



Final Gondwana breakup: The Paleogene South American native ungulates and the demise of the South America–Antarctica land connection



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ABSTRACT

The biogeographic hypothesis more accepted today is that Antarctica (West Antarctica) and southern South America (Magellan region, Patagonia) were connected by a long and narrow causeway (Weddellian Isthmus) between the Antarctic Peninsula and South America since the Late Cretaceous (Campanian) until the Early Paleogene allowing terrestrial vertebrates to colonize new frontiers using this land bridge. Stratigraphically calibrated phylogenies including large, terrestrial native ungulates Litopterna and Astrapotheria taxa reveal long ghost lineages that extended into the Late Paleocene and provide evidence for the minimum times at which these “native ungulates” were present both on Antarctica and South America. Based on these results we estimate that the Weddellian Isthmus was functional as a land bridge until the Late Paleocene. Our data place the disconnection between Antarctica and South America in the Late Paleocene, indicating that the terrestrial faunistic isolation (Simpson’s “splendid isolation”) in South America begun at the end of the Paleocene (~56 to 57 m.y.). This faunistic isolation is documented to have occurred at least 25 Ma before the existence of deep-water circulation conditions in Drake Passage (~30 m.y.) based on the onset of seafloor spreading in the west Scotia Sea region. We hypothesize that in the early stages of extension (Late Paleocene, ~55 m.y.) a wide and relatively shallow epicontinental sea developed between the Antarctic Peninsula and South America drowning the Weddellian Isthmus and preventing the faunal interchange for obligate cursorial terrestrial forms.

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1. Introduction

The Southern Hemisphere today has a fauna and flora distinct from those of the Northern Hemisphere. This unique biota is, in part, the result of the geographic isolation of South America, Antarctica, and Australia from other world continents since the Late Cretaceous and, for South America, ending only in the Neogene (Pliocene or earlier) with

the permanent establishment of the Panamanian Isthmus reconnecting the American continents (Iturralde-Vinent, 2006; Lawver et al., 2011; Montes et al., 2012) and initiating the Great American Biotic Interchange (Burnham and Graham, 1999; Webb, 2006; Woodburne, 2010).

Breakup of the Gondwana started in the Late Jurassic, and by the beginning of the Late Cretaceous (~99.6 Ma) the continents South America, Australia, and Antarctica conformed a very large-scale Noah’s arks (McKenna, 1973) with their biota rifted and moved away. The drifting of these arks throughout latitudinal climate zones was the first-order cause for environmental changes to which the biota, living on the drifting Gondwana fragments, was subjected, and then geographically isolated from one another showing increasing degrees of endemism over time.

Continental dispersal of terrestrial mammals during the final breakup of the Gondwana seems to have been strongly controlled by the presence or absence of seas, their distribution, extent and depth. In particular, the biogeographic relationships of the terrestrial fauna of West

Abbreviations: ACC, Antarctic Circumpolar Current; Ma, megannum in the isotopic time scale; m.y., an abstract consideration of elapsed time not directly tied to the isotopic scales; SAANU, South American and Antarctic native ungulate; SALMA, South American Land Mammal Age.

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Antarctica (Antarctic Peninsula, James Ross Basin) with South America seem to be the result of the combined effects of changing paleogeography and organismal evolution. Continental breakup and assembly, eustatic sea-level changes, tectonic cycles, and climate shifts all influenced the geographic context within which the development of a particular paleobiotic unit took place.

Evidence of Paleogene Antarctic terrestrial faunas come almost exclusively from the James Ross Basin, Antarctic Peninsula (e.g., Woodburne and Zinsmeister, 1982; Marenssi et al., 1994; Reguero et al., 1998, 2002, 2013), and the knowledge of the Paleogene terrestrial mammals in Antarctica is almost exclusively based on fossils from several horizons representing sedimentation in coastal and shallow-marine environments of the Eocene La Meseta Formation (Marenssi et al., 1998) in Seymour (= Marambio) Island, northeast of the Antarctic Peninsula (Fig. 1), and secondly from the Eocene of the Fildes Peninsula, 25 de Mayo (King George) Island (Covacevich and Rich, 1982; Jianjun and Shuonan, 1994).

