

The Gondwanan and South American Episodes: Two Major and Unrelated Moments in the History of the South American Mammals

Rosendo Pascual · Edgardo Ortiz-Jaureguizar

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Abstract The first steps in the history of South American mammals took place ca. 130 Ma., when the South American plate, still connected to the Antarctic Peninsula, began to drift away from the African-Indian plate. Most of the Mesozoic history of South American mammals is still unknown, and we only have a few enigmatic taxa (i.e., a Jurassic Australosphenida and an Early Cretaceous Prototribosphenida) that pose more evolutionary and biogeographic questions than answers. The best-known Mesozoic, South American land-mammal fossils are from Late Cretaceous Patagonian beds. These fossils represent the last survivors of non- and pre-tribosphenic Pangaean lineages, all of them with varying endemic features: some with few advanced features (e.g., ?Eutriconodonta and “Symmetrodonta”), some very diversified as endemic groups (e.g., ?Docodonta Reigitheriidae), and others representing vicariant types of well known Laurasian Mesozoic lineages (e.g., Gondwanatheria as vicariant of Multituberculata). These endemic mammals lived as relicts (although advanced) of pangeic lineages when a primordial South American continent was still connected to the Antarctic Peninsula and, at the northern extreme, near the North American Plate. By the beginning of the Late Cretaceous, the volcanic and diastrophic processes that finally led to the differentiation of the Caribbean region and Central America built up transient geographic connections that permitted the initiation of an overland inter-American exchange that included, for example, dinosaurian titanosaurs from South America and hadrosaurs from North America. The immigration of other vertebrates followed the same route, for example, polydolopimorphian marsupials. These marsupials were assumed to have differentiated in South America prior to new discoveries from the North American Late Cretaceous. The complete extinction of endemic South American Mesozoic mammals by the Late Cretaceous-Early Paleocene, and the subsequent and in part coetaneous immigration of North American therians, respectively, represent two major moments in the history of South American mammals: a

R. Pascual (✉)
Facultad de Ciencias Naturales y Museo, Paseo del Bosque s/n, B1900FWA La Plata, Argentina
e-mail: ropascua@museo.fcnym.unlp.edu.ar

E. Ortiz-Jaureguizar
LASBE (Laboratorio de Sistemática y Biología Evolutiva), Facultad de Ciencias Naturales y Museo, Paseo del Bosque s/n, B1900FWA La Plata, Argentina
e-mail: eortiz@fcnym.unlp.edu.ar

Gondwanan Episode and a South American Episode. The Gondwanan Episode was characterized by non- and pre-tribosphenic mammal lineages that descended from the Pangeic South American stage (but already with a pronounced Gondwanan accent, and wholly extinguished during the Late Cretaceous–Early Paleocene span). The South American Episode, in turn, was characterized only by therian mammals, mostly emigrated from the North American continent and already with a South American accent obtained through isolation. The southernmost extreme of South America (Patagonia) remained connected to the present Antarctic Peninsula at least up until about 30 Ma., and both provided the substratum where the primordial cladogenesis of “South American” mammals occurred. The resulting cladogenesis of South American therian mammals followed Gould’s *motto*: early experimentation, later standardization. That is to say, early cladogenesis engendered a great variety of taxa with scarce morphological differentiation. After this early cladogenesis (Late Eocene–Early Oligocene), the variety of taxa became reduced, but each lineage became clearly recognizable distinctive by a constant morphologic pattern. At the same time, those mammals that underwent the “early experimentation” were part of communities dominated by archaic lineages (e.g., brachydont types among the native “ungulates”), whereas the subsequent communities were dominated by mammals of markedly “modern” stamp (e.g., protohypsodont types among the native “ungulates”). The Gondwanan and South American Episodes were separated by a critical latest Cretaceous–earliest Paleocene hiatus, it is as unknown as it is important in which South American land-mammal communities must have experienced extinction of the Gondwanan mammals and the arrival and radiation of the North American marsupials and placentals (with the probable exception of the xenarthrans, whose biogeographic origin is still unclear).

Keywords Mesozoic · Cenozoic · Gondwana · South America · Patagonia · Antarctica · Paleobiogeography · Paleocology

Introduction

Fossil mammals that are not related to modern groups may have little effect on generalizations concerning Recent taxa. Notwithstanding, they are of intrinsic importance in permitting not only a classification that accounts for the greatest diversity of taxa, but also, for example, showing that monotremes and therians arose as just two of many possible alternatives offered by Pangea in the two derived subsequent and separate supercontinents, Laurasia and Gondwana (Pascual, 1996; Pascual and Goin, 2001; Pascual et al., 2002c). Fossil taxa related to modern groups often provide insights into the primitive states of characters that were markedly transformed in Recent representatives; fossils are also useful for testing the broadest generalizations of evolutionary biology laws (Novacek, 1992). On this latter topic, the Late Mesozoic Gondwanan mammals that recently began to be recorded for the first time in Patagonia (see Bonaparte, 1996, and literature therein) provide numerous and varied examples. These examples attest to at least one major Late Cretaceous Gondwanan Episode, as distinct as it is unexpected (Gondwanan “Stage,” *sensu* Pascual, 1996). Among its mammals, we can recognize some of the most outstanding examples of vicariant taxa (see below). This Episode records an unexpected evolutionary experiment (“the other history,” *sensu* Pascual, 1997) mainly because, with the exception of the Monotremata in the Australian-Papuan region, and probably the Xenarthra in South America, it left no extant representatives. The Gondwanan taxa include an advanced non-tribosphenic gondwanathere and a likewise advanced pre-tribosphenic dryolestoid, both known from relict representatives discovered in early (but not earliest) Paleocene beds, with another gondwanathere represented in middle Eocene deposits of the Antarctic Peninsula (Reguero et al., 2002; Goin et al., 2006b).

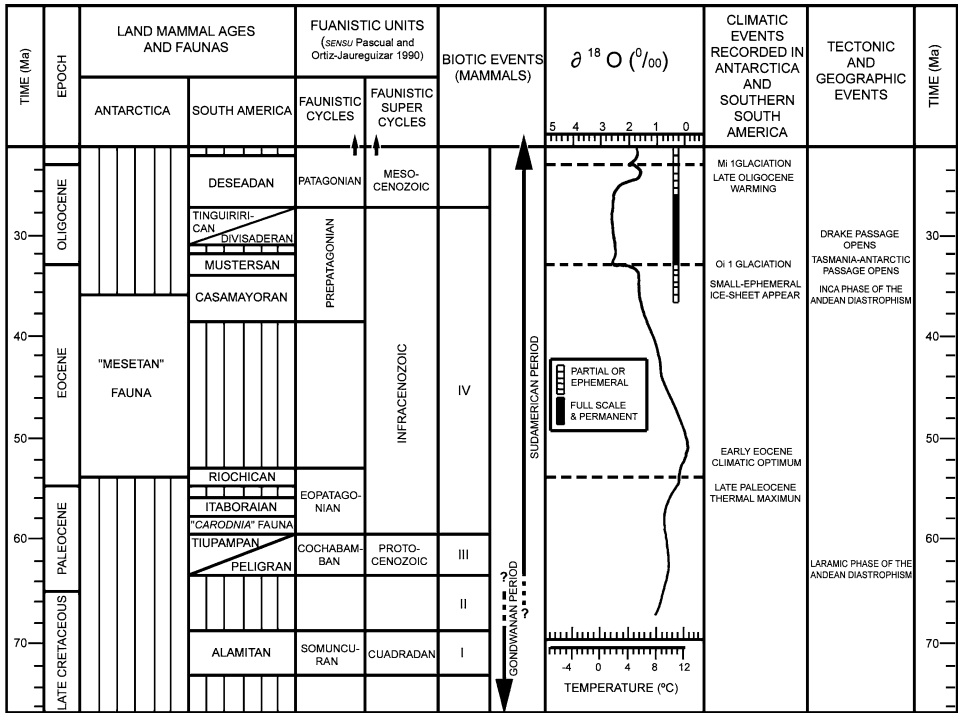


Fig. 1 Correlation of Antarctic and South American Land-Mammal Ages and Faunas, with $\delta^{18}\text{O}$ (‰) temperatures ($^{\circ}\text{C}$), climatic events recorded in Antarctica and Southern South America, and Southern tectonic and geographic events. The absolute ages are related to the standard GPTS (Geomagnetic Polarity Time Scale; Berggren et al., 1995). The last three parameters were taken from Zachos et al., 2001

To these three early Cenozoic taxa, which are the only known relicts of Gondwanan clades, have been added an advanced toothed immigrant monotreme (Ornithorhynchidae). This latter group has not been recorded in South American Late Cretaceous beds. If it means absence, the South American platypus quite probably emigrated by the earliest Paleocene from Australia, obviously through Antarctica (Pascual et al., 1992a,b, 2002c), or probably directly from Antarctica (see below).

In summary, South American land mammal history is radically divided into two major and unrelated episodes (Fig. 1) that occurred on two distinct geographical platforms. These two episodes were unconnected, involved a complete change of the actors, and were separated by a ca. 9 million year Late Cretaceous-earliest Paleocene hiatus, with a diminished mammal fauna (see below). The two major episodes are the Gondwanan and South American episodes (Fig. 1). The Gondwanan Episode is represented by the Alamitan South American Land Mammal Age (SALMA), the Somuncurian Faunistic Cycle, and the Cuadradian Faunistic Supercycle. The South American Episode is, in part, composed of the Peligran through the Deseadan SALMAs, the Cochabambian through Patagonian Faunistic Cycle, and the Proto-Cenozoic through Meso-Cenozoic Supercycle.

The Gondwanan Episode, almost exclusively known on the basis on the Patagonian record (see below), is characterized mainly by fragmentary Late Cretaceous remains of isolated molars of non-tribosphenic and pre-tribosphenic mammals of central Patagonia, but also by several dentaries of native dryolestoids. Several partial skeletons of an advanced pre-tribosphenic

mammal (*Vincelestes neuquenianus* Bonaparte, 1986b; see below) are known from Early Cretaceous beds of NW Patagonia. These fossils apparently represent an episode that is distinct from the Gondwanan Episode. Likewise, those ichnites from the Late Jurassic (Callovian or Oxfordian) of Southern Patagonia, assigned by Casamiquela (1961, 1975) to a mammal he nominated *Ameghinichnus patagonicus* and considered as representing a therian stock ancestral to marsupials and possibly eutherians, as well as a tiny dentary coming from beds of likewise Callovian-Oxfordian age in central-northern Patagonia, considered to be the first South American tribosphenic mammal (Rauhut et al., 2002), might represent another Mesozoic episode distinct from the Late Cretaceous Gondwanan Episode.

The South American Episode (= “Stage”) from the Early Paleocene (or probably from the Late Cretaceous; see Bertini et al., 1993) to Present, has involved immigrant metatherians and eutherians as its exclusive actors. However, the recently discovered middle-late Jurassic mammal suggests at least one previous pre-Cretaceous instance in which mammals evolved tribosphenic molars, a process that (according to the record) preceded the Laurasian one (e.g., Luo et al., 2002; Rauhut et al., 2002; Kielan-Jaworowska et al., 2004). Thus, the Jurassic form supports the alternative suggested by Flynn et al. (1999) that “Tribosphenic molars evolved independently in two ancient (holotherian) mammalian groups with different geographic distributions during the Jurassic/Early Cretaceous . . .”

As defined here, the two major episodes suggest that their respective mammal communities offer examples of vicariance and dispersal biogeography, and a hard testimony to one of the most obvious truisms in the history of life: “*Earth and Life evolve together*” (Croizat, 1958, 1964). After the final separation of Africa and South America, the geographical events that governed South American mammalian history favored a predominantly north-south emplacement of the American continents that finally led to the present western coast of the Southern Atlantic Ocean. This favored the dispersion of mammals between the North American sector of the Laurasian continent in the North, and Australia in the southern sector of Eastern Gondwana (e.g., marsupials from North America to Australia *via* South America-Antarctica [see Cox, 2000; Case et al., 2005]; monotremes from Australia to South America *via* Antarctica [see Pascual et al., 1992a,b, 2001, 2002c]). Particularly in this case, as well as in the global contact between the long time separated Laurasian and Gondwanan continents, we have to bear in mind the realities of timing and direction of continental ruptures and drifting as related with the timing of origins of taxa and their disjunctions and dispersal, as well as “... the often rapid and distant dissemination of organisms about the (present) world” (Thorne, 1978, p. 299). In this regard, the question of the origin, dispersion and dominance of the tribosphenidans (see above) is a good example.

It is notable that our knowledge of South American mammal history while the continent was part of the Gondwanan Supercontinent is solely derived from the Patagonian fossil record. In addition, there is a fragmentary record that comes from northern and central Patagonia and mostly represents the Campanian-Early Maastrichtian span. The Early Cretaceous and the Late Jurassic are so far poorly recorded, as well as the Triassic recently recorded in Brazil (see below). However, the exclusive record of some Laurasian mammal taxa in Late Paleocene Bolivian beds (Tiupampan SALMA; see Appendix) suggests that Patagonian Mesozoic mammal history must be viewed with caution when interpreting details of the broader history of South American Gondwanan mammals (Rougier et al., 2002). Despite the persistence of an inherited biogeographical difference between Patagonia (with an East Gondwana accent) and central-northern South America (with a West Gondwana accent) (see Crisci et al., 1991, 1993), the present record changes little the general South American mammalian history we derived from the known, predominantly Patagonian, Late Cretaceous-Early Paleocene record. The South American record is so poorly known at the critical time (latest Cretaceous-earliest Paleocene) that the above mentioned observation posed by Rougier et al. (2002) cannot even be addressed.

Taking into account the above considerations, the basic objective of this paper is summarize the evolution of the South American (plus the Antarctic Peninsula) land-mammal communities, using as a conceptual framework the two episodes that characterized the history of South American mammals. In this paper we will restrict our analysis to the Gondwanan Episode and the first part of the South American Episode, taking as its termination what in South America we regard (Pascual et al., 1985; Ortiz-Jaureguizar, 1986; Pascual, 1986) by its faunistic consequences as the equivalent to the European “Grande Coupure” (Stehlin, 1909; see below).

Methodology and basic assumptions

We have used as basic unit the land-mammal fauna of the ten SALMAs that represent the Late Cretaceous-Oligocene span (Fig. 1): Alamitan (Late Cretaceous, Patagonia); Peligran (Early Paleocene, Patagonia); Tiupampan (Late Paleocene, Bolivia and Peru); Itaboraian (Late Paleocene, Patagonia, northwestern Argentina and Brazil); Riochican (Late Paleocene-Early Eocene, Patagonia and northwestern Argentina); Casamayoran (Middle and Late Eocene, Patagonia and northern Argentina); Mustersan (Late Eocene-Early Oligocene, Patagonia and northwestern Argentina); Tinguirirican (Early Oligocene, Chile); and Divisaderan (Early Oligocene, central-western Argentina). Notwithstanding, and with the purpose of having a higher chronological resolution, we also use the faunas of some land mammal bearing formations that in previous papers were included in some of those SALMAs (e.g., Marshall et al., 1983; Pascual et al., 1996) or that were not considered as SALMAs. More specifically, we consider as yet un-named SALMAs: (1) the land-mammal fauna of the “*Carodnia* faunal zone” of Simpson (1935), i.e., Peñas Coloradas Fm. (Late Paleocene, Patagonia), previously included in the Itaboraian SALMA (see Bond et al., 1995), or included in the Tiupampan (Marshall et al., 1997) (Fig. 1); (2) the land-mammal fauna of the La Meseta Fm. (Eocene, Antarctica; see Reguero et al., 2002, and Fig. 1); and (3) the land-mammal fauna of the “Astraponotéen plus supérieur” of Ameghino (1901, 1902) or “Astraponotense más superior” of Bond et al. (1996), Sarmiento Fm. (Early Oligocene, Patagonia), previously included in the Mustersan SALMA, and presently considered younger than the original Astraponotéen, and as such the Patagonian approximate correlative to the Chilean Tinguirirican land-mammal fauna and SALMA (see Bond et al., 1995; Reguero, 1999; and Fig. 1). Systematic lists and biochronological ranges (SALMAs and faunas) of the land-mammal genera of the Gondwanan and South American Episodes can be found in the Appendix.

We hypothesized that the SALMAs, recognized mainly from the southern record (Fig. 1), represent relatively balanced mammal communities developed during periods of stasis, related to episodes of eustatic rise and geodynamic quiescence (Pascual, 1984a,b). On the other hand, we hypothesized that these periods of stasis were disrupted by severe climatic changes related to eustatic fall and geodynamic events. We have been using primarily dental characters, and more specifically the height of the cheekteeth crowns of native herbivorous mammals, to infer dietary behavior and habitat preferences (Pascual and Ortiz-Jaureguizar, 1990). With the addition of other biological and/or geological evidence we have recognized how closely related were the turnovers in mammal communities, and migratory events, with the above-mentioned physical environmental and climatic changes. Native herbivorous mammals, from the oldest to the youngest, successively grade from low-crowned to high-crowned animals, following the general environmental and climatic trend: from predominantly widely distributed close-forested, warm and wet habitats, to relatively confined open temperate grasslands, to hot deserts, and to cold habitats, which also appear as being related to the astronomical phenomena that produced the progressive retraction of the climatic belts (Pascual and Ortiz-Jaureguizar, 1990; Pascual

et al., 1996; Ortiz-Jaureguizar, 1998). Nevertheless, the land mammal record indicates that this general trend fluctuated over time.

The analysis of the inferred ecological types composing each of the southern SALMAs, compared with the lithogenetic facies and the geographic distribution of the mammal-bearing formations, lead us to recognize the following general patterns:

- (1) From the oldest to the youngest mammal communities we note progressive changes, from those composed of subtropical types, sylvan and forest dwellers, to ecological types adapted to temperate grasslands, to desert habitats.
- (2) From the oldest to the youngest we see a change from communities composed of a high diversity at suprageneric levels, and with species having a low degree of anatomical differences, to those composed of a low diversity at suprageneric level with species having a higher degree of anatomical differences. Gould's *motto* of "early experimentation and later standardization" (Gould, 1983) is perfectly applicable to the evolutionary pattern of South American mammals.
- (3) The oldest communities, representing warmer environments (particularly indicated by the associated biota; see Pascual and Ortiz-Jaureguizar, 1990), had a wider latitudinal distribution (Pascual et al., 1996), including at least the Peninsula Antarctica (Vizcaíno et al., 1998).
- (4) With distributional oscillations, up to approximately the Middle Miocene, mammal-bearing formations persisted within very southern latitudes.
- (5) Gradually, the Late Miocene mammal-bearing formations are situated northward of the Patagonian region, i.e., from approximately 41°S northward.
- (6) The Patagonian Late Paleocene to Miocene land mammal formations are mainly composed of pyroclastic sediments. From the Late Miocene on, they changed to epiclastic, having strong reduced amount of pyroclastic sediments. Abundant phytoliths in the pyroclastic sediments suggest that grasslands were relatively wide-ranging environments, particularly indicated, early by the protohypsodont (*sensu* Mones, 1979, 1982) native "ungulates" of the Late Eocene SALMAs, and then by euhypsodont native "ungulates" of most of the Late Miocene-Pleistocene SALMAs. Both were important part of the Neogene mammal communities (see Pascual and Ortiz-Jaureguizar, 1990). The Tertiary mammal-bearing sediments exposed northward of Patagonia are predominantly epiclastic, although those from the pampas plains contain reduced pyroclastic components (known as "loessoid").
- (7) From the latest Miocene on, Patagonian mammal-bearing formations are rare, because the depocenters had been shifted northeastward. Apparently by then Patagonia was still propitious territory for mammals, as it was before (see Pascual, 1970; Pascual and Odreman Rivas, 1971).
- (8) Throughout the Tertiary, the general trend of shifting the continental depocenters northward and eastward appears to have been causally related to two notable phenomena: (I) the processes related to the definition of southernmost South America after its separation from Antarctica, passing from former thalassocratic environments to finally epeirocratic ones, the latter formerly composed of "subtropical" biomes, and later, gradually, by temperate grasslands to semi-desert biomes, and (II) the progressive rise of the Patagonian Cordillera gradually decreased the distribution of the humidity, generated in the Southern Pacific Anticyclone, and shifted the propitious environments for land mammals toward eastern and northern Patagonia. Obviously, these processes were related with global tectonic and astronomical phenomena that concomitantly produced the retraction of the climatic belts toward the equator.

The hierarchical arrangement of the SALMAs shows clusters of related episodes of mammal community evolution, not only according to taxonomic changes, but more importantly according to ecological modifications. Ortiz-Jaureguizar (1986) carried out a multivariate analysis of SALMAs similarity, a method that later on was revisited and updated by Pascual and Ortiz-Jaureguizar (1990), and Pascual et al. (1996). They used SALMAs as operational “taxonomic” units (OTUs) and the families of Cenozoic and Late Cretaceous land mammals as “characters.” They were able to recognize four hierarchical ranks of organization of SALMAs, distinguished as Faunistic Units. From lower to higher they were called: Faunistic Subcycles, Faunistic Cycles, Faunistic Supercycles, and Faunistic Megacycles. The recorded major changes in mammal communities (Pascual, 1984a, *in press*; Pascual and Ortiz-Jaureguizar, 1990; Pascual et al., 1996) appear to be concomitantly related to major changes in the environmental conditions related to worldwide tectonic phenomena.

Although the apparent regional relation of those physical and biological phenomena is more clearly expressed by Faunistic Cycles, Faunistic Subcycles, and Land-Mammal Ages, the major events that characterized the Faunistic Supercycles (Fig. 1) appear to be more closely related with worldwide phenomena. Thus, to characterize and summarize the major ecological and biogeographic changes recorded on the land-mammal communities characterizing the Gondwanan and South American Episodes, we will employ the Faunistic Supercycles.

Also, to graphically represent the faunistic changes recorded during the Late Cretaceous–Oligocene lapse, we will consider two parameters following Pascual et al. (1996): (1) taxonomic richness; and (2) trophic diversity. Both parameters were measured using genera as units. In the first case, genera were grouped into orders; in the second, genera were grouped into ten trophic types on the basis of cheekteeth crown morphology and height. The ten trophic types recognized were: (1) insectivorous; (2) insectivorous-frugivorous; (3) omnivorous-insectivorous; (4) frugivorous; (5) crustacean-mollusks eaters; (6) omnivorous-browsers; (7) browsers; (8) mixed-feeders; (9) grazers; and (10) carnivorous.

Gondwanan episode

Simpson’s milestone studies (see Simpson, 1980, and his own literature therein) were the first that established the base for the modern interpretation of the history of South American land mammals (see Marshall et al., 1983, 1984; Pascual and Ortiz-Jaureguizar, 1990; Pascual et al., 1996; Pascual, 1996, 1998). In addition, he ordered and synthesized a vast quantity of data originally published in at least six languages. A good deal of his interpretations, particularly those on the beginning of the Age of Mammals in South America, were mainly based on his original work, but critically also based on the work of the Ameghino brothers (see Simpson, 1948, 1967).

