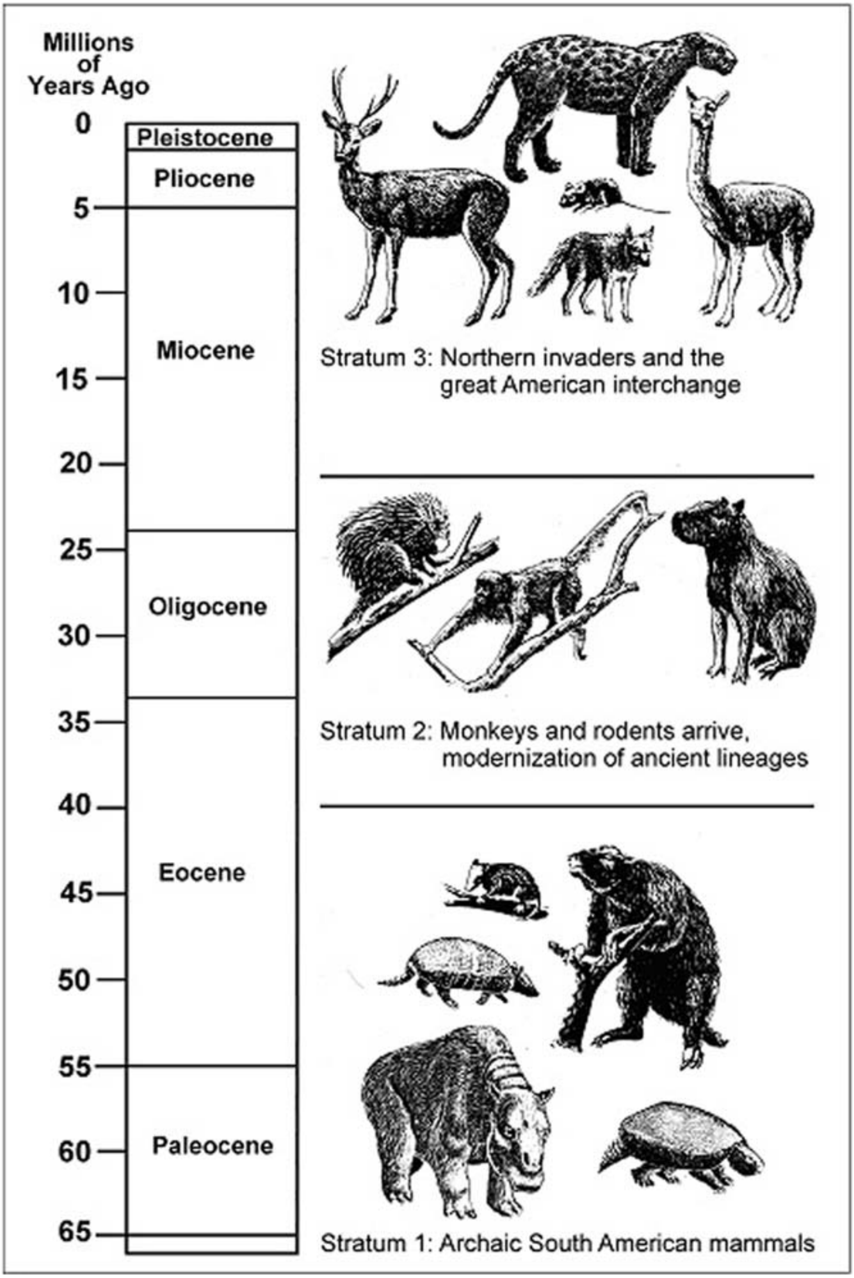

Fig. 4.2 The three major faunal strata in Cenozoic South America (from Flynn and Wyss 1998)

and Middle Miocene, 15–20 Ma. The final phase, Stratum 3, is when North American mammals began their sally into SAM to become an inexorable ecological force, while southern animals also filtered into the north. This is the Great American Biotic Interchange (Stehli and Webb 1985).

Although we assume that primates must have landed in SAM as rain forest-adapted animals, they arrived on a continent which was already becoming dominated by open country herbivorous mammals. Grasslands began to emerge during the Oligocene in the far south in Patagonia. While this may roughly coincide with the first appearance of primates in the fossil record, the oldest primate bearing locality is much nearer the equator, in Bolivia. Nevertheless, multiple lines of evidence (MacFadden 2000) show the shift from browsing to grazing occurred over a vast area, reaching from Patagonia to Bolivia, so that by Late Oligocene times the major mammalian faunas were adapted to and co-evolving with emergent grasslands. The native notoungulates provide a stunning example of this transition. This hoofed order of mammals was always abundant and taxonomically diverse in the Paleogene record (Cifelli 1985; Bond 1986; Pascual et al. 1996), with brachyodont (low-crowned) and bunodont teeth well suited for an herbivorous diet. But by the Miocene, notoungulates were characterized by high-crowned (hypsodont) and selenodont (shearing) cheek teeth, grazing adaptations. Jacobs et al. (1999) also note the presence of grasses in SAM even during the Paleocene and the dominance of mammalian herbivores in the early Oligocene Tinguiririca fauna of Chile. Today, grasslands cover about 60% of the continent (Fig. 4.1a).

Still, there are indications of non-grazing niches among Stratum 1 and Stratum 2 mammals as well. Several SAM orders and families evolved bunodont (round, low cusps) molars during the Paleogene, some with specialized morphologies designed for a variety of diets. For example, polydolopines, caroloameghiniids and protodidelphids were probably frugivorous marsupials with procumbent incisors and very low-crowned molars (*see* Goin 2003, and references therein). Didolodontids and protolipterniids were primitive ungulates ("condylarths") that also included small, primate-sized animals that were diverse and abundant (Cifelli 1985; Muizon and Cifelli 2000; Gelfo 2006). This varied fauna probably was widespread during the EECO at its peak around 52–50 Ma. Afterwards, the Eocene turned cooler for a long period of time, up until the early Oligocene (*see* Zachos et al. 2001). In the late Oligocene, during the Deseadan South American Land Mammal Age (SALMA), platyrrhines first appear in the record, in Bolivia (Table 4.1). One would expect this to have been the critical period for primates to appear in Patagonia as well, since we know that SAM caviomorph rodents existed then in Chile and Argentina (Flynn et al. 2003; Vucetich et al. 2005). However, no Patagonian localities of this age have produced primates thus far.

The Tinguiririca SALMA, which was recently identified in Chile and is probably about 31–33 Ma, has an interesting fauna because it documents the simultaneous occurrence of dentally primitive herbivorous mammals and more advanced, hypsodont forms (Flynn et al. 2003: Hitz et al. 2006), thus probably reflecting major environmental changes near the base of the Oligocene. The transition toward high-crowned teeth in several groups of herbivorous mammals is also well documented

Table 4.1 The fossil record of platyrrhine primates. Pre-Pleistocene genera marked with an asterisk are possibly "living fossils," forms closely related to modern genera as actual or possible congeners, sister-taxa or clade members classified within the same tribe as the moderns

Epoch	Platyrrhine fossils	Geographic source	Fossil locality or formation	Age
Holocene	*Antillothrix*	Hispaniola	Samaná Bay, DR; Cueva de Berna, DR; Trouing Jeremie #5, Haiti; Trouing Marassa, Haiti; Trou Jean Paul, Haiti; Trouing Carfineyis, Haiti	*ca.* 3,580 BP
Pleistocene	*Xenothrix*	Jamaica	Long Mile Cave; Skeleton Cave	*ca.*.6,730 BP
	Paralouatta varonai	Cuba	Cueva del Mono fósil; Cueva Alta	Holocene – Miocene
	Protopithecus	Brazil	Minas Gerais; Toca da Boa Vista, Bahia	*ca.* 20,000 BP
	Caipora	Brazil	Toca da Boa Vista, Bahia	*ca.* 20,000 BP
	Alouatta	Brazil	Gruta dos Brejoes, Bahia	*ca.* 20,000 BP
Late Miocene	*Acrecebus*	Brazil	Solimoes Fm, Acre	9–6.8 Ma, Huayquerian
	Solimoea	Brazil	Solimoes Fm, Acre	9–6.8 Ma, Huayquerian
Middle Miocene	*Neosaimiri*∗	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Laventan
	Laventiana	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Laventan
	Mohanamico∗	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Lamentan
	Patasola	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Laventan
	Lagonimico	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Lamentan
	*Aotus**	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Laventan
	*Cebupithecia**	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Lamentan
	Nuciruptor	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Laventan

Table 4.1 (continued)

	*Miocallicebus**	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Laventan
	*Stirtonia**	Colombia	La Venta, Upper Magdalena Valley	13.5–11.8 Ma, Laventan
	*Proteropithecia**	Argentina	Collon Cura Fm, Neuquen Province	15.8 Ma, Colloncuran
	Paralouatta marianae	Cuba	Domo de Zaza, Lagunitas Formation	~14.68–18.5 Ma
Early Miocene	*Homunculus*	Argentina	Santa Cruz Fm, Santa Cruz Province	16.5 Ma, Santacrucian
	Killikaike	Argentina	Santa Cruz Fm, Santa Cruz Province	16.5 Ma, Santacrucian
	Soriacebus	Argentina	Pinturas Fm, Santa Cruz Province	17.5–16.5 Ma, Santacrucian
	Carlocebus	Argentina	Pinturas Fm, Santa Cruz Province	17.5–16.5 Ma, Santacrucian
	*Dolichocebus**	Argentina	Sarmiento Fm, Chubut Province	~20 Ma, Colhuehuapian
	*Tremacebus**	Argentina	Sarmiento Fm?, Chubut Province	~20 Ma, Colhuehuapian
	Chilecebus	Chile	Abanico Fm, central Chile	20 Ma, Colhuehuapian
Late Oligocene	*Branisella*	Bolivia	Salla	26 Ma, Deseadan
	Szalatavus	Bolivia	Salla	26 Ma, Deseadan

at the locality of Gran Barranca, in central Patagonia, which presents a relatively continuous stratigraphic sequence from the Middle Eocene through the Eocene-Oligocene transition and the Early Miocene (Madden et al. 2005). Thus the Gran Barranca spans the EECO, the cooling phase that followed it, and also a brief period of warming, the Middle Miocene Climatic Optimum (MMCO) (Zachos et al. 2001, and references therein). Mammals are most abundant at Gran Barranca around the Eocene-Oligocene boundary, including caviomorphs, but primates are not possibly because they were rare if at all present.

The non-herbivorous mammals may have used woodland or forested habitats of some kind, interspersed within the grasslands. In fact, there is abundant paleobotanical evidence that forests of enormous species diversity existed deep in Patagonia in the early Eocene, coincident with the EECO (Wilf et al. 2003; Hinojosa 2005; Wilf et al. 2005), after which climatic cooling accompanied the extinction of some of their tropical elements (Zamaloa et al. 2006). In the north, in Colombia and Venezuela, Jaramillo et al. (2006) show a rapid increase in plant diversity during the EECO which, by early Middle Eocene, culminates in greater diversity than is found in the Holocene neotropics. Diversity drops thereafter until the early Oligocene. Thus SAM must have been a complex and changing mosaic of grasslands and forests during the Cenozoic, long before and all throughout the reign of primates in the north.

4.2.1 Before Platyrrhines: Climatic Influence of Antarctica

In the southern cone of SAM in particular, temperature and habitat during the Paleogene and early Neogene were influenced profoundly by proximity to Antarctica, by the climate and cryospheric history of that continent in what was then a uni-polar world. Early Eocene plant and pollen records from Antarctica, although sparse and fragmentary, provide a consistent view of a warm equable climate with a temperate forested continent at least along the coastline (e.g., Askin 1997; Francis and Poole 2002). Mean annual temperatures are estimated to have ranged up to 7–15°C during the PETM and early EECO on the Antarctic Peninsula (Francis and Poole 2002), oxygen isotope data from calcite cements provide paleotemperature estimates of 5–13° C (Pirrie et al. 1998), and deep-sea oxygen isotope records suggest that the warmest bottom water temperatures of the Cenozoic occurred during the early Eocene (up to 13°C) (Zachos et al. 2001).

After the EECO, Antarctica experienced a long-term cooling trend (Fig. 4.3), culminating with the expansion of continental sized ice sheets at the start of the Oligocene (e.g., Miller, Fairbanks, and Mountain 1987; Zachos et al. 2001; Francis and Poole 2002). During the middle and late Eocene, pollen and plant studies, while scant, indicate a deterioration of the environment from warm temperate to cool temperate climates (Francis and Poole 2002). Deep-sea isotopic records also suggest a cooling of bottom water from 12°C to 13°C during the early Eocene to perhaps 2–6° C by the late Eocene (e.g., Zachos et al. 2001). There is stratigraphic evidence for glaciers reaching the coast in the western Ross Sea during the late Eocene,

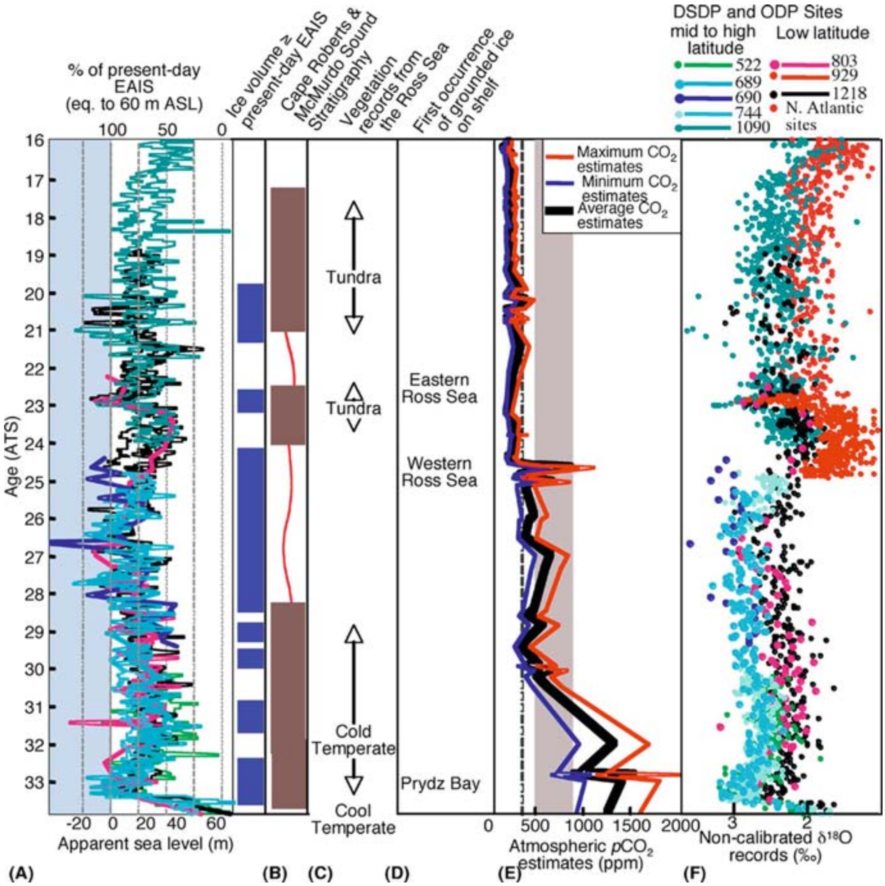

Fig. 4.3 Antarctica paleoenvironmental reconstruction from Early Oligocene to Middle Miocene (modified from Pekar and Christie-Blick, 2008). (**A**) Apparent sea-level (ASL) is global sea level plus the effects of water loading on the crust. The upper x-axis is the percent of the present-day East Antarctic Ice Sheet (EAIS) (equivalent to ~60 m ASL). The lower x-axis is ASL change: zero represents sea level resulting from ice volume lent to the present-day EAIS; increasing values represents sea-level rise; negative values represent ice volume greater than the present-day EAIS. Thick blue lines represent times when ice volume was ≥ than present-day EAIS. (**B**) Composite stratigraphy of cores drilled in the western Ross Sea. Thick brown lines represent times when sediment was preserved; red wavy lines represent hiatuses identified in cores. Note the excellent agreement when ice volume was ≥ than present-day EAIS and the timings of the hiatuses. (**C**) Reconstructed vegetation. (**D**) First occurrence of grounded ice based on core and seismic data around Antarctica. (**E**) Partial Pressure of Carbon Dioxide ($p\mathrm{CO}_2$) estimates show decreasing values during the Oligocene reaching pre-industrial levels by the latest Oligocene and continuing into the early Miocene. Dashed line represents pre-industrial values (280 ppm); shaded box represents values predicted to occur this century. (F) Deep-sea oxygen isotope (δ^{18}O) values. The abrupt decrease circa 24.5 Ma is due to a change in the source of data from high latitude to low latitude sites, with Southern Ocean sites below and mainly western equatorial Atlantic Site 929 above. (modified from Pekar and Christie-Blick, 2008.) *See* Color Insert.

although it is uncertain whether they were smaller tidewater glaciers or continental in scale (Barrett 1989). However, a growing consensus from a number of different data sources indicate that small to moderately sized ice sheets existed in Antarctica (presumably on the interior plateaus) during the middle and late Eocene (Browning et al. 1996; DeConto and Pollard 2003; Pekar et al. 2005; Miller et al. 2005).