The history of dispersal and evolution of the Antarctic Eocene land mammal faunas in the James Ross Basin, Antarctic Peninsula is closely related to the existence of land bridges between West Antarctica

(Antarctic Peninsula) and South America, and East Antarctica and Australia (Tasman Gateway) (Bijl et al., 2013) (Fig. 2). Based on the composition of the paleofloras of the western part of the Antarctic Peninsula Leppe et al. (2012) suggested that the entity of a hypothetical isthmus between Antarctic Peninsula and the Magellan region and Patagonia started in the Late Cretaceous (late Campanian or early Maastrichtian).

Terrestrial mammals with South American affinities (including marsupials, xenarthrans and native ungulates; Reguero and Gasparini, 2007; Reguero et al., 2013; Table 1) have been exhumed from the shallow marine La Meseta Formation, Seymour Island, Antarctic Peninsula. This fauna exhibits high levels of species endemism for marsupials and two groups of South American native ungulates (Fig. 3), and is also taxonomically imbalanced in that it is not typically an Eocene South American fauna (Reguero et al., 2002), as might be expected if most of its ancestors dispersed over a “land bridge” between these two continents or eventually used several intervening islands in a stepping-stone chain facilitated by past lower sea levels. So, Early Paleogene terrestrial mammal localities from West Antarctica (Antarctic Peninsula) and Patagonia (South America) reflect the final breakup of