The record of South American mammals was almost absolutely restricted to the Cenozoic, and not just to the earliest Cenozoic but to the medial Paleocene (*sensu* Woodburne and Swisher, 1995) onward until 1983. In that year, Bonaparte and staff discovered the first unquestionable Mesozoic mammals in northern Patagonia (Late Cretaceous; see Bonaparte et al., 1984; Bonaparte and Soria, 1984), and almost simultaneously Pascual and staff found the first Early Paleocene mammals in central Patagonia (Scillato-Yané and Pascual, 1984, 1985). This last finding proved to be Early Paleocene in age, although not the earliest (see Pascual and Ortiz-Jaureguizar, 1991; Ortiz-Jaureguizar et al., 1999). The mammal-bearing levels are exposed in the Hansen Member (known as “Banco Negro Inferior”) of the Salamanca Formation (for its stratigraphical relationships and geographical situation see Pascual et al., 1992b; Legarreta and Uliana, 1994; Bond et al., 1995; Ortiz-Jaureguizar et al., 1999). Until these two findings, we had

not realized how notable was the very first span of the “Age of Mammals” in South America. Although presently somewhat restricted, the transitional K-T span still persists almost unknown (Pascual, 1998), although a recent finding apparently began to fill in part this transitional span (Goin et al., 2006a, and see below). The restricted knowledge of the history of South American mammals from the medial Paleocene onward contributed to the ignorance that in South America during its existence as part of Gondwana (i.e., most of the Mesozoic), there developed a notable mammalian episode, although phylogenetically not as spectacular as that occurred in Laurasia. Our ignorance of the presence of a distinct Mesozoic Gondwanan Episode in the history of South American mammals contributed to our failure to recognize the idea that the Australo-Papuan monotremes and South American xenarthrans were not suspected of being extant representatives of the Gondwanan Mesozoic unrecorded “other history.” In fact, they have not been recorded in the South American Gondwanan and earliest Paleocene beds. However, particularly from Reig’s paper (1981) to the most recent paper by Woodburne et al. (2003), using different lines of evidence, xenarthrans began to be regarded as South American in origin and considered to have had a Gondwanan root (but see below, The South American Episode). They both were seen as two of the most primitive living mammals, monotremes as Prototheria Gill 1872 (see McKenna, 1975; McKenna and Bell, 1997), xenarthrans as the most primitive clade with respect to the remaining advanced Theria, the so called Epitheria (McKenna, 1975; McKenna and Bell, 1997). Simply, the critical Late Cretaceous-Early Paleocene span in the history of South American mammals remained unknown until 1983. Of course, the oldest Mesozoic history still remains unknown.

Although by the 1980s the evidence supporting continental drift had been accepted as unquestionable, explanations of the biogeographic history on the Cenozoic South American mammals did not require application of the plate tectonic rationale as a *sine qua non* condition. Under Simpson’s arguments, which were basically followed by many other researchers (e.g., Patterson and Pascual, 1968, 1972), his sweepstake routes could solely explain the biogeographic history of South American mammals. But the subsequent record of early (but not earliest) Paleocene mammals in Bolivia and Patagonia, and much more the Late Cretaceous land mammals found also in Patagonia, opened a distinct historical perspective, drastically challenging Simpson’s original conceptions. Together these both suggest that:

- (1) The entire history of South American mammals cannot be explained without using the plate tectonics rationale (see Pascual, 1996, 1998, *in press*; Vizcaíno et al., 1998).
- (2) Most Late Cretaceous mammals represent known, major Pangeic Mesozoic clades, but also show marked endemism (Bonaparte, 1986a,b,c). So, these mammals were recognized as representing an endemic “Gondwanan Stage” (Pascual, 1996), which resulted from the fragmentation of the old Pangaea Supercontinent (ca. 180 Ma.) in the northern Laurasian continent, and the southern Gondwanan continent (Bonaparte, 1986b). Consequently, the ancestral Pangean populations were fragmented, leading to their subsequent isolation both on Laurasia and Gondwana. This led to the differentiation of a vicariant Gondwanan biota with respect to a Laurasian one that, with regional differentiation, persisted approximately until the end of the Cretaceous.
- (3) There was a long and critical unrecorded latest Cretaceous-earliest Paleocene hiatus, which is now becoming partially filled. Recent discoveries have added original information and suggestions, which have helped to elucidate the first steps of the Age of Mammals in South America, i.e., the unknown beginnings of the South American Episode (Bond et al., 1995; Pascual, 1996, 1998).
- (4) The long Tertiary isolation of South American mammal communities from those of the Antarctic Peninsula did not occur, neither from the beginning of the Tertiary or throughout

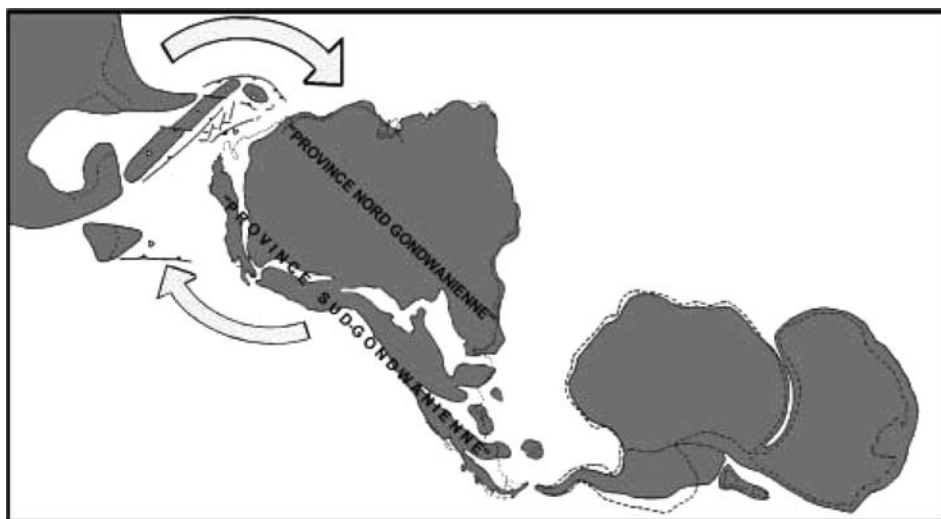


Fig. 2 First Great Turnover, Terrestrial Weddellian Province, first steps of the South American Episode, and the differentiation of the inferred “nord-gondwanienne” and the “sud-gondwanienne” provinces, differentiated between ca. 85–63 Ma. (Based on Zambrano, 1987; Legarreta et al., 1989; de Broin and de la Fuente, 1993)

most of the Tertiary, as commonly thought (e.g., Simpson, 1980). Rather, the beginning of the southern continental isolation still maintained a loose connection with the Antarctic Peninsula, at least potentially, that was part of the landscape up to the first part of the Paleogene, and quite probably also including part of the remaining Antarctic continent. The Drake Passage was completely opened by 30 million years (Zachos et al., 2001; see also Fig. 4). Thus, until ca. 30 million years the Antarctic Peninsula, at least, was part of the landscape on which the first steps of the Cenozoic (and probably also the latest Cretaceous) “South American” mammalian evolution occurred. For a long time, Antarctica was regarded just as a “stepping stone” (e.g., Keast, 1972), or as an “intermediate area” (Simpson, 1978). This restricted vision of Antarctica’s role reflects the paucity of the oldest fossil mammals known at that time, marsupials in Australia, and marsupials and some placentals in South America. However, Keast (1972, p. 207) recognized that monotremes “... might have enjoyed a Cretaceous and Early Tertiary radiation (in Australia) prior to the ascendancy of the marsupials...” They were not known as fossil at the time. Presently, the oldest fossil monotremes are the primitive steropodontids *Teinolophos trusleri* (Rich et al., 1999; Aptian) and *Steropodon galmani* (Archer et al., 1985; Albian), and the relatively specialized Kollikodontidae (*Kollikodon ritchiei*; Flannery et al., 1995; Albian). These fossils support Keast’s suggestion of an early radiation in the Australian sector of Gondwana. The recent record of the monotreme *Monotrematum sudamericanum* (Pascual et al., 1992a,b, 2002c), in Early Paleocene beds of Patagonia, and its apparent absence in Late Cretaceous land mammal-bearing beds of South America, indirectly support an early radiation in Australia, or in the Antarctic-Australian sector of Gondwana as Flannery et al. suggested (1995). *Monotrematum sudamericanum* is a quite advanced member of the Ornithorhynchidae, characterized by a “stage of evolution” resembling that of the Australian Oligo-Miocene *Obdurodon dicksoni* (Archer et al., 1992) and indicating a long evolutionary history. By at least the Early Paleocene, ornithorhynchids had acquired some other derived features that distinguish this family. According to some researchers (e.g., Woodburne and Case, 1996),

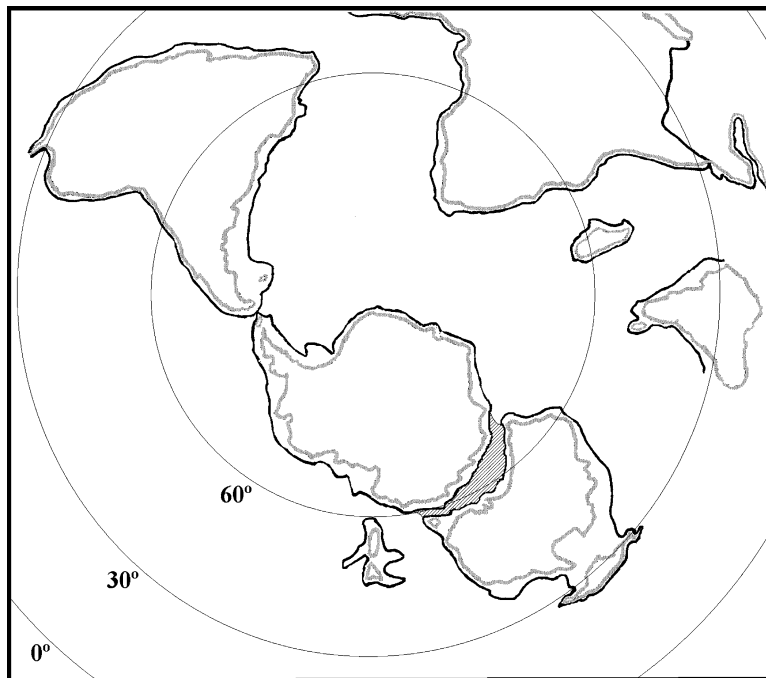


Fig. 3 Paleogeographic reconstruction of the southern continents (Gondwana) by 64 Ma. Shallow marine conditions began to separate Antarctica from Australia. (Based on Woodburne and Case, 1996)

the oldest marine barrier was a shallow marine seaway (cf. Figs. 2–4) between Australia and Antarctica that was as old as 64 million years. Thus, Antarctica may have been part of the territory where monotremes originated and evolved. The presence of four families of monotremes (Kollikodontidae, Steropodontidae, Ornithorhynchidae, and Tachyglossidae) in the Australian sector of Gondwana suggests (Flannery et al., 1995, p. 419) an origin and diversification within the Australian (or Australian-Antarctic) sector. This taxonomic diversity also suggests, according to Flannery et al. (1995), that monotremes may have dominated the Early Cretaceous mammal assemblages of at least the Australian portion of Eastern Gondwana. In addition, they thought that the order Monotremata probably originated no later than the Jurassic. The immigration (or extension of their range) of marsupials into the primordial Australian continent must have occurred no later than 64 Ma, which implies that Antarctica may have also been part of the territory where the “Australian marsupials” evolved. Woodburne and Case (1996) suggested that the most likely time of dispersal (or expansion) of marsupials to Australia was prior to the sundering of the South Tasman Rise at about 64 Ma (Fig. 3). Further, based on the available paleontological and biochemical data, Woodburne and Case (1996) suggested that species ancestral to the present *Peramelina*, *Dasyuromorpha*, and *Diprotodontia* evolved in Antarctica (at least) prior to the entry into Australia. The role of Antarctica in the evolution of other non-tribosphenic and pre-tribosphenic mammals is unknown. A non-tribosphenic mammal, the gondwanatherian *Sudamerica ameghinoides* (see below), was recorded in Early Paleocene beds of Patagonia (see below), when a connection between most of the southern continents still persisted (the “Weddellian Province,” see Fig. 2 and Case, 1988), and later on Late Eocene beds

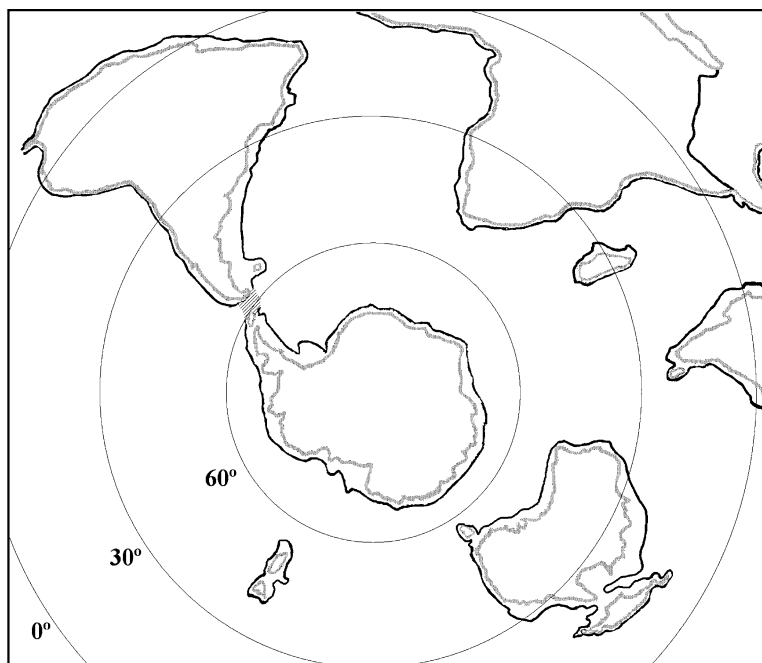


Fig. 4 Paleogeographical reconstruction of southern continents (Gondwana) by 35 Ma. According to Zinsmeister (1982) the Drake Passage included shallow and intermediate waters. According to Zachos et al. (2001, fig. 2) the Drake Passage was totally open by 30 Ma. Australia and Antarctica became separated by oceanic crust

of Antarctic Peninsula (Reguero et al., 2002; Goin et al., 2006b). Thus, it is obvious that Antarctica had to be part of the territory where the cladogenesis of the southern non-tribosphenic and pre-tribosphenic mammals occurred (Bonaparte, 1990). In turn, native South American therian mammals were recorded in the same Late Eocene beds of Antarctic Peninsula (Seymour Island; see Reguero et al., 2002; Bond et al., 2006) where *Sudamerica ameghinoi* was collected. Thus, it is also obvious that at least the Antarctic Peninsula was part of the scenery where Early Paleocene, or later Cretaceous evolutionary radiation of “South American” therian mammals occurred.

- (5) While still part of the Gondwanan continent, what was destined to become the South American continent and its biota, withstood a long standing Mesozoic isolation (Bonaparte, 1986b), i.e., Pascual’s “Gondwana Stage” (Pascual, 1986). Up to now the Gondwanan mammal-bearing sediments have not provided the forebearers of any of those mammals identified by Simpson (1950) as the “Ancient immigrants.” A primary “Ancient Immigrant” could be the supposed placental found in Late Cretaceous beds (Adamantina Formation, Turonian?) of the Baurú Group in Southcentral Brazil (Bertini et al., 1993).

Simpson never explicitly denied the existence of “Mesozoic mammals” in South America, but apparently he did not envision that South America was ever inhabited by non-tribosphenic and pre-tribosphenic mammals. So it is that the record of supposedly Late Cretaceous primitive marsupial and placental mammals in the high Andean plateau of Peru led him to state that “... it would have been expected that mammals like these would occur in the Cretaceous of South America” (Simpson, 1980, p. 39). These mammals, as well as those from Bolivia, also

supposedly Cretaceous in age (e.g., de Muizon et al., 1984; de Muizon and Marshall, 1985; Marshall and de Muizon, 1988), were later demonstrated to be Paleocene in age (Gayet et al., 1991; de Muizon, 1991), although not representing the earliest Paleocene. In short, up to the end of the 1970's Simpson's extremely influential papers on mammalian zoogeography in some way reinforced Matthew's statement: Holarctica (actually, we should say formerly Laurasia and later Holarctica) was the source for all "South American" mammals (Matthew, 1915). For example, Simpson (1941) correctly considered that the affinity between the South American borhyaenids and the Australian thylacines was the result of parallel evolution from a common ancestor, but didn't remark that these marsupials (and marsupials in general) were a paleobiological evidence for a connection between both continents. However, later on he abandoned his stabilist concept stating that "... the early dispersal of marsupials involved North America, South America, Antarctica, and Australia." He changed his mind because he had accepted that "... plate tectonic evidence as usually interpreted at present obviously opens up another possibility for faunal connection between Australia and South America, with Antarctica as the intermediate area" (Simpson, 1978, p. 323).

Those relictual Gondwanan mammals found in Paleogene Patagonian and Antarctic mammal-bearing beds (two gondwanatheres and a Dryolestida remains; see above) represent the South American Episode. The subsequent absolute dominance of therians (*sensu* McKenna and Bell, 1997) suggest that there was a relatively abrupt turnover, the First Great Turnover (Pascual et al., 2001) in South American mammalian communities, in contrast with what happened in North America (see South American Episode below).

We have to bear in mind that the record of the Gondwanan Episode was almost restricted to the Late Cretaceous of north-central Patagonia, and to the Early Cretaceous from northwestern Patagonia (e.g., *Vincelestes neuquenianus* Bonaparte, 1986b; see below). However, recent finds of notable Jurassic remains drastically began to change the restricted knowledge we had heretofore, suggesting, for example, that in pre-Cretaceous Gondwanan extremely noteworthy evolutionary novelties occurred. Among others, we began to discover that in South America, as in various continents of Gondwanaland, groups of mammals evolved tribosphenic molars vicariously with respect to the northern Hemisphere Tribosphenida, i.e., a dual origin of tribosphenic mammals (Rich et al., 1997, 1999, 2002; Flynn et al., 1999; Luo et al., 2001, 2002; Rauhut et al., 2002), and in advance of the Laurasian "model," as remarked by Flynn et al. (1999). These discoveries attest to a distinct episode.

As pointed out by Vizcaíno et al. (1998, pp. 202–203) "... those mammals characteristic of the ... Gondwanan Stage are endemic taxa that seem to have differentiated in the isolated Gondwanan Continent, and to have evolved from Pangean groups. Therefore, besides the Middle to Late Jurassic Episode, there had to be at least an older Pangean Episode, which, apparently was recorded in Late Triassic-Early Jurassic beds of Southern Africa (Crompton, 1964, 1974; Crompton and Jenkins, 1968, 1978)." Quite recently, Ribeiro et al. (2001, p. 169) announced the record of a morganucodontoid in Late Triassic-Early Jurassic beds of the Caturrita Formation, Rio Grande do Sul (Brazil), opening the high probability that these lower Mesozoic mammals were represented also in Argentine beds, mainly because a dicynodont therapsid, *Jachaleria*, was originally found in Late Triassic beds of western Argentina (Bonaparte, 1970).

As remarked by Cifelli (2001, p. 1218) "... a hiatus in the fossil record separates well-known taxa and assemblages from Early and Late epochs of that (Jurassic) period (Rowe, 1993)." If we correlate the above mentioned South African record with the South American Early Jurassic record, and admit Rauhut et al.'s (2002, p. 165) statement "... that mammalian faunas from the Southern Hemisphere already showed a marked distinction from their northern counterpart by the Middle to Late Jurassic," the likewise distinctive Late Cretaceous Gondwanan Episode appears as the South American record of the last events of the Gondwanan mammalian history.

In summary, the present record of mammals in the Gondwanan continents, even with its limitations, suggests that the major Gondwanan Episode is divisible into at least three minor and distinct episodes: (1) Late Triassic-Early Jurassic, so far only recorded in Southern Africa (see Crompton, 1964, 1974; Crompton and Jenkins, 1968, 1978 for the known taxa) and South America (Ribeiro et al., 2001); (2) Late Middle-Late Jurassic (see Casamiquela, 1961, 1964; Heinrich, 1998, 1999; Flynn et al., 1999; Rauhut et al., 2002 for the known taxa); and (3) Early-Late Cretaceous (see Archer et al., 1978; Bonaparte et al., 1984; Bonaparte and Soria, 1984; Bonaparte, 1986a,b,c, 1988, 1990, 1992, 1996; Bonaparte and Kielan-Jaworowska, 1987; Bonaparte and Crompton, 1990; Krause and Bonaparte, 1990; Pascual et al., 1993, 1996, 1999, 2000b; Kielan-Jaworowska and Bonaparte, 1996; Pascual, 1996, 1998; Rich et al., 1997, 2001; Pascual and Goin, 2001; Vizcaíno et al., 1998 for the known taxa).

Brief comparative analysis of South American Gondwanan Mammal Taxa

Although still very poor, the record of Gondwanan Jurassic mammals confirms what is also evident in the Laurasian record. Namely, that the Jurassic period is an important stage in early mammalian evolution wherein we first see diversification of this group, leading to the stem lineages of monotremes and modern therian mammals (Luo et al., 2001; Rauhut et al., 2002). The fossil record of Jurassic and Early Cretaceous mammals in southern continents, and particularly within the South American sector of Gondwanaland, although sketchy, is still eloquent enough to suggest that tribosphenic therians were part of a clade, named Australosphenida by Luo et al. (2001), that is markedly distinct from its Laurasian tribosphenic counterpart, the clade Boreosphenida of Luo et al. (2001). In contrast to many other recent authors (e.g., Rauhut et al., 2002; Kielan-Jaworowska et al., 2004), we exclude *Steropodon* and the remaining toothed monotremes (see above and Pascual and Goin, 2001) from Australosphenida. On the other hand, the most conspicuous non-therian taxa appear as vicariant counterparts of Laurasian taxa. The Gondwanan record suggests that the South American Australosphenida originated, radiated and became widespread in Gondwana well before the end of the Jurassic. According to the record, no mammal belong to Australosphenida has been reported from the Cretaceous Period of South America, i.e., from Pascual's (1996) Gondwana Stage. The South American mammalian fauna during the Late Cretaceous Alamitian SALMA (see Appendix) was dominated by Dryolestida, with only one species of Symmetrodonta and two dubious Eutriconodonta, scarce but quite endemic Gondwanatheria, and strongly advanced Docodonta, "... which may indicate that the Australosphenida had already largely been replaced on this continent by that time" (Rauhut et al., 2002, p. 167). Whether or not they belong to Australosphenida, monotremes appear to have originated in the Antarctica-Australia sector of Gondwana rather than the South American one, where they immigrated by the early Paleocene, or at most by the latest Cretaceous (see above).

As noted above, the Gondwanan mammalian fauna provides outstanding examples of vicariant groups. A simple comparative analysis of the mammal taxa so far recorded in the South American sector of Gondwanaland with those recognized as related from Laurasia, suggests that the vicariant groups were a consequence of the disjunction of Pangaea and the differentiation of Laurasia in the northern hemisphere and Gondwana in the southern one. On the one hand, the long isolation of Gondwana led to a marked endemism. On the other hand, some groups differentiated higher native taxa, with advanced features that are so distinct as make difficult to hinder the recognition of their relationships with Laurasian taxa. A conspicuous example are the Gondwanatheria, whose mandibular and dental features formerly led to their being considered as multituberculates, and lately to be regarded as "... *Mammalia incertae sedis*" (Pascual et al., 1999, p. 382; but see below). However, the remaining groups show different grades of advanced

dental features that do not obliterate the main diagnostic features that relate them to Laurasian higher taxa.