The most significant climate shift of the Cenozoic occurred across the Eocene and Oligocene boundary (Miller et al. 1991; Zachos et al. 2001; Pekar et al., 2002), with relatively small ephemeral ice sheets expanding in the latest Eocene to large permanent ice sheets at the base of the Oligocene. In some instances, they expanded out onto the shelf during glacial maxima (e.g., Cooper et al. 1991), extending up to 500 km outboard of the present-day ice grounding lines in Prdyz Bay (Hambrey et al. 1991). This is confirmed by cores obtained from around Antarctica and a variety of other studies, which support the notion that the Oligocene ice sheets may have been 30–40% larger than the present-day East Antarctic Ice Sheet (EAIS) (Kominz and Pekar 2001; Lear et al. 2004; Pekar et al. 2002; Miller et al. 2005; Pekar and Christie-Blick 2008). In contrast, ice volume decreased to as little as 30–40 % of the present-day EAIS during glacial minima, suggesting a dynamic ice sheet during the Oligocene (Pekar et al. 2002; Lear et al. 2004; Pekar et al. 2006; Pekar and Christie-Blick 2008). Additionally, palynology records suggest that during glacial minima, climate changed from a cool temperate in the latest Eocene to a cold temperate climate in the earliest Oligocene to near tundra-like conditions by the late Oligocene (Francis and Poole 2002; Prebble et al. 2006).

The opening of the Drake Passage, which provided separation between SAM and the remnants of Gondwana, is believed to have been the final barrier to circum-Antarctic circulation. However, the timing of the opening is still uncertain with estimates of the opening to shallow waters ranging from the late middle Eocene (∼41 Ma) to early Oligocene (Lawver and Gahagan 1998; Scher and Martin 2004). A deep-water passage developed somewhat later in the Oligocene (Livermore et al. 2004; Pekar et al. 2006). Numerical modeling studies suggest the deep water Drake Passage significantly altered oceanic circulation patterns and in turn may have affected the climate on Antarctica and SAM (Mikolajewicz et al. 1993; Nong et al. 2000; Toggweiler and Bjornsson 2000; Sijp and England 2004).

During the early Miocene (23–16 Ma), Antarctica remained heavily glaciated, with ice volume being up to 30% larger than the present-day EAIS during glacial maxima, shrinking to about 40–50% of the present-day EAIS during glacial minima (Lear et al. 2004; Pekar and DeConto 2006). The coastline was sparsely vegetated, with near tundra like conditions during glacial minima (Francis and Poole 2002; Prebble et al. 2006). This is consistent with the evidence that grasslands prevailed at this time in nearby Patagonia (*see* above). Interpretations of Antarctic climate and cryosphere conditions during the middle and late Miocene through the Pliocene (15–2 Ma) are more controversial. Data from outcrops located in East Antarctica suggest a warmer, more dynamic ice sheet during the late Neogene (Webb and Harwood 1991, 1993; Francis and Hill 1996; Ashworth et al. 1997), while evidence from the geomorphologic landscape evolution of the ice-free Dry Valleys region of the continent suggests persistent cold polar condition since the Middle Miocene

(Marchant et al. 1993; Marchant et al. 1996; Sudgen et al. 1993) Fossil plants as well as insects, invertebrates and palaeosols dated as late Neogene, indicate the presence of tundra-like conditions with estimates of mean annual temperature of –12°C, and a short summer season with temperatures up to +5°C (Wilson et al. 1998; Francis et al. 2007). The relevance of a more dynamic ice sheet is that warming and cooling phases may be relatable to Patagonian climate, possibly corresponding to the flux of warmer and more forested habitats that primates prefer.

4.3 NWM: the Temporospatial and Ecophylogenetic Setting

Sites producing fossil platyrrhines (Fig. 4.4a) occur across the entire length of the Andean backbone of SAM. The outstanding fact here is their occurrence at very low latitudes in Argentina and Chile, with one locality, Killik Aike Norte, situated about 1500 km away from the tip of the Antarctic Peninsula. Paleontologists first discovered fossil NWM in 1836 (Lund 1840) but concerted efforts to recover them by mounting frequent, systematic expeditions began only in the 1980s. Thus, the New World fossil record cannot be expected to match the abundance of fossil catarrhines. What we can safely assume about the SAM record is that we have only a few clues to a small portion of the story. Most critically, we are probably missing the very beginning. The oldest fossil NWM are the Bolivian *Branisella boliviana* and *Szalatavus attricuspis* (*see* Fleagle and Tejedor 2002), about 26 Ma from the Deseadan SALMA, but this date may be long after the time when anthropoids first entered the continent.

It is generally thought that platyrrhines arrived in SAM along with caviomorph rodents, for neither order is present early in the Paleogene, both seem to first appear at about the same time, and many believe both originated in Africa and dispersed across the Atlantic Ocean. The earliest radiometric ages of the mammal assemblage where caviomorph fossils are found is ~31–32 Ma for the Chilean fossils (Flynn et al. 2003) and no more than 33.4 Ma for the Patagonian forms (Vucetich et al. 2005). But in both cases, the taxonomic diversity of the rodents is very low, and they are not abundant among the various fossil specimens collected. Even more, the Patagonian caviomorphs present a very primitive pattern of enamel microstructure (Vucetich et al. 2005, and references therein), leading to the suggestion that their SAM origins are not much older than the early Oligocene or latest Eocene. Since rodents are always by far more abundant than primates later in the SAM record, monkeys could have been even more rare proportionately early in their history. The absence of platyrrhines from some pre-Deseadan faunas may thus be an artifact of sampling, but it may also reflect different ecological requirements.

However, Poux et al. (2006) use molecular data to place the date of the caviomorph's origin at 37–45 Ma, in the Eocene. The latest date they give for platyrrhine origins is ~39 Ma, also Eocene, about 13 million years before the fossils of Salla. In contrast, in Africa, archaic fossil anthropoids are known in abundant diversity from the upper Eocene, 36 Ma (Seiffert et al. 2005) and onwards,

Fig. 4.4a Geographic distribution of continental South American fossil and subfossil platyrrhines

but modern-looking catarrhines are only well established in the early Miocene (Harrison 2002). So, it is no surprise that many platyrrhine fossils, relatively young, are of a modern aspect and relatable to the living forms. Except for questions about the earliest genera, *Branisella* and *Szalatavus*, whose affinities are not at all clear, what we have sampled thus far appears to be earlier forms of the one radiation that produced modern lineages (e.g., Rosenberger 2002). Once the NWM record becomes readable in the early and middle Miocene in terms of morphological

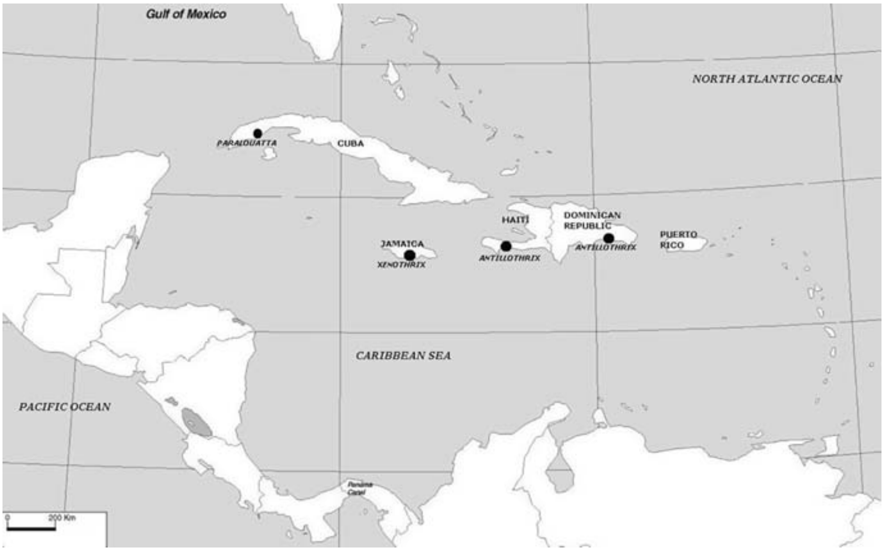

Fig. 4.4b Geographic distribution of Caribbean fossil and subfossil platyCarib map

diversity that is interpretable with some degree of confidence, controversy notwithstanding, the fossils appear to be quite closely related and adaptively similar to modern counterparts (e.g., Stirton 1951; Rosenberger 1979; Delson and Rosenberger 1984; Setoguchi and Rosenberger 1987). A preponderance of long lived genera, generic lineages and morphological stasis may be a defining feature of the platyrrhine radiation over the past 15–20 million years – the Long Lineage Hypothesis. This idea has obvious significance when considering the evolution of communities.

Rosenberger, Delson and colleagues (Rosenberger 1979; Delson and Rosenberger 1984; Setoguchi and Rosenberger 1987; Rosenberger 1992) suggested that the platyrrhine and catarrhine radiations may be fundamentally different in this regard, for Old World anthropoids have evolved as a succession of replacing adaptive radiations and few genera or lineages reveal the relatively great time depth seen in SAM. In contrast, in the New World one can identify several forms that may have congeners, sister-taxa or potential ancestors in the Miocene fossil record between 12 Ma and 20 Ma, or are so closely related that they are classified in the same tribe (Table 4.1).

By the same token, sampling error is a difficulty when interpreting the history of living communities. For example, the semi-arid Cerrado grasslands of central east Brazil supports small assemblages of two or three monkey species, often living as riverine pioneers. The composition of small mammals in these communities indicate that they are extensions of both the Amazonian forests and the Mata Atlantica (Mares et al. 1986); either may be a potential source for the primates. The adaptable *Callithrix*, *Cebus* and *Alouatta* often occur in sympatric species dyads, which is consistent with the low biological productivity of these areas. But the subfossils discovered at sites squarely within the present day Cerrado, or at the interface between Cerrado and the Mata Atlantica, the mega-sized *Protopithecus* and *Caipora* (**? ?**; Cartelle and Hartwig 1996; Hartwig and Cartelle 1996), strain the imagination: How they, too, could have coexisted with *Cebus* and *Alouatta* as the evidence indicates they did (*see* Tejedor, Rosenberger and Cartelle 2008), in the sparsely forested environs suggested by other contemporaneous mammals, such as giant ground sloths and grazing, fleet footed notoungulates (*see* Cartelle 1994)? At the same time, it is hard to fathom how *Protopithecus* and *Caipora* could have lived in a proto-Mata Atlantica if its structure closely resembled the present day forest.

Our final caveat relates to the fact that we give scant attention to the smallest platyrrhines, the callitrichines. While there are a few points of interest that arise below concerning them, marmosets and tamarins are minimally represented in the platyrrhine record and we suspect that this situation, the bias against finding small-sized specimens, will continue until there is an extensive, concerted effort to find them by adopting screen washing techniques at appropriate localities.

4.4 The Platyrrhine Provinces in Space and Time

With fossils occurring far beyond the domain of the Amazonian basin, which represents only 40% of the continent in area, rather than presuming a "center of evolution" around a monolithic Amazonia, we divide NWM into four regional groups or provinces based on fauna, geography and habitat: Amazonian, Atlantic, Caribbean and Patagonian. Each has interesting ecophylogenetic connections to fossil and subfossil species. Absent living non-human primates, the Caribbean province includes animals that are entirely extinct. Evidence indicates they have affinities with fossil SAM as opposed to living Central American species. The Patagonian province is also represented exclusively by fossils, ranging from the late Oligocene through the middle Miocene. Our concept of Patagonia is an extension of conventional usage. In addition to the common characterization of it as the region of Argentina east of the Andes and south of the Río Colorado, we also include places that encompass primate bearing sites within the southern Andes, such as the Abanico Formation of central Chile that yielded *Chilecebus carrascoensis* (Flynn et al. 1995). The growing Andean cordillera was certainly not a difficult barrier for the primates during the early Miocene, and there is no geographical or ecological reason to separate central Chile from Patagonia as different provinces.

We have not included Salla, Bolivia, with its two (or three, *see* below) important primate genera, in either the Amazonian or Patagonian provinces. Despite its geographical proximity to the former, the mammal fauna is distinctly different and there are indications of a semi-arid environment (MacFadden 1990). Comparisons of the Deseadan mammal faunas of Patagonia and Salla also highlight important ecological differences, especially among the rodents (Vucetich 1986; Pascual and Ortíz Jaureguizar 1990; Vucetich et al. 2005). Greater aridity is indicated in the south. Additionally, the pre-Deseadan rodents of Patagonia differ from Salla and from the

Oligocene rodents from Peru (Vucetich et al. 2005; Frailey and Campbell 2004). Thus while this Bolivian locale likely represents another ecological community, we still know too little about its primates to warrant much elaboration. Similarly, the various regions on the continent with distinctive habitats that currently support primates as low-diversity/density faunas, notably the Cerrado and Caatinga of east and central Brazil and the Llanos of Venezuela, are not distinguished. They are important to our thesis as analogues of several fossil assemblages, but do not merit recognition as separate provinces.