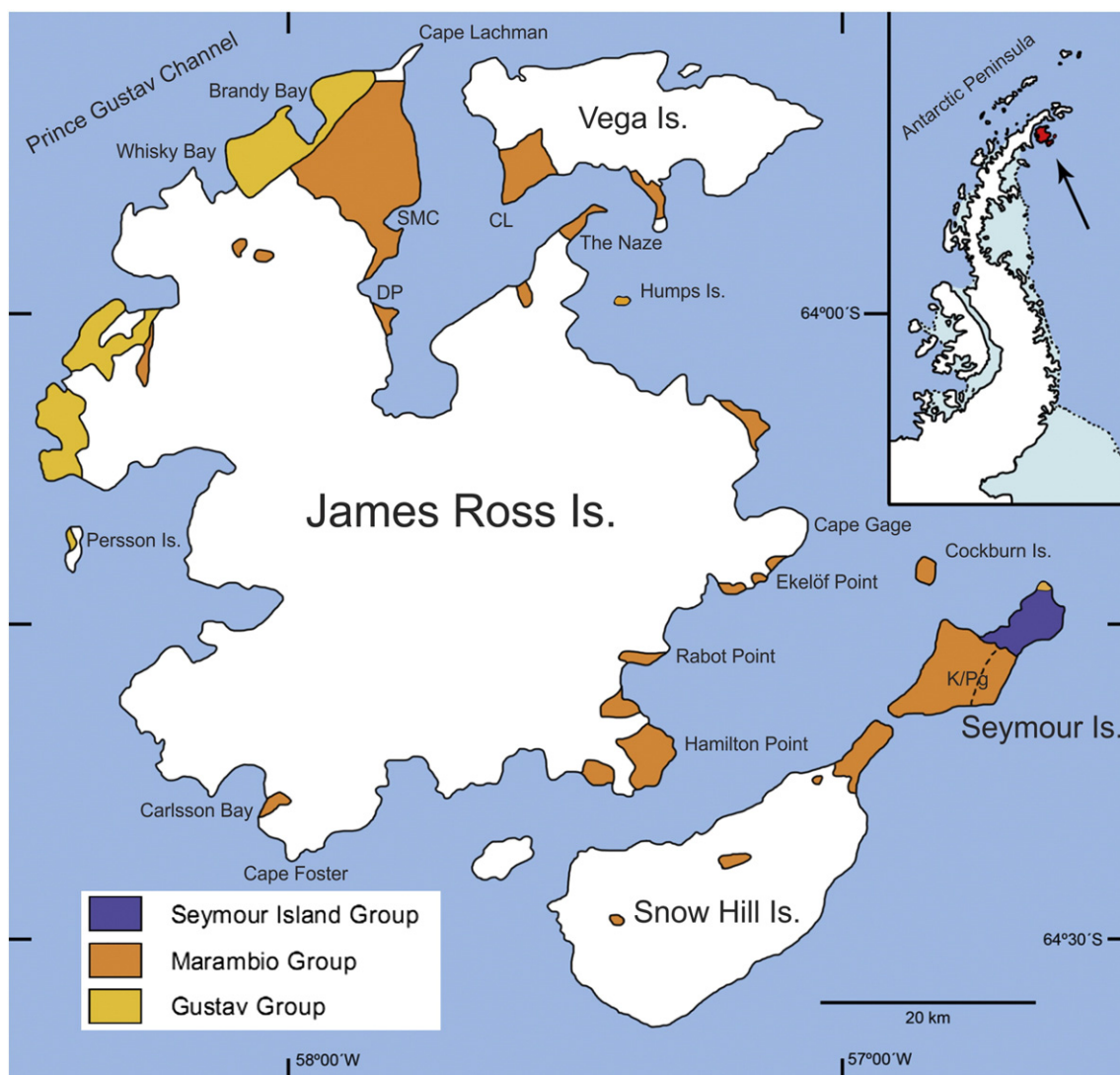


Fig. 1. Schematic geological map of the James Ross Basin, Weddell Sea, north-eastern Antarctic Peninsula. White areas are either the James Ross Island Volcanic Group or snow/ice cover. Locality key: DP, Dreadnought Point; BB, Brandy Bay; CL, Cape Lamb; SMC, Santa Marta Cove. Position of the Cretaceous–Paleogene boundary on Seymour (= Marambio) Island indicated by the symbol K/Pg.