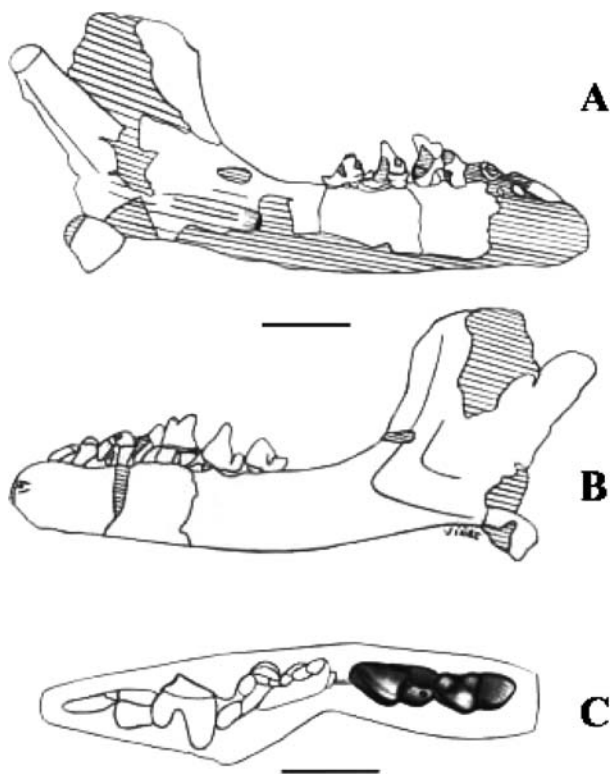
Contrary to his original conclusion (e.g., Bonaparte, 1986b), recently Bonaparte (1996), with disputable arguments, tried to demonstrate, on the one hand, that "... the dryolestoid assemblage from the Late Cretaceous of Patagonia (Bonaparte, 1996) might not be a isolated groups of therian mammals which evolved separately in South America (as stated by Ensom and Sigogneau-Russell, 1998), but instead are only a sample of a larger, unknown Late Cretaceous radiation of Dryolestida related to the North African, Iberian, and English forms" (Bonaparte, 2002, p. 340). On the other hand, the analysis of the biogeography of the tetrapods recorded in the central Patagonia Late Cretaceous Los Alamos Formation, led Bonaparte to consider that "If the geographic isolation of the Iberian Peninsula (Ziegler, 1988; Lillegraven and Krusat, 1991) favored the diversity of the Dryolestidae, we can conclude that they were able to colonize North Africa, and from there South America and finally North America in the Late Cretaceous" (Bonaparte, 2002, p. 365). The South American separation from Africa was initiated in the southern part about 130 Ma (Storey, 1995), and culminated by 110 Ma (Sclater et al., 1977; Parrish Totman, 1993). Thus, the colonization by land of South America by African Dryolestidae had to occur before these dates. In turn, if the immigration was overseas, we have to remember that during the time when the South American continent was completely isolated, the immigration of hystricomorph rodents and platyrrhine primate ancestors took place at about 30 Ma, approximately coincident with the time of final opening of the Drake Passage (see Fig. 4 and Pascual, in press). By this time dryolestoids were long extinct. Late Cretaceous Gondwanan land mammal bearing sites, showing a relatively rich diversity, are certainly only known in Central Patagonia. However, a single mammal specimen, consisting of the anterior part of a right dentary with part of the canine alveolus, alveoli of p1–2, a complete p3, and part of posterior alveolus of ?p4, was collected in the Adamantina Formation, of the Baurú Group (Aptian?-Maastrichtian), of south-central Brazil, from levels probably of Turonian age. Based on the presence of four premolars, the authors (Bertini et al., 1993) regarded this specimen as a placental, although the fragmentary nature of this specimen made it impossible to determine more precisely its affinities. However, it is a quite important document since it could be: (1) the record of the last australosphenidan (in such a case it means that they lived up to the Late Cretaceous); (2) related to Vincelestidae; or (3) the first record of the "Ancient Immigrants" (Simpson, 1950) or "Old Timers" (Simpson, 1980), that initiated the "The First Great Turnover" (*sensu* Pascual et al., 2001), and with them the peculiar South American Cenozoic placental mammalian history.

Our treatment of Late Cretaceous mammals, up to now only relatively well known from Central Patagonia, will not follow a systematic sequence, as mentioned in the Appendix, but will consider in the first place those groups that show the most advanced and derived features that in South America are hallmarks of the peculiar history of Gondwanan mammals.

The present Patagonian Gondwanan record indicates (Rauhut et al., 2002) that the most outstanding feature evidenced by Gondwanan mammals is the great age (Middle Jurassic) and advanced morphology of tribosphenic mammals (Flynn et al., 1999; Luo et al., 2001, 2002). This led to the alternative suggestion of a Gondwanan origin for the group (Flynn et al., 1999), long thought to have arisen on northern continents. Further, all of the recorded Jurassic Gondwanan tribosphenic mammals, as well as the peculiar South American Early Cretaceous pre-tribosphenic *Vincelestes neuquenianus* Bonaparte, 1986a (but see Sigogneau-Russell, 1999), have been phylogenetically related to the ancestral Peramure, as were the Laurasian Boreosphenida. Curiously enough, no representatives of Peramure have been recorded as yet in the South American and Australian Jurassic and Cretaceous Gondwanan land-mammal bearing beds.

Setting aside *Ameghinichnus patagonicus*, regarded by Casamiquela (1975) as a primitive therian (see Introduction), the first tribosphenic Jurassic osseous mammal remain found in South

Fig. 5 *Asfaltomylos patagonicus* Rauhut et al., 2002. Left mandible with roots and crown fragments of the last three premolars (holotype). **A.** Lingual view. Scale bar = 1 mm. **B.** Labial view. **C.** Occlusal view. Scale bar = 2 mm (Based on Rauhut et al., Figs. 1 and 2)



America is *Asfaltomylos patagonicus* (Rauhut et al., 2002; Martin and Rauhut, 2005) (Fig. 5A–C), represented by a dentary with roots and crown fragments of the last three premolars, and m1–3. The molars are tribosphenic with a fully basined talonid, but with a labially inflated, large hypoconid, that on m3 is connected to a well-developed hypoconulid by the talonid rim, which forms a large wear facet. From this wear facet the authors inferred the presence of a functional protocone on the upper molars, which makes *Asfaltomylos* a fully tribosphenic mammal. The trigonids are lingually open, with an angle of m1 about 130°, whereas for m2 and m3 it is about 80°. All preserved teeth are double-rooted, and m1–m3 has faint lingual cingulid at the base of the paraconid. Based on this character the authors referred *Asfaltomylos patagonicus* to the Australosphenida of Luo et al. (2001), to distinguish this clade from the Boreosphenida clade, characteristic of the Northern Hemisphere. The slender dentary did not possess a pterygoid fossa, neither is there a post-dentary through. Although it is likely that Australosphenida were living in Gondwana during the Jurassic, they have not been recorded up to date in the relatively rich mammal-bearing Late Cretaceous of Patagonia. It appears to support our hypothesis that there was a distinct Jurassic episode, during which there differentiated endemic taxa more closely related to Jurassic forms of northern continents.

In the Early Cretaceous La Amarga Formation (Hauterivian-Barremian) of northwestern Patagonia, Bonaparte (1986a) find the best-preserved representative of South American Mesozoic mammals, he named *Vincelestes neuquenianus* (Fig. 6). This mammal has molars with the “reverse triangle” occlusal pattern, but with a small low protocone and a small talonid without a true basin. As remarked by Bonaparte and Rougier (1987) and Butler (1990), its molars are not quite as advanced as those of tribosphenic molars and are at a level of organization

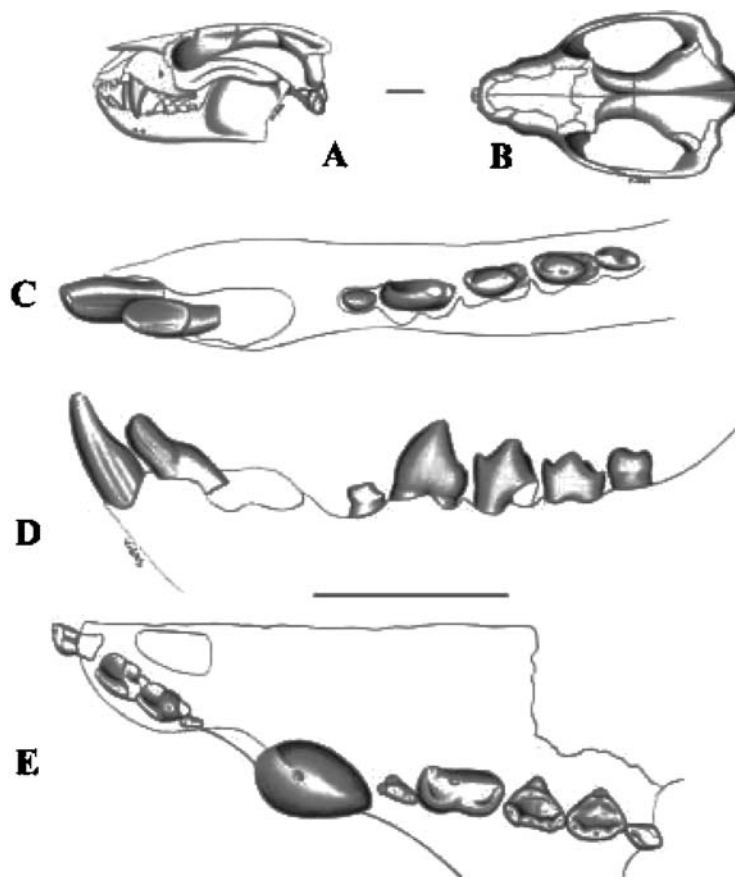
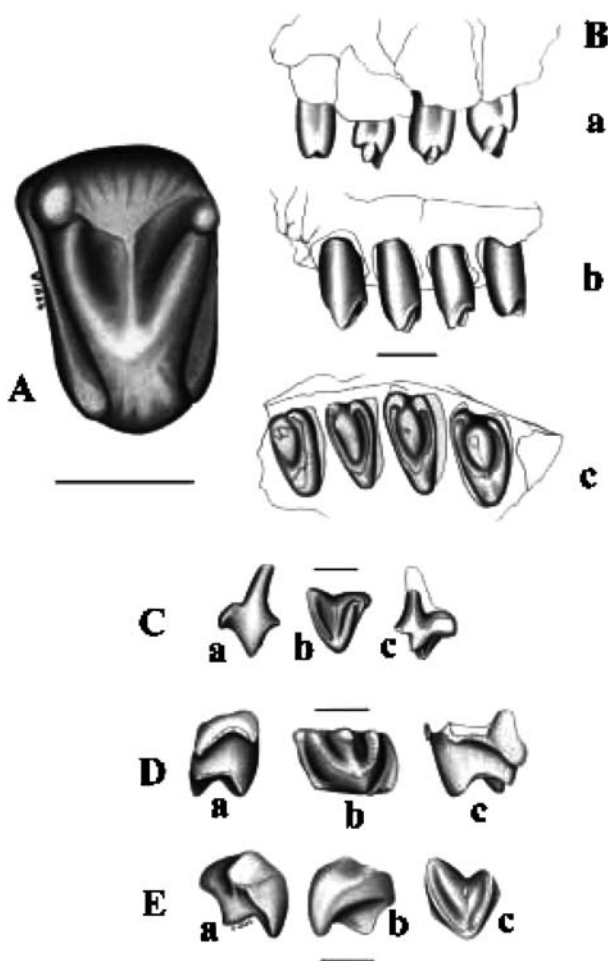


Fig. 6 *Vincelestes neuquenianus* Bonaparte, 1986a,b,c. Skull: **A**. Lateral view. **B**. Dorsal view. Lower dentition: **C**. Occlusal view, **D**. Labial view. **E**. Upper dentition: Occlusal view. Scale bar = 10 mm (Based on Bonaparte, 1986a; Bonaparte and Rougier, 1987)

between that of the Late Jurassic *Peramus* and the Early Cretaceous *Aegialodon*. Besides, in many features of the skull *Vincelestes* resembles Mesozoic “non-therian” mammals (e.g., morganucodontids and multituberculates). Like them, *Vincelestes* has a large anterior lamina of the petrosal in the sidewall of the braincase. In marsupials and placentals the petrosal makes no significant contribution to the lateral braincase wall of the braincase. Wible (1990), Wible and Hopson (1993), and Wible et al. (1995) have identified several derived basicranial characters shared by *Vincelestes*, Marsupialia, and Placentalia that are absent in known Mesozoic “non-therian” mammals and in monotremes. Included are a true cochlear aqueduct for the perilymphatic duct and a caudal tympanic process on the petrosal (Rougier et al., 1992).

In summary, *Vincelestes neuquenianus* possesses characters that position it as an intermediate between “non-therian” and therian mammals. Rougier (1993) grouped this advanced taxa with therians in a clade named Prototribosphenida, which, in a reappraisal of Mammaliaform interrelationships (Rougier et al., 1996a,b), was regarded as one of the most robustly supported clades. More recently, on the basis of the petrosal and skeletal characters, Kielan-Jaworowska et al. (2004) accept that Prototribosphenida is the clade that includes the common ancestor of

Fig. 7 *Mesungulatum houssayi* Bonaparte and Soria, 1984. **A.** M¹? Occlusal view. Scale bar = 5 mm. **B.** *Leonardus cuspidatus* Bonaparte, 1990. Fragment of left maxilla with four molars. **a.** Labial view; **b.** Lingual view; **c.** Occlusal view. Scale bar = 2 mm. **C.** *Brandonia intermedia* Bonaparte, 1990. Right upper molar. **a.** Lingual view; **b.** Occlusal view; **c.** Labial view. Scale bar = 1 mm. **D.** *Paraungulatum rectangularis* Bonaparte, 2002. Left upper molar. **a.** Distal view; **b.** Occlusal view; **c.** Mesial view. Scale bar = 2 mm. **E.** *Casamiquelia rionegrina* Bonaparte, 2002. Right upper molar (holotype). **a.** Mesial view; **b.** Distal view; **c.** Occlusal view. Scale bar = 1 mm. (Based on Bonaparte, 1986a, 1990, 2002).



Vincelestes and Zatheria (i.e., *Peramus* + Boreosphenida) plus all of its descendants (see also Luo et al., 2002).

From a biogeographic point of view, the presence of *Vincelestes* in Early Cretaceous beds of Patagonia, and the absence of Prototribosphenida into the Late Cretaceous ones, is enigmatic. According to the most recent cladograms (e.g., Luo et al., 2001; Rauhut et al., 2002; Kielan-Jaworowska et al., 2004), *Vincelestes* is not related with *Asfaltomylos* and, consequently, it is not a Cretaceous derivative of the australosphenidans. It could be a Gondwanan derivative of the pangeic dryolestoids. Curiously, however, Patagonian beds from the Late Cretaceous only record derived representatives of the Dryolestida (e.g., *Groebertherium*, *Leonardus*) but not prototribosphenic mammals. This fact is notable because *Vincelestes* is closely related to boreosphenidans, which apparently displaced (replaced?) all of the most “primitive” prototribosphenids during the Late Cretaceous in Laurasia.

According to Bonaparte (1996), “pretribosphenid” Dryolestida were the most conspicuous and diverse Gondwanan mammals (Fig. 7A–E) from the Late Cretaceous of the Los Alamitos Formation Fauna (Alamitian SALMA; see Appendix). However, Rougier et al. (2002) remarked that this diversity could be lesser than assumed, since some of the supposedly distinct taxa could

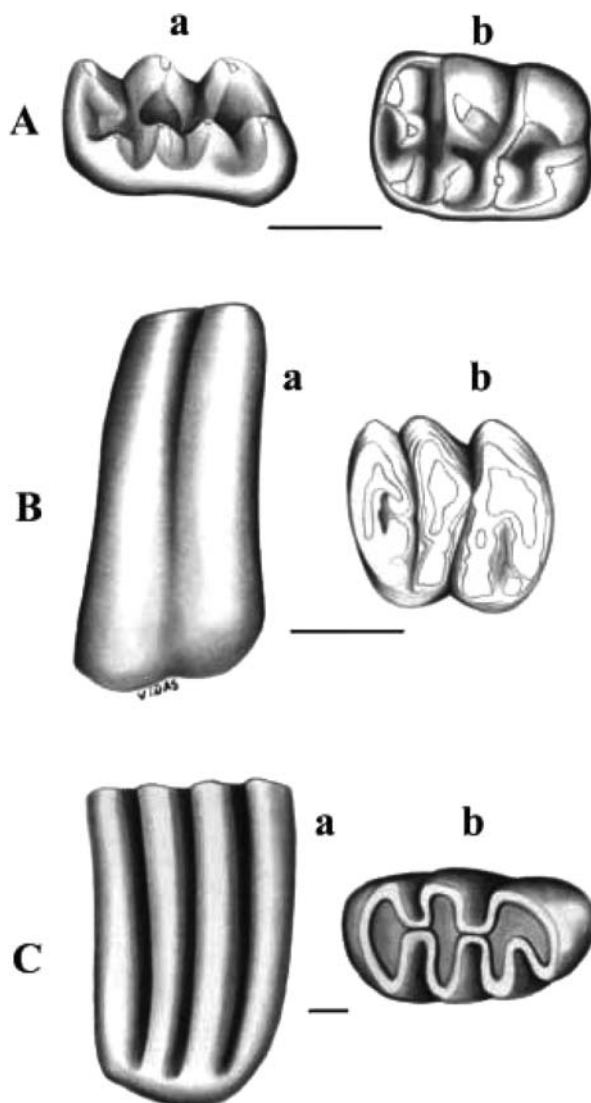
be based on molariform teeth of the same species that occupied different loci in the tooth row. As an example, originally Bonaparte (1990) assigned both *Barberenia araujoae* and *Quirogatherium major* to the Symmetrodonta. The assignment of the former to Symmetrodonta was supported by Sigogneau-Russell and Ensom (1998), but in Rougier's view (pers. comm. to Bonaparte, 2002) the holotype of this species might be the P3 or P4 of the dryolestoid *Groebertherium* or *Brandonia*. In addition, Rougier has suggested that the upper molar holotype of *Quirogatherium* may correspond to the P3 or P4 of *Mesungulatum* sp. (pers. comm. to Bonaparte, 2002). If these observations are correct, the only symmetrodont recorded in the Patagonian Late Cretaceous is *Bondesius ferox*.

Notwithstanding, in other aspects the Los Alamos dryolestoids show quite unexpected advanced characters. For example, some petrosals assigned by Rougier et al. (2001) to the endemic family Mesungulitidae show a mixture of primitive and quite advanced features. Among the former are a perilymphatic evolutionary process withstood by the Gondwanan representatives. Up to date, this is only applied to the Jurassic Gondwanan mammals, because the South American ones representing the Late Cretaceous, for sure only known from Central Patagonia and based on what we called the Gondwanan Episode (= Stage), represent a quite distinct evolutionary event during which tribosphenic mammals apparently became extinct, and the non-tribosphenic and pre-tribosphenic radiated, giving origin to incomparable and quite advanced ecological types. For example, the extensive morphological variation of dental types that is found among dryolestids indicates that they withstood an unmatched diversification (but see above). If the advanced features showed by some petrosals assigned by Rougier et al. (2001) to the endemic dryolestoid Mesungulitidae were convergently acquired with the Laurasian Tribosphenida (*vide* Rougier et al., 2001), this is one more example that the isolation led to the differentiation of advanced features in Gondwanan non-tribosphenic, pre-tribosphenic and australosphenidan mammals that were previously known only in boreosphenid ones. For example this is the case of the upper molars of the advanced Early Paleocene Gondwanan Dryolestida *Peligrotherium tropicalis* (see Gelfo and Pascual, 2001, Fig. 2) respect to the upper molar of some Laurasian Paleogene “ungulates” as the Dinocerata, e.g. the Early Eocene *Proathyopsis praecursor* (see Simpson, 1929, Fig. 1).

Among the most endemic mammals of the Gondwanan Episode are the gondwanatherians. These mammals, as peculiar and enigmatic as evolutionary precocious, were recorded in Late Cretaceous beds of Patagonia, Madagascar, and India, in Early Paleocene beds of Patagonia, and in Eocene beds of Antarctica (Krause et al., 1997; Kielan-Jaworowska et al., 2004; Goin et al., 2006b).

On the basis of isolated teeth, *Gondwanatherium patagonicum* Bonaparte, 1986c (Fig. 8B) from the Late Cretaceous, and *Sudamerica ameghinoi* Scillato-Yané and Pascual, 1984 (Fig. 8C), from the Early Paleocene (both from Patagonia) were described, and each assigned to a monotypic family, respectively, Gondwanatheriidae and Sudamericidae. Based on their close similarity in dental morphology, particularly by their quite advanced hypsodontism, precocious according to the global record of mammals (cf. B with C in Fig. 8), they were wrongly considered to be the earliest known edentates (Scillato-Yané and Pascual, 1984, 1985; Bonaparte, 1986a,b, 1990). At the same time, Bonaparte (1986a) described the m2 of a brachyodont Late Cretaceous Patagonian taxon, *Ferugliotherium windhausenii*, which he assigned to Multituberculata. Mones (1987) included *Gondwanatherium* and *Sudamerica* in a new order of Xenarthra that he named Gondwanatheria. Krause and Bonaparte (1990) concluded that Gondwanatheria is a new suborder of the Order Multituberculata Cope, 1884, with two families, Sudamericidae (including the hypsodont *Sudamerica* and *Gondwanatherium*), and Ferugliotheriidae (including the brachyodont *Ferugliotherium*). Later, Krause and Bonaparte (1993) changed the suborder Gondwanatheria to a superfamily, Gondwanatherioidea, which they tentatively assigned to the

Fig. 8 Homologous left m1s of: **A.** *Ferugliotherium windhauseni* Bonaparte, 1986a. **a.** Lingual-occlusal view. Scale bar = 1 mm; **b.** Occlusal view. **B.** *Gondwanatherium patagonicum* Bonaparte, 1986b; **a.** Labial view; **b.** Occlusal view. **C.** *Sudamerica ameghinoi* Scillato-Yané and Pascual, 1984. **a.** Lingual view. (Based on Scillato-Yané and Pascual, 1985).



multituberculate suborder Plagiaulacida. Kielan-Jaworowska and Bonaparte (1996) described a fragmentary dentary with p4 of multituberculate pattern, which they tentatively assigned to *Ferugliotherium*. Later, Krause et al. (1997) described the gondwanatherian genus *Lavanify* from the Late Cretaceous of Madagascar, and an unnamed genus and species of India, which they assigned to the Subclass ?Allotheria Marsh, 1879, an assignment that tacitly suggests that Gondwanatheria may be a sister group of multituberculates. The multituberculate affinities of gondwanatherians were challenged by Pascual et al. (1999), who described a right dentary of *Sudamerica ameghinoi* (with two molariform teeth and two more molar loci posterior to them) from the Early Paleocene of Argentina. This study made evident a series of uncertainties that led Pascual et al. (1999) to disregard Gondwanatheria as multituberculates. Coupled with the controversial relationships of multituberculates, they concluded that the Gondwanatheria

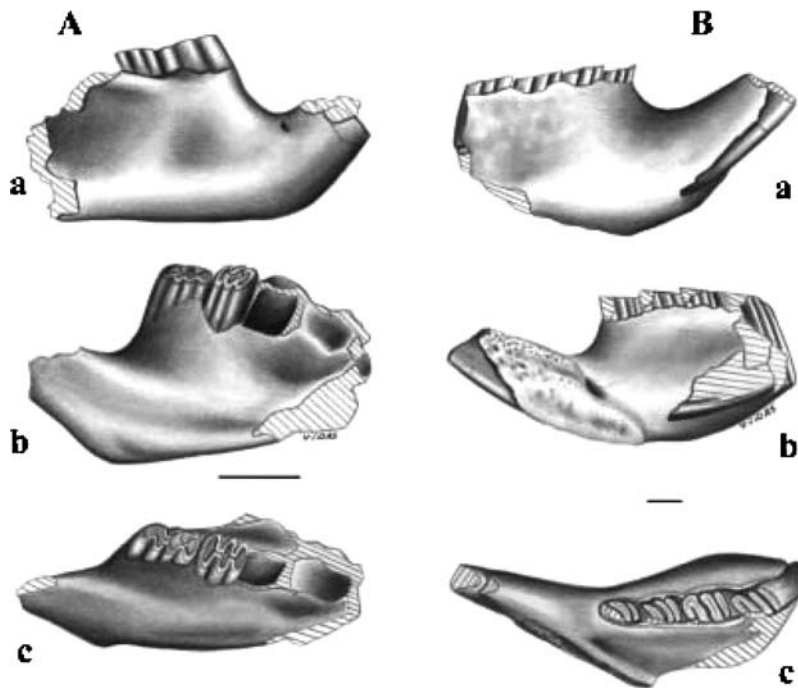


Fig. 9 Comparison of the right dentaries of the early Paleocene Gondwanatherian *Sudamerica ameghinoi* (A) with the late Miocene caviomorph rodent (Dinomyidae) *Tetrastylus* sp. (B) Note the similarity between the number and shape of the “elasmodont” cheekteeth, and the shape and extension of the incisive up to below the last cheek tooth. The cement filling the flexids and the cement layer covering the whole molar prisms of *S. ameghinoi* have spontaneously fell down after the fossilization. (Respectively based on specimens of the Museo Paleontológico “Egidio Feruglio” MPEF 534, and of the Museo de La Plata, MLP 52-IX-30-66). a. Labial view; b. Lingual view; c. Occlusal view

are *Mammalia incertae sedis*, a conclusion that more recently was also accepted by Kielan-Jaworowska et al. (2004).