4.4.1 The Amazonian Province

The Amazon rainforest is the most dynamic terrestrial ecological region in the world, as it annually transforms with rainfall patterns, from being a river and then a lake, as seasons cycle from dry to wet (*see* Hess et al. 2003). More than a dozen primate species and as many as a dozen genera can easily be found at many lowland locations within the province. How these primates operate within a structured community has been the subject of excellent discussions by Terborgh (1983, 1985) who explains the general ecological factors and species specific feeding, locomotor and behavioral strategies that enable local species packing. His studies shed light on the overall picture of Amazonia that has meaning for our ecophylogenetic assessment of fossils throughout SAM.

Six of the 16 extant primate genera we recognize taxonomically are endemic to the region: *Cebuella, Callimico, Pithecia, Chiropotes, Cacajao* and *Lagothrix*. Others found within the lowland forests that would be considered endemic had they not dispersed into Central America (relatively recently, after uplift of the isthmus ca. 3 Ma (Stehli and Webb 1985)) include *Saguinus, Saimiri, Aotus*, and *Ateles*. None of the latter genera occur in the other major tropical forest of SAM, the Mata Atlantica. Of the four northern out-dispersers, *Ateles* has been able to penetrate deep into Mexico; *Saimiri* only goes as far as Costa Rica; *Saguinus* and *Aotus* are limited to Panama. This pattern means that a static, present-day definition of Amazonian endemism is rather arbitrary. The effective pre-Pleistocene measure of primate endemism in the Amazonian Province is higher than a literal count implies, closer to 10 genera. There is one endemic tribe, Pitheciini (*Pithecia, Chiropotes* and *Cacajao*). The latter's geographic exclusivity (they even cluster close to the river, or are sparsely distributed away from it) is instructive as to the ecological basis of their endemism, for they are not present in Central America or the Mata Atlantica even though habitat (Central America) or close relatives (*Callicebus* in the Mata Atlantica) would suggest this is an anomaly. Instead, this pattern probably means that seed-eaters cannot make it in the Mata Atlantica, just as extreme soft-fruit feeders, i.e., *Ateles*, also cannot be supported there or in sympatry with other large-bodied atelines, *Alouatta*, *Brachyteles*, or their local predecessors (e.g., *Protopithecus*, *Caipora*).

Three other modern platyrrhines that live in Amazonia have distributions overlapping into other tropical forests and are clearly non-endemics. *Callicebus, Cebus* and *Alouatta* occur in the Mata Atlantica, and *Cebus* and *Alouatta* occur in Central America. *Alouatta*, like *Ateles*, occupies Mexico in its northernmost limit, and it also co-occurs with *Cebus* in many marginal, sparsely forested habitats in the tropical grasslands of the Cerrado and Llanos. These taxa are critical to understanding the low-diversity communities of Patagonia, as discussed below.

Fossils are known from a few localities that are actually within Amazonia today, but the most important source of paleontological information comes from the La Venta fauna of Colombia, which is now situated in the arid Magdalena Valley. There is a consensus that before the uplift of the Cordillera Oriental, which now walls off the Magdalena river from the Amazon basin, this region was part of the latter's drainage system and biotically part of the Amazonian province. The evidence for this has been growing since primates were first discovered there the 1940s. Kay (1997) cogently review much of this information. La Venta is a subsample of the cohesive, ∼12–14 Ma Amazonian community, the best fossil representations of that biome that we know. In the fossiliferous Acre basin of western Brazil is a second, younger area, approximately 8 Ma, which has produced primates (Kay and Cozzuol 2006) and other tropical forms. It is also part of the Amazonian province.

4.4.2 The Atlantic Province

Outside the lowland Amazon basin there is a second major tropical forest now situated along the eastern margin of the continent, within Brazil, the Mata Atlantica. Our primate-centric use of the term is restricted to the relatively humid semi-deciduous forests in southeastern Brazil, bordering the margin of Atlantic Ocean and extending plume-like in the south to the vicinity of Paraguay. This habitat is quite different from Amazonia. It has a radically different physiography, lacking the basin and river-network system that defines the Amazon, for example, and so large volumes of moisture are not held within it for long periods of time. In addition to rainfall, these humid forests rely on trade winds off the Atlantic Ocean for moisture, but they are also given to more intense dry seasons.

For all its biodiversity, the Atlantic province is by comparison with Amazonia a low-productivity habitat. Only six primate genera live there: *Brachyteles, Leontopithecus, Callicebus, Callithrix, Alouatta* and *Cebus*. The first two are endemic to the region, very highly endangered and now confined to small tracts of forest, but records indicate that *Brachyteles* was once almost as widely distributed in the Mata Atlantica as *Alouatta* and *Cebus* are today. *Callicebus* is also very widely distributed. Furthermore, not all of the six platyrrhine genera occur at any one place, another indication of the lower carrying capacity of the environment. The most common sympatric combinations involve one (rarely two together) of the callitrichines, plus *Cebus, Alouatta* and, in areas where they have escaped the holocaust of human habitation, *Brachyteles, Callithrix* and *Leontopithecus* tend to replace one another. Overall, this assessment probably underestimates primate biodiversity somewhat because the present composition of the Mata Atlantica flora and fauna was also strongly influenced by the Pleistocene refugial phenomenon (e.g., Cerqueira 1982), which may have pushed some forms to extinction recently without recruiting others.

The character of the Atlantic fauna is defined, in a sense, by *Cebus, Alouatta* and *Brachyteles*. The ecological adaptability of *Cebus* and *Alouatta* has already been stressed, and *Brachyteles* appears to fall into a similar category. The convergence of the endemic *Brachyteles* on howler-like semi-folivory (Rosenberger and Strier 1989; Rosenberger 1992; *see* also Anthony and Kay 1993) is a measure of the inability of the Mata Atlantica to support even one large-bodied, committed soft-fruit frugivore like the closely related *Ateles*, with which *Brachyteles* shares many positional and locomotor specializations (e.g., Rosenberger and Strier 1989). Amazonian localities often support two large frugivores, *Ateles* and *Lagothrix*.

The presence of only one pitheciine in the Atlantic province, the non-seed-eating *Callicebus*, also attests to its non-Amazonian floristic character. The success of the widespread *Callicebus* may mean that in the Mata Atlantica primates occupying the middle body size range do not have seeds as a protein option. Evolving sympatrically with *Cebus* monkeys who target deftly proteinaceous prey, leaves offer a viable, necessary option, for *Callicebus*, here and in Amazonia (*see* Norconk 2007). The smaller cebids of the Mata Atlantica, phylogenetically canalized to rely on arthropod and insects for protein, are also distinguished by derived feeding and foraging specializations relative to their Amazonian counterparts. Thus *Leontopithecus* is derivedly large in body size and preys more on vertebrates than other callitrichines. And, *Callithrix* is gumivorous. In a sense, *Leontopithecus* and *Callithrix* combine to exemplify the *Saguinus*-like niche.

Generally, the Atlantic region assembles a relatively small collection of primates that are either pioneers, adept generalists or targeted dietary specialists when it comes to exercising the protein needs – animals or leaves – of their diets, but neither seed-eating, nor hyper-frugivory seems to be available as a strategy. Each of the four major monophyletic groups of platyrrhines are represented by at least one genus, thus, making it easy to envision the fauna as a product of vicariance, the splitting of a once continuous connection between Mata Atlantica and Amazonas. *Cebus*, *Alouatta* and *Callicebus* are most prone to be successful in such a scenario, being ecologically the most generalized members of their subfamilies or tribes; their anatomical specializations (autapomorphies) make them so. But they each also require different resources and get them by using different feeding strategies. *Cebus* is the highly omnivorous predaceous frugivore; *Alouatta* is able to rely heavily on leaves; *Callicebus* can eat relatively hard fruits as well as insects and also a fair proportion of leaves. It also is interesting that the subfamilies that have succeeded in establishing two new genera, callitrichines and atelines, have in each case produced distinctly different forms from those living in Amazonia. *Leontopithecus*, the largest living callitrichine, is highly predatory and specialized for foraging in microhabitats such as the large bromeliad bowels that are typical of the Mata Atlantica habitat. *Brachyteles*, phyletically an atelin and postcranially adapted to a high-energy lifestyle that differs radically from the low-energy existence of an *Alouatta*, has secondarily become a semi-folivore.

The Brazilian subfossils mentioned above also have bearing on the evolution of the Atlantic province. Two genera are even larger than extant atelines, *Protopithecus* and *Caipora*, both one and a half to twice the weight of any extant ateline. These come from the states of Minas Gerais and Bahia (where the Mata Atlantica is almost now entirely extinct). The ages of these fossils cannot be determined; they are considered to be late Pleistocene or Holocene (MacPhee and Woods 1982). In addition to their surprisingly large size, one other factor is pertinent here. Both appear to be decidedly frugivorous (e.g., Cooke et al. 2007), and neither has a dental morphology that suggests a howler-like compromise between fruit and leaves (*see* Rosenberger and Kinzey 1976). Other subfossil mammals (megatheres, ungulates) that have come from the same caverns as *Protopithecus* and *Caipora* indicate presence of a more open country environment than humid tropical forest. The proposition that terrestrially is a possible form of locomotion in one or both of these mega-platyrrhines (Heymann 1998) needs to be investigated, but preliminary morphological studies of the postcranium (Cartelle and Hartwig 1996; Hartwig and Cartelle 1996) have failed to find evidence for this.

What the subfossil primates point to is the existence of a former habitat in the Atlantic province that was probably more productive than the current forest, one that could support one or more large bodied, highly active frugivores that might have generally resembled *Lagothrix* in diet and locomotion. This is consistent with the evolutionary model that a continuous connection between the Amazon and the Atlantic provinces existed in the past. *Protopithecus* and *Caipora* may have been users of large trees in mature, continuous-canopy forests that preceded the drier, semi-deciduous Mata Atlantica.

4.4.3 The Caribbean Province

Three genera of subfossil primates have been described from the Caribbean, and a fourth new form is now under study. One of the most prominent facts about the Caribbean primates is that all are endemic. There is also pointed debate about the relationships of these forms and we caution that little is known regarding their functional morphology. Thus, our interpretations regarding the lifestyles of these NWM are meant to be provisional. A second crucial point is that so far we are only certain that one monkey genus occurs on each of the islands bearing primates. If an artifact, this means more exciting forms await discovery. If real, it opens up new lines of questioning regarding insularity.

Three of the islands of the Greater Antilles, Cuba, Hispaniola, and Jamaica have fossil and subfossil primates. These islands probably were not modern in appearance until the late Miocene at the earliest, but there were certainly subaerial portions of the major islands exposed as early as the Eocene (Iturralde-Vinent and MacPhee 1999). Unfortunately, few mammalian fossils exist from this early period, but there is a considerable fossil record of the sloths, rodents, insectivores, bats, and (a few) primates from the Miocene through the Holocene.

There are alternative hypotheses explaining how the Caribbean was colonized by terrestrial mammals and other vertebrates. For example, Hedges and colleagues (e.g., Hedges 1996, 2001; Hass et al. 2001) have largely supported an overwater dispersal model, where many separate propogules arrived from the South American mainland onto the islands since the early Oligocene. Another view is that of Iturralde-Vinent and MacPhee (1999; MacPhee and Iturralde-Vinent 1994, 1995), who posit that a landspan once existed where the Greater Aves Ridge now lies, which connected the mainland of South America and Cuba, Hispaniola and Puerto Rico as well as the islands of the Lesser Antilles. This landspan, termed GAARlandia, was subaerial only briefly during the Eocene-Oligocene transition and allowed in at least two lineages of sloths (White and MacPhee 2001), a primate, bats, and numerous rodents. MacPhee and colleagues believe a single primate species was ancestral to the entire primate fauna, a notion contested by Rosenberger (2002). Either way, the mammals experienced a significant adaptive radiation, and today we know of 60 extant and 75 extinct non-introduced land mammal species (Daválos 2004). There is a striking degree of endemism in this fauna, with fifty percent of (non-introduced) bat species, and one hundred percent of the non-volant mammals being native (Hedges 2001). These newcomers would have encountered an earlier fauna of likely North American derivation, including the relatives of the insectivores *Solenodon* and *Nesophontes* that may have entered the Antilles sometime during the Eocene (e.g, MacDowell 1958).

The earliest evidence for primates in the Greater Antilles is from the Cuban Miocene (14.68–18.5 Ma) site of Doma de Zaza, where a lone primate astragalus was recovered in the early 1990s and described as *Paralouatta marianae* (MacPhee et al. 2003). Other terrestrial mammals known from Domo de Zaza are a megalonychid sloth and a capromyid rodent. The geological evidence, and the presence of marine fauna, indicates that the site lay along the banks of the sea where several depositional environments were present (MacPhee et al. 2003). Afterwards, the primate fossil record is silent until the late Pleistocene or Holocene when at least four species of primates were present in the Greater Antilles. These include *Xenothrix mcgregori, Antillothrix bernensis, Paralouatta varonai* and the new form.

The Jamaican monkey *Xenothrix* has a peculiar dentition (*see* Rosenberger 1977; MacPhee and Horovitz 2004) characterized by large, bunodont, thick-enameled cheek teeth and, most likely, broad upper incisors (Rosenberger 2002). Postcranially, its morphology is consistent with a slow-climbing positional repertoire (MacPhee and Fleagle 1991; MacPhee and Meldrum 2006). *Paralouatta* also has cheek teeth that are crested and wear down in a conspicuously flat fashion, indicating thick enamel. Its postcranials have been interpreted as possibly indicating semi-terrestriality (MacPhee and Meldrum 2006). Early studies of *Antillothrix* have also emphasized the bunodont shape of its crowns (MacPhee and Woods 1982), and postcranial remains are indicative of arboreal quadrupedalism with some leaping (*see* Ford 1990; MacPhee and Meldrum 2006). A common functional thread here appears to be protection against exogenous dietary abrasives. This may imply diets including fibrous and/or woody materials, such as pith, hard-shelled fruits or tough seeds, or a *Cebus*-like omnivory. More exotic adaptations, such as an embedded grub eating diet like Aye-Ayes, can also be entertained, e.g., *Xenothrix*. Wear resistance would also be consistent with the suggestion of a semi-terrestrial habit in *Paralouatta*. Basically, in the hypersensitive selective environment of enforced insularity on a small landmass, each of the Caribbean primates may have been adapting to the ultimate fallback, critical-function foods (*see* Rosenberger and Kinzey 1976), which may have meant omnivory.

4.4.4 Patagonian Province

As discussed above, during the Cenozoic the relatively flat eastern Patagonian lowlands would have been gradually evolving into its modern form – arid, cold and windy, strongly influenced by the nearby Antarctic, recipient of its cold winds and bottom waters, rain-blocked on the Pacific side by the uplifting Andes. Patagonia would have lacked the humid eastern trade winds that feed the higher subequatorial latitudes and the semi-deciduous Atlantic coastal forest. The environment has become most suitable to grasslands, which began to proliferate 30 million years ago, almost 10–15 million years before they rooted in North America (Flynn and Wyss 1998; MacFadden 2000; Jacobs et al. 1999). Even the localities that have produced primates evidence grazing and/or browsing notoungulates and rodents, and fleet predatory phorusrhacid birds that also signal open environments. Savanna, with sparse, spaced trees and an established herbaceous ground layer, is a possibility.