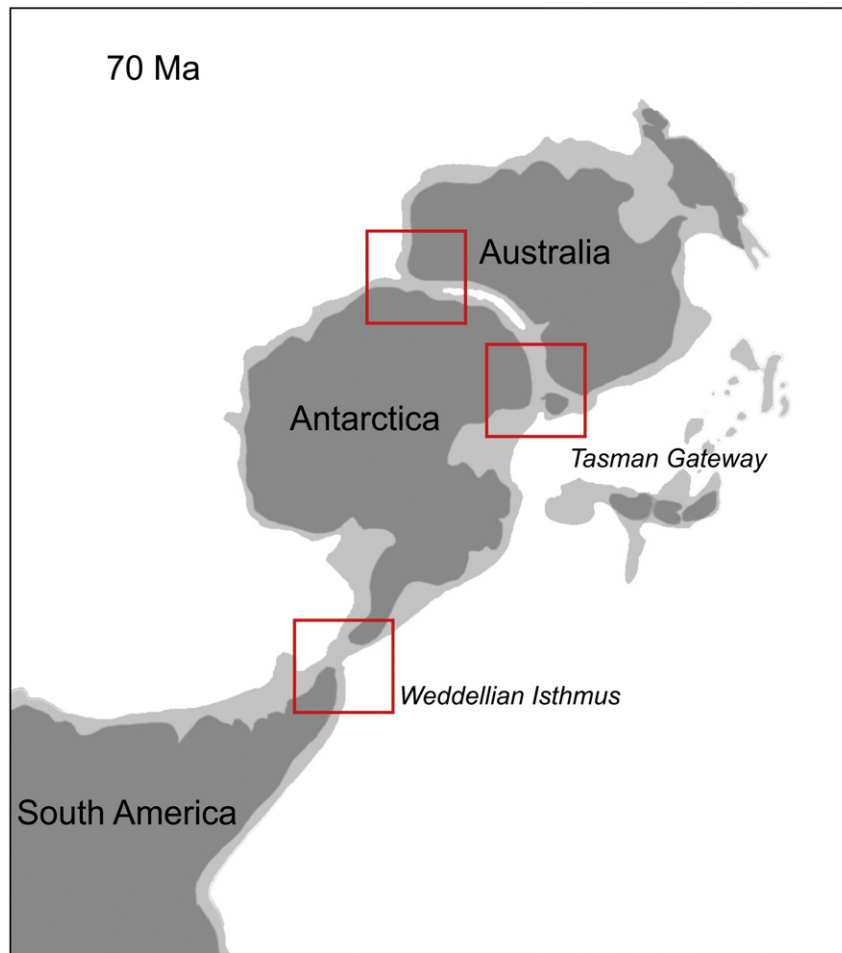


Fig. 2. Polar stereographic projection to 45°S of the southern oceans at 70 m.y. Hypothesized land connections between South America, Antarctica and Australia are indicated by red squares.

Gondwana into its present-day components and their dispersal to their present positions on the globe. The final breakup of Gondwana brought about first-order biogeographic changes for all its component terrestrial biota (Reguero and Marensi, 2010; Abello et al., 2013; Gelfo et al., 2013).

Since the Early Paleogene and for most of the Cenozoic, South America lacked connections with other major landmasses and was an island continent, leading George Gaylord Simpson (1980) to recognize the evolution and diversity of their mammals as the product of a “splendid isolation.” The evolution of South American Cenozoic terrestrial mammals was conceived, during several decades, as episodic and described as a succession of three “faunal strata” (Simpson, 1980). The oldest of them—Stratum 1 (Fig. 4), spanning roughly the Paleocene–Eocene—consists of communities dominated by the continent’s “original inhabitants” (e.g., “South American native ungulates,” marsupials, xenarthrans).

McKenna (1975) suggested the common origin of South American native ungulates, and grouped Litopterna, Astrapotheria, Notoungulata, Pyrotheria and Xenungulata, in the Meridiungulata. This division of the Grandorder Ungulata separated South American forms of other extant and extinct ungulates (McKenna and Bell, 1997).

These orders are examples of ungulate mammals that arose independently in “splendid isolation” on the island continent of South America. Like Australia, South America was isolated completely from all other continents following the breakup of Gondwana. Litopterna and Astrapotheria are native ungulates that were part of the “Stratum

1” of Simpson (1980) with Paleogene records in South America and Antarctica continents. These observations suggest that these clades possessed a wider geographic distribution than previously assumed, and that caution is necessary when attempting to establish paleobiogeographic patterns on the basis of a patchily distributed fossil record.

Litopterna and Astrapotheria were extinct groups of Cenozoic South American and Antarctic native ungulates (SAANU) which convergently resemble other Holarctic hoofed mammals in several characters. Some litopterns are convergent with “archaic ungulates” (Protolipternidae), equids (Proterotheriidae) and camelids (Macraucheniiidae). Astrapotheres resemble in some cases rhinoceros with their lophodont molars and tusk-like canines. Sparnotheriodontidae litopterns were medium- to large-sized ungulates with bunolophodont dentition. The family is known in the Late Paleocene/Early Eocene Itaboraian South American Land Mammal Age (SALMA) of Brazil, the Early Eocene Riochican and Casamayoran SALMAS of Patagonia, and the ?Middle Eocene of Mendoza, Argentina. The other taxon belongs to an Astrapotheriidae, forms with a known biochron in South America that ranges from the Late Paleocene until the Late–Early Eocene (Itaboraian SALMA) until the Middle Miocene (Laventan SALMA).