The dentary, incisors and cheekteeth of the Paleocene and last Patagonian survivor of this clade (i.e., *Sudamerica ameghinoi*) show the most striking similar features characterizing some of the most advanced Mio-Pliocene South American caviomorph rodents (Fig. 9B; and see below). The rodent-like incisor is strongly compressed laterally, with a ventrolabially restricted enamel band, and extended within the alveolus along the lingual face of the dentary, although not along the lower border, as in rodents (cf. A with B, in Fig. 9) up to the distal border of the last cheek-tooth alveolus apparently having affected the root extension of this molar, as in the living South American rodent *Ctenomys*. The cheekteeth are very high-crowned, although they did not grow throughout life since their roots are closed (Fig. 8C); they are elasmodont, i.e., composed by parallel laminae of enamel, bordering the lateral extension of the dentine; these lophids are formed by lateral and opposed invagination of the enamel (flexids) and are very deep but unconnected to each other. Each flexid is full of cement, which separates the lophids from each other, and extends as a thin film enveloping the whole molar prism.

Isolated brachydont lower molars of *Ferugliotherium windhausenii* were found in the same Late Cretaceous Los Alamitos Formation, which also produced the holotype of *Gondwanatherium patagonicum* Bonaparte, 1986c [Los Alamitos Formation; see Bonaparte et al.,

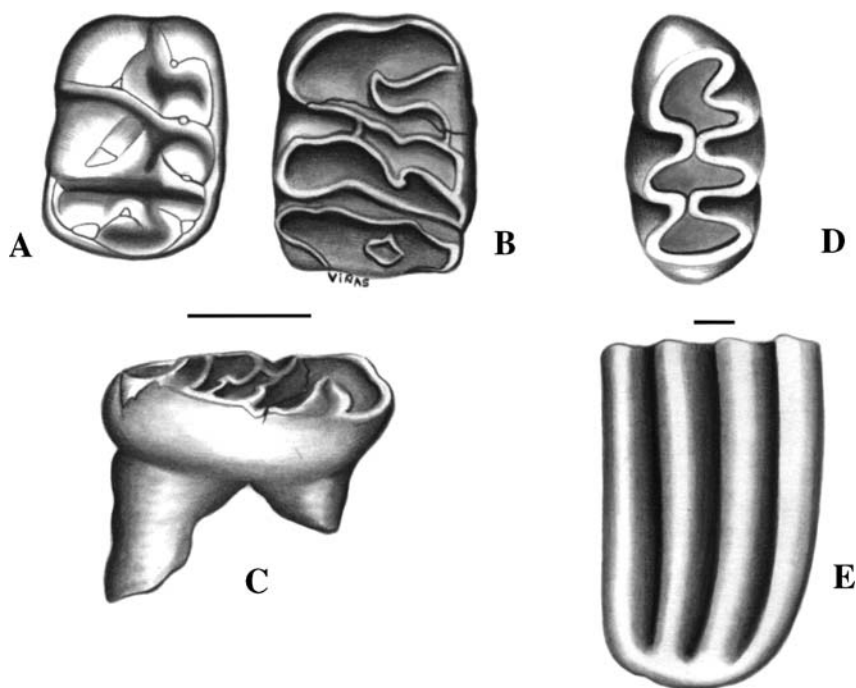


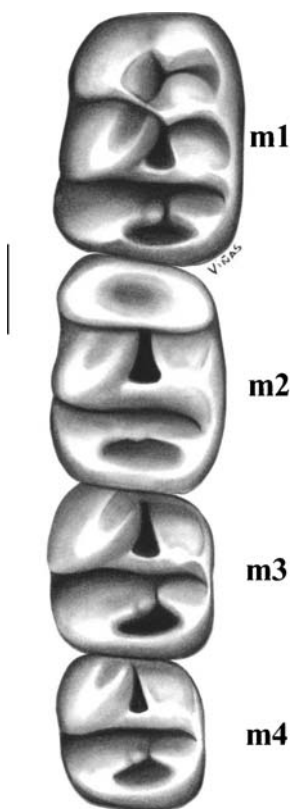
Fig. 10 Comparison of occlusal view of left m1 of *Ferugliotherium windhausenii* (A. Unworn tooth. B. Very worn tooth. C. Lateral view of B showing its brachyodonty and roots) with the left m1 (D and E) of *Sudamerica ameghinoi*. D. Occusal view. E. Lingual view. Scale bars 1 mm

1984. They were also recorded in the correlative La Colonia Formation (see Pascual et al., 2000b, pp. 398–402, Fig. 1)]. The molar pattern of *Ferugliotherium windhausenii* is the basic pattern that led to the advanced Gondwanatheria Sudamericiidae (cf. Fig. 10A–C with D, E; see also Krause and Bonaparte, 1990; Krause et al., 1997; Pascual et al., 1999; Kielan-Jaworowska et al., 2004). These bunolophodont molars, with their peculiar crown features, were the basis for:

- (1) Recognizing taxa bearing these molars as a distinct family, Ferugliotheriidae, tentatively as ?Multituberculata, and dubiously related to the native Gondwanatheriidae, and as such being a dubious ?Multituberculata (Bonaparte, 1986c).
- (2) Assessing that they show the primitive state for molar characters that are diagnostic of the Late Cretaceous *Gondwanatherium patagonicum* and the Early Paleocene *Sudamerica ameghinoi* (cf. Fig. 8A with B and C). In this latter figure we have depicted what we regard as the homologous lower cheekteeth, which is the first one of the specimen of *Sudamerica ameghinoi* (Fig. 9A), originally described and figured by Pascual et al. (1999).
- (3) Kielan-Jaworowska and Bonaparte's (1996) ratification of *Ferugliotherium windhausenii* as a Multituberculata; by extension, all three species were argued to be multituberculates, and ultimately allocated to the multituberculate suborder Gondwanatheria, name originally applied by Mones (1987) in the understanding that they were a new order of ?Xenarthra.

With respect to the “plagiaulacoid” premolar present in the specimen of *Ferugliotherium windhausenii* described by Kielan-Jaworowska and Bonaparte (1996, fig. 4; cf. with our Fig. 11), recently Kielan-Jaworowska et al. (2004) concluded that it shows a multituberculate pattern,

Fig. 11 *Ferugliotherium windhausenii* Bonaparte 1986a. Reconstruction of an inferred left m_1 – m_4 series. The m_1 is an unworn specimen from the La Colonia Formation (MLP 88-III-28-1); m_2 and m_3 are based on a worn specimen from the Los Alamitos Formation (MACN, Chubut, 1484). The number of molars and some crown features were made according to worn specimens and those of the most advanced known Gondwanatheria *Sudamerica ameghinii* (MPEF 534). Scale bar ~ 1 mm

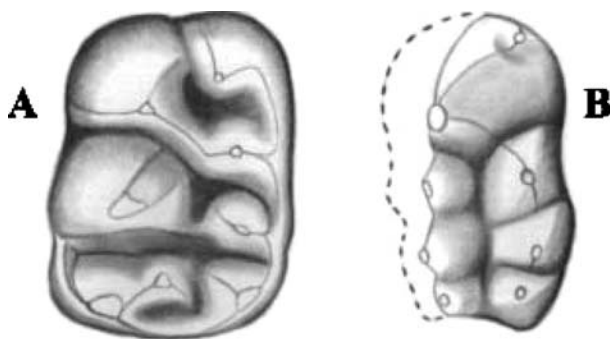


covered on labial and lingual sides with oblique ridges. This p4 “... differs from that of Cimolodonta in apparently being rectangular rather than arcuate in labial view...” (Kielan-Jaworowska et al., 2004, pp. 335–336) and shares this character with the paraphyletic “Order Plagiaulacida” (sensu Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004, p. 336). As Pascual et al. (1999) demonstrated that Gondwanatheria have four molarized lower teeth and no bladelike premolars, Kielan-Jaworowska et al. (2004, p. 336) “... remove this dentary and tentatively also upper premolars from Gondwanatheria and assign them to Multituberculata *incertae sedis*. This suggests that multituberculates might have lived during the Late Cretaceous in South America, but their radiation there is as yet poorly known.”

From an evolutionary point of view, we believe that the molar pattern of *Ferugliotherium windhausenii* appears to be one more variant of the common pattern of the order Haramiyida (Hahn et al., 1989), but with the opposite cusps of the lingual and buccal rows connected by transverse ridges, otherwise insinuated in most of the taxa of the order Haramiyida (Hahn et al., 1989; see also our Fig. 8A, and fig. 1 in Butler, 2000). The molar pattern of *F. windhausenii* appears to be an earliest offshoot of the Haramiyida that diverged by the acquisition of transversal ridges connecting the opposite cusps of lingual and labial rows, subequal in height. This is the basic pattern that led to the advanced Gondwanatheria Sudamericae (see Fig. 8C).

According to Butler (2000), the more likely hypothesis is that multituberculates were specialised haramiyid derivatives, a hypothesis also considered as probable by Kielan-Jaworowska et al. (2004). In our opinion, the pangeic order Haramiyida, with the almost exclusively Laurasian order Multituberculata and the Gondwanan order Gondwanatheria, integrate the subclass

Fig. 12 Compared crown view of left m1 of *Ferugliotherium windhauseni* (A) with right m1 of *Haramiyavia clemmensensi* (B), showing that the relatively well defined cristae (or ridges) extended between lingual and labial cusps in the former were already insinuated in *Haramiyavia*, as in most of the Haramiyida. [Respectively based on the original (Museo de La Plata 88-III-28-1) and in Jenkins et al., 1997]. Not to scale.



Allotheria, probably “... with a separated history going back to the Triassic,” as stated by Butler just for the Haramiyida and Multituberculata (Butler, 2000, p. 333). Thus, the Gondwanatheria and the Multituberculata had to be sister-groups, and since each of them evolved in the two isolated new supercontinents (Gondwana and Laurasia, respectively), they became one more example of vicariant taxa.

From a morphofunctional point of view, we think that the change in masticatory pattern from a haramiyid-like ancestor to gondwanatheres was due to the shift of a molariform with longitudinal grooves separating longitudinal rows of cusps, to molariforms having prominent ridges connecting opposite lingual and buccal cusps, and prominent transverse furrows that extend nearly or completely across crowns between cusps of adjacent rows, with two big roots (Fig. 12). This brachydont tooth is represented in *Ferugliotherium* (Fig. 8A), which led to molars with very high crowns separated by furrows fulfilled with cement, but although showing different deep crown [*Gondwanatherium* (Late Cretaceous) versus *Sudamerica* (Early Paleocene)], but, never growing throughout life since, in a different grade, in both states always their roots are closed (Fig. 8B–C).

In relation to the state of evolution of the remaining taxa from the same Patagonian Late Cretaceous and Early Paleocene beds, the acquisition of hypsodonty molar teeth in Gondwanatheria appears as precocious, representing an advanced evolutionary state that in South America repeatedly succeeded within diverse mammalian lineages (e.g., marsupial taxa such as the Argyrolagidae [Pascual et al., 1988] and Patagonidae [Pascual and Carlini, 1987]; some notoungulates such as the typotherian [Patterson and Pascual, 1972; Pascual and Ortiz-Jaureguizar, 1990; Pascual et al., 1996]) during the Eocene to Pliocene span. Less frequently, but likewise occurring during the same Cenozoic geological time, is the concomitant elongation of the incisors and progressive hypsodontism of the cheek teeth, as it occurred in the later Gondwanatheria, and particularly in *Sudamerica ameghinoi*, the last gondwanatherian from the Early Patagonian Paleocene. This phenomenon has also been recorded as a convergent adaptation in various groups of Late Miocene and Pliocene caviomorph rodents (see Pascual and Ortega Hinojosa, 1966, figs. LII–LV). In *Sudamerica ameghinoi*, the tendency to extend the root of the incisor up to the base of the last molar’s alveolus impeded the whole intralveolar developing of the molar, which remained quite short and somewhat curved. Among caviomorph rodents the same process reached its acme in the living species of the eremic octodontid genus *Ctenomys*, where the m3 became diminutive (see Pascual et al., 1988, fig. 1F).

One of the most outstanding examples of vicariant taxa is represented by the so advanced Docodonta *Reigitherium bunodontum* (but see Kielan-Jaworowska et al., 2004), represented by an isolated lower molar of the Los Alamos Formation, and a left dentary with p4–m2 (Figs. 13 and 14), found in the likewise Patagonian Campanian–Maastrichtian La Colonia Formation (see

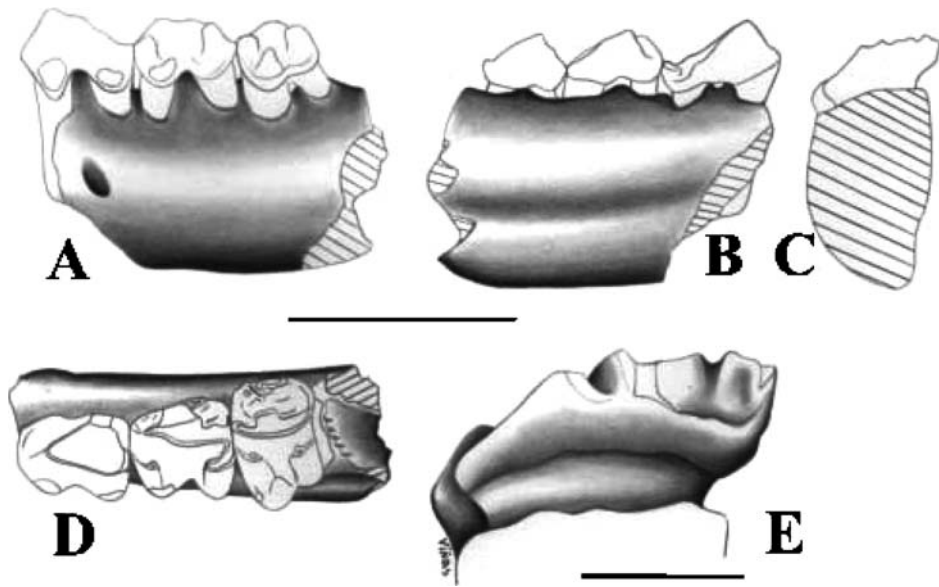


Fig. 13 *Reigitherium bunodontum* Bonaparte, 1990 (A, B, C, D and E, fragment of a left dentary with p₄-m₂). A Labial view; B Lingual view; C Posterior view behind the m₂. D Occlusal view of p₄-m₂. E Posterior view of m₂. A–D, scale bar = 5 mm. E, scale bar = 1 mm. (Based on Pascual et al., 2000a,b)

Pascual et al., 2000b). It is the first known docodont mammal from the southern hemisphere. Even though its lower dentition resembles more closely the North American Late Jurassic *Docodon* than other Eurasian docodonts (e.g., intermolar basins formed by the adjacent halves of molars, and vertical crenulations [ribs and furrows]), it differs radically from Laurasian docodonts in that the crowns of the lower cheekteeth are transversely enlarged; several lingual cusps are incorporated into the masticatory surface. The evolution of the reigitheriid lower molar pattern appears as an advanced state of that of *Docodon*, as it was with respect to the ancestral *Morganucodon* (Jenkins, 1969; Kermack et al., 1973, 1981). It appears to have originated in a *Morganucodon*-like pattern, evolving three main modifications (fig. 5 in Pascual et al., 2000b), resulting in a step-like process: (1) expansion of the lingual cingulum; (2) elevation of the lingual cingular cusps, becoming interconnected to each other by a crest as high as or higher than the labial one, and enlargement of the masticatory surface by the close connection of both lingual and buccal crests; and (3) aggregation of labial pilar-shaped cusps. *Reigitherium bunodontum* adds support to the hypothesis that Gondwanaland mammals evolved as vicariants of the Laurasian ones. Further, it is an example that the universal trend to increase the masticatory surface of the cheekteeth was also accomplished by non-therian mammals, without passing through the reversed triangle state that led to the tribosphenic pattern. Because the primitive state of *Docodon*'s cheekteeth characters were so markedly transformed in *Reigitherium bunodontum*, its assignment to a quite distinct genus is beyond doubt. Further, we think that from an evolutionary point of view this taxon is so advanced to merit being separated from Docodonta as a distinct order, and maybe within a higher new rank. This evolutionary phenomenon, in many aspects, appears to be similar to that leading to the differentiation of the order Gondwanatheria with respect to the order Multituberculata, both regarded by us as sister-groups. Both appear as the result of allopatric speciation, as an example of vicariant groups, consequently related to the subdivision of the supercontinent Pangaea, in the Northern Hemisphere Laurasia, and in the Southern Hemisphere Gondwana.

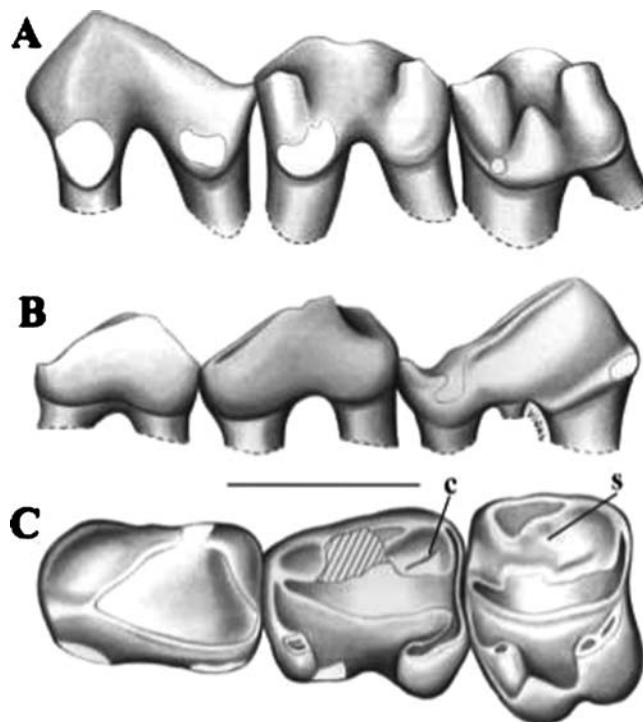


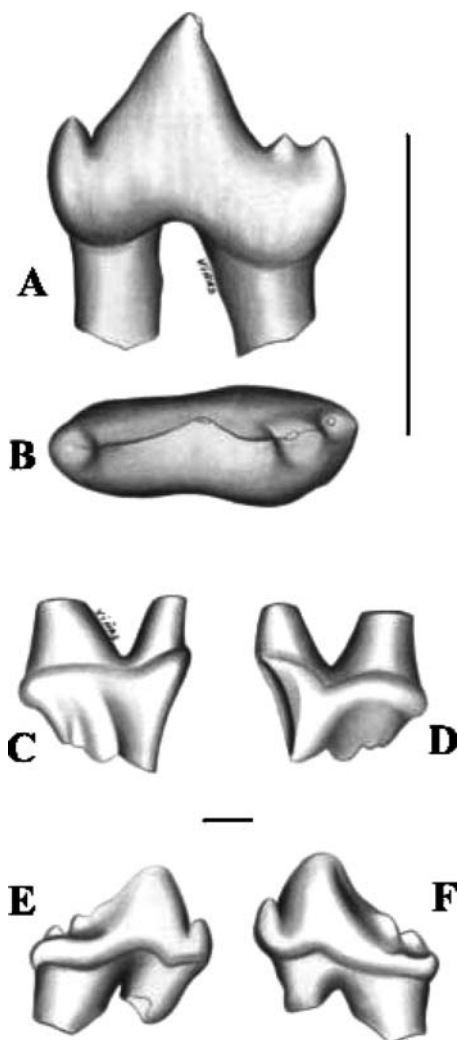
Fig. 14 *Reigitherium bunodontum* Bonaparte, 1996. **A.** Detailed labial view of right p₄-m₂ series (note the labial shearing surfaces on the base of the anterior and posterior lobes of the crown); **B.** Lingual view of p₄-m₂; **C.** Occlusal view of p₄-m₂; c, crenulations; s, sulcus. (Based on Pascual et al., 2000a,b). Scale bar = 2 mm

From beds of the Campanian-Maastrichtian Los Alamitos Formation from North-central Patagonia, Bonaparte (1986b, 1992) named and described two new species, both assigned to the new genus *Austrotriconodon*, and represented by isolated upper and lower molars: *A. mackennai* Bonaparte 1986b, and *A. sepulvedai* Bonaparte, 1992. Bonaparte (1992) assigned both species to the monotypic family Austrotriconodontidae, which he included in the order Triconodonta. However, recent cladistic analyses consistently show that this “Order” is paraphyletic, based largely on a plesiomorphic molar pattern, i.e., three main cusps placed in antero-posterior alignment on a crown that is somewhat compressed transversely. Consequently, the “Order Triconodonta” was divided into two orders, Morganucodonta and Eutriconodonta, the former occupying a basal location among mammals, and the last located among (or near to) the living mammals (for more details, see Kielan-Jaworowska et al., 2004, and references therein).

According with this new classification, Kielan-Jaworowska et al. (2004) tentatively assigned both species of Austrotriconodontidae to the order Eutriconodonta, because it has “... very derived upper molars; cusps arranged “in palisade,” little differentiated in external view, with cusp B the largest. Upper molars with distinctive, cirque-like mesial embayment, extending to the apex of cusp B. Lower molars with hypertrophied cusp a and posterior accessory cusp c vestigial; internal cingulum reduced” (Kielan-Jaworowska et al., 2004, pp. 235–236).

We agree with Kielan-Jaworowska et al. (2004) that the discovery of advanced characters in species recognized as “triconodonts” only by the possession of a basic tricusate molar, joint to the aberrant molar features of one of the Late Cretaceous Patagonian species, makes it difficult to recognize their relationships. It is at least clear that there exist notable morphological

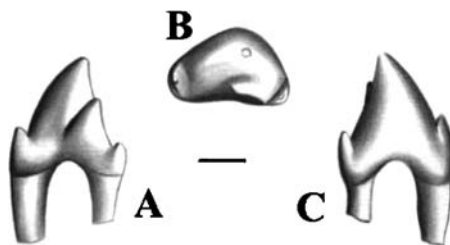
Fig. 15 (A and B)
Austrotriconodon mckennai
 Bonaparte, 1986a. Left lower molar.
 A. Labial view; B. Occlusal view.
 Scale bar = 2.8 mm. C–F
“Austrotriconodon” sepulvedai
 Bonaparte 1992. Scale
 bar = 1 mm. C–D. Right upper
 molar, in labial (C) and lingual
 views (D). E–F Right lower molar
 in labial (E) and lingual (F) views.
 (Based on Bonaparte, 1986a, 1992).



differences between the holotypes of both *Austrotriconodon mckennai* (Fig. 15A and B) and *Austrotriconodon sepulvedai* (Fig. 15C–F). According to Kielan-Jaworowska et al. (2004), the teeth of *Austrotriconodon mckennai* were probably misidentified as lower molars by Bonaparte (1986c, 1992), because “... they have more of the appearance of premolars, perhaps from the middle of the series, and more likely belonging to the upper than lower dentition.” (Kielan-Jaworowska et al., 2004, p. 236). Additionally, these authors write that “... *A. sepulvedai* is represented by two teeth that we tentatively regard as anterior lower premolars, together with an upper molar” (Kielan-Jaworowska et al., 2004, p. 236).

Although *A. mckennai* shows the standard molar (premolar?) pattern characterizing the canonic molar pattern of Late Jurassic “triconodonts” (Fig. 15A and B), the upper and lower molariforms of *A. sepulvedai* (Fig. 15C–F) shows some apparently aberrant features for a “triconodont.” The lower molar has a peculiar postcingulum, extended lingually to cover almost half of that face; its labial extension is shorter, although likewise prominent; both surrounding a sort of a basin occupied by two on-line cusps, on the whole conforming a sort of a “taloid” as

Fig. 16 *Bondesius ferox*
Bonaparte, 1990. Right lower molar,
in lingual (A), occlusal (B) and
labial (C) views. Scale bar = 1 mm.
(Based on Bonaparte, 1996)



those seen on some primitive tribosphenic molars. One specimen assigned by Bonaparte (1992) to the last lower premolar on the whole has the same basic features as the molar. Both the molar and premolar lack a precingulum, and only the molar has a prominent cusp; both have two strong roots that make the crown appear as disproportionately low, more apparent in the premolar due to its advanced sub-horizontal wear, which also appears as a distinct character for a “triconodont.” The features of a molar that Bonaparte (1992) considered an upper molar of *A. sepulvedai* are even more aberrant for a “triconodont.” The labial and lingual faces are totally distinct. The four cusps are aligned on the labial face, and are particularly united one to another, in a palisade manner, forming in such a way a serrate crest. This crest is clearly separated from a lower lingual face. Further, the crown is clearly divided by a lingual flexid and a labial lower cut of the crest, just behind the higher cusp—from where takes origin a prominent cingulum—in an anterior, trigonid-like portion, and a posterior and lower shelf-like and talonid-like posterior portion. An anterior notch, apparently for a close contact with the precedent cheek-tooth, marks the most anterior and wider portion of the trigonid-like feature.