The phases of warmer and colder periods suggested by the dynamism of ice sheets in the Antarctic during the Miocene (Fig. 4.3) likely drove episodic expansion and contraction of more treed habitats where local conditions permitted. The source of warm-adapted flora that perhaps crept in from the north may have included proto-Amazonian or proto-Atlantic elements, but this would have involved habitat expansion over vast distances, accompanied by change reflecting local adaptation. Evolving native vegetation may have been even more important. The forests that developed during the EECO in Patagonia (Wilf et al. 2003; 2005; Hinojosa 2005) probably was a resource base for the later emergence of treed habitats that occurred in Patagonia during the Miocene. This could have included large swaths of forested terrain, sparse savanna and also riverine corridors where small communities of primates could have easily lived as they do now in the Atlantic province and in the Cerrado, Llanos and Chaco grasslands of Brazil, Venezuela and Bolivia.

The local Patagonia flora may have been a sort that was not conducive to high primate diversity. Two lines of evidence suggest that it was unlikely to have been a transplanted “Amazonia of the South”, with similarly high productivity. First, new syntheses of the geological evidence pertaining to the topographic and rainfall features forming the foundation of Amazonia suggest the basin had a relatively late origin, coming long after primates are known to have occupied Patagonia (Campbell et al. 2006). Thus, if far north botanical elements were drawn to the southern cone, they were likely to have been different from the substance that makes today's Amazonian province what it is. Additionally, there may have been a physical barrier limiting southward dispersal. During the middle and late Miocene there is evidence of a large inland sea, the Paranaian Sea, situated north of Patagonia. It reached as far north as Bolivia and stretched from the Atlantic Ocean in the vicinity of northern Argentina and Uruguay to the base of the Andes (Aceñolaza 2000; Alonso 2000; Cozzuol 2006). This could have acted as a strong barrier for dispersal of terrestrial plants and animals either from or to the north.

In a mixed regional environment that favored grasslands but also allowed forests to exist, the primates that came to live in the Patagonian province during the late Oligocene and early Miocene were likely to have been adaptively similar to the pioneers and colonists that today inhabit second tier and marginal primate habitats in SAM. This means we might expect animals having lifestyles consistent with the Mata Atlantica and even the Cerrado, adaptable taxa like *Alouatta*, *Cebus* and *Callicebus*. But gum-eating marmoset-like species, quite successful in Cerrado and even in the drier Caatinga, are able to co-exist with other primates and would probably have done well also.

How do these predictions fit with the empirical evidence? An interesting ecophylogenetic feature of the Patagonian primate faunas as it is currently known is the dominance of pitheciines, and the general resemblances of some to the inferred formative pitheciine feeding strategies (*see* Rosenberger 1992). These include *Homunculus*, *Tremacebus*, *Soriacebus* and *Carlocebus*. First, they are all small- to middle-sized NWM. In *Homunculus* and *Soriacebus*, prognathic incisors and premolar morphology indicate hard-fruit harvesting. *Homunculus* cheek teeth, of which we only have several, are also interesting in that they are worn but in a pattern that exposes rows of molar shearing crests on the crown surface. Their cheek teeth also seem to be relatively large. This is suggestive of at least some folivory, and a lifestyle in which *Homunculus* may resemble *Callicebus* living in the Mata Atlantica. In her summary, Norconk (2007) notes that the percentage of leaves in the diet of *Callicebus* in four field studies ranges from 4% to 23%– 66%. The spread at the end of the range reflects seasonal variation. Like *Callicebus*, *Homunculus* may have relied on leaves more than insects to fulfill its protein needs.

Homunculus also has small, non-projecting canines. As is well known, this is associated with monogamy and territorial defense in *Callicebus* and *Aotus* (e.g., Fernandez-Duque 2007). Additionally, *Homunculus* has jaws that deepen posteriorly, as in most *Aotus* but less than the extent seen in *Callicebus*. It may be that this feature is connected with the development of a vocal sac that enables the animals to produce powerful calls as a component of ritualized territorial behavior. One of the advantages of this syndrome is that it makes it possible for group sizes to remain small and efficiently spaced apart, which would be an advantage in low-productivity environments.

Soriacebus clearly had advanced, pitheciin-like prising incisors and the massive canines and anterior premolars associated with cracking hard-covered fruits, but it had unique cheek teeth that do not resemble pitheciins morphologically. So, while possible, there is insufficient anatomical evidence to argue by way of detailed analogy that *Soriacebus* was already an advanced seed-eater comparable to sakis and uakaris, where seeds comprise two-thirds or more of the diet (Norconk 2007). Rosenberger (1992) argued that *Soriacebus* was a primitive pitheciine, adaptively, able to ingest unripe, woody fruit, but without specializing on the seed for protein. Bown and Larriestra (1990) saw evidence of a varied environment in the Pinturas Formation where *Soriacebus* occurs, including tropical forest, areas that were perhaps partly forested and adequately watered, and areas sufficiently arid to allow sand dunes to form. They say (pg. 108), "...if appreciable climatic drying did accompany dune formation, some forest-dwelling mammals (including monkeys) were either unaffected by it or quickly reestablished themselves following dune formation." This description bears little resemblance to Amazonia.

Tremacebus molar teeth, known only from fragments of very badly worn teeth, are nonetheless grossly similar to some molars allocated to *Homunculus*, which show deep pockets of gross crown wear. Skull shape and measures of orbit size indicates eyeball proportions intermediate between small-eyed *Callicebus* and large-eyed modern *Aotus* (Fleagle and Rosenberger 1983; Kay et al. 2004). There is little reason to doubt that *Tremacebus* was nocturnal or crepuscular or cathemeral, roughly like *Aotus*, even though its eyes may have been slightly smaller and its olfactory lobe may not have been as enlarged relatively as *Aotus* (*see* also Kay et al. 2004). There is no reason to expect a 20 million year old owl monkey to be identical to an extant owl monkey. *Tremacebus* may have been quite similar in its use of time and light conditions to *Aotus* populations that live in the southern, more temperate limits of its distribution in Argentina and Paraguay, where their activity is conditioned by ambient temperature and moon-light phases (Fernandez-Duque 2007). They are more active during daytime hours when the nighttime temperature is low and/or nightlight is limited.

Only two non-pitheciine genera are known in Patagonia, *Dolichocebus* and *Killikaike*, although we fully expect more of the adaptable cebines and alouattins will eventually be discovered The skull shapes of both (Rosenberger 1992; Tejedor et al. 2006) suggest they had typically large cebine brains, thus perhaps similar foraging systems. The dentition of *Dolichocebus* is still hardly known.

Recent paleoecological studies are consistent with this scenario. Among the subregions where fossil primates are found in Argentina, the Santa Cruz Formation is an early Miocene stratigraphic unit deposited in Santa Cruz province (Ameghino 1906; Russo and Flores 1972). The duration of the Santa Cruz was probably under a million years (Tejedor et al. 2006). Yet it is one of the most representative, diverse, and rich vertebrate assemblages in South America, and is exposed from the Atlantic coast west to the Andean foothills. The most complete and best preserved fossils come from the coast, especially at sites between the rivers Coyle and Gallegos. Primates are not anomalies at these localities because they have also produced other mammals that tend to inhabit humid forests, such as sloths and some caenolestoid marsupials.

Tauber (1994, 1997a,b), who recorded hundreds of specimens of vertebrates, including mammals and a primate skull (Tauber 1991), developed a broad basis for biostratigraphic and paleoecologic studies of this area. He found several indications that from the latest, early Miocene onward climate changed from being warm and humid toward becoming drier and more seasonal. This was associated with a reduction in arboreal habitats and a shift toward open grasslands. Tauber showed there was a decrease in mammalian diversity over time, especially of the smaller forms such as microbiotheres and palaeothentid marsupials, and the small rodents. In contrast, armored glyptodontids and cursorial toxodontids, both herbivores, became larger and more diverse; hypsodont dentitions became more common among notoungulates; and, brachydont ungulates showed a progressive shift in body size frequencies.

That Patagonia was not uniformly tropical across the land mammal ages and geographical areas occupied by primates is shown in other ways as well, including palynological studies in the Pinturas Formation (Zamaloa 1993) that found temperate families of trees, and sedimentology (Bown and Larriestra 1990). Palinostratigraphic work in coastal Patagonia (Barreda and Palamarczuck 2000) showed that xerophytic plants were replaced by more tropical elements during the latest Early Miocene-earliest Middle Miocene. From the mammals, Vucetich (1994; *see* also Vucetich and Verzi 1994) concluded that the paleoenvironment of the western Santacrucian exposures could have been similar to the coastal Santa Cruz Formation in the east; probably woodland savannahs, or possibly more arid than that.

4.5 Discussion

4.5.1 Landscapes and Early History

The Cenozoic geographic isolation of SAM has been an important factor in shaping the evolution of platyrrhines. As we have proposed elsewhere (Delson and Rosenberger 1984), this situation enforced intra-community interactions among the NWM – potentially for 26 million years or more – while eliminating the sort of competitive faunal mixing that happened in the Old World among primate communities that met when anthropoids moved between continents. Continental scale isolation is possibly one of the correlates of the long lineage syndrome; strongly differentiated niches evolving early in the platyrrhine radiation followed by the establishment of an ecophylogenetic balance among the differentiating sublineages. Because no competing guilds were injected wholesale into the continent, the greater platyrrhine community may have arrived at a relatively steady-state ecological framework that allowed various lineages to survive for long periods in conditions of relative stasis, without being subject to massive faunal turnover.

Other important factors of continental scale that shaped the evolution of NWM involved the size and contour of the landmass, its deep extension into southern latitudes, and its tectonic history. These elements had profound consequences for regional communities and the radiation as a whole. It meant that the widest segment of the continent, in the north, was strongly influenced by a hot house equatorial climatic regime, while the long, narrow southern cone was influenced by its proximity to the ice box climatic engine of Antarctica, more powerful during much of the Cenozoic. Three major tectonic events also had crucial consequences. In the south, separation of the Fuegan tip of SAM from Antarctica and the deepening of the Drake Passage strongly influenced climate for more than 30 million years. It molded and enforced cold-adapted Patagonian habitats that may only have been interrupted locally and intermittently. In the north and west, episodes of Andean uplift during the past 15 million years may have effectively created the physiographic foundations of the Amazon basin. In the Caribbean, crustal movements opened a pre-isthmian exit for primates out of the continent and into the Greater Antilles.

Of course, the truly seminal event in NWM history was the coming of anthropoids to the continent. In the absence of any resident ecological cognates, upon encountering a conducive tropical habitat the newly arrived anthropoids probably underwent an explosive adaptive radiation driven by competitive release, comparable to what happened in Madagascar long before. There are still no fossils that bear witness to this process for the record probably does not extend deeply enough in time, and the oldest site, Salla, Bolivia, 26 Ma, has produced only 2–3 genera (by our count) so far, all difficult to interpret. The caviomorph rodents, better represented as early fossils, were possibly co-immigrants although here, too, there is still no corroborating fossil evidence of contemporaneity.

Early caviomorphs, known from Chile and Argentina, have a long history in Patagonia. They occur for perhaps 5–7 million years before any evidence for NWM on the continent. The near absence of NWM from Argentina's Gran Barranca, from localities older than the Colhuehuapian that produce rodents, is interesting. Gran Barranca has been well sampled (using screen washing) and spans several millions of years in time. The rarity of platyrrhines there may be another indication that the far southern latitudes were inhospitable to primates for long periods until the early Miocene, when the earliest NWM begin to appear at the 20 Ma Abanico Formation of Chile (Wyss et al. 1994). Or, it may mean that the rate of dispersal of caviomorphs, much more cosmopolitan in their distribution and more labile in their habitat requirements, was much higher than the primate rate. But none of the Colhuehuapian primates (Table 4.1) can be considered stem platyrrhines, contra Flynn et al. (1995) and Kay et al. (2008). Quite the opposite, *Dolichocebus* and *Tremacebus* are assignable to extant lineages, cebines and aotins, respectively. *Chilecebus* is still insufficiently described, but it appears to be phylogenetically nested among the cebids, possibly within a derived clade. Therefore, the Patagonian forms are neither near the ancestry of the radiation nor is there evidence that they arose in the southern cone.

It is tempting to position Salla, Bolivia, as a central datum in the early history of NWM for it is the oldest site that has produced monkeys thus far. MacFadden (1990:19) did so in speculating that his reconstruction of Salla's habitat as semi-arid was evidence that "…the earliest South American primates may have lived in a non-rainforest environment and is therefore in contrast to the dominant adaptive/environmental setting for platyrrhines today…. Perhaps this was the original environment into which platyrrhines radiated and the tropical, rain-forest environments of today represents secondary evolution into a new adaptive zone." We consider this a stretch. A more tempered explanation is that Salla primates, like various modern NWM and many extinct Patagonian forms with close affinity to the moderns, were able to exist in marginal (gallery forest?) habitats as part of their arborealist heritage. We still have no indications from the postcranium, except for one possibility in the Caribbean, of terrestrially adapted platyrrhines, which should have thrived in the south if they ever passed the arbo-terrestrial Rubicon. Even though Salla primates exhibit high-crowned wear resistant teeth (Kay et al. 2001), we believe these would have been advantageous in a forested habitat adjacent to dust-producing grasslands. There is also one Salla specimen, a mandible, whose allocation has been largely ignored (but *see* Rosenberger 1981; Rosenberger et al. 1991), that has a bunodont *Cebus*-like molar and a thick, shallow jaw. It may be a cebine, i.e., a part of the most adaptable, derived platyrrhine guilds. Thus we see it more profitable to regard Salla not as a mirror of the adaptive profile of ancestral platyrrhines; rather, as another example of the meandering evolutionary pathways taken by splinters of the NWM adaptive radiation as they evolved locally under shifting climatic and environmental conditions, including milieus that were non-Amazonian in aspect.

4.5.2 Evolving in the SAM Provinces

Eventually, the platyrrhine radiation “settled” in the Amazonian and Atlantic provinces. From our modern perspective, the immense diversity of the Amazonian community became the centerpiece of the evolving platyrrhine fauna, starting at least in the middle Miocene. However, it would be wrong to assume all the taxa and adaptive profiles represented there evolved *in situ* as responses to the ecology of that great lowland forest. South America is a large continent with a complex history, and monkeys have colonized different regions across time and space. The Amazonian primate community may be a composite fauna that includes forms drawn from other provinces or areas of SAM.

An integration of paleontology, phylogenetics and the phylogeography (i.e., of important primate fruit foods) may be employed in testing this composite fauna hypothesis. Although the evidence is probably not sufficiently robust at this time to address the problem in depth, we offer several ideas for exploration. Among the atelid endemics, it seems likely that the most committed seed-eaters, *Chiropotes* and *Cacajao*, and fruit-eaters, *Ateles*, originated in Amazonia. No fossils particularly close to any of these have been found yet but molecular evidence suggests relatively recent origins for them (Opazo et al. 2006), at about 9 Ma and 13 Ma respectively, which postdates the time when mountain building in the west initiated the transformational geological processes that produced the basin (*see* below).