Deep-water conditions did not develop in Drake Passage until about 30 m.y. ago; the youngest estimates for deep-water circulation via Drake Passage are based on the ca. 28 m.y. onset of seafloor spreading in the west Scotia Sea region (Barker, 2001; Eagles et al., 2005; Lodolo et al., 2006). Prior to the opening of Drake Passage and the establishment

Table 1

Taxonomic list, stratigraphy, age, and references for the terrestrial and marine mammals from the Eocene La Meseta Formation of Seymour Island, James Ross Basin, Antarctic Peninsula.

Taxon	Stratigraphy (allomembers)	Age	Source
MAMMALIA			
POLYDOLOPIMORPHIA			
Fam. Prepidolopidae			
<i>Perrodolophys coquinense</i>	Cu I	Early Eocene	Goin et al. (1999)
Fam. Polydolopidae			
<i>Antarctodolops dailyi</i>	Cu I	Early Eocene	Woodburne and Zinsmeister (1984)
<i>Antarctodolops mesetaense</i>	Cu I	Early Eocene	Chornogubsky et al. (2009)
MICROBIOTHERIA			
Fam. ?Microbiotheriidae			
<i>Marambiotherium glacialis</i>	Cu I	Early Eocene	Goin et al. (1999)
Fam. Woodburnodontidae			
<i>Woodburnodon casei</i>	Cu I	Early Eocene	Goin et al. (2007)
"DIDELPHIMORPHIA" *			
Fam. Derorhynchidae			
<i>Derorhynchus minutus</i>	Cu I	Early Eocene	Goin et al. (1999)
<i>Pauladelphys juanjoii</i>	Cu I	Early Eocene	Goin et al. (1999)
Derorhynchidae, gen. et sp. indet.	Cu I	Early Eocene	Goin et al. (1999)
Family indet.			
<i>Xenostylos peninsularis</i>	Cu I	Early Eocene	Goin et al. (1999)
?MARSUPIALIA			
Family, gen. and sp. indet.	Cu I	Early Eocene	Goin et al. (1999)
GONDWANATHERIA			
Fam. Sudamericidae			
<i>Sudamerica? sp.</i>	Cu I	Early Eocene	Goin et al. (2006a)
XENARTHRA			
Tardigrada indet.	Cu I	Early Eocene	Carlini et al. (1990)
SANU			
LITOPTERNA			
Fam. Sparnotheriodontidae			
<i>Notiolofo arquinotiensis</i>	Aca, Cu I, Cu II, Sub	Early Eocene/Late Eocene	Bond et al. (2006)
ASTRAPOTHERIA			
Fam. Astrapotheriidae			
<i>Antarctodon sobrali</i>	Cu I	Early Eocene	Bond et al. (2011)
"INSECTIVORA" or DRYOLESTIDA			
gen. et sp. indet.	Cu I	Early Eocene	MacPhee et al. (2008)
MAMMALIA INCERTAE SEDIS			
gen. et sp. indet. 1	Cam	Early Eocene	Vizcaíno et al. (1997)
gen. et sp. indet. 2	Cu I	Early Eocene	Marensi et al. (1994)
CETACEA			
Fam. Basilosauridae			
<i>Zeuglodon sp.</i>	Sub	Late Eocene	Borsuk-Bialynicka (1988)
<i>Pelagiceti</i> gen. et sp. nov.	Cu I	Early Eocene	Buono et al. (2011)
MYSTICETI			
CRENATICETI			
<i>Llanocetus denticrenatus</i>	Sub	Late Eocene	Mitchell (1989)

Abbreviations: Aca, Acanthilados; Cam, Campamento; Cu I, *Cucullaea* I; Cu II, *Cucullaea* II; Sub, Submeseta.

* "Didelphimorphia" in its traditional concept and contents is not regarded as a natural group.

of the Antarctic Circumpolar Current, a land connection between South America and the Antarctic Peninsula is thought to have lasted until approximately 41 m.y. (Scher and Martin, 2006), although continental lithospheric stretching preceding the final breakup may have begun ca. 50 Ma (Livermore et al., 2005; Ghiglione et al., 2008).