In summary, we agree with Kielan-Jaworowska et al. (2004) that the dental pattern of the Austrotriconodontidae (and, particularly, that of *A. sepulvedai*) is unique for a “triconodont,” making quite dubious such affiliation. We also think that the tentative affiliation of Austrotriconodontidae to the Eutriconodonta proposed by Kielan-Jaworowska et al. (2004) is a plausible hypothesis. We also believe that in line with the peculiar radiation of most of the other Gondwanan mammals, it could be one more example of a highly derived native group that shared with Eutriconodonta a common pangeic ancestor.

Bondesius ferox, the only “symmetrodont” species known from Argentina, is also represented in the Late Cretaceous Los Alamitos Formation, although based on only one isolated lower molar (Bonaparte, 1990). As noted by Bonaparte, it shows very distinctive features that justify inclusion in a different Gondwanan family of its own, Bondesiidae (Fig. 16). *B. ferox* is an obtuse-angle only “symmetrodont” species, with a peculiar asymmetrical distribution of cusps and without cingulids. The talonid situated behind a prominent and postero-internal metaconid; the paraconid is the lower cusp, mesially situated and following the line of the higher and backward inclined protoconid; two well developed and separated roots distinguish this species.

Ecologic and biogeographic changes in land-mammal fauna during the Gondwanan episode

During this time, land-mammal communities are basically represented by those recorded both in the Los Alamitos Formation (Río Negro Province) and the correlative La Colonia Formation (Chubut Province). They are the richest and so far the only eloquent mammal-bearing South American Mesozoic localities, and according to the vertebrate remains, they are assigned to the Campanian-Early Maastrichtian span. However, and according to microfossils and molluscan taxa, these stratigraphic units extend up to the earliest Paleocene. The land mammals so far recorded are Late Cretaceous in age, and were recognized as representing a distinctive SALMA,

the Alamitan SALMA. The Alamitan SALMA is the only recognized SALMA of the Gondwanan Episode, and thus, it is also the only SALMA of the Cuadradan Supercycle (Fig. 1).

Cuadradan supercycle

The Cuadradan communities included only advanced non- and pre-tribosphenic mammals, showing a high Gondwanan endemism. Some exclusive orders as Gondwanatheria—originally taken as primitive edentates, and later on as specialized multituberculates—are so far known from the Campanian up to the Early Paleocene in Patagonia, and up to the Middle Eocene in Antarctica, and represented by a phylogenetic sequence that goes from a taxon whose cheekteeth show a haramiyida-like crown (*Ferugliotherium*) up to an anachronous taxon (*Sudamerica*), almost hypsodont (protohypsodont *sensu* Mones, *op.cit.*), on the whole quite similar to the most advanced Late Miocene-Pliocene eumegamylinae caviomorph rodents.

Most of the families, if not most of the superfamilial taxa, are endemic, particularly in some groups, as for example within the varied cladotherian Dryolestida. Among the most endemic families are the Reigitheriidae, dubiously assigned to the order Docodonta because of the retention of some autopomorphic features distinguishing the genus *Docodon* (see above, and Pascual et al., 2000b).

From a taxonomic point of view, Cuadradan communities were dominated by Dryolestida (67%; but see Rougier et al., 2002), followed at a great distance by the Gondwanatheria (13%; see Fig. 17). Although most of the Cuadradan species pertain to native South American families, most of the orders they represent have been basically known by their Late Jurassic Laurasian record. By the Late Cretaceous most of them were scarce in the northern continents, and the

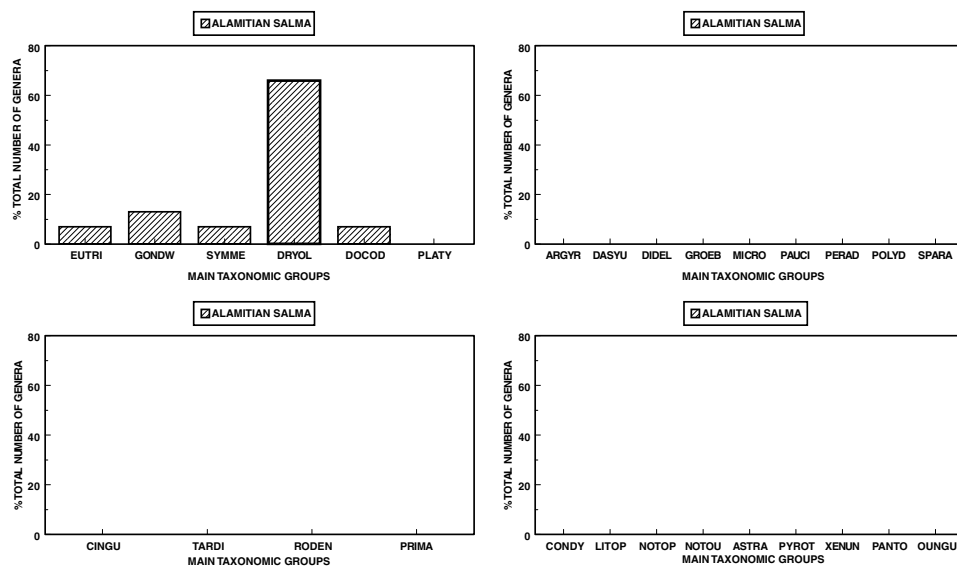


Fig. 17 Pattern of taxonomic diversity during the Cuadradan Faunistic Supercycle (Alamitan SALMA). Abbreviations: EUTRI, Eutriconodonta; GOND, Gondwanatheria; SYMME, Symmetrodonta; DRYOL, Dryolestida; DOCOD, Docodonta; ARGYR, Argyrolagida; DASYU, Dasyurida; DIDELF, Didelphimorphia; GROEB, Groeberida; MICROB, Microbiotheria; PAUCI, Paucituberculata; PERAD, Peradectia; POLYD, Polydolopimorphia; SPARA, Sparassodonta; CINGU, Cingulata; TARDI, Tardigrada; RODEN, Rodentia; PRIMA, Primates; CONDY, Condylarthra; LITOP, Litopterna; NOTOP, Notopterna; ASTRA, Astrapotheria; PYROT, Pyrotheria; XENUN, Xenungulata; PANTO, Pantodontia; OUNGU: Other “ungulates”

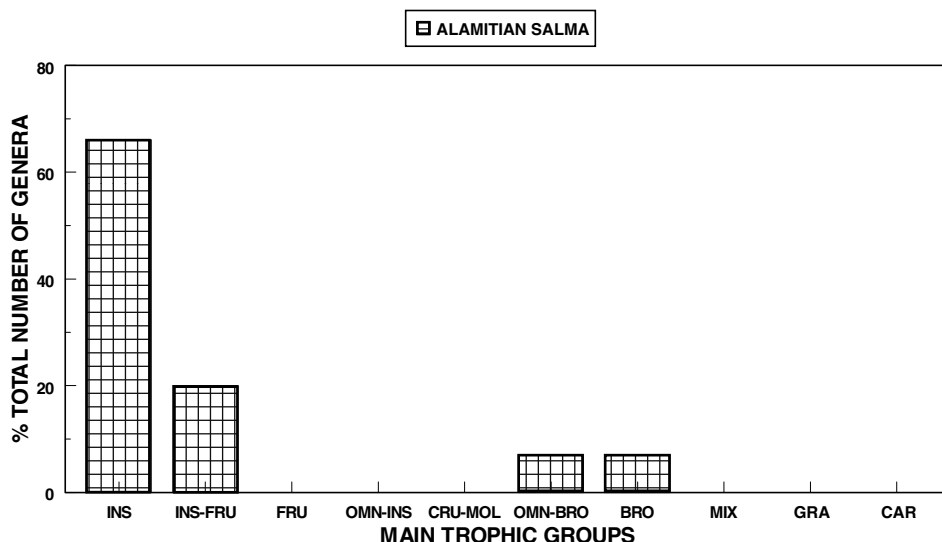


Fig. 18 Pattern of trophic diversity during the Cuadrado Faunistic Supercycle (Alamitan SALMA). Abbreviations: INS, insectivorous; INS-FRU, insectivorous-frugivorous; FRU, frugivorous; OMN-INS, omnivorous-insectivorous; CRU-MOL, crustacean-mollusc eaters; OMN-BRO, omnivorous-browsers; BRO, browsers; MIX, mixed feeders; GRA, grazers; CAR: carnivorous

tribosphenic mammals progressively became predominant. So it is that by the Campanian 70% of the Laurasian genera of mammals were tribosphenic forms, while in South America there were only pre-tribosphenic or non-tribosphenic forms. Thus, the Late Cretaceous persistence in South America of an assemblage of only pre-tribosphenic or non-tribosphenic forms was logically explained as due to long-standing geographic isolation, otherwise supported by their high endemism (see Bonaparte, 1990; Pascual and Ortiz-Jaureguizar, 1992; Ortiz-Jaureguizar, 1996).

From a trophic point of view, the land-mammal communities were dominated by insectivores (68%) followed by insectivore-frugivores (20%; see Fig. 18). As in the other continents, in South America the Late Cretaceous herbivorous and carnivorous adaptive zones were mainly occupied by dinosaurs. Notwithstanding, some of the Late Cretaceous South American mammals apparently shifted to some kind of specialized herbivorous diet, among which the Gondwanatheria Sudamericidae *Gondwanatherium patagonicum* highlighted this trend. This shift was increased in the most derived Sudamericidae (i.e., the Paleocene South American *Sudamerica ameghinoides* and the Late Cretaceous Madagascan *Lavanify miolaka*, apparently related to the absence of placentals, making one more difference with the coeval Laurasian scenario (Pascual and Ortiz-Jaureguizar, 1992; Ortiz-Jaureguizar, 1996).

The critical latest Cretaceous-earliest Paleocene Hiatus

During this interval, as unknown as important, South American land-mammal communities must have experienced notable evolutionary changes. According to the Patagonian record, the principal events that characterize The First Great Turnover had to occur during the long hiatus between the Late Cretaceous (Campanian-earliest Maastrichtian) and the earliest Paleocene. It is opportune to remember that the stratigraphical data indicate that by the Late Cretaceous-Early Paleocene span the South American continent was geographically divided by a sea corridor in

two main geographical regions: one North-eastern Region (= “province nord-gondwanienne”) and another South-western Region (= “province sud-gondwanienne” *sensu* de Broin and de la Fuente, 1993) (Fig. 2). According to the record, it appears that some organisms were sensitive to this transient geographic feature (barrier?, filter?) since biogeographically we can distinguish a North-eastern Region from a South-western one. It is suggestive that distinct Late Cretaceous–Paleocene land faunistic and floristic elements recorded in Patagonia show closer relationships with those of East Gondwana. In turn, those correlatives from northern South America show closer relationships with the African ones. On this account, two eloquent examples are the dipnoan Lepidosirenidae fishes (Pascual and Bondesio, 1976) and the Pelomedusidae and Chelyidae tortoises (de Broin, 1991). According to de Broin and de la Fuente (1993), the northern Pelomedusidae and the Patagonian Chelyidae indicate that by the Late Cretaceous–Early Paleocene span there probably existed “... deux provinces gondwaniennes,” one “nord-gondwanienne” and another “sud-gondwanienne” (see also Crisci et al., 1991, 1993; Pascual et al., 1996, 2001; Wilson and Arens, 2001). However, no Late Cretaceous mammal have been yet recorded in the North-eastern Region that could modify the concept of a Gondwanan Episode got from the Patagonian record, although admittedly their eventual record could change some details of the picture we presently have.

The main evolutionary events that mark the end of the Gondwanan Episode and the beginning of the South American Episode were as follows:

- (1) Extinction of most of non-tribosphenid (*sensu* McKenna and Bell, 1997) mammals, with the exception of the Gondwanatheria (e.g., the Early Paleocene *Sudamerica ameghinoi* [Pascual et al., 1999; and an Antarctic Middle Eocene taxon *aff.* to *Sudamerica*], and the Dryolestida [*Peligrotherium tropicalis* Bonaparte et al., 1993; see Fig. 19, and Gelfo and Pascual, 2001]).
- (2) Survival up to the Late Eocene in Antarctic Peninsula of one species of a gondwanatherian sudamericid (Goin et al., 2006b).
- (3) Immigration of monotremes¹ (the Patagonian Early Paleocene ornithorhynchid *Monotrematum sudamericanum* [Pascual et al., 1992a,b, 2002c]), otherwise the only known non-Australian monotreme (Fig. 20).
- (4) Emigration from Laurasia (North America) to South America of marsupials and placentals (see Pascual and Ortiz-Jaureguizar, 1991; Pascual et al., 1996; Ortiz-Jaureguizar, 1996; Goin et al., 2006a; and see below).
- (5) Emigration from South America to Australia of marsupials, quite probably following the same Antarctic route and at the same time that monotremes were on the way to South America. Although less probable, placentals could also have immigrated to Australia (see Godthelp et al., 1992; Rich et al., 1999).
- (6) A marked cladogenetic radiation of marsupials, and the first steps of the placental radiation (both immigrated from Laurasia, specifically from the rising North American Continent). The more advanced cladogenetic radiation of marsupials than placentals was, probably, because marsupials migrated to South America earlier than placentals (Pascual and Ortiz-Jaureguizar, 1991), to finally populate, *via Antarctica*, the present Australo-Papuan Region.

The recent description by Goin et al. (2006a) of an isolated lower molar of the polydolopimorphian *Cocatherium lefipanum* in Danian-equivalent strata of central-western Patagonia, represents the first step conducive to fill the latest Cretaceous–earliest Paleocene hiatus between

¹ It is equally probably that monotremes were broadly distributed across Australia, Antarctica and southern South America during Cretaceous times. In this alternative scenario, the absence of monotremes in Cretaceous land-mammal bearing formations can be explained by a poor fossil record.

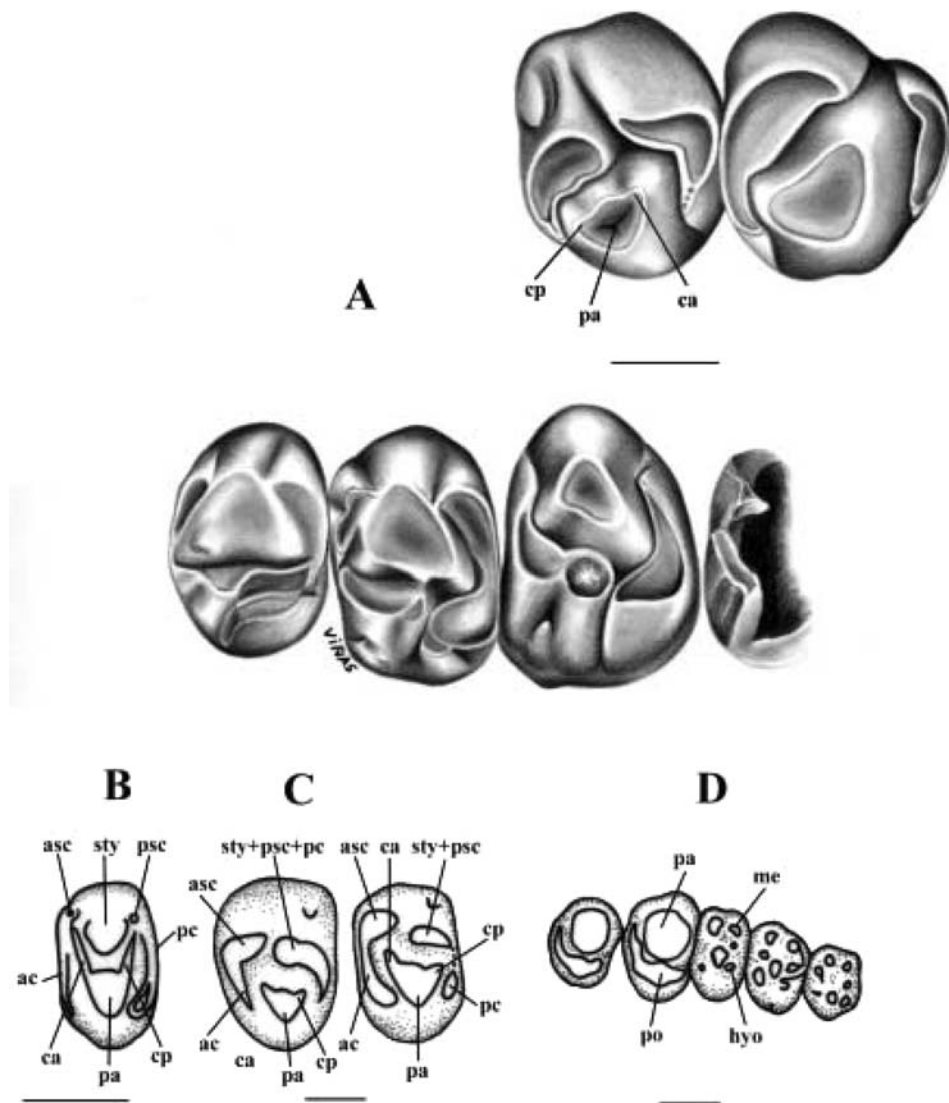
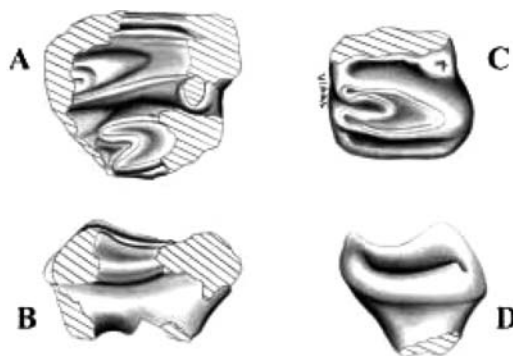


Fig. 19 *Peligrotherium tropicalis* Bonaparte et al., 1993 (MLP 90-II-12-58). Above: **A**. Maxillary fragment with M^1 – M^2 and left M^1 fragment, and M^2 – M^4 , occlusal view. Abbreviations: ca, anterior crista; cp, posterior crista; pa, paracone. Scale bar: 5 mm. Below: Homologies in upper molars of Mesungulatidae and Peligrotheriidae, and comparison with Peripitychidae cheekteeth. **B**, left M^3 of *Mesungulatum housayi* Bonaparte and Soria, 1984; **C**, left M^2 – M^3 of *Peligrotherium tropicalis* Bonaparte et al., 1993; **D**, left $P3$ – $M3$ of *Peripitychus* Cope, 1882. Abbreviations: ac, anterior cyngulum; asc, anterior styler cusp; ca, anterior crista; cp, posterior crista; hyo, hypocone; me, metacone; pa, paracone; pc, posterior cyngulum; psc, posterior styler cusp; po, protocone; sty, stylocone. Scale bars: **B** and **C** = 5 mm; **D** = 10 mm

the Gondwanan and South American Episodes. This marsupial is the oldest South American Tertiary therian mammal from South America, and pertains to a group known from the Late Cretaceous of North America (Case et al., 2005) as well as later Paleocene and Eocene deposits of South America (see Marshall, 1982) and Middle Eocene deposits of Western Antarctica (see Case et al., 1988; Goin et al., 1999). According to Goin et al. (2006a), this polydolopimorphian

Fig. 20 *Monotrematum sudamericanum* Pascual et al., 1992a. Right M² (MPEF 1634) in occlusal (A) and posterior (B) views. Right m1 (MPEF 1635), in occlusal (C) and posterior (D) views. Not to scale



provides evidence for an evolutionary radiation of marsupials in the earliest Paleocene or Late Cretaceous of the Americas. Additionally the record of polydolopimorphians in Late Cretaceous beds of North America also raises questions about the timing, as well as the place of evolution of other “typical” South American marsupials (e.g., some didelphimorphians, some sparassodonts) that can be phylogenetical related to North American clades (Goin, 2003; Goin et al., 2006a). Finally, we suggest that the regression of the Late Cretaceous-Danian submeridian seaway, that so drastically divided the South American continent, and also because of its archipelagic character (particularly along the southern part, i.e., Patagonia), appears as one of the most proximate influential causes of the South American Gondwanan mammal extinction. A similar pattern was proposed by Archibald (1985, 1998) to explain the partial extinction and survival of land-mammals during the K/T transition in North America. With respect to this, Archibald (1998, p. 35) wrote “... the proximate causes resulting from marine regression explain the highly selective pattern of vertebrate extinctions and survival through the K/T transition in the Western Interior of North America better than do those attributed to asteroid impact or possible massive volcanism.”

The South American Episode

Although apparently contradictory, the Cenozoic mammalian history began during the Latest Cretaceous, when South America was not yet a completely isolated island continent (Fig. 2). We note that at least by the Campanian we have the oldest dated record of Laurasian (North America) land vertebrate immigration (Hadrosauridae), and probably tribosphenic mammals (see Gondwanan Episode above). Gondwanan pre and non-tribosphenic relicts (i.e., the gondwanathere *Sudamerica*, the dryolestan *Peligrotherium*, and the monotreme *Monotrematum*) are together with the Laurasian mammals (e.g., the didelphid *Derorhynchus*, the notoptern *Requisia*, and the condylarth *Escribania*) that initiated the record of the South American Episode (Fig. 1). Actually, the very beginning of the South American Episode has not been recorded (Pascual, 1998). This unrecorded interval includes at least the Latest Cretaceous and the earliest Paleocene span, during which had to occurred the most important phenomena that mark the transition from the Gondwanan Episode to the South American Episode, i.e., the root of the endemic South American islanders (see above “The Critical, Latest Cretaceous-Earliest Paleocene Hiatus”).

As we said above, to make more discernible the marked distinction between the Gondwanan and the South American Episodes, we will briefly consider only the first part of the latter, arbitrarily taking as the early and late limits of this span two well recognized mammal community turnovers, respectively, known as the First Great Turnover (K-T) (Pascual et al., 2001), and the South American Middle Cenozoic land-mammal turnover (see Wyss et al., 1994). We previously

regarded this latter turnover as the South American equivalent (e.g., Pascual et al., 1985, 1996; Ortiz-Jaureguizar, 1986; Pascual, 1986; Pascual and Ortiz-Jaureguizar, 1990) to the European “*La Grande Coupure*” (Stehlin, 1909), which was qualified by Stehlin as the greatest and most sudden change known during all of Tertiary time on that continent. So it is the Late Eocene-Early Oligocene Turnover in South America.

During Late Cretaceous, a risen South American continent, separated from the Gondwanan supercontinent, began to receive the first Laurasian immigrants from the North American continent (according to the record, Gondwanan tribosphenic mammals were already extinct by the end of the Cretaceous; see above Gondwanan Episode). Thus, the replacement of Gondwanan by Laurasian mammals had commenced. The First Great Turnover was on the way and with it the birth of the autochthonous South American mammal communities. During almost the last half of the Tertiary, the latter kept evolving in isolation (Fig. 4), and up to the very beginning of the Great American Biotic Interchange (Marshall et al., 1979; Marshall, 1985; Stehli and Webb, 1985). This last interchange was recognized as the Second Great Turnover (Pascual et al., 2001), but in fact it should be the third one, because the second was the above-mentioned Late Eocene-Early Oligocene turnover.