As examples of taxa that may have had an extra-Amazonian origin, *Alouatta* and *Cebus* are good candidates due to their highly generalized ecological nature. Paleontology (e.g., Rosenberger 1979) and molecules (e.g., Opazo et al. 2006) indicate a pre-20 Ma origin for the *Cebus* lineage and, as discussed above, alouattins may have had a long pre-Laventan history as well. In a sense, *Alouatta* and

Cebus exhibit derived feeding and foraging adaptations that enabled them to become successful ecological generalists, seasonally adaptable, flexible in diet and substrate requirements, and comparatively undeterred by ecological barriers that geographically limit other monkeys. They are also intermediate in body size relative to the full range of Amazonian primates, neither too small nor too large to mandate a narrow zone of ecological tolerance. *Cebus*, a phyletic giant among modern cebids (Rosenberger 1992; but *see* Kay and Cozzuol 2006), has eluded the small-body size energetic and foraging constraints imposed by the ecophyletic inertia of its ancestry within the fundamentally insectivorous, cebid guild. *Alouatta* is the smallest living ateline genus, contrary to what might be expected as the member most prone to leaf eating, and its smallest living species occur in the Mata Atlantica (Table 4.2). This means howlers have fewer substrate constraints than heavier forms which need large canopies to support foraging and feeding requirements. Thus *Alouatta* and *Cebus*, well known across the continents as ecological pioneers, could easily have arisen in habitats defined by lower productivity, more seasonality, and less physical majesty than the big-canopy, multi-tiered, lush forests of Amazonia.

A second set of forms that may have arisen outside Amazonia are *Aotus* and *Callicebus*. As a non-endemic, living also in the Atlantic province, it is easy to see *Callicebus* evolving in connection with a low-productivity habitat, able to use leaves as a protein source even at a body size much smaller than *Alouatta*. Even more interesting is the point that both may have close evolutionary ties to extinct early middle Miocene forms from the southern cone. *Callicebus* has been potentially linked with *Homunculus*, and *Tremacebus* is closely related to *Aotus* (including the Laventan *A. dindensis* (*see* Fleagle and Tejedor 2002 for a review). While neither of these fossils is sufficiently well known anatomically to reveal characters barring them from a direct ancestry of the moderns, the possibility that they may be sister-taxa to the

Table 4.2 Body weights of extinct and extant atelines

Species	Weight (kg)
Alouatta fusca	**4.418**[1]
Alouatta caraya	**5.206**[1]
Alouatta belzebul	**5.585**[1]
Alouatta palliata	**6.015**[1]
Alouatta seniculus	**6.228**[1]
Lagothrix lagothricha	**6.875**[1]
Ateles belzebuth	**8.076**[1]
Ateles belzebuth	**8.076**[1]
Ateles geoffroyi	**8.168**[1]
Ateles geoffroyi	**8.168**[1]
Paralouatta varonai	**9.55–10.17**[2]
Brachyteles arachnoides	**13.500**[1]
Caipora bambuiorum	**20.5**[3]
Protopithecus brasiliensis	**24.85**[4]

Sources: [1]Rosenberger (1992), [2]MacPhee and Meldrum (2006), [3]Cartelle and Hartwig (1996), [4]Hartwig and Cartelle (1996) living forms means it is also possible that *Aotus* and *Callicebus* have had a long, extra-Amazonian history.

Segments of the NWM adaptive radiation, probably through episodes of vicariance and dispersal, became fixed in the Atlantic province, where they remain today. Another satellite evolved in the Caribbean, where they recently became extinct. These two groups each underwent modest adaptive radiations, probably arising from an ancestral community of primates in each region as opposed to a single-species last common ancestor seeding the two communities. Otherwise, multiple biogeographic events and multiple adaptive parallelisms must be postulated to explain the ecophylogenetic complimentarily of the Amazonian, Atlantic and Caribbean provinces.

The Patagonian offshoot has been extinct for nearly 15 Ma. This assemblage was species-poor by comparison with the Amazonian province and all forms seem to have been short lived in the region. Of the seven platyrrhine genera occurring in Argentina during the early middle Miocene over a five million year span, there may only be one genus that lived through any of the time horizons denoted by four geological formations. It is important that several are related to monkeys or lineages found later in the north, and they are generally more primitive than the La Venta forms. The apparently short duration and low diversity in the southern cone is probably a result of the progressive cooling and proliferation of grassland habitats that occurred after the EECO, when warm, moist environments were probably transient, short-term phenomena. In the nearby Falkland (Malvinas) Islands, sometime between the Middle Oligocene and Early Pliocene, there was a temperate broadleaf coniferous forest (Macphail and Cantrill 2006). Thus, the primate communities of Patagonia may have largely been consigned to pioneering taxa able to live in marginal habitats, more similar in character to a Mata Atlantica profile than to an Amazonian pattern. While only cebines and pitheciines are known to have been present, there are hints of alouattins as well (Tejedor 2002).

Sampling error must be partly responsible for this next point, but in all of the sites that have yielded any of these primates no more than two genera appear to co-occur. In the modern north, in the modest Mata Atlantica fauna, it is not unusual for four or five primate genera to live in sympatry. In the Caribbean, thus far we only have one genus per island, but this almost surely will change. Nevertheless, with respect to their limited diversity, the Patagonian localities do resemble islands. Were they subject to the same heightened extinction risks of insularity?

When the Patagonian primates became extinct is difficult to say. There is no record of them in formations younger than the Collon Cura, at about 16 Ma; they may not have survived into the middle Miocene. The “Mesopotamian” outcrops of eastern Argentina (Paraná Formation, *see* Aceñolaza 2000), for example, have been well prospected but without producing any primates, although it is believed to represent the same biogeogaphic province as the Acre Formation of the western Amazon. Acre has produced three primate genera thus far, at approximately 8 Ma (Kay and Cozzuol 2006). Younger primates may have been largely excluded from the southern cone by entrenched long-term trends toward increasing aridity, increasingly open, sparsely vegetated environments and geographical barriers that also limited dispersal (*see* below). Whatever were the immediate conditions in the early middle Miocene, the larger point here is that primates may have been almost predestined to extinction because NWM never did take root in Patagonia in the form of viable enduring communities resembling Amazonia or the Mata Atlantica forests.

There is evidence that during the late Middle Miocene and early Late Miocene, from about 11–9.5 Ma, the terrestrial faunas of the Patagonian region were separated from the mid-continent by an extensive marine incursion, the Paranaian Sea. Reconstructions of this embayment indicate it reached from the region of northern Argentina and Uruguay northwest to Bolivia, with its western edge running along the base of the rising Andes (e.g., Cozzuol 2006; Potter 1997). This would have been a barrier or strong filter against dispersal between Patagonia and Amazonia. Cozzuol (2006) argues that it coincided with tectonic, hydrogeologic and climatic events that divided the Patagonian and Amazonian biotas, and soon thereafter led to the extinction of northern, aquatic faunal elements that bridged between the western Amazonian and Paranaian basins. The recession of the Paranaian Sea may mark the beginnings of the terrestrial biota that evolved into the current configuration of the southern grasslands terrain.

In the far north, at the younger sites of Acre and La Venta, there is clear evidence of pitheciines, cebines and atelines, some quite advanced (*see* Hartwig and Meldrum 2002). From Acre, Kay and Cozzuol (2006) recently described a new, very large monkey closely related to *Cebus*, *Acrecebus fraileyi*, and a primitive atelin, *Solimoea acrensis*. The Acre fauna also includes a second species of *Stirtonia*, a genus known from two species at La Venta. There is a consensus that *Stirtonia* is very closely related to, and adaptively similar to, modern *Alouatta*, so much so that Delson and Rosenberger (1984) suggested modern howlers are living fossils, possibly descended directly from *Stirtonia*. Similar proposals have been made concerning *Neosaimiri* (or *Saimiri* (*Neoaimiri*)) *fieldsii* and *Aotus dindensis* being parts of the squirrel monkey and owl monkey generic lineages, respectively. Considering that the entire fauna is quite modern in the abundance of primate genera and their ecophylogenetic composition, we would infer that the role of atelines in that community was comparable to what it is today in Amazonia, even though at this point we have only one alouattin represented. Overall, it is likely that La Venta, and the lesser known Acre, form an ecological time-continuum with modern Amazonia. This suggests that the primates of the Amazonian province have been evolving as a regional community for at least 12 million years. It must be one of the reasons why a high proportion of La Venta genera are so closely related to modern forms. One would expect that latitudinal gradients, exacerbated by the Antarctic effect, would limit southern expansion of this biota, and there is evidence that the province was geographically contained. Well-sampled faunas of equivalent age, with abundant mammals but apparently no primates, are known from Quebrada Honda, Bolivia, but they are more similar in composition to high-latitude formations than to La Venta (Croft 2007).

Another critical facet of La Venta relates to callitrichines, a subject we have intentionally ignored since there is little question that a large part of the explanation for their rarity in the fossil record reflects our coarse collecting techniques. However, modern SAM platyrrhine communities are incomplete without them, so their presence would be an important indicator of ecological structure in a paleocommunity.

Four La Venta species have been proposed as possible callitrichines. No additional material has been assignable to the three teeth first allocated to *Micodon kiotensis* (Setoguchi and Rosenberger 1987), and this animal remains too poorly known to pursue much further. At the least, it tells us species of the right size range and morphology were present in this primate communinty. A second small-sized taxon is *Patasola magdalenae* (Kay and Meldrum 1997), based on a subadult lower jaw. Here, too, the evidence is compelling but not unquestionable. More controversial is a crushed skull, *Callicebus*-sized, that Kay (1994) described as a “giant tamarin,” *Lagonimico conclucatus*, and a lower jaw, *Mohanamico hershkovitzi* (Lutcherhand et al. 1986). The latter has been vigorously debated (e.g., Rosenberger et al. 1990; Kay 1990). We believe that *Lagonimico* is a pitheciine (Rosenberger 2002) and *Mohanamico* is probably a callimiconin callitrichine (Rosenberger et al. 1990). Thus La Venta, in keeping with its ecological modernity, did support callitrichines.

4.5.3 Subfossils of a Miocene Aspect

The Caribbean province and the Brazilian subfossils, while comprised of forms that are quite distinct, echo signals of the Miocene. *Protopithecus brasiliensis* and *Caipora bambuiorum* (Hartwig and Cartelle 1996; Cartelle and Hartwig 1996; *see* also MacPhee and Woods 1982) are a very large-sized alouattin and atelin, respectively. Their ecological role in the eastern Brazilian community is not easily discernable at this point; more functional morphology is required. However, preliminary work indicates that *Protopithecus* is considerably *less* folivorous than expected in an alouattin. It differs markedly from *Alouatta* and *Stirtonia*. Its dentition strongly emphasizes frugivory (Cooke et al. 2007). Other new specimens from the cave collections that produced these primates include a new species of *Alouatta* (Tejedor et al. 2008), a *Cebus*, and the original series collected at Lagoa Santa by Lund (1838) probably includes *Callicebus*. Thus the Quaternary of this region supported various forms of a modern ecological cast but, as noted above, the picture of their habitat is still fuzzy. Like Simpson’s (1981; Fig. 4.2) stratified faunas of SAM, we think these giant subfossils reflect an earlier faunal layer of primates possibly derived from a greater Amazonia-Mata Atlantica continuum that existed during the Miocene. *Protopithecus* and *Caipora* were probably replaced by other forms such as *Brachyteles*, perhaps evolving *in situ*, when grasslands intervened and the Atlantic province began to take on its current physiographic shape. This involved the intrusion of the open country mega mammals that are associated with *Protopithecus* and *Caipora* (Cartelle 1993).

In the Greater Antilles, there are three known genera (*see* MacPhee and Woods 1982) and a fourth that is currently being described. There are strong disagreements about the origins and interrelationships of these forms (e.g., MacPhee and

Horovitz 2004) but we follow the arguments put forth by Rosenberger (2002) pending further study now underway. This suggests that atelines, pitheciines and cebines are present. *Paralouatta varonai* (and *P. marianae*) is, by cranial evidence (Rivero and Arredondo 1991), an alouattin, but its dentition, like *Protopithecus*, is adapted for frugivory (Cooke et al. 2007). MacPhee and Meldrum (2006) suggest it may have been semi-terrestrial. The two-molared *Xenothrix mcgregori*, which we consider a pitheciine, has very bunodont cheek teeth (Williams and Koopman 1952; Hershkovitz 1970; Rosenberger 1977, 1992) with large, broad premolars and thickly enameled cheek teeth superficially resembling *Cebus*, only relatively enlarged. The postcranial skeleton appears to be odd, but also quite arboreal (MacPhee and Fleagle 1991). *Xenothrix* may have had very broad incisor teeth (Rosenberger 2002). The dentition overall suggests a frugivorous diet, probably of hard-shelled fruits or grit-covered foods. Seed-eating cannot be disqualified, either, but leaf-eating as a staple seems unlikely. The enormously deepened mandible is a pitheciine feature. *Antillothrix bernensis* (MacPhee et al. 1995), which we regard as a cebid, is still difficult to interpret functionally, though a mandible attributed to it is relatively thick and it carries a molar that appears to be quite bunodont. This is a combination of features found in *Cebus*.

Thus the complexion of the Caribbean fauna, in spite of the fact that none of the three known genera have yet to be found on a single island, reflects the diversity of the NWM eco-clades but in a combination that fuses primitiveness with autapomorphy, and also new adaptive nuances within clades. *Xenothrix* is a stunning example of the latter. One of the implications of *Paralouatta* is that the dispersal of alouattins into the Caribbean was likely to have antedated La Venta times, or that it involved a form that existed elsewhere on the continent. This is consistent with the suggestion (Rosenberger 1978), now receiving confirmation from a radiometric date of 14.68 Ma, and a more likely stratigraphic date of 17.5–18.5 Ma, associated with *Paralouatta marianae* (MacPhee et al. 2003) – NWM have an ancient origin in the Caribbean. While MacPhee and colleagues (*see* MacPhee and Woods 1982) argue that these forms are the monophyletic issue of a single dispersal event, our view is that the ancestral population (assuming there was only one) was more likely a fauna, a splinter community of SAM primates comprised of at least three ecophylogenetic groups experiencing joint range extensions onto a newly accessible archipelago during the Miocene.

4.5.4 Origins and Evolution of the Amazonian Community – or, How Life in the Flooded Forest Weighed Against a Terrestrial Radiation

The Miocene date for *Paralouatta* thus becomes even more intriguing, as it is about as old as the Patagonian primates and several millions of years older than the La Venta primates (*see* also MacPhee 2005). With Caribbean platyrrhines having roots as deep as these, we need to entertain complex scenarios implied by NWM occupying continental space vastly larger than Amazonia, perhaps not all at once but surely over the expanse of geological time. Amazonia can no longer be considered the seat of platyrrhine evolution if Patagonian and Caribbean and the Quaternary platyrrhines of Brazil involve lineages more primitive than their ecophylogenetic counterparts living in the Amazonian province.