The South American mammal record distinguishes this Late Eocene-Early Oligocene event as a quite important continental mammalian turnover, apparently related to environmental changes, mainly associated to the regional Inca Diastrophic Phase, and to the final opening of the Drake Passage (Figs. 1 and 4), which affected ocean heat transport and more intense high-latitude climate change. This climatic-environmental change has been clearly recorded in Southern Patagonia (see Pascual, 1984a,b, 1986, *in press*; Pascual and Ortiz-Jaureguizar, 1990; Pascual et al., 1996, 2002b), and recently in Chile (Wyss et al., 1994). A multivariate analysis of South American Land Mammal Ages similarity clearly distinguished this event as the limit between the two major Faunistic Units, the Paleo-Cenozoic Megacycle and the Neo-Cenozoic Megacycle (see Fig. 1 and Ortiz-Jaureguizar, 1986; Pascual and Ortiz-Jaureguizar, 1990). Furthermore, this Middle Cenozoic biological change marks the only common limit between any of the faunistic units we have recognized, dating a very important Middle Cenozoic faunal turnover. From a biological point of view this limit is not only marked by the first appearance of the immigrant primates and rodents, but also by a general and crucial faunal transition, from mammal communities dominated by archaic lineages (e.g., brachydont native “ungulates”; Figs. 21 and 22) to communities characterized by mammals of a markedly more “modern” stamp (i.e., protohypsodont [*sensu* Mones, 1979, 1982]; Figs. 23 and 24) of native “ungulates” (see Pascual et al., 1985, 1996; Pascual and Ortiz-Jaureguizar, 1990; Wyss et al., 1994). This is the most

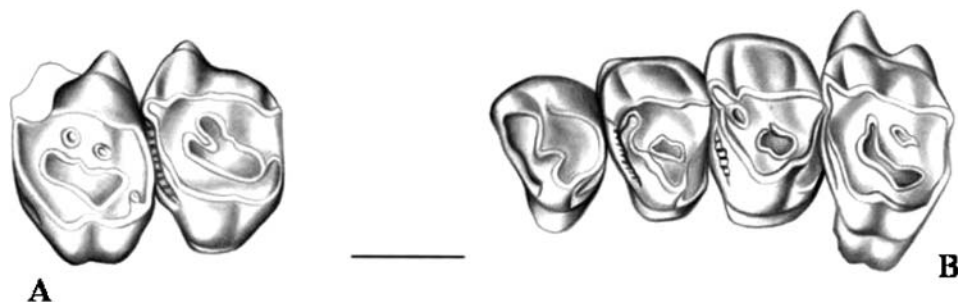


Fig. 21 *Kibenikhoria get* Simpson, 1935. **A**, left M^{2-3} ; **B**, left P^2-M^1 (occlusal view). Scale bar = 1 cm. This taxon is representative of mammal communities that were dominated by archaic lineages (e.g., brachydont native “ungulates”) and is precedent to the most important Middle Cenozoic Mammal Turnover

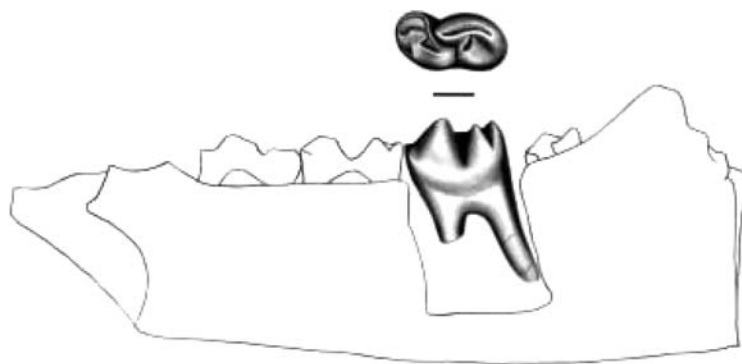


Fig. 22 *Pleurostylodon* sp. Ameghino, 1897. Right m_2 (occlusal view). This taxon represents another case of an archaic lineage (as in Fig. 21). Scale bar = 5 mm

important Middle Cenozoic mammalian turnover event. It occurred over a long span, estimated at approximately 15 million years by Wyss et al. (1994). Certainly, this is a hiatus in our knowledge, which had been already noticed by the paleontologists working on the history of South American mammals, although such long extension was unexpected by them.

The relictual Gondwanan mammals that were part of the oldest known communities that initiated The South American Episode remained long unknown because the earliest Paleocene Patagonian mammal-bearing beds presently known were unprospected by the most outstanding paleontologists that made known the South American mammalian history, from the Ameghinos to Simpson, and until the 1980s, and even quite recently by subsequent researchers. Simpson's

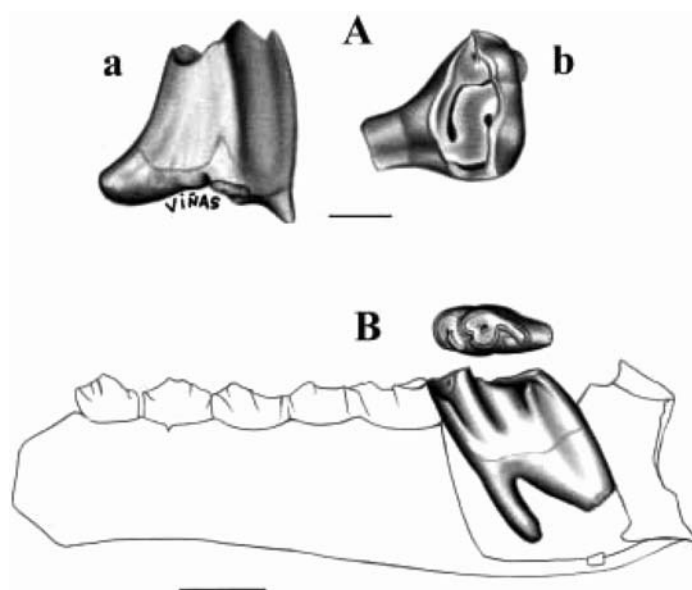


Fig. 23 *Pseudohyrax eutrachytheroides* Ameghino, 1901. This taxon, with protohypsodont molars, represents mammal communities subsequent to the Middle Cenozoic Turnover. **A**, left M^2 , **a**: posteroexternal view, and **b**: occlusal view. Scale bar = 5 mm. **B**, right m_3 lingual view. Scale bar = 1 cm

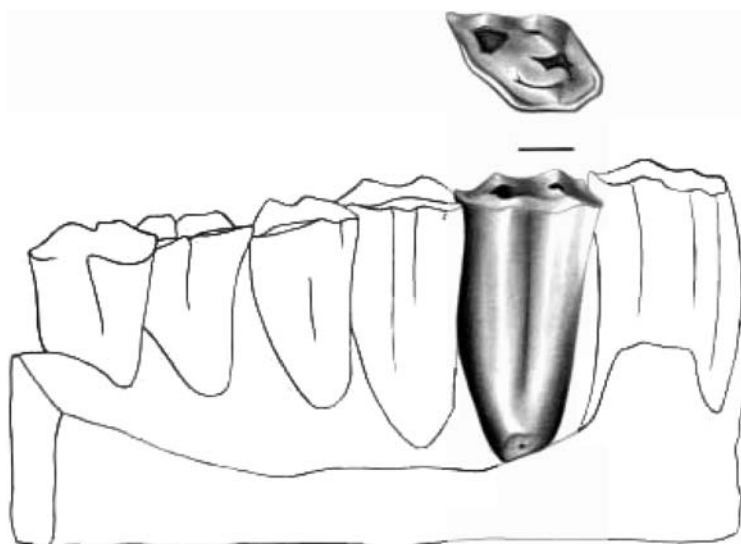


Fig. 24 *Archaeototherium propheticus* Ameghino, 1901 (= *Bryanpattersonia* sp.). This protohypsodont taxon is representative of mammal communities subsequent to the Middle Cenozoic Turnover and is more advanced than *Pseudohyrax eutrachytheroides* Ameghino, 1901 (Fig. 23). Scale bar: 5 mm

studies exalted the uniqueness of South American Cenozoic and Recent mammals (Simpson, 1948, 1980). Subsequent studies have reinforced Simpson's concept (1980, p. 53) about the immigrant "old timers" (e.g., didelphimorphs and condylarths). At the same time, these studies also suggest a pre-Cenozoic history not envisioned by Simpson that includes three Patagonian Paleogene Gondwanan relictual species—one dryolestoid and two gondwanatherians.

The earliest Paleocene Patagonian mammal-bearing beds so far known were discovered at the same time that the first Late Cretaceous mammals were recovered, also from Patagonia (see above). These two findings notably changed not only our knowledge and perspective of South American mammal evolution but promoted original insights into the study of mammalian evolution in general. It is necessary to iterate that relatively eloquent and unquestionable Mesozoic mammals were unknown in South America until 1983, when Bonaparte and staff found the first and unquestionable South American Late Cretaceous mammals in northern Patagonia. If this mammal-bearing Early Paleocene would have been recorded years before, the unexpected Gondwanan Episode could have been inferred.

With the probable exception of the Xenarthra, the ultimate phyletic origin of the clades (i.e., Marsupialia and Placentalia) that inhabited the South American continent almost throughout the whole Cenozoic (including at least the Antarctic Peninsula during the first part of the Paleogene), as well as the one living at Present, was North America, with the exception of primates and rodents that emigrated from Africa (Simpson, 1950, 1980; Lavocat, 1971, 1976; Patterson and Pascual, 1972; Pascual and Ortiz-Jaureguizar, 1990; Wyss et al., 1993, 1994; Flynn et al., 1995; Pascual, *in press*). Excluded are, of course, that relictual Mesozoic gondwanatherian (see below), apparently confined up to the Middle Eocene in the Antarctic Peninsula.

The absolute dominance of therians (*sensu* McKenna and Bell, *op.cit.*) in the continent after the earliest known Paleocene, when Gondwanan relictual mammals were apparently extinct, suggests the occurrence of a relatively abrupt turnover, i.e., The First Great Turnover (Pascual et al., 2001) in South American mammalian evolution. This phenomenon contrasts with what

happened in North America (Archibald and Clemens, 1984; see Pascual and Ortiz-Jaureguizar, 1992; Clemens, 2001), and in the remaining Laurasian continents. The extinction at the K/T boundary reduced the total diversity of the mammalian fauna, but did not produce the almost complete extinction as the one we have recorded in South America. For example, approximately 60% of the Lancian (latest Cretaceous) lineages became extinct in northeastern Montana (Clemens, 2001). Notwithstanding, the Laurasian history of mammals was comparatively continuous from the oldest Late Triassic on, always having as actors only mammals that ultimately originated in one or another of the Laurasian continents, without any influential interchange with Gondwana. There was not such a turnover as that recorded in the South American sector of Gondwana throughout the Campanian-Danian interval, which apparently succeeded in the whole Gondwana continent. Immediately after or during the Late Cretaceous-Early Paleocene Gondwanan mammal extinction, in the South American sector of Gondwana began the replacement of the Gondwanan mammals by Laurasian therians. Further, mammals that originated in Laurasia spread all over most of the continents, and in such a way that they presently represent the majority of the extant mammals. The Late Cretaceous-earliest Paleocene extinction of the Gondwanan mammals and the consequent absence in South America of representatives of the Gondwanan Episode (with the probable exception of the enigmatic Xenarthra) throughout the remaining Cenozoic has only recently been appreciated.

Ecologic and biogeographic changes in the land-mammal fauna during the South American Episode

Land-mammal communities of this time were best represented in Patagonia. Some other communities were recorded out of Patagonia and in other countries, e.g., Bolivia (Santa Lucía Formation, Tiupampan SALMA, Early-middle Paleocene); Perú (Umayo Formation, ?Tiupampan SALMA, Early-middle Paleocene); Brazil, central Patagonia, and northern Argentina (respectively, Itaboraí Formation, Las Flores Formation, and Rio Loro Formation, Late Paleocene, Itaboraian SALMA [see Ortiz-Jaureguizar and Pascual, 1989; Pascual and Ortiz-Jaureguizar, 1990, Pascual et al., 1996]); northern Argentina (Mealla Formation, Lumbraera Formation, Casa Grande Formation, Geste Formation, Pozuelos Formation, Late Paleocene-Middle-Late Eocene-?Early Oligocene), Central Chile [Abanico Formation (*vide* Charrier et al., 1990), approximately 31–37 Ma, Tinguirirican SALMA, i.e., Late Eocene-Early Oligocene (*vide* Flynn and Swisher, 1995)]; and the Antarctic Peninsula (La Meseta Formation, Middle Eocene). The land mammals so far recorded are Early Paleocene to Early Oligocene in age, and were recognized as representing at least eight distinctive SALMAs [Peligran; Tiupampan; “*Carodnia* fauna” or “*Carodnia* zone” of Simpson (1935), whose characteristic mammal remains were recorded from Peñas Coloradas Formation of Legarreta and Uliana (1994) (see also Bond et al., 1995; Ortiz-Jaureguizar et al., 1999); Itaboraian; Riochican; Casamayoran; Mustersan; Tinguirirican and Divisaderan], grouped into two different Supercycles: (1) Protocenozoic Supercycle, comprised by the Peligran and Tiupampan SALMAs; and (2) Infracenozoic Supercycle, comprised by the “*Carodnia* fauna,” Itaboraian, Riochican, Casamayoran, Mustersan, Tinguirirican and Divisaderan SALMAs (see below, Fig. 1, and Appendix).

Protocenozoic supercycle

The mammals characterizing this supercycle include the oldest Cenozoic communities so far known, including the oldest Laurasian therian immigrants, together with a few Gondwanan relicts in southernmost latitudes. They initiate the South American Episode. These

mammals are represented in three main but quite separated localities, where Early Paleocene land mammal-bearing formations are exposed. The two first are present within intertropical regions, while the third is situated in central Patagonia. The three localities are as follows:

- (1) Southern Peru, nearby Laguna Umayo, about 20 km Northwest of Puno, at a latitude about 15°S. Originally, the mammal-bearing sediments were wrongly assigned to the farther north exposed Late Cretaceous Vilquechico Formation (Grambast et al., 1967; Branisa et al., 1969), mainly based on charophytes of this age, egg shell fragments identified as dinosaurs (Kerourio and Sigé, 1984), and on stage of evolution of the fauna (Sigé, 1972). Supposedly this age was confirmed by the presence of the marsupial *Alphadon austrinum*, a genus characteristic of the Late Cretaceous of North America. This marsupial material was later restudied by Crochet (1979, 1980), who demonstrated that *Alphadon austrinum* should be referred to the genus *Peradectes* (*P. austrinus*), characteristic of the North American and European Paleocene. Presently this mammal-bearing formation is called the Umayo Formation because of its distinct facies (see Marshall et al., 1997, p. 55). According to the latter authors, this unit would be equivalent of the Santa Lucía Formation from Bolivia (Early-middle Paleocene i.e., Tiupampan SALMA), as suggested by species of its fauna content (Gayet et al., 1991).
- (2) A “quarry” excavated in sediments of the Santa Lucía Formation, situated five km southeast of Vila-Vila, Cochabamba, Bolivia (see Marshall and Hoffstetter, 1991; de Muizon, 1991), at a latitude about 18°S.
- (3) The Hansen Member (“Banco Negro Inferior”) of the Salamanca Formation, exposed at Punta Peligro, marine cliffs of the Golfo de San Jorge, about 20 km north of Comodoro Rivadavia (Chubut Province), at a latitude about 45°S (see Legarreta and Uliana, 1994).

The three land mammal-bearing stratigraphic units were referred to the same SALMA, Tiupampense (*sic*) by Pascual and Ortiz-Jaureguizar (1991). However, the study of new mammal remains obtained from the Patagonian “Banco Negro” led Bonaparte et al. (1993) to make them the type of a new land-mammal age, the Peligran. Both SALMAs have a unique association of mammals that includes the first native, advanced “condylarths” as well as marsupials, but there are also differences in relative taxonomic richness and in the anatomical state of evolution.

The Tiupampan SALMA was characterized by a relative taxonomic richness (see Appendix). In the course of this SALMA the didelphimorphian marsupials and the “condylarths” were co-dominant (30% each one), while in the Patagonian Peligran SALMA the didelphimorphian, polydolopimorphian and “condylarths” were equally dominants (20% each one; see Fig. 25). Taking into account the state of evolution of mammals, in the Tiupampan SALMA the Laurasian Mioclaenidae became differentiated in a native subfamily, that is, the Kollpaniinae, and are represented by the following species: *Molinodus suarezi* de Muizon and Marshall, 1987b; *Tiucclaenus minutus* de Muizon and Marshall, 1987c; *Tiucclaenus colasi* de Muizon and Cifelli, 2000; *Tiucclaenus robustus* de Muizon and Cifelli, 2000; *Pucanodus gagnieri* de Muizon and Marshall, 1991; *Andinodus boliviensis* de Muizon and Marshall, 1987c; *Simoclaenus sylvaticus* de Muizon and Cifelli, 2000. In turn, in the Peligran SALMA (see Appendix) the immigrant “condylarths” were represented by two endemic mioclaenids (*Escribania chubutensis* Bonaparte et al., 1993 and *Raulvaccia bunodonta* Bonaparte et al., 1993), and by one of the first and most primitive taxa of the native Litopterna, the Notonychopidae *Requisia vidmari* Bonaparte and Morales, 1997. The genotype of the new family Notonychopidae, *Notonychops powelli* Soria, 1989, was based on one specimen recorded in Paleocene strata (Río Loro Formation) exposed in northwestern Argentina (Tucumán). This new family was referred to the new order Notopterna (Soria, 1989), which has not been unanimously accepted and is sometimes considered another family (Notonychopidae) of the order Litopterna, e.g., Bonaparte and Morales (1997). In turn,

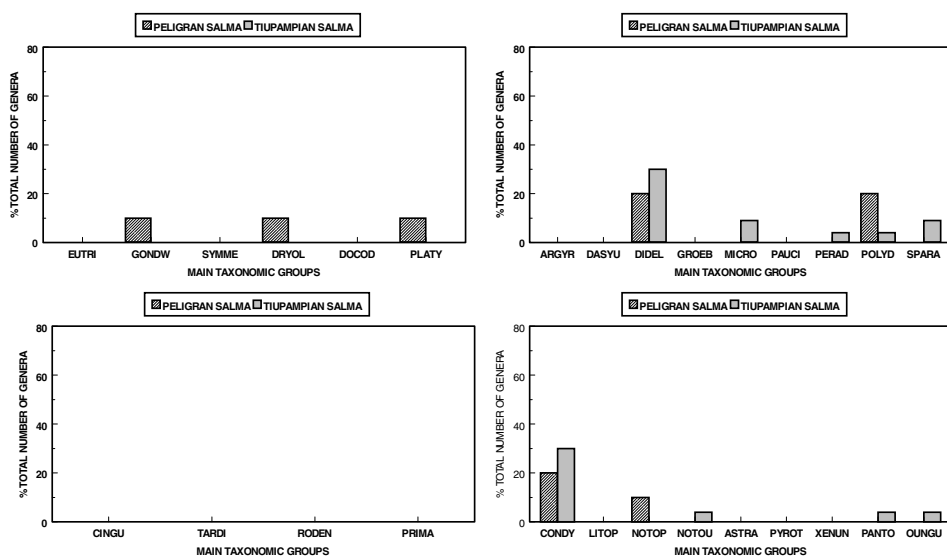


Fig. 25 Pattern of taxonomic diversity during the Protocenozoic Faunistic Supercycle (Tiupampan and Peligran SALMAs). Abbreviations as in Fig. 17

the correlation of the Río Loro Formation with the Bolivian Tiupampa Formation has not been established with certitude, and much less with the Patagonian Peligran beds. Consequently, it is unclear if this family originated within the lower latitudes or within the higher Patagonian latitudes. In this paper, we include the Paleocene strata of the Río Loro Formation in the Itaboraian SALMA, following Ortiz-Jaureguizar and Pascual (1989), Pascual and Ortiz-Jaureguizar (1990), and Pascual et al. (1996).

Beside the “condylarths” recorded in the Tiupampan and Peligran SALMAs, there were Laurasian immigrants in the Northern Bolivian Tiupampan beds, e.g., Leptictida (Palaeoryctidae?, cf. *Cimolestes* sp.) and Pantodonta (the Alcidedorbignyidae *Alcidedorbignya inopinata* de Muizon and Marshall, 1987c), and survivors of the Gondwanan radiation, such as the gondwanatherian *Sudamerica ameghinoi* (see Pascual et al., 1999) and the dryolestida *Peligrotherium tropicalis* Bonaparte et al., 1993 (see Gelfo and Pascual, 2001), in the Patagonian Peligran beds. To these Gondwanan relictual taxa must be added the Australian or Antarctic immigrant monotreme ornithorhynchid *Monotrematum sudamericanum* (Pascual et al., 1992a,b, 2002c). Although both SALMAs were recognized as Early Paleocene, the distinct composition of mammal taxa, and particularly the distinct state of dental characters in the “condylarths,” led some workers to distinguish the Tiupampan SALMA as older than the Peligran SALMA (e.g., Bonaparte et al., 1993). Notwithstanding, on the basis of geologic evidences another authors considered that the Peligran SALMA is older than the Tiupampan (Marshall et al., 1997). In spite of these different interpretations, we note that both SALMAs are characterized by the regional presence of Laurasian immigrants (Tiupampan), and relictual Gondwanan taxa in the Patagonian Peligran, although none of them have been recorded in the subsequent SALMAs. Examples include (1) the marsupial Peradectia, the placental Laurasian Pantodonta, Leptictidae and “condylarth” Mioclaenidae Kollpaniinae in the Tiupampan SALMA of Cochabamban region, and (2) the immigrant ornithorhynchid *Monotrematum sudamericanum*, aside to relictual taxa of the Gondwanan Episode, as the Gondwanatheria Sudamericiidae *Sudamerica ameghinoi*, and the dryolestoidan *Peligrotherium tropicalis* in the Peligran SALMA of Patagonia.

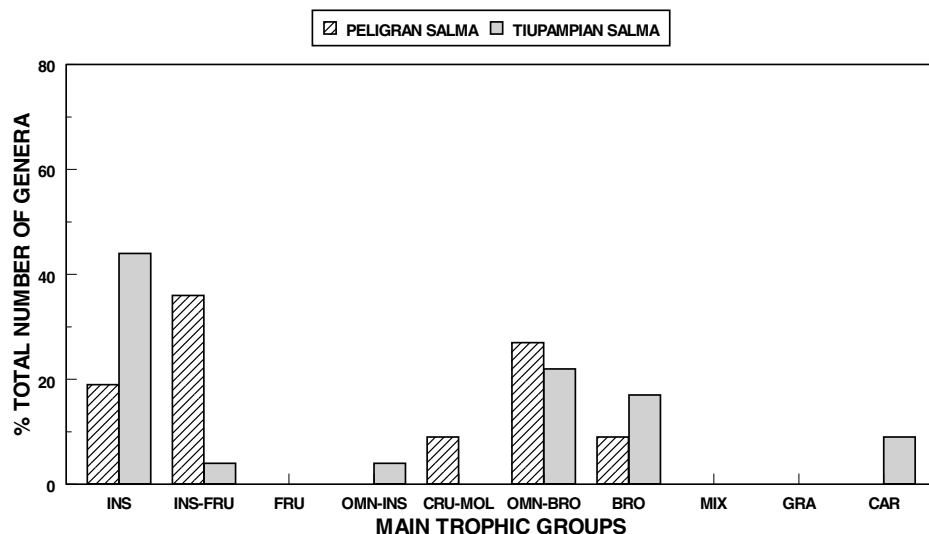


Fig. 26 Pattern of trophic diversity during the Protocenoic Faunistic Supercycle (Tiupampan and Peligran SALMAs). Abbreviations as in Fig. 18

Although the Tiupampan and the Peligran land mammals show that they were not coetaneous, the two mammal-bearing stratigraphical units, on which were based, respectively, the Tiupampan and the Peligran SALMAs, appear as lithogenetically subsequent and conformable to apparently the same Late Cretaceous-Early Paleocene marine transgressive beds deposited in a sort of sea-way that divided the South American continent in two territories (Fig. 2). Mainly the short-lived immigrants in both units, mentioned above, suggest that these two territories were, respectively, two distinct paleobiogeographical regions, whose limits cannot be precisely established because both records are presently too restricted and quite separated in space. Although the mammals recorded in each of these territories are not coetaneous, the different taxonomic composition can be attributed not only to diachronism but also to different ecological situations, which are related to the latitudinal differences of the type-localities (about 18°S for the Tiupampan locality, and 45°S for the Peligran one; see above).

From a trophic point of view, Tiupampan land-mammal communities were dominated by insectivores (44%), followed by omnivore-browsers (22%) and browsers (17%; see Fig. 26). However, Peligran communities were dominated by insectivore-frugivores (36%), followed by omnivorous-browsers (27%) and insectivores (19%) (see Fig. 26). According to the flora (Petriella and Archangelsky, 1975) and vertebrate fauna (see Gayet et al., 1991; Pascual and Ortiz-Jaureguizar, 1991; Marshall et al., 1997, table 2) so latitudinally distant localities as Tiupampa and Punta Peligro had intertropical forested environments. Notwithstanding, the trophic differences between land-mammal communities suggest that both areas were relatively different. The higher number of browsers and insectivores in Tiupampan communities can be correlated with closer, wetter and warmer woodlands than the Patagonian Peligran ones.

Differences in taxonomic and trophic composition provide additional evidence for two Late Cretaceous-Early Paleocene biogeographical provinces: (1) “Province Nord-gondwanienne,” and (2) “Province Sud-Gondwanienne,” originally recognized by the tortoises (de Broin and de la Fuente, 1993; see above “Brief Comparative Analysis...” and our Fig. 2). As above mentioned, among the Laurasian immigrants in the “Province Nord-gondwanienne” are the

marsupial taxon Peradectia, and the placental taxa Leptictida, Pantodonta, and mioclaenid condylarths (subfamily Kollpaniinae), none of which are yet recorded in the Peligran Patagonian beds. In contrast, the only condylarths so far recorded in the Peligran beds of Patagonia are the advanced and native Didelodontidae (*Escribania chubutensis* = *Raulvacchia bunodonta*, *cf.* J. Gelfo, pers. comm.), a family derived from the immigrant Mioclaenidae (Gelfo, pers. comm.). Among marsupials, the Tiupampan Peradectia and Microbiotheria (*sensu* Marshall et al., 1990, 1997) have been not recorded yet in the Patagonian Peligran beds. Instead, advanced Didelphimorphia (species belonging to the genera *Derorhynchus* and *Didelphopsis*), together with the oldest native polydolopid and bonapartheriid Polydolopimorphia, have been recorded in the Peligran beds of Patagonia (Goin et al., unpublished). Thus, the mammals so far recorded from the Bolivian Tiupampan beds show a quite distinct composition. The most outstanding difference is the distinct origin of the immigrants of each SALMA, which, with the exception of the condylarths, became extinct by the Early-Middle Paleocene. No remains of them have been recorded in the subsequent SALMAs. The record shows that by Peligran times the radiation of the Laurasian therian immigrants had occurred, giving origin to native South American taxa, such as the “condylarths” Didelodontidae and the first Litopterna or Notopterna Notonychopidae (Soria, 1989; Bonaparte and Morales, 1997), among the placentals.

Infracenozoic supercycle

For the first time, the only mammalian inhabitants were marsupials and placentals, with the above mentioned exception of a gondwanathere up to the Middle Eocene “Mesetan” land-mammal fauna in the Antarctic Peninsula (see Appendix). As their basic diversification had been achieved, this lapse of time is the longest autochthonous part of the South American history, consequently related to the longest continental isolation. From a strict point of view this span of isolation, as we said above, includes the Antarctic Peninsula, if not also part or all of the remaining Antarctic Continent. Although the early part of this Supercycle is beginning to be better known (Bond et al., 1995), the relatively scarce record suggests that this lapse of time was characterized by the highest diversity of native mammals. Along this interval there occurred the radiation climax of most of the native marsupials and “ungulates,” e.g., Sparassodonta and Polydolopimorphia among the marsupials, and Condylartha, Astrapotheria, Litopterna, “Notopterna,” Notoungulata, Pyrotheria, and Xenungulata among the placentals.

From a taxonomic point of view, during the first part of this Supercycle (“*Carodnia* Fauna” and Itaboraian SALMA; see Appendix and Fig. 1) land-mammal communities were dominated by marsupials (particularly didelphimorphians and polydolopimorphians), but from the Riochican SALMA to the end of this Supercycle notoungulates replaced marsupials as the dominant mammals (Fig. 27). Thus, the Marsupalia reach its climax during the first part of this Supercycle. This is evidenced by the presence of the most varied marsupials ever known in South America, that radiated into peculiar adaptive types, as well as the plesiadapid-like Polydolopimorphia (Fig. 28) and the arboreal primate-like Groeberiidae (Fig. 29). During the later second part of this Supercycle, at least in southern South America, was added one saltatorial ecological group, the Argyrolagidae (Fig. 30), otherwise better represented in the subsequent Supercycles, particularly during the Mio-Pliocene Supercycles. Another important aspect of the last part of the Infracenozoic Supercycle is the increase in the diversity of xenarthrans, and the first appearance of the caviomorph rodents (Tinguirirican SALMA; see Appendix and Fig. 1), two of the groups that, together with the notoungulates, will be the dominant mammals during most of the rest of the Cenozoic (Pascual et al., 1996). The first recorded xenarthrans were the Dasypodidae (Itaboraian SALMA), and by the end of the Supercycle (Tinguirirican SALMA) is recorded an enigmatic group of tardigrades, represented by *Pseudoglyptodon*. Fossil evidence suggests that

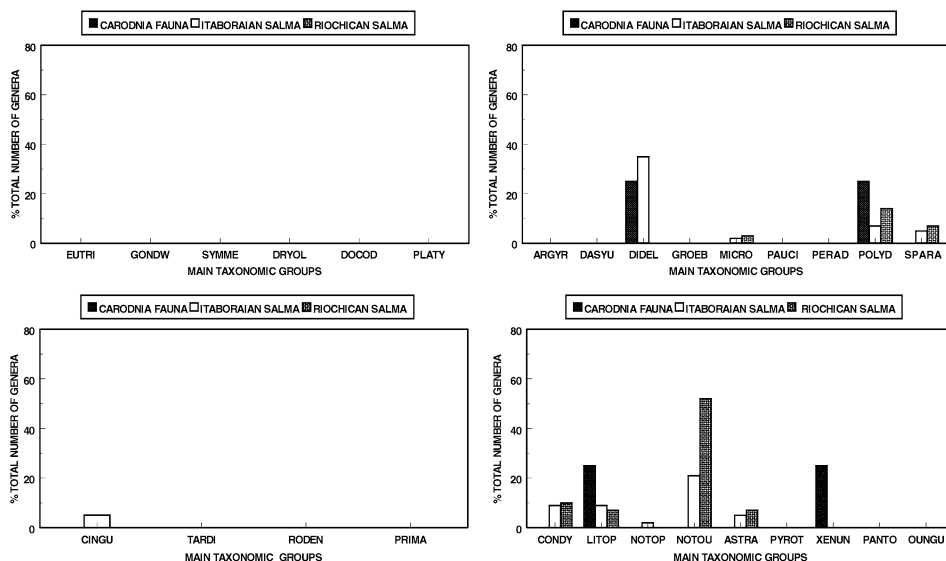


Fig. 27 Pattern of taxonomic diversity during the Patagonian “*Carodnia* Fauna,” and the Itaboraian and Riochican SALMAs. Abbreviations as in Fig. 17

caviomorph rodents came from Africa, apparently following two immigratory events. Already by then they were well differentiated as caviomorph South American mammals (see Wyss et al., 1993).

From a trophic point of view, land-mammal communities were dominated by browser-types during all of the Infracenozoic Supercycle. During the first part of this Supercycle the insectivorous types maintained a relatively high diversity, but this diversity diminished during the last part of the Supercycle (Fig. 31). Conversely, during the first part of the Infracenozoic Supercycle the mixed-feeders and grazers show a low diversity, but the diversity of these types rises during the final part of the Supercycle (Fig. 33). This rise of the mixed-feeders and grazers in southern beds (Patagonia) suggests a wider extension of grasslands. The brachyodonty of the coeval and related groups in lower latitudes suggests the beginning of more marked latitudinal environmental differences (see Pascual et al., 1996).

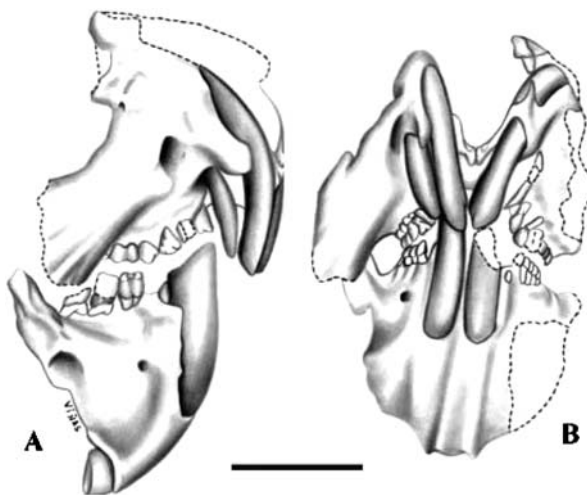
In spite of the trend from more homogeneous and wooded habitats to more varied and open ones recorded during the Infracenozoic Supercycle, an exception exists: the “Mesetan” land-mammal fauna (Fig. 1). This is a peculiar Eocene fauna, recorded near the northernmost tip of the Antarctic peninsula (Seymour Island). From a taxonomic point of view, the “Mesetan” land-mammal fauna was dominated by didelphimorphian (39%) and polydolopimorphian (15%) marsupials (Appendix and Fig. 32). From a trophic point of view, this fauna was clearly dominated by insectivores (62%), followed by insectivore-frugivores (23%) and browsers (15%) (Fig. 33). According to Reguero et al. (2002) and Bond et al. (2006), closed woodland developed under wet and cold-temperate climatic conditions during the deposition of the La Meseta Formation. However, Case (2006 and references therein) reports that mean annual temperatures were cooler (11–13°C) with a highly seasonal climate, in which the mean winter temperature could have ranged from -3 to 2°C . Case (2006) found that the body size distribution of the “Mesetan” land fauna was U-shaped and bimodal, with small (i.e., 50–300 g) marsupials and gondwanatheres, large (i.e., 10–150 kg) “ungulates,” pilosans, ratites, and phororhacoids, and

Fig. 28 *Epidolops ameghinoi*
Paula Couto, 1952. Mandible with
right i_{1-2} - c - pm_{2-3} - m_{1-4} and left
 c - m_4 . Scale bar = 1 cm



without medium-sized mammals (i.e., with a size from a rabbit to a small ungulate). Case (2006) concluded that this body size pattern is similar to those of the modern boreal mammalian faunas of North America, wherein there is a low frequency of species in the medium body size range as a consequence of the cold winter temperatures. Notwithstanding, some of Case's (2006) body size estimations could be controversial. For example, in the same volume, Bond et al. (2006) estimated that the Antarctic Sparnotheriodontidae (see below) had a body mass of 395–400 kg, more than two times the body size of the heaviest vertebrate estimated by Case (2006). Another example is found in the polydolopid *Polydolops dailyi*. According to Case (2006) this species

Fig. 29 *Groeberia minoprioi*
Patterson, 1952. Rostral portion of
the skull and anterior portion of the
mandible. **A**, right lateral view of
both skull and mandible mounted in
the articulated position as they were
found. **B**, same as **A** in frontal view.
Scale bar = 1 cm



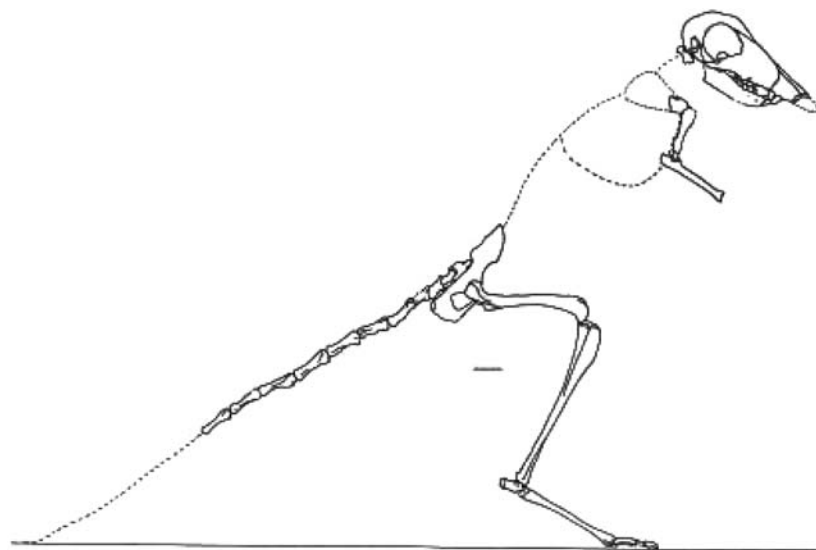


Fig. 30 *Argyrolagus scagliai* Simpson 1970. Skeleton in right lateral view. Scale bar = 1 cm. Modified from Simpson (1970)

falls into the category extended between 50–300 g. However, when the allometric equation of Dumont et al. (2000) for the m2 is applied to *P. dailyi*, it has a body mass of 644.37 g. Similarly, when using the allometric equation of Gordon (2003) for the same molar, it has a body mass of 587.86 g (see also Ortiz-Jaureguizar, 2003, for body mass comparisons of other plagiaulacoid-like South American marsupials). Consequently, we think that the conclusions of Case (2006)

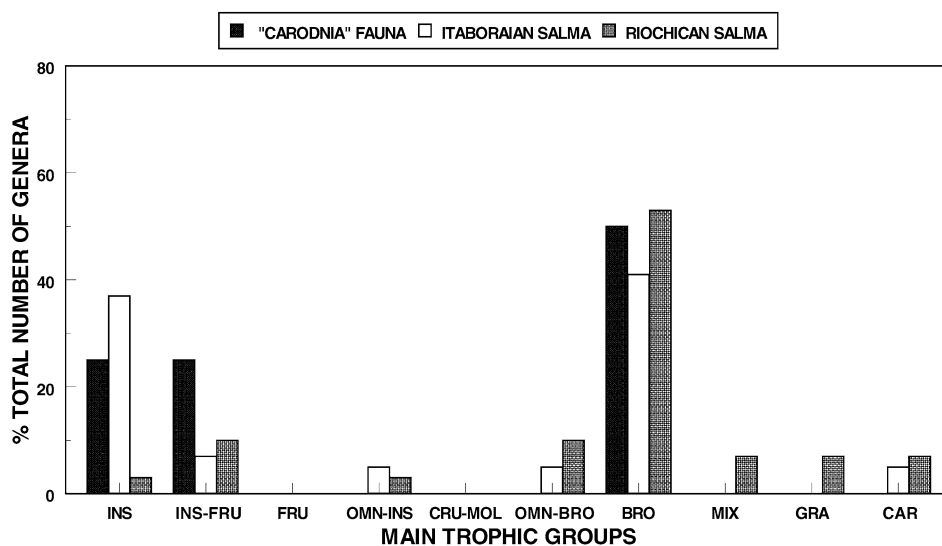


Fig. 31 Pattern of trophic diversity during the Patagonian "Carodnia Fauna," and the Itaboraian and Riochican SALMAs. Abbreviations as in Fig. 18

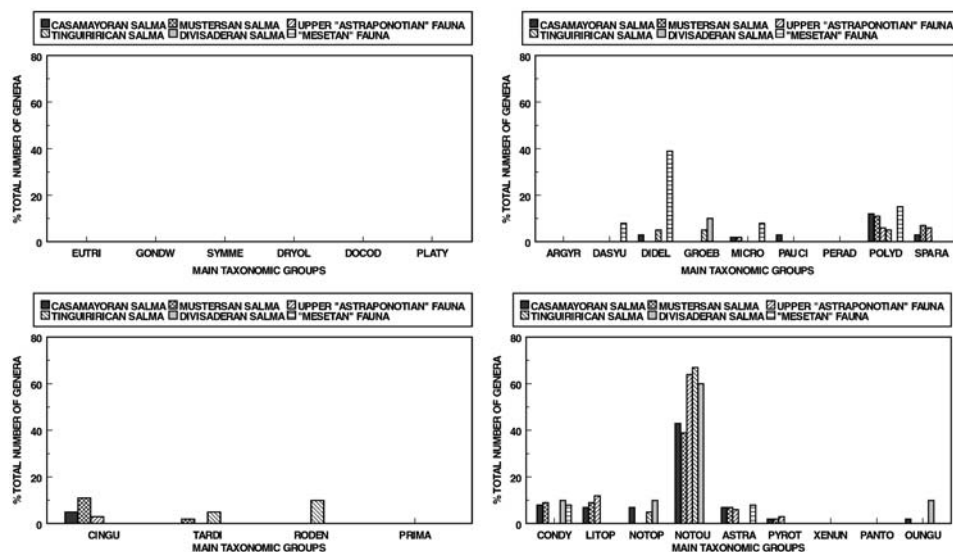


Fig. 32 Pattern of taxonomic diversity during the Casamayoran, Mustersan, “Astraponotéen supérieur,” Tinguirirican, Divisaderan, and “Mesetan” Faunas and SALMAs. Abbreviations as in Fig. 17

may be based on underestimated body mass, being probably that medium-sized mammals were present in the “Mesetan” fauna. If this is true, the body size distribution in this fauna is unimodal and not bimodal, and then the application of a boreal model is wrong. Consequently, we think that the environmental conditions proposed by Reguero et al. (2002) and Bond et al. (2006) are more probable than those proposed by Case (2006). Also, the environmental conditions proposed in Reguero et al. (2002) and Bond et al. (2006) are in agreement with the taxonomic and trophic composition of its land-mammal fauna. However, these taxonomic and trophic composition patterns are anomalous for an Eocene austral fauna, and are more similar to the oldest South American faunas, like those of the Paleocene (except the Riochican; see Figs. 32 and 33).

According to Reguero et al. (2002), the “Mesetan” fauna can be derived from the Riochican and Early Casamayoran (Vacan) land-mammal faunas, and its persistence on the late Eocene of the Antarctic Peninsula is a consequence of the presence of some kind of barrier. These authors also underlined that the more unexpected characteristic of this fauna is the absence of Notoungulata. This absence, according to Reguero et al. (2002), can be explained by differential extinction, taphonomic bias, or the existence of a geographic or ecological barrier, but Reguero et al. (2002) believe that the evidence is in favor of differential extinction. In this sense, they consider that the Notoungulata reached the Antarctic Peninsula during the latest Paleocene, and then became extinct there at the onset of the climatic cooling recorded during the middle-Late Eocene (Fig. 1). Also, they postulated that most of the “Mesetan” mammals could have reached West Antarctica during the warmest phases of the Paleogene, i.e., the latest Paleocene and the earliest Eocene (Fig. 1). The only exception could be the Sudamericidae, whose presence in the “Mesetan” fauna and its Gondwanan origin fits better with vicariance scenarios than with dispersal scenarios (Reguero et al., 2002). On this matter, these authors postulated that “... 1) the group originated before the major continental fragmentation of Early Cretaceous, and spread throughout most of Gondwana (the absence of gondwanatheres in Africa is attributable to poor sampling, differential extinction, or both), or 2) the group originated sometime in the Early Cretaceous after the tectonic isolation of Africa.” (Reguero et al., 2002, p. 205).

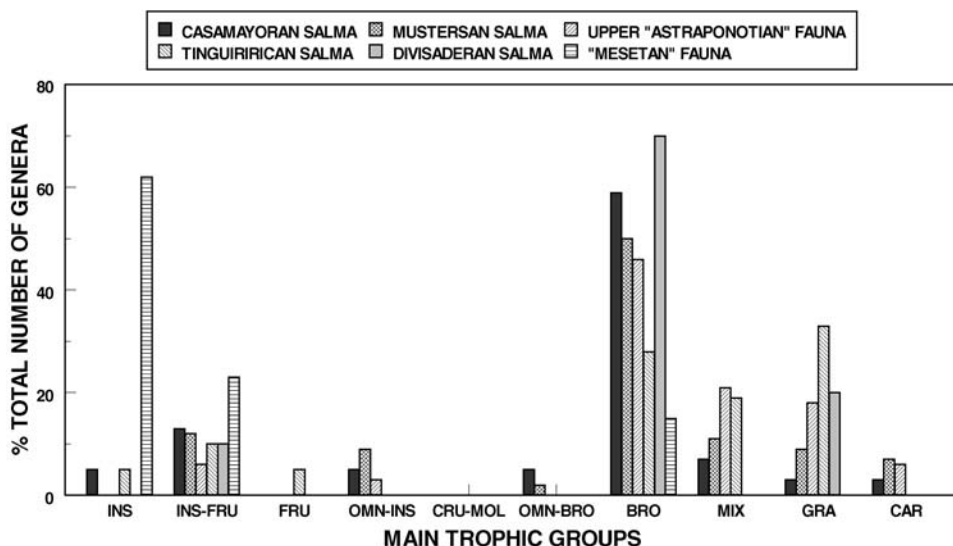


Fig. 33 Pattern of trophic diversity during the Casamayoran, Mustersan, “Astraponotéen supérieur,” Tinguirirican, Divisaderan, and “Mesetan” Faunas and SALMAs. Abbreviations as in Fig. 18

Another scenario is also possible based on Reguero et al. (2002) and new evidence (see below). According to the evidence available when Reguero et al. (2002) wrote their paper:

- (1) Antarctic sudamericids were probably derived from the Peligran *Sudamerica ameghinoides*.
- (2) Antarctic derorhynchids showed close similarities with two unpublished species of *Derorhynchus* from the Itaboraian of Patagonia.
- (3) The Antarctic microbiothere closely resembles a microbiothere species of the Itaboraian from Patagonia.
- (4) The endemic Antarctic polydolopid *Polydolops dailyi* is closely related to the species *P. thomasi* from the Casamayoran (Vacán and Barrancan) of Patagonia.
- (5) The Antarctic sparnotheriodontid is very close (perhaps representing the same species) to an unpublished new Early Casamayoran (Vacán) species from Patagonia, and some dental features of the Antarctic species seems to be more derived than those of the Riochican and Vacán genus *Victorlemoinea*.
- (6) The Antarctic trygonostylopod was tentatively referred to the genus *Trygonostylops*, previously recorded in the Riochican and Casamayoran (Vacán and Barrancan) of Patagonia.
- (7) The Antarctic Pilosa share plesiomorphic features with primitive Tardigrada and Vermilingua, two orders recorded for the first time in Deseadan beds of Patagonia and Bolivia (Tardigrada), and Colhuehuapian beds of Patagonia (Vermilingua).

Notwithstanding, new data on the marsupials of the Peligran SALMA (Goin et al., unpublished), a previous paper on new “Mesetan” marsupials (Goin et al., 1999), as well as a different analysis of the remaining evidence, led us to propose a different scenario. Thus, the unpublished data of Goin and colleagues indicates that derorhynchids and polydolopids appear for the first time during the Peligran SALMA. This fact, plus the proposed relationships of the Peligran and Antarctic sudamericids (see Goin et al., 2006a,b), and the common absence of notoungulates during the Peligran and “Mesetan” faunas, suggest that under a dispersalist point of view, the land-mammals of the “Mesetan” fauna could not arrive to Antarctica at the same time, as is inferred from the paper of Reguero et al. (2002). This hypothesis was also formulated by Goin

et al. (1999) for the marsupials, and by Bond et al. (2006) for the new “Mesetan” litoptern. In this last paper, these authors named the Antarctic Sparnotheriodontidae *Notolophus arquinotiensis*, and discuss its phylogenetic and biogeographic relationships with some Patagonian native “ungulates.”

If a dispersal scenario is accepted, we suggest that some mammals of the “Mesetan” fauna arrived earlier than the Riochican-Early Casamayoran (Vacan) span (e.g., sudamericids and marsupials during the Peligran-Itaboraian span; sparnotheriodontids during the Itaboraian-Vacan span). Also, in this scenario it is unnecessary to appeal for immigration and subsequent extinction to explain the absence of notoungulates in the “Mesetan” fauna. The notoungulates were recorded for the first time in South America during the Tiupampan SALMA and for the first time in Patagonia during the Itaboraian SALMA (Fig. 1). According to the geologic evidence, Patagonia and the rest of South America were separated by the widespread Danian transgression during the Peligran-Tiupampan times (Fig. 2). In spite of this seaway barrier, Tiupampan and Peligran faunas shared some marsupials and “condylarths” in common (see above), but there are no notoungulates recorded in Patagonia. According to the record, notoungulates reach Patagonia only after the Danian regression, a lapse represented in Patagonia by the poorly known “*Carodnia*” fauna and the Itaboraian one (Fig. 1). Additionally, we infer that notoungulates did not have the ability to move across marine barriers, since this group did not participate in the emigratory events from South America. As an example, rodents and tardigrads reached the West Indies during the Miocene (see Pascual et al., 1990, 1996), and tardigrads arrived to North America during Late Miocene, as forerunners of the Great American Biotic Interchange (Stehli and Webb, 1985; Marshall and Cifelli, 1990; Pascual et al., 1996).