Thus, for Amazonia a key question is: How old is the basin? In a wide ranging synthesis, Cambpell et al. (2006) provide a detailed model and scenario of its evolution during the last 15 million years. They suggest that its beginnings were set in motion by middle Miocene tectonism in the Andes, as the eroding cratonic shields of the east filled the landscape with a massive amount of sediment to form a single, enormous flat plain. Rivers drained toward the northwest and into the Pacific, in the region of Ecuador, and in the north into the Caribbean through Venezuela. At about 9.5–9.0 Ma, Andean uplift began to block the northwest portal. The basin began to pool, forming a vast shallow lake, Lago Amazonas, or a system of coalescing lakes, swamps, and rivers. The whole environment was subject to tropical, seasonal monsoonal rains. The modern eastward drainage flow was initiated later, at about 2.5 Ma, when the mouth of the Amazon opened to funnel the immense river system into the Atlantic Ocean. But what type of environment was evolving within this gigantic inland sea? According to Campbell et al. (2006: 206):

> . . .it rarely preserved fossils, plant or animal. This is explained most readily by two factors. The first is that deposition occurred in a highly oxidizing, shallow water environment, which resulted in the rapid decomposing of most organic debris. Second, unlike Lago Pebas [an older paleo-lake complex to the south west], which had an abundant vegetation complex in and around it, Lago Amazonas probably had as its modern analog the llanos of eastern Bolivia. There, long-term, seasonal flooding effectively curtails much vegetation growth, including on the banks of numerous lakes that fill the region. Compared to the Amazonian forests that cover the modern landscape, lowland Amazonia of the late Neogene was probably a vast complex of shallow mega-lakes surrounded by swampy, grassland savanna that endured months-long periods of seasonal inundations. It is also reasonable to expect that climatic cycles leading to extended periods of exceptional precipitation could have produced years-long periods of inundation.

If Campbell et al. (2006) are correct – and there are other models which they review that posit the beginnings of the Rio Amazonas and its tributaries to 27 Ma – vast areas of the Amazonian province would at times have been a spongy, wet desert as far as monkeys are concerned. The llanos of Bolivia, which is the modern habitat analog of Campbell et al., does not support a primate fauna, and the Bolivian Chaco is depauperate. But in some areas of the basin, the long-term influence of inundation must have been an important source of selection for monkeys and their foods. For example, it may have been a crucial factor in selecting for viable dispersal mechanisms of falling fruits, enabling them to withstand being drenched for long periods. Ayres (1989) has argued cogently that a regime of pervasive forest floor inundation is behind the coevolution of water tight hard-shelled fruits and the husking and seed-eating adaptations in *Cacajao* and *Chiropotes.* Special locomotor adaptations in saki and uakaris, pedal hanging (Meldrum 1993), like-tail hanging in atelines, may also have been an advantageous way for larger-sized primates to hover safely beneath boughs and canopies in order to forage on a lower tier of vegetation arising from the flooded forest floor.

And, if our analysis of the Patagonian situation for primates is correct, that it was long ephemeral to the mainline evolutionary history of NWM that was taking place elsewhere on the continent, the Campbell et al. (2006) model of Amazonia's evolution exposes an old conundrum from a different perspective, i.e., why platyrrhines never produced a terrestrial radiation, or even heavily committed terrestrial sublineages or genera. The presence of NWM fossils woven into southern cone communities where other ground dwelling mammals were present accentuates this problem: terrestrial opportunities had definitely been broadly available there since the Miocene, even if they were less common later in the Amazonian province. While this matter will remain an open issue until someone finds a fossil that is an obligate terrestrialist, additional light can be shed on why the odds have been against NWM evolving terrestriality as an environmental adaptation. It relates to the basic structure of Amazonia and the profound depths to which NWM have adapted to it.

Unlike most Old World rain forest habitats, the Amazonian lowlands are flooded for six months of the year, when it grows to cover an area about three times the surface its encompasses during the dry season. This means there is simply no *terra firme* available to modern monkeys for much of the year (and half their lives). Following Campbell et al. (2006), this condition may have existed for millions of years, may even have been exaggerated for long stretches of geological time and would have been less cyclical before 2.7 Ma, when the newly opened eastern portal to the Atlantic began the massive drainage of accumulating inland rainwater. For lineages, this means eons of selection in a waterworld swamp. It also means that the monkeys who might be best able to find a transitional opportunity to shift activities from canopy to forest floor would be those that best exploit the subcanopy niches, the callitrichines. But on account of their small body size they are unlikely candidates for evolving terrestrial offshoots. The largest platyrrhines, on the other hand, are also adept at exploiting the subcanopy by using their feet and/or their tails in hanging toward it.

Thus, specialized positional behaviors that evolved within the Amazonian province would have included a large proportion of NWM adapting to efficiently use arboreal space above the seasonally flooded forest floor. This represents an environmental scenario and evolutionary trajectory that is the antithesis of adaptive scenarios toward terrestriality, for it reinforces arboreality. In other words, by maximizing subcanopy specializations in positional behavior, NWM would have minimized terrestriality as a selective option among callitrichines, atelines and pitheciines, barring the evolution of an additional layer of autapomorphies enabling an arbo-terrestrial transition. On the other hand, it would be interesting to consider the shortened tails of uakaris and the less acrobatic quadrupedalism of howlers and cebus monkeys (*see* also MacPhee and Meldrum 2006), all possibly secondary specializations within their larger clades, as potential solutions to enable some degree of ground use in these taxa. For uakaris, this would have evolved within the flooded forest regime, as Ayres (1989) anticipated. For *Alouatta* and *Cebus*, it would have evolved in marginal

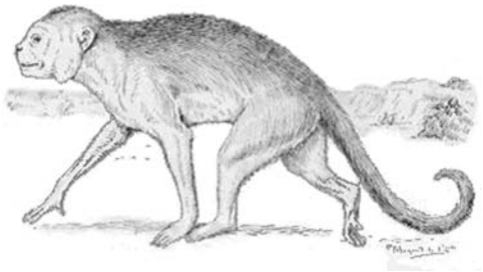

Fig. 4.5 Rusconi's behavioral reconstruction of *Tremacebus harringtoni* (Rusconi 1935)

habitats, possibly outside the Amazon. Even so, the central point is that the *probability* of Amazonian platyrrhines evolving terrestrial taxa would have been very low across geological time.

A final point is that terrestriality within and among primate clades is a demonstrably rare phenomenon. Thus there is no cause to anticipate terrestriality evolving in platyrrhines even though it has been highly successful among catarrhines; our own catarrhine sensibilities may have falsely exaggerated the chances (Fig. 4.5). Among all the modern and subfossil strepsirhines, fossil adapiforms, living and extinct tarsiiforms, plesiadpiforms, all stem catarrhines – and platyrrhines so far as we know them – no more than a handful of genera appear to be obligate terrestrialists. Primates, as an order, are almost universally arboreal. As a radiation, platyrrhines are no different.

4.6 Summary

Platyrrhines have been evolving in parts of South America for more than 26 million years, adapting to many changes in the continent's structure, climate, flora and fauna. The Amazonian rain forest where New World monkeys are now most abundant may have begun to evolve its current configuration only 15 million years ago, long after platyrrhines arrived. Today's largest primate communities, in Amazonia and the Mata Atlantica, are different in character, and provide contrasting models for reconstructing past primate communities. The Patagonian province was inhabited by primates from the early to middle Miocene for at least 5 million years before becoming extinct. It was strongly influenced by proximity to Antarctica and the evolution of the Antarctic ice sheets, supporting a low-diversity primate community analogous to the Mata Atlantica but with a primate fauna that may have been dominated by middle-sized, non-seed eating, primitive pitheciines, able to tolerate highly seasonal resources and feeding predominantly on a mixture of tough fruits and leaves. The late middle Miocene La Venta region of Colombia was a very modern, diverse, tropical primate community, an extension of the Amazonian province.

The poorly known Greater Antilles forms may have first entered in the Miocene as a small community involving at least three groups, pitheciines, atelines and cebines.

We propose that some platyrrhines that are now successful and very widely distributed in tropical forests across much of the South and Central American landscape, such as *Cebus* and *Alouatta*, are actually members of pioneering lineages that may have been more prone in the past to using the ground. However, we also argue that the modern platyrrhines more generally, as a consequence of exceptional and myriad adaptations to canopy and subcanopy locomotion and posture, have been unlikely candidates for evolving terrestrial lineages or communities. Apart from the earliest forms, most of the fossil record is consistent with the Long Lineage Hypothesis, that lengthy, enduring ecophylogenetic lineages have shaped the evolution of the platyrrhine adaptive radiation. Since some of these lineages, namely pitheciines and cebines, existed in Patagonia possibly before the modern wet lowlands in the north took on their contemporary aspect, it is an oversimplification to interpret the evolution of New World monkeys as a product of the Amazonian rain forest. The modern Amazonian primate community is an evolutionary mix of genera including: (1) ecologically flexible forms that may have arisen elsewhere and were first adapted to very different conditions, such as relatives of *Callicebus, Aotus* and other early pitheciines, and relatives of *Cebus* and *Alouatta*; (2) derived descendants of lineages who radiated and became increasingly specialized to unique habitat features of Amazonia, such as *Chiropotes* and *Cacajao*; and (3) a variety of monkeys that may have arisen *in situ*, including *Ateles*, *Lagothrix* and an assortment of callitrichines.

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References

Aceñolaza, F.G. (2000) La Formación Paraná (Mioceno medio); estratigrafía, distribución regional y unidades equivalentes. In: Aceñolaza, F.G. and Herbst, R. (Eds.), *El Neógeno de Argentina* INSUGEO, Serie Correlación Geológica, 14, 9–27.

Alonso, R. (2000) El Terciario de la Puna en tiempos de la ingresión marina paranense. In: Aceñolaza, F.G. and Herbst, R. (Eds.), *El Neógeno de Argentina* INSUGEO, Serie Correlación Geológica, 14, 163–180.

Ameghino, F. (1906) Les formacions sédimentaires du Crétacé supérieur et du Tertiare de Patagonie avec un paralélle entre leur faunes mammalogiques et celles de l'ancien continent. Anales Museo de Historia Natural, Buenos Aires, ser. III 15, 1–568.

Anthony, M.R.L. and Kay, R.F. (1993) Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. American Journal of Science, 283A, 356–382.

Ashworth, A.C., Harwood, D.M., Webb, P.-N. and Mabin, M.C.G. (1997) A weevil from the heart of Antarctica: Ion Studies in Quaternary entomology – an inordinate fondness for insects. Quaternary Proceedings, 5, 15–22.

Askin, R.A. (1997) Eocene-? earliest Olgicoene terrestrial palynology of Seymour Island, Antarctica, In: Ricci, C. (Ed.), the Antarctic Region: geological Evolution and Processes, Terra Antarctica Publications, Siena, pp. 993–996.

Ayres, J.M. (1989) Comparative, feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. Journal of Human Evolution, 18, 697–716.

Barreda, V. and Palamarczuck, S. (2000) Estudio palinoestratigráfico del Oligoceno tardío- Mioceno en secciones de la costa patagónica y plataforma continental argentina. In: Aceñolaza, F.G. and Herbst, R. (Eds.), *El Neógeno de Argentina* INSUGEO, Serie Correlación Geológica, 14, 103–138.

Barrett, P.J. (1989) Antarctic Cenozoic history from the CIROS-1 Drillhole, McMurdo Sound. *DSIR Bulletin*, 245, 1–254.

Beard, K.C. (2002) East of Eden at the Paleocene/Eocene boundary. Science, 295, 2028–2029.

Bigarella, J.J. and Ferreira, A.M.M. (1985) Amazonian geology and the Pleistocene and the Cenozoic environments and paleoclimates. In: Prance, G.T. and Lovejoy, T.E. (Eds.), *Amazonia. Key Environments Series*. Pergamon Press, New York, pp. 49–71.

Bond, M. (1986) Los ungulados fósiles de Argentina: evolución y paleoambientes. *Actas Congreso Argentino de Paleontología y Bioestratigrafía*, 2, 173–185.

Bown, T.M. and Larriestra, C.N. (1990) Sedimentary paleoenvironments of fossil platyrrhine localities, Miocene Pinturas Formation, Santa Cruz Province, Argentina. Journal of Human Evolution, 19, 87–119.

Browning, J.V., Miller, K.G. and Pak, D.K. (1996) Global implications of lower to middle Eocene sequence boundaries on the New Jersey coastal plain: The icehouse cometh. Geology, 24, 639–642.

Campbell, K.E., Frailey, C.D. and Romero-Pittman, L. (2006) The Pan-Amazonian Ucayali Peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. Palaeogeography, Palaeoclimatology, Palaeoecology, 239, 166–219.

Cartelle, C. (1993). Achado de Brachyteles do Pleistoceno Final. Neotropical Primates, 1, 8.

Cartelle, C. and Hartwig, W.C. (1996) A new extinct primate among the Pleistocene megafauna of Bahia, Brazil. Proceedings of the National Academy of Science, 93(13), 6405–6409.

Cartelle, C. (1994) *Tempo Passado. Mamíferos do Pleistoceno em Minas Gerais.* Editora Palco, ACESITA. Assessoria de Comunicação da Compania Aços Especiais Itabira, Belo Horizonte, 131pp.

Cerqueira, R. (1982) South American landscapes and their mammals. In: Mares, M.A. and Genonways, H.H. (Eds.), *Mammalian Biology in South America*, University of Pittsburgh, Linesville, pp. 53–75.

Cifelli, R.L. (1985) South American ungulate evolution and extinction. In: Stehli, F. and Webb, S.D. (Eds.), *The Great American Biotic Interchange*, Plenum Press, New York, pp. 249–266.

Cooke, S.B., Halenar, L., Rosenberger, A.L., Tejedor, M.F. and Hartwig, W.C. (2007) *Protopithecus, Paralouatta*, and *Alouatta:* The making of a platyrrhine folivore. American Journal of Physical Anthropology, 132(S44), 90.

Cooper, A.K., Barrett, P.J., Hinz, K., Traube, V., Leitchenkov, G. and Stagg, H.M.J. (1991) Cenozoic prograding sequences of the Antarctic continental margin: A record of glacio-eustatic and tectonic events. Marine Geology, 102, 175–213.

Cozzuol, M.A. (2006) The Acre vertebrate fauna: Age, diversity, and geography. Journal of South American Earth Sciences, 21, 185–203.

Croft, D.A. (2007) The middle Miocene (Laventan) Quebrada Honda fauna, southern Bolivia and a description of its notoungulates. Palaeontology, 50, 277–303.

Daválos, L.M. (2004) Phylogeny and biogeography of Caribbean mammals. Biological Journal of the Linnaean Society, 81, 373–394.

DeConto, R.M., Pollard, D. (2003) Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO_2. Nature, 421, 245–249.

Delson, E. and Rosenberger, A.L. (1984) Are there any anthropoid primate living fossils? In: Eldredge, N. and Stanley, S.M. (Eds.), *Living Fossils*. Springer Verlag, New York pp. 50–61.

Fernandez-Duque, E. (2007) Aotinae: Social monogamy in the only nocturnal haplorhines. In: Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. and Bearder, S.K. (Eds.), *Primates in Perspective*, Oxford, New York, pp. 139–154.

Fleagle J. and Rosenberger A.L. (1983) Cranial morphology of the earliest anthropoids. In: Sakka, M. (Ed.), *Morphologie, Evolutive, Morphogenese du Crane et Anthropogenese*. Paris: Centre National de la Recherche Scientifique, pp. 141–153.

Fleagle, J. and Tejedor, M.F. (2002) Early platyrrhines of southern South America. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record.* Cambridge University Press, Cambridge, pp. 161–173.

Flynn, J.J. and Wyss, A.R. (1998) Recent advances in South American mammalian paleontology. TREE, 13(11), 449–454.

Flynn, J.J., Wyss, A.R., Charrier, R. and Swisher III, C.C. (1995) An Early Miocene anthropoid skull from the Chilean Andes. Nature, 373, 603–607.