If a dispersal scenario is rejected, we suggest that most of the “Mesetan fauna” represents an Eocene Antarctic relict of a widespread Paleocene Patagonian-Antarctic land-mammal fauna (Fig. 3). Taking into account the paleogeographic reconstructions of Zachos et al. (2001; see Fig. 1) for the Paleocene, Eocene and earliest Oligocene, a physical connection between Patagonia and Antarctic persisted before disappearing 30 Ma ago during the Early Oligocene (Figs. 1–4). During the “Mesetan” times the Patagonian land-mammal fauna was dominated by most advanced taxa than those recorded in the “Mesetan” fauna (see above). If we consider both the paleogeographic and the faunistic evidence, this fact can be explained only by the presence of some kind of ecological barrier, that avoided to the Patagonian mammals extend its home range to Antarctica, and *vice versa*. This barrier, absent during the Paleocene, can explain the taxonomic and ecological differences observed on both areas, and the relictual aspect of the “Mesetan” land-mammal fauna.

An interesting problem derived from the “Mesetan” fauna is the presence of an unequal phalanx of an enigmatic non-Cingulata xenarthran. This phalanx may belong to Tardigrada or a Vermilingua, two orders of the xenarthran superorder Pilosa undisputedly recorded for the first time in South America during the Deseadan (Tardigrada) and Colhuehuapian (Vermilingua) SALMAs. An isolated third left metacarpal from Patagonia was assigned by Carlini et al. (1990) to a non-Cingulata Paratheria (i.e., Xenarthra + Pholidota); this specimen shares some characters with the Vermilingua and other characters with the Tardigrada and Pholidota (the affinities of this specimen with the xenarthran Pleiodonta can not be determined, because there are not homologous parts of the fore limb skeleton). According to these authors, this specimen come from beds of Late Casamayoran (Barrancan) SALMA, but now the precise lithostratigraphic and biochronologic provenance is uncertain (Carlini, person. comm.). The other xenarthran order (Cingulata) is recorded by the first time in South America during Itaboraian SALMA, but this group is absent in the “Mesetan” fauna. The provenance of the Antarctic Pilosa is unclear, because is very difficult to prove that this group: (a) was a member of the Patagonian mammal communities that emigrated to Antarctica from Patagonia; (b) was a member of the

Antarctic communities that emigrated to Patagonia from Antarctica; or (c) was a relict of a previous widespread Antarctic-Patagonian land-mammal fauna. The first hypothesis could be correct only if the absence of the Pilosa in the Patagonian faunas during the Paleocene and Eocene is due to bias in the fossil record. However, this is not very probable, because several of the Paleocene and Eocene land-mammal faunas (e.g., Riochican, Casamayoran, Mustersan, see Appendix) have been relatively well sampled and the Pilosa are systematically absent. The second hypothesis is more probable, because in this scenario it is unnecessary to appeal to sampling problems to explain the absence of Pilosa in the Paleocene-Eocene Patagonian fossil record. Finally, the third hypothesis has a mix of the problems and advantages of the other two. In this scenario, it is necessary to appeal to record bias or regional extinction to explain the absence of Pilosa in Patagonia during the Paleocene and Eocene, and a subsequent emigration from Antarctica during the latest Eocene or earliest Oligocene.

In relation to these hypotheses, the radically different biogeographic patterns of the two principal groups of Xenarthran, Cingulata and Pilosa, requires some consideration. If we accept that the absence of Cingulata in the Eocene “Mesetan fauna” is not due to record bias, and that the absence of Pilosa in the Paleocene and Eocene Patagonian fossil record is not due to record bias or regional extinction, we may conclude that both groups had distinct areas of differentiation: South America for the Cingulata and Eastern Antarctica (or Southern Africa?) for the Pilosa. Thus, the presence of Cingulata during the Late Paleocene of Patagonia and Brazil suggests that this group had already differentiated in some place on this continent. Conversely, the presence of Pilosa in Antarctica during the “Mesetan” time, its absence in both older and relatively coetaneous Patagonian land-mammal faunas (Fig. 1), and the sudden record of Tardigrada and Vermilingua during the Late Oligocene-Lower Miocene in South America, suggest that Pilosa are not South American natives. Its presence in the Eocene “Mesetan” fauna could suggest an Antarctic origin for this group. But taking into account: (1) that recent phylogenetic analyses based on molecular data proposed that Xenarthra originated 125 Ma ago (i.e., during Hauterivian) probably in South America and/or Africa, and (2) that Africa initiated its separation from Antarctica 135 Ma ago, and finalized its separation with South America 110 Ma ago (Storey, 1995; Sclater et al., 1977; Parrish Totman, 1993), it is also probable that the Pilosa could have originated in Eastern Antarctica or in Southern Africa. Unfortunately, we do not have a good fossil record of the Cretaceous and Paleocene evolution of Antarctic and South African mammals.

Appendix

Systematic and chronological ranges (SALMAs and Faunas) of Late Cretaceous-Recent mammal genera (with the suprageneric taxa that include each of them) of Southern South America

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
Order?Eutriconodonta												
Family Austrotriconodontidae												
<i>Austrotriconodon</i>	1	0	0	0	0	0	0	0	0	0	0	0
Order Multituberculata												
Suborder “Plagiaulacoidea”												
Gen. et sp. indet.	1	0	0	0	0	0	0	0	0	0	0	0
Order Gondwanatheria												
Family Ferugliotheriidae												
<i>Ferugliotherium</i>	1	0	0	0	0	0	0	0	0	0	0	0

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
Family Sudamericiidae												
Gondwanatherium	1	0	0	0	0	0	0	0	0	0	0	0
<i>Sudamerica</i>	0	1	0	0	0	0	0	0	0	0	0	1
“Symmetrodonta”												
Family Bondesiidae												
<i>Bondesius</i>	1	0	0	0	0	0	0	0	0	0	0	0
Order Dryolestida												
Family Barbereniidae												
<i>Barberenia</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>Quirogatherium</i>	1	0	0	0	0	0	0	0	0	0	0	0
Family Brandoniidae												
<i>Brandonia</i>	1	0	0	0	0	0	0	0	0	0	0	0
Family Casamiquelidae												
<i>Alamitherium</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>Casamiquelia</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>Roughtherium</i>	1	0	0	0	0	0	0	0	0	0	0	0
Family Dryolestidae												
<i>Groebertherium</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>Leonardus</i>	1	0	0	0	0	0	0	0	0	0	0	0
Family Mesungulidae												
<i>Mesungulatum</i>	1	0	0	0	0	0	0	0	0	0	0	0
Family Peligrotheriidae												
<i>Peligrotherium</i>	0	1	0	0	0	0	0	0	0	0	0	0
Fam. inc. sedis												
<i>Paraungulatum</i>	1	0	0	0	0	0	0	0	0	0	0	0
Order Docodonta												
Family Reigitheriidae												
<i>Reigitherium</i>	1	0	0	0	0	0	0	0	0	0	0	0
Order Platypoda												
Family Ornithorhynchidae												
<i>Monotrematum</i>	0	1	0	0	0	0	0	0	0	0	0	0
Order Peradectia												
Family Caroloameghiniidae												
<i>Caroloameghinia</i>	0	0	0	0	0	0	1	0	0	0	0	0
Family Peradectidae												
<i>Peradectes</i>	0	0	1	0	0	0	0	0	0	0	0	0
Order Didelphimorphia												
Family Derorhynchidae												
<i>Derorhynchus</i>	0	1	0	1	1	0	0	0	0	0	0	1
<i>Gaylordia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Minusculodelphis</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pauladelphys</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Xenostylus</i>	0	0	0	0	0	0	0	0	0	0	0	1
Gen. Nov.	0	0	0	0	1	0	0	0	0	0	0	0

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
Family Didelphidae												
<i>Andinodelphis</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Coona</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Didelphopsis</i>	0	1	0	0	1	0	0	0	0	0	0	0
<i>Marmosopsis</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Monodelphopsis</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Tiulordia</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Zeusdelphys</i>	0	0	0	0	1	0	0	0	0	0	0	0
Family Herpetheriidae												
<i>Eobrasilia</i>	0	0	0	0	1	0	0	0	0	0	0	0
Family Jaskhadelphyidae												
<i>Jaskhadelphys</i>	0	0	1	0	0	0	0	0	0	0	0	0
Family Protodidelphidae												
<i>Bobbschaefferia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Guggenheimia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Procaroloameghinia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Protodidelphis</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Robertbutleria</i>	0	0	0	0	1	0	0	0	0	0	0	0
Gen Nov.	0	0	0	0	0	0	0	0	0	0	0	1
Family Pucadelphidae												
<i>Incadelphys</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Mizquedelphys</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Pucadelphis</i>	0	0	1	0	0	0	0	0	0	0	0	0
Family Sternbergiidae												
<i>Itaboraidelphis</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Sternbergia</i>	0	0	0	0	1	0	0	0	0	0	0	0
Didelphimorphia inc. sed.												
<i>Pascualdelphys</i>	0	0	0	0	0	0	0	0	0	1	0	0
<i>Szalinia</i>	0	0	1	0	0	0	0	0	0	0	0	0
Gen. nov.	0	0	0	0	0	0	0	0	0	0	0	1
Order Groeberida												
Family Groeberiidae												
<i>Groeberia</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Klohnia</i>	0	0	0	0	0	0	0	0	0	1	0	0
Order Microbiotheria												
Family Glasbiidae												
<i>Chulpasia</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Palangania</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Reigia</i>	0	0	0	0	0	0	0	1	0	0	0	0
Family Microbiotheriidae												
<i>Eomicrobiotherium</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Khasia</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Mirandatherium</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Marambiotherium</i>	0	0	0	0	0	0	0	0	0	0	0	1

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
Order Polydolopimorphia												
Family Bonapartheriidae												
<i>Bonapartherium</i>	0	0	0	0	0	0	1	1	0	0	0	0
<i>Epidolops</i>	0	0	0	0	1	0	0	0	0	0	0	0
Gen nov.	0	1	0	0	0	0	0	0	0	0	0	0
Family Gashterniidae												
<i>Gashternia</i>	0	0	0	0	1	1	0	0	0	0	0	0
<i>Sillustania</i>	0	0	1	0	0	0	0	0	0	0	0	0
Family Polydolopidae												
<i>Amphidolops</i>	0	0	0	1	1	1	1	0	0	0	0	0
<i>Eudolops</i>	0	0	0	0	0	0	1	1	1	0	0	0
<i>Polydolops</i>	0	0	0	0	0	1	1	1	1	1	0	1
<i>Pseudolops</i>	0	0	0	0	0	0	1	0	0	0	0	0
Gen. nov.	0	1	0	0	0	0	0	0	0	0	0	0
Family Prepidolopidae												
<i>Prepidolops</i>	0	0	0	0	0	1	1	0	0	0	0	0
<i>Perrodelpheys</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Punadolops</i>	0	0	0	0	0	0	0	1	0	0	0	0
Polydolopimorphia incertae sedis												
<i>Roberthoffstetteria</i>	0	0	1	0	0	0	0	0	0	0	0	0
Polydolopimorphia?												
<i>Hondonadia</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Rosendolops</i>	0	0	0	0	0	0	1	0	0	0	0	0
Order Paucituberculata												
Family Caenolestidae												
<i>Quirogalestes</i>	0	0	0	0	0	0	1	0	0	0	0	0
Order Sparassodonta												
Family Borhyaenidae												
<i>Nemolestes</i>	0	0	0	0	1	1	0	0	0	0	0	0
<i>Pharsophorus</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Plesiofelis</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Procladosictis</i>	0	0	0	0	0	0	0	1	0	0	0	0
Family Hatliacynidae												
<i>Allqokirus</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Patene</i>	0	0	0	0	1	1	1	0	0	0	0	0
Family Mayulestidae												
<i>Mayulestes</i>	0	0	1	0	0	0	0	0	0	0	0	0
Family Proborhyaenidae												
<i>Arminiheringia</i>	0	0	0	0	0	0	1	1	0	0	0	0
<i>Proborhyaena</i>	0	0	0	0	0	0	0	0	1	0	0	0
Order Dasyurida?												
Gen nov.	0	0	0	0	0	0	0	0	0	0	0	1
Order indet.												
Gen. nov.	0	0	0	0	0	0	0	0	0	0	0	1

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
Order Cingulata												
Family Dasypodidae												
<i>Machlydotherium</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Meteutatus</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Pseudeutatus</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>"Pseudostegotherium"</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Prostegotherium</i>	0	0	0	0	1	0	1	0	0	0	0	0
<i>Riostegotherium</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Sadypus</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Utaetus</i>	0	0	0	0	0	0	1	0	0	0	0	0
Family Glyptodontidae												
<i>Glyptatelus</i>	0	0	0	0	0	0	0	1	0	0	0	0
Family Palaeopeltidae												
<i>Palaeopeltis</i>	0	0	0	0	0	0	0	1	0	0	0	0
Order Tardigrada												
Family Megalonychidae												
<i>Proplatyarthrus?</i>	0	0	0	0	0	0	0	1	0	0	0	0
Tardigrada inc. sed.												
<i>Pseudoglyptodon</i>	0	0	0	0	0	0	0	0	0	1	0	0
Order Condylarhra												
Family Didolodontidae												
<i>Decaconus</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Didolodus</i>	0	0	0	0	0	0	1	1	0	0	0	0
<i>Enneoonus</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Ernestokokenia</i>	0	0	0	0	1	1	1	0	0	0	0	0
<i>Lamegoia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Megacrodon</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Paulacoutoia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Paulogervasia</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Xesmodon</i>	0	0	0	0	0	0	0	1	0	0	0	0
Family Hyopsodontidae												
<i>Andinodus</i>	0	0	1	0	0	0	0	0	0	0	0	0
Family Mioclaenidae												
<i>Escribania</i>	0	1	0	0	0	0	0	0	0	0	0	0
<i>Kollpania</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Molinodus</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Pucanodus</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Raulvaccia</i>	0	1	0	0	0	0	0	0	0	0	0	0
<i>Simoclaenus</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Tiucclaenius</i>	0	0	1	0	0	0	0	0	0	0	0	0
Family Periptichidae												
<i>Mimatuta</i>	0	0	1	0	0	0	0	0	0	0	0	0
Order Notopterna												
Family Amilnedwardsidae												
<i>Amilnedwardsia</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Rutimeyeria</i>	0	0	0	0	0	0	1	0	0	0	0	0

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
Family Indalecidae												
<i>Adiantoides</i>	0	0	0	0	0	0	1	0	0	0	1	0
<i>Indalecia</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Gen nov.</i>	0	0	0	0	0	0	0	0	0	1	0	0
Family Notonychopidae												
<i>Requisia</i>	0	1	0	0	0	0	0	0	0	0	0	0
<i>Notonychops</i>	0	0	0	0	1	0	0	0	0	0	0	0
Order Litopterna												
Family Adianthidae												
<i>Proectocion</i>	0	0	0	0	0	0	1	0	0	0	0	0
Family Macraucheniiidae												
<i>Coniopternium</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Polymorphis</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Pternoconius</i>	0	0	0	0	0	0	0	0	1	0	0	0
Family Proterotheriidae												
<i>Anisolambda</i>	0	0	0	0	0	1	1	1	1	0	0	0
<i>Guilielmofloweria</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Heteroglyphis</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Paranisolambda</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Polyacrodon</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Ricardolydekkeria</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Wainka</i>	0	0	0	1	0	0	0	0	0	0	0	0
Family Protolipterniidae												
<i>Asmithwoodwardia</i>	0	0	0	0	1	0	1	0	0	0	0	0
<i>Miguelsoria</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Protolipterna</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Protheosodon</i>	0	0	0	0	0	0	0	0	1	0	0	0
Family Sparnotheriodontidae												
<i>Phoradiadus</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Sparnotheriodon</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Victorlemoinea</i>	0	0	0	0	1	1	1	0	0	0	0	0
<i>Notolophus</i>	0	0	0	0	0	0	0	0	0	0	0	1
Order Notoungulata												
Family Archaeohyracidae												
<i>Archaeohyrax</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Bryanpattersonia</i>	0	0	0	0	0	0	0	0	1	1	0	0
<i>Acoelohyrax</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Eohegetotherium</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Eohyrax</i>	0	0	0	0	0	1	1	1	0	0	0	0
<i>Pseudhyrax</i>	0	0	0	0	0	0	0	1	1	1	0	0
Gen nov. A	0	0	0	0	0	1	0	0	0	0	0	0
Gen nov. B	0	0	0	0	0	0	0	1	0	0	0	0
<i>Protoarchaeohyrax</i>	0	0	0	0	0	0	0	0	0	1	0	0
<i>Archaeotypotherium</i>	0	0	0	0	0	0	0	0	1	1	0	0
Gen nov. D	0	0	0	0	0	0	0	0	0	1	0	0
Gen nov. E	0	0	0	0	0	0	0	0	0	1	0	0
Gen nov. F	0	0	0	0	0	0	0	0	0	1	0	0

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
<i>Acropithecus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Archaeopithecus</i>	0	0	0	0	0	1	1	0	0	0	0	0
Family Campanorciidae												
<i>Campanorco</i>	0	0	0	0	0	0	1	0	0	0	0	0
Family Hegetotheriidae												
<i>Ethegetherium</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Prohegetotherium</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Propachyrucos</i>	0	0	0	0	0	0	0	0	1	0	0	0
Gen. nov. A	0	0	0	0	0	0	0	0	1	0	0	0
Family Henricosborniidae												
<i>Henricosbornia</i>	0	0	0	0	1	1	1	0	0	0	0	0
<i>Othnielmarshia?</i>	0	0	0	0	0	1	1	0	0	0	0	0
<i>Peripantostylops</i>	0	0	0	0	1	1	1	0	0	0	0	0
<i>Simpsonotus</i>	0	0	0	0	0	1	0	0	0	0	0	0
Family Homalodotheriidae												
<i>Asmodeus</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Trigonolophodon</i>	0	0	0	0	0	0	0	0	1	1	0	0
Family Interatheriidae												
<i>Antepithecus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Eopachyrucos</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Guilielmoscottia</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Notopithecus</i>	0	0	0	0	0	1	1	1	0	0	0	0
<i>Proargyrohyrax</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Punapithecus</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Santiagorothia</i>	0	0	0	0	0	0	0	0	1	1	0	0
<i>Transpithecus</i>	0	0	0	0	1	1	1	0	0	0	0	0
Gen. nov. A	0	0	0	0	0	0	0	0	0	1	0	0
Gen. nov. B	0	0	0	0	0	0	0	0	1	0	0	0
Family Isotemniidae												
<i>Anisotemnus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Coelostylodon</i>	0	0	0	1	0	0	0	0	0	0	0	0
<i>Distylophorus</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Edvardocopeia</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Isotemnus</i>	0	0	0	0	1	1	1	0	0	0	0	0
<i>Pampatemnus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Pleurostylodon</i>	0	0	0	0	0	1	1	0	1	0	0	0
<i>Periphragnis</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Rhyphodon</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Thomashuxleya</i>	0	0	0	0	0	0	1	0	0	0	0	0
Family Leontiniidae												
<i>Ancylocoelus</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Leontinia</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Martinniguelia</i>	0	0	0	0	0	0	0	1	0	0	0	0
Family Mesotheriidae												
<i>Plesiotrachytherus</i>	0	0	0	0	0	0	0	0	0	0	1	0
Family Notohippidae												
<i>Eomorphippus</i>	0	0	0	0	0	0	0	0	1	1	0	0
<i>Morphippus</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pampahippus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Plexotemnus</i>	0	0	0	0	0	0	1	0	0	0	0	0

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
<i>Puelia</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Rhynchippus</i>	0	0	0	0	0	0	0	0	1	0	0	0
Gen nov. A	0	0	0	0	0	0	0	0	0	1	0	0
Gen nov. B	0	0	0	0	0	0	0	0	0	1	0	0
Family Notostylopidae												
<i>Brandmayria</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Boreastylops</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Edvardotrouessartia</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Homalostylops</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Notostylops</i>	0	0	0	0	0	1	1	1	1	0	0	0
<i>Otronia</i>	0	0	0	0	0	0	0	1	0	0	0	0
Gen nov.	0	0	0	0	0	0	0	0	0	1	0	0
<i>Seudenius</i>	0	0	0	0	0	1	0	0	0	0	0	0
Family Oldfieldthomasiidae												
<i>Acoelodus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Allalmenia</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Brachystephanus</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Camargomendesia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Colbertia</i>	0	0	0	0	1	1	1	1	0	0	0	0
<i>Itaboraiterium</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Kibenikhoria</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Maxschlosseria</i>	0	0	0	0	0	1	1	0	0	0	0	0
<i>Oldfieldthomasia</i>	0	0	0	0	0	1	1	0	0	0	0	0
<i>Paginula</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Suniodon</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Tsamnichoria</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Ultrapiethecus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Xenostephanus</i>	0	0	0	0	0	0	0	0	0	0	1	0
Gen nov. A	0	0	0	0	0	0	0	0	0	0	1	0
Family Toxodontidae												
<i>Proadinotherrum</i>	0	0	0	0	0	0	0	0	1	0	0	0
Not. inc. sedis												
<i>Palaeocladosictis</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pseudopachyrucos</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Satshatennus</i>	0	0	0	0	1	0	0	0	0	0	0	0
Order indet.												
Family Perutheriidae												
<i>Perutherium</i>	0	0	1	0	0	0	0	0	0	0	0	0
Order Astrapotheria												
Family Astrapotheriidae												
<i>Albertogaudrya</i>	0	0	0	0	0	0	1	1	1	0	0	0
<i>Astraponotus</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Parastrapotherium</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Scaglia</i>	0	0	0	0	0	0	1	0	0	0	0	0
Family Eoastrapostylopidae												
<i>Eoastrapostylops</i>	0	0	0	0	1	0	0	0	0	0	0	0

Continued

	ALA	PEL	TIU	CAR	ITA	RIO	CAS	MUS	AST	TIN	DIV	MES
Family Trigonostylopidae												
<i>Shectenia</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Tetragonostylops</i>	0	0	0	0	1	1	1	0	0	0	0	0
<i>Trigonostylops</i>	0	0	0	0	0	1	1	1	0	0	0	1
Order Pyrotheria												
Family Pyrotheriidae												
<i>Carolozittelia</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Propyrotherium</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Pyrotherium</i>	0	0	0	0	0	0	0	0	1	0	0	0
Order Xenungulata												
Family Carodniidae												
<i>Carodnia</i>	0	0	0	1	0	0	0	0	0	0	0	0
Order Pantodonta												
Family Alcyledorbignyidae												
<i>Alcyledorbignya</i>	0	0	1	0	0	0	0	0	0	0	0	0
Order indet.												
<i>Florentinoameghinia</i>	0	0	0	0	0	0	1	0	0	0	0	0
Order indet.												
Family indet.												
<i>Acamana</i>	0	0	0	0	0	0	0	0	0	0	1	0
Order Rodentia												
Family Chinchillidae												
Gen nov.	0	0	0	0	0	0	0	0	0	1	0	0
Family Dasyproctidae												
Gen nov.	0	0	0	0	0	0	0	0	0	1	0	0

Note. ALA, Alamitan; PEL, Peligran; TIU, Tiupampan; CAR, *Carodnia* Fauna; ITA, Itaboraian; RIO, Riochican; CAS, Casamayoran; MUS, Mustersan; AST, “Astraponotéen” supérieur Fauna; TIN, Tinguirirican; DIV, Divisaderan; MES, “Mesetan” Fauna.

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