Flynn, J.J., Wyss, A.R., Croft, D.A. and Charrier, R. (2003) The Tinguiririca Fauna,Chile: Biochronology, paleoecology, biogeography, and a new earliest OligoceneSouth American Land Mammal “Age”. Palaeogeography, Palaeoclimatology, Palaeoecology, 195, 229–259.

Ford, S.M. (1990) Locomotor adaptations of fossil platyrrhines. Journal of Human Evolution, 19, 141–173.

Frailey, C.D. and Campbell, K.E. (2004) The rodents of the Santa Rosa local fauna. In: Campbell, K.E. (Ed.), *The Paleogene Mammalian Fauna of Santa Rosa, Peru.* Natural History Museum of Los Angeles County, Science Series, 40, 71–130.

Francis, J.E. and Hill, R.S. (1996) Fossil plants from the Pliocene Sirus Group, Transantarctic Mountains: Evidence for climate from growth rings and fossil leaves, Palaios, 11, 389–396.

Francis, J.E., Haywood, A.M., Ashworth, A.C. and Valdes, P.J. (2007) Tundra environments in the Neogene Sirius Group, Antarctica: evidence from the geological record and coupled atmosphere–vegetation models. Journal of the Geological Society, 164, 317–322.

Francis, J.E. and Poole, I. (2002) Cretaceous and early Tertiary climates of Antarctica: evidence from fossil wood: Palaeogeography, Palaeoclimatology, Palaeoecology, 182, 47–64.

Gebo, D.L. (2002) Adapiformes: Phylogeny and adaptation. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 21–43.

Gelfo J.N. (2006) *Los Didolodontidae (Mammalia: Ungulatomporpha) del Terciario Sudamericano. Sistemática, origen y evolución.* PhD thesis, Universidad Nacional de La Plata, Argentina.

Goin, F.J. (2003) Early marsupial radiations in South America. In: Jones, M., Dickman, C. and Archer, M. (Eds.), *Predators with Pouches: The Biology of Carnivorous Marsupials.* Commonwealth Scientific & Industrial Research Organization, Sydney, pp. 30–42.

Groves, C. (2001) *Primate Taxonomy*. Smithsonian Institution Press, Washinton, DC.

Gunnell, G.F. and Rose, K.D. (2002) Tarsiiformes: Evolutionary history and adaptation. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 45–82.

Hambrey, M.J., Ehrmann, W.U. and Larsen, B. (1991) Cenozoic glacial record of the Prydz Bay continental shelf, East Antarctica. In: Barron, J., et al. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results 119*, Ocean Drilling Program, College Station, pp. 77–132.

Harrison, T. (2002) Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record.* Cambridge University Press, Cambridge, pp. 311–338.

Hartwig, W. and Meldrum, D.J. (2002) Miocene platyrrhines of the northern Neotropics. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record.* Cambridge University Press, Cambridge, pp. 175–187.

Hartwig, W.C. and Cartelle, C. (1996) A complete skeleton of the giant South American primate *Protopithecus*. Nature, 381(6580), 307–311.

Hass, C.A., Maxson, L.R. and Hedges, S.B. (2001) Relationships and Divergences Times of West Indian Amphibians and Reptiles: Insights from Albumin Immunology. In: Woods, C.A. and Sergile, F.E. (Eds.), *Biogeography of the West Indies: Patterns and Perspectives.* CRC Press, New York, pp. 157–174.

Hedges, S.B. (1996) The Origin of the West Indian Amphibians and Reptiles. In: Powell, R. and Henderson, R.W. (Eds.), *Contributions to West Indian Herpetology: a tribute to Albert Swartz.* Society for the Study of Amphibians and Reptiles, Ithaca, pp. 95–128.

Hedges, S.B. (2001) Biogeography of the West Indies: An Overview. In: Woods, C.A. and Sergile, F.E. (Eds.), *Biogeography of the West Indies: Patterns and Perspectives.* CRC Press, New York, pp. 15–33.

Hershkovitz, P. (1977) *Living New World Monkeys (Platyrrhini): with an introduction to Primates.* University of Chicago Press, Chicago.

Hess, L.L., Melack, J.M., Novo, E.M.L.M., Barbosa, C.C.F. and Gastil, M. (2003) Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. Remote Sensing of Environment, 87, 404–428.

Heymann, E.W. (1998) Giant fossil New World primates: arboreal or terrestrial? Journal of Human Evolution, 34, 99–101.

Hinojosa, L.F. (2005) Cambios climáticos y vegetacionales inferidos a partir de paleofloras cenozoicas del sur de Sudamérica. Revista. Geologica Chile, 32, 95–115.

Hinojosa, L.F., (2005) Historia Terciaria de la Cordillera de la Costa: relaciones fisionómicas y fitogeográficas de la vegetación de la Cordillera de la Costa y las Paleofloras Terciarias del sur de Sudamérica. In: Smith, C., Armesto, J.J. and Valdovinos, C. (Eds.), *Biodiversidad y Ecología de los Bosques de la Cordillera de la Costa de Chile*, Editoral Universitaria, Santiago, pp. 90–104.

Hitz, R.B., Flynn, J.J. and Wyss, A.R. (2006) New Basal Interatheriidae (Typotheria, Notoungulata, Mammalia) from the Paleogene of Central Chile. America Museum Novitates, 3520, 1–32.

Horovitz, I. and MacPhee, R.D.E. (1996) New materials of *Paralouatta* and a new hypothesis for Antillean monkey systematics. Journal of Vertebrate Paleontology, 16, 42A.

Horovitz, I. and MacPhee, R.D.E. (1999) The quaternary Cuban platyrrhine *Paralouatta varonai* and the origin of the Antillean monkeys. Journal of Human Evolution, 36, 33–68.

Horovitz, I. (1997) *Platyrrhine Systematics and the Origin of the Greater Antillean Monkeys.* PhD dissertation. State University of New York, Stony Brook.

Horovitz, I. (1999) A Phylogenetic Study of the Living and Fossil Platyrrhines. American Museum Novitates, 3269, 1–40.

Iturralde-Vinent, M.A. and MacPhee, R.D.E. (1999) Paleogeography of the Caribbean Region: Implications for Cenozoic Biogeography. Bulletin of the American Museum of Natural History, 238, 1–95.

Jacobs, B.F., Kingston, J.D. and Jacobs, L.L. (1999) The Origin of Grass-Dominated Ecosystems. Annals of the Missouri Botanical Garden, 86(2), 590–643.

Jacobs, B.F., Kingston, J.D and Jacobs, L.L. (1999) The origins of grass-dominated ecosystems. Annals of the Missouri Botanical Gardens, 86, 590–643.

Jaramillo, C., Rueda, M.J. and Mora, G. (2006) Cenozoic Plant Diversity in the Neotropics. Science, 311, 1893–1896.

Kay, R.F. and Cozzuol, M.A. (2006) New platyrrhine monkeys from the Solimoes Formation (late Miocene, Acre State, Brazil). Journal of Human Evolution, 50, 673–686.

Kay, R.F. (1990) The phyletic relationships of extant and extinct fossil Pitheciinae (Platyrrhini, Anthropoidea). Journal of Human Evolution, 19, 175–208.

Kay, R.F. (1994) “Giant” Tamarin from the Miocene of Colombia. American Journal of Physical Anthropology, 95, 333–353.

Kay, R.F., Fleagle, J.G., Mitchell, T.R.T., Colbert, M., Bown, T. and Powers, D.W. (2008) The anatomy of *Dolichocebus gaimanensis*, a stem platyrrhine monkey from Argentina. Journal of Human Evolution, 54, 323–382.

Kay, R.F., Williams, B.A. and Anaya, F. (2001) The adaptations of *Branisella boliviana*, the earliest South American monkey, In: Plavcan, J.M., Kay, R.F., Jungers, W.L. and van Schaik, C. (Eds.), *Reconstructing Behavior in the Primate Fossil Record (Advances in Primatology)*, Kluwer/Plenum, New York, pp. 339–370.

Kay, R.F., Campbell, V.M., Rossie, J.B., Colbert, M.W. and Rowe, T. (2004) The olfactory fossa of *Tremacebus harringtoni* (Platyrrhini, early Miocene, Sacanana, Argentina): Implications for activity pattern. Anatomical Record, 281A, 1157–1172 .

Kay, R.F., Madden, R.H., Cifelli, R.L. and Flynn, J.J. (1997) *Vertebrate paleontology in the neotropics : the Miocene fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C.

Kay, R.F. and Meldrum, D.J. (1997) A new small platyrrhine from the Miocene of Colombia and the phyletic position of the callitrichines. In Kay, R.F., Madden, R.H., Cifelli, R.L. and Flynn, J. (eds.): *A History of Neotropical Fauna: Vertebrate Paleontology of the Miocene of Tropical South America*. Smithsonian Institution Press, Washington D.C., pp. 435–458.

Kinzey, W.G. (ed). (1997) *New World Primates: Ecology, Evolution, and Behavior*. Aldine de Gruyter, New York.

Kominz, M.A. and Pekar, S.F. (2001) Oligocene eustasy from two-dimensional sequence stratigraphic backstripping. Geological Society of America Bulletin, 113, 291–304.

Lawver, L.A. and Gahagan, L.M. (1998) The initiation of the Antarctic circumpolar current and its impact on Cenozoic climate. In: Crowley, T. and Burke, K. (Eds.), *Tectonic Boundary Conditions for Climate Model Simulations*, Oxford University Press, New York, pp. 213–226.

Lear, C.H., Rosenthal, Y., Coxall, H.K. and Wilson, P.A. (2004) Late Eocene to early Miocene ice sheet dynamics and the global carbon cycle. Paleoceanography, 19, PA4015.

Livermore, R., Eagles, G., Morris, P. and Maldonado, A. (2004) Shackleton Fracture Zone: No barrier to early circumpolar ocean circulation. Geology, 32, 797–800.

Lund, P.W. (1838) Blik paa Brasiliens dyreverden for sidste jordomvaeltning. *Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger*, 8, 61–144.

Lund, P.W. (1840) View of the fauna of Brazil, previous to the last geological revolution. Charlesworth's Magazine of Natural History, 4, 1–8; 49–57; 105–112; 153–161; 207–213; 251–259; 3-7-317; 373–389.

Lutcherhand, K., Kay, R.F. and Madden, R.H. (1986) *Mohanimico herkovitzi*, gen. sp. nov. un primate du Miocene moyen d'Amerique du Sud. Comptes rendus de l'Academie de science de Paris, 303, 1753–1758.

MacDowell, S.B. (1958) The Greater Antillean insectivores. Bulletin of the American Museum of Natural History, 115, 117–214.

MacFadden, B.J. (1990) Chronology of Cenozoic primate localities in South America. Journal of Human Evolution, 19, 7–21.

MacFadden, B.J. (2000) Cenozoic Mammalian Herbivores from the Americas: Reconstructing Ancient Diets and Terrestrial Communities. Annual Review of Ecology and Systematics, 31, 33–59.

Macphail, M. and Cantrill, D. (2006) Age and implications of the Forest Bed, Falkland Islands, southwest Atlantic Ocean: Evidence from fossil pollen and spores. Palaeogeography, Palaeoclimatology, Palaeoecology, 240, 602–629.

MacPhee, R.D.E. (2005) "First" appearances in the Cenozoic land-mammal record of the Greater Antilles: significance and comparison with South American and Antarctic records. Journal of Biogeography, 32, 551–564.

MacPhee, R.D.E. and Iturralde-Vinent, M. (1994) First Tertiary Land Mammal from Greater Antilles: An Early Miocene Sloth (Xenarthra, Megalonychidae) From Cuba. American Museum Novitates, 3094, 1–13.

MacPhee, R.D.E. and Iturralde-Vinent, M. (1995) Origin of the Greater Antillean Land Mammal Fauna, 1: New Tertiary Fossils from Cuba and Puerto Rico. American Museum Novitates, 3141, 1–31.

MacPhee, R.D.E. and Fleagle, J.G. (1991) Postcranial Remains of *Xenothrix mcgregori* (Primates, Xenotrichidae) and Other Late Quaternary Mammals from Long Mile Cave, Jamaica. Bulletin of the American Museum of Natural History, 206, 287–321.

MacPhee, R.D.E. and Horovitz, I. (2004) New Craniodental Remains of the Quaternary Jamaican Monkey *Xenothrix mcgregori* (Xenotrichini, Callicebinae, Pitheciidae), with a Reconsideration of the *Aotus* Hypothesis. American Museum Novitates, 3434, 1–51.

MacPhee, R.D.E. and Meldrum, J. (X) Postcranial Remains of the Extinct Monkeys of the Greater Antilles (Platyrrhini, Callicebinae, Xenotrichini), with a Consideration of Semiterrestriality in *Paralouatta*. American Museum Novitates, 3516, 1–65.

MacPhee, R.D.E. and Horovitz, I. (2002) Extinct Quaternary platyrrhines of the Greater Antilles and Brazil. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record.* Cambridge University Press, Cambridge pp. 189–200.

MacPhee, R.D.E. and Woods, C. (1982) A New Fossil Cebine from Hispaniola. American Journal of Physical Anthropology, 58, 419–436.

MacPhee, R.D.E., Horovitz, I., Arredondo, O. and Vasquez, O.J. (1995) A New Genus for the Extinct Hispaniolan Monkey *Saimiri bernensis* Rímoli, 1977, with Notes on Its Systematic Position. American Museum Novitates, 3134, 1–21.

MacPhee, R.D.E., Iturralde-Vinent, M. and Gaffney, E. (2003) Domo de Zaza, an Early Miocene Vertebrate Locality in South-Central Cuba, with Notes on the Tectonic Evolution of Puerto Rico and the Mona Passage. American Museum Novitates, 3394, 1–42.

Madden, R.H., Bellosi, E., Carlini, A.A., Heizler, M., Vilas, J.J., Re, G., Kay, R.F. and Vucetich, M.G. (2005) Geochronology of the Sarmiento Formation at Gran Barranca and elsewhere in Patagonia: Calibrating middle Cenozoic mammal evolution in South America. *Actas XVI Congreso Geológico Argentino*, La Plata, Tomo IV, 411–412.

Marchant, D.R., Denton, G.H., Swisher, C.C. and Potter, N. (1996) Late Cenozoic Antarctic paleoclimate reconstructed from volcanic ashes in the dry valleys region of southern Victoria Land. Geological Society of America Bulletin, 108, 181–194.

Marchant, D.R., Swisher, C.C., III, Lux, D.R., West, Jr. D. and Denton, G.H. (1993) Pliocene paleoclimate and East Antarctic ice sheet history from surficial ash deposits. Science, 260, 667–670.

Mares, M.A., Ernest, K.A. and Gettinger, D.D. (1986) Small Mammal Community Structure and Composition in the Cerrado Province of Central Brazil. Journal of Tropical Ecology, 2(4), 289–300.

Meldrum, D.J. (1993) Postcranial adaptations and positional behavior in fossil platyrrhines. In: Gebo, D.L. (Ed.), *Postcranial Adaptations in Nonhuman Primates*. Northern Illinois University, DeKalb, pp. 235–251.

Mikolajewicz, U., Maier-Reimer, E., Crowley, T.J. and Kim, K.-Y. (1993) Effect of Drake and Panamanian gateways on the circulation of an ocean model. Paleoceanography, 8(4), 409–426.

Miller, K.G., Wright, J.D. and Fairbanks, R.G. (1991) Unlocking the ice house: Oligocene-Miocene oxygen isotopes, eustasy, and margin erosion. Journal of Geophysical Research, 96, 6829–6848.

Miller, K.G., Fairbanks, R.G. and Mountain, G.S. (1987) Tertiary oxygen isotope synthesis, sea-level history, and continental margin erosion. Paleoceanography, 2, 1–19.

Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.J., Christie-Blick, N. and Pekar, S.F. (2005) The Phanerozoic Record of Global Sea-Level Change. Science, 310, 1293–1298.

Muizon, C. De and Cifelli, R. (2000) The "condylarths" (archaic Ungulata, Mammalia) from the early Paleocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. Geodiversitas, 22(1), 47–150.

Napier, P.H. (1976) *Catalogue of primates in the British Museum (Natural History) I. Families Callitrichidae and Cebidae.* British Museum Natural History, London.

Nong, G.T., Najjar, R.G., Seidov, D. and Peterson, W. (2000) Simulation of ocean temperature change due to the opening of Drake Passage. Geophysical Research Letters, 27, 2689–2692.

Norconk, M.A. (2007) Sakis, uakaris, and titi monkeys. In: Campbell, C.J., Fuentes, A., MacKinnon, K., Panger, M. and Bearder, S. (Eds.), *Primates in Perspective.* Oxford University Press, New York. pp. 123–138.

Opazo, J.C., Wildman, D.E., Prychitko, T., Johnson, R.M. and Goodman, M. (2006) Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). Molecular Phylogenetics and Evolution, 40, 274–280.

Pascual, R. (2006) Evolution and geography: The biogeographic history of South American land mammals. *Annals of the Missouri Botanical Garden*, 93, 209–230.

Pascual, R. and Ortíz Jaureguizar, E. (1990) Evolving climates and mammal faunas in cenozoic South America. Journal of Human Evolution, 19(1–2), 23–60.

Pascual, R., Ortíz Jaureguizar, E. and Prado, J.J. (1996) Land Mammals: Paradigm for Cenozoic South American geobiotic evolution. In: Arratia, G. (Ed.), *Contributions of Southern South America to Vertebrate Paleontology.* Münchner Geowissenschaftliche abhandlungen Verlag Dr. F. Pfeil (A) 30, 265–319.

Patterson, B. and Pascual, R. (1972) The fossil mammal fauna of South America. In: Keast, A., Erk, F. and Glass, B. (Eds.), *Evolution Mammals and Southern Continents.* State University of New York Press, Albany, pp. 247–309.

Pekar, S.F. and DeConto, R.M. (2006) High-resolution ice-volume estimates for the early Miocene: Evidence for a dynamic ice sheet in Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology, 231, 101–109.

Pekar, S.F., Hucks, A., Fuller, M. and Li, S. (2005) Glacioeustatic changes in the early and middle Eocene (51–42 Ma) greenhouse world based on shallow-water stratigraphy from ODP Leg 189 Site 1171 and oxygen isotope records. Geological Society of America Bulletin, 117(7), 1081–1093.

Pekar, S.F. and Christie-Blick, N. (2008) Resolving apparent conflicts between oceanographic and Antarctic climate records and evidence for a decrease in $p\mathrm{CO}_2$ during the Oligocene through early Miocene (34–16 Ma). Palaeogeography, Palaeoclimatology, Palaeoecology, 260/1–2, 41–49.

Pekar, S.F., Christie-Blick, N., Kominz, M.A. and Miller, K.G. (2002) Calibrating eustasy to oxygen isotopes for the early icehouse world of the Oligocene. Geology, 30, 903–906.

Pekar, S.F., Harwood, D.M. and DeConto, R.M. (2006) Resolving a late Oligocene conundrum: deep-sea warming versus Antarctic glaciation. Palaeogeography, Palaeoclimatology, Palaeoecology, 231, 29–40.

Pirrie, D., Marshall, J.D., Crame, J.A. (1998) Marine high Mg calcite cements in Teredolites bored fossil wood: evidence for cool palaeoclimates in the Eocene La Meseta Formation, Seymour Island. Palaios, 13, 276–286.

Potter, P. E. (1997) The Mesozoic and Cenozoic paleodrainage of South America: a natural history. Journal of South American Earth Science, 10, 331–344.

Poux, C., Chevret, P., Huchon, D., DeJong, W.W. and Douzery, E.J.P (2006) Arrival and Diversification of Caviomorph Rodents and Platyrrhine Primates in South America. Systematic Biology, 55(2), 228–244.

Prebble, J.G., Raine, J.I., Barrett, P.J. and Hannah, M.J. (2006) Vegetation and climate from two Oligocene glacioeustatic sedimentary cycles (31 and 24 Ma) cored by the Cape Roberts Project, Victoria Land Basin, Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology, 231, 41–57.

Rivero, M. and Arredondo, O. (1991). *Paralouatta varonai*, a new Quaternary platyrrhine from Cuba. Journal of Human Evolution, 21, 1–11.

Rosenberger, A.L. and Strier, K.B. (1989) Adaptive radiation of the ateline primates. Journal of Human Evolution, 18, 717–750.

Rosenberger, A.L. (1977) *Xenothrix* and ceboid Phylogeny. Journal of Human Evolution, 6, 461–481.

Rosenberger, A.L. (1978) A new species of Hispaniolan primate: a comment. Anuario Cientifico Universidad Central Este 3, 248–251.

Rosenberger, A.L. (1979) Cranial anatomy and implications of *Dolichocebus*, a late Oligocene ceboid primate. Nature, 279, 416–418.

Rosenberger, A.L. (1980) Gradistic views and adaptive radiation of platyrrhine primates. Zeitschrift für Morphologie und Anthropologie, 71, 157–163.

Rosenberger, A.L. (1981) A mandible of *Branisella boliviana* (Platyrrhini, Primates) from the Oligocene of South America. International Journal of Primatology, 2, 1–7.

Rosenberger, A.L. (1992) Evolution of feeding niches in new world monkeys. American Journal of Physical Anthropology, 88(4), 525–562.

Rosenberger, A.L. (2002) Platyrrhine paleontology and systematics: The paradigm shifts. In: Hartwig, W. (Ed.), *The Primate Fossil Record.* Cambridge University Press, Cambridge, pp. 151–159.

Rosenberger, A.L. and Kinzey, W. (1976) Functional Patterns of Molar Occlusion in Platyrrhine Primates. American Journal of Physical Anthropology, 45, 281–298.

Rosenberger, A.L., Hartwig, W. and Wolf, R.G. (1991) *Szalatauus attricuspis*, an early platyrrhine primate from Salla, Bolivia. Folia Primatologica, 56, 225–233.

Rosenberger, A.L., Setoguchi, T. and Shigerhara. N. (1990) The fossil record of callitrichine primates. Journal of Human Evolution, 19, 209–236.

Rosenberger, A.L. and Tejedor, M.F. (in press) The misbegotten: long lineages, long branches and the interrelationhsips of Aotus, Callicebus and the saki-uakaris. In: Barnett, A., Viega, L., Ferrari, S., Norconk, M. Cambridge University Press, Cambridge. Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge University Press, Cambridge.

Rusconi, C. (1935) Los especies de primates del oligoceno de Patagonoa (gen. *Homunculus*). Revista argentina de paleonologia y anthropologia ameghinia, 1, 39–126.

Russo, A. and Flores, M.A. (1972) Patagonia Austral extra-Andina. In Leanza, A.P. (ed.) Geología Regional Argentina, Academia Nacional de Ciencias, 1, 707–725, Córdoba.

Scher, H.D. and Martin, E.E. (2004) Circulation in the Southern Ocean during the Paleogene inferred from neodymium isotopes. Earth and Planetary Science Letters, 228, 391–405.

Seiffert, E.R., Simons, E.L., Clyde, W.C., Rossie, J.B., Attia, Y., Bown, T.M., Chatrath, P. and Mathison, M.E. (2005) Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. Science, 310, 300–304.

Setoguchi, T. and Rosenberger, A.L. (1987) A fossil owl monkey from La Venta, Colombia. Kyoto Univ. Overseas Res. Rep. New World Monkeys, 6, 1–6.

Sijp, W.P. and England, M.H. (2004) Effect of the Drake Passage in controlling the stability of the ocean's thermohaline circulation. Journal of Climate, 18, 1956–1966.

Simons, E.L. (1972) *Primate Evolution: An Introduction to Man's Place in Nature*. MacMillan Company, New York.

Simpson, G.G. (1981) *Splendid Isolation: The Curious History of South American Mammals*. Yale University Press, New Haven, p. 266.

Smith, T., Rose, K.D. and Gingerich, P.D. (2006) Rapid Asia–Europe–North America geographicdispersal of earliest Eocene primate Teilhardinaduring the Paleocene–Eocene Thermal Maximum. Proceedings of the National Academy of Sciences, 103(30), 11223–11227.

Stehli, F.G. and Webb, S.D. (1985) The Great American biotic interchange. Plenum Press, New York, p. 550.

Stirton, R.A. (1951) Ceboid monkeys form the Miocene of South America. Bulletin of the University of California Publications in Geology, 28, 315–356.

Sudgen, D.E., Marchant, D.R. and Denton, G.H. (1993) The case for a stable East Antarctic ice sheet: the background. Geografiska Annaler, 75A, 151–155.

Szalay, F. and Delson, E. (1979) *Evolutionary History of the Primates*. Academic Press, New York.

Tauber, A. (1991) *Homunculus patagonicus* Ameghino 1891 (Primates, Ceboidea), Mioceno temprano de la costa atlántica austral, Provincia de Santa Cruz, República Argentina. *Academia Nacional de Ciencias*, Córdoba, 82, 1–32.

Tauber, A. (1994) Estratigrafía y vertebrados fósiles de la Formación Santa Cruz (Mioceno inferior) en la costa atlántica entre las rías del Coyle y Río Gallegos, Provincia de Santa Cruz, República Argentina. Unpublished PhD Thesis, Facultad de Ciencias Exactas, Físicas y Naturales. Universidad Nacional de Córdoba, Argentina. p. 422.

Tauber, A.A. (1997a) Bioestratigrafía de la Formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. Ameghiniana, 34(4), 413–426.

Tauber, A.A. (1997b) Paleoecología de la Formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. Ameghiniana, 34(4), 517–520.

Tejedor, M.F. (2002) Primate canines from the early Miocene Pinturas Formation, Southern Argentina. Journal of Human Evolution, 43, 127–141.

Tejedor, M.F., Tauber, A.A., Rosenberger, A.L., Swisher, C.C. and Palacios, M.E. (2006) New primate genus from the Miocene of Argentina. Proceedings of the National Academy of Sciences, 103(14), 5437–5441.

Tejedor, M.F., Rosenberger, A.L. and Cartelle, C. (2008) Nueva Especie de *Alouatta* (Primates, Atelinae) del Pleistoceno Tardío de Bahía, Brasil. Ameghiniana, 45, 247–251.

Terborgh, J. (1983) *Five New World primates: a study in comparative ecology*. Princeton, New Jersey, p. 260

Terborgh, J. (1985) The ecology of Amazonian primates. In: Prance, G.T. and Lovejoy, T. (Eds.), *Key environments: Amazonia.* Pergamon, Oxford, pp. 284–304.

Toggweiler, J.R. and Bjornsson, H. (2000) Drake Passage and paleoclimate. Journal of Quaternary Science, 15, 319–328.

Vucetich, M.G. (1986) Historia de los roedores y primates en Argentina: su aporte al conocimiento de los cambios ambientales durante el Cenozoico. Actas Congreso Argentino de Paleontología y Bioestratigrafía, 2, 157–165.

Vucetich, M.G. (1994) La fauna de roedores de la Formación Cerro Boleadoras (Mioceno Inferior?) en la provincia de Santa Cruz (Argentina). Acta Geológica Leopoldensia, 39, 365–374.

Vucetich, M.G., Deschamps, C.M., Olivares, A.I. and Dozo, M.T. (2005) Capybaras, size, shape, and time: A model kit. Acta Palaeontologica Polonica, 50(2), 259–272.

Vucetich, M.G. and Verzi, D.H. (1994) Las homologías en los diseños oclusales de los roedores Caviomorpha: un modelo alternativo. Mastozoología Neotropical, 1, 61–72.

Webb, P.-N. and Harwood, D.M. (1993) Pliocene fossil *Nothofagus* (Southern beech) from Antarctica: phytogeography, dispersal strategies, and survival in high latitude glacial-deglacial environments. In: Alden, J., Mastrontonio, J.C and Ødum, S. (Eds.), *Forest Development in Cold Climates.* Plenum Press, New York, pp. 135–165.

Webb, P.-N. and Harwood, D.M. (1991) Late Cenozoic glacial history of the Ross Embayment, Antarctica. Quaternary Science Reviews, 10, 215–223.

Wesselingh, F.P. and Salo, J.A. (2006) A Miocene perspective on the evolution of the Amazonian biota. Scripta Geologica, 133, 439–458.

White, J.L. and MacPhee, R.D.E. (2001) The sloths of the West Indies: A systematic and Phylogenetic Review. In: Woods, C.A. and Sergile, F.E. (Eds.), *Biogeography of the West Indies: Patterns and Perspectives.* CRC Press, New York, pp. 35–54.

Wilf, P., Cúneo, N.R., Johnson, K.R., Hicks, J.F., Wing, S.L. and Obradovich, J.D. (2003) High Plant Diversity in Eocene South America: Evidence from Patagonia. Science, 300, 122–125.

Wilf, P., Labandeira, C.C., Johnson, K.R. and Cúneo, N.R. (2005) Richness of plant–insect associations in Eocene Patagonia: A legacy for South American biodiversity. Proceedings of the National Academy of Sciences, 102(25), 8944–8948.

Williams, E.E. and Koopman, K.F. (1952) West Indian Fossil Monkeys. American Museum Novitates, 1546: 16 p.

Wilson, G.S., Harwood, D.M., Askin, R.A. and Levy, R.H. (1998) Late Neogene Sirius Group strata in Reedy valley, Antarctica: a multiple-resolution record of climate, ice-sheet and sea-level events. Journal of Glaciology, 44, 437–447.

Wyss, A.R., Flynn, J.J., Norell, M.A., Swisher, C.C., Novacek, M.J., McKenna, M.C. and Charrier, R. (1994) Paleogene mammals from the Andes of central Chile: a preliminary taxonomic, biostratigraphic, and geochronologic assessment. American Museum Novitates, 3098, 1–31.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. and Billups, K. (2001) Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. Science, 292, 686–693.

Zamaloa, M.C. (1993) Hallazgos palinológicos en la Formación Pinturas, Sección Cerro de los Monos (Mioceno inferior), Provincia de Santa Cruz, Argentina. Ameghiniana, 30, 353.

Zamaloa, M.C., Gandolfo, M.A., Gonzalez, C.C., Romero, E.J., Cúneo, N.R. and Wilf, P. (2006) Casuarinaceae From The Eocene Of Patagonia, Argentina. International Journal of Plant Science, 167(6), 1279–1289.