This article analyzes phylogenetic and biogeographic patterns for two Paleogene SAANU, Astrapotheria and Litopterna, that inhabited both Antarctica and South America before the final breakup of these continents, within the context of major prevailing geologic and oceanographic conditions throughout the Early Paleogene to provide insights into the mechanisms that resulted in their existence on the Antarctic continent at that time.

2. Materials and methods

The cladograms of Astrapotheria and Notoungulata were taken from Bond et al. (2011) and Reguero and Prevosti (2010) respectively. Until now, no published cladistic analysis has focused on a detailed phylogeny of the Sparnotheriodontidae (Litopterna). We built a data matrix with 34 dental characters and 7 taxa (Appendices 1 and 2). All the

characters were considered as unordered and equally weighted. The tree was rooted with: *Tiuculaenus minutus* (Kollpaniinae) because as this taxon is part of one of the oldest "archaic ungulates" that appear in South American fossil record and with close affinities with North American taxa (de Muizon and Cifelli, 2000), and *Didolodus multicuspis* which is thought to be close to the ancestry of sparnotheriodontid litoptern (Gelfo, 2006). The analysis was performed using TNT software (Goloboff et al., 2003) under the implicit enumeration option.

The incompleteness of the fossil record means that minimum divergence times must be established through the calculation of "ghost lineages" (Norell, 1996), which extend the temporal range of a lineage prior to its appearance in the fossil record based on information from its sister lineage. We identify "ghost lineages" following the methodology proposed by previous authors, considering the age of first appearance of each terminal taxon in the fossil record as the only relevant temporal information (Pol et al., 2004).

The sequence of South American Land Mammal "Ages" (SALMAs) referred to in the present study essentially follows Gelfo et al. (2009a). Geologic time units follow current standards (Gradstein et al., 2012).



Fig. 3. Reconstruction of four endemic Early Eocene terrestrial mammals from Seymour (= Marambio) Island, Antarctic Peninsula. Above on the trees: on the left log, *Antarctodolops daily* (Marsupialia, Polydolopidae); on the right log, *Marambiotherium glaciaris* (Marsupialia, Microbiotheriidae). Underground: on the left, *Antarctodon sobrali* (Astrapotheria, Astrapotheriidae). On the right, *Notiolofos arquinotiensis* (Litopterna, Sparnotheriodontidae). They represent an Early Paleogene endemic radiation in West Antarctica in the final breakup of Gondwana. Artist: Jorge González.

3. Discussion

3.1. Weddellian Isthmus: Danian paleogeographic reconstruction (Fig. 5)

Recent reconstruction of the Early Paleogene paleogeography of the Antarctic Peninsula and South America show a continuous land-mass extending from South America to Antarctica (Lawver et al., 2011). No major marine barriers were present between South America and Antarctica at this time. However, the hypothesized existence in the Miocene of an “ancestral South Sandwich arc” east of the Drake Passage that could have served as an early proximal barrier to deep Pacific–Atlantic flow was suggested by Barker (2001) and Dalziel et al. (2013).

Here we propose to name “Weddellian Isthmus” this continuous, although probably narrow land-mass, extending from South America to the Antarctic Peninsula after the original name erected by Zinsmeister (1979, 1982) for his high latitude Weddellian Biogeographic Province. This province was defined on the basis of marine molluscan, echinoderm

and arthropod faunas as a cool temperate, shallow water region which extended from southern South America (Magellan Region in Chile, and Patagonia in Argentina), along the Antarctic Peninsula and West Antarctica, to New Zealand, Tasmania and southeastern Australia. Later, Case (1988) expanded this concept with the inclusion of terrestrial plants and mammals. This province existed from the Late Cretaceous through the Eocene when Australia, Antarctica, and southernmost South America were in proximity (Zinsmeister, 1979, 1982; Woodburne and Zinsmeister, 1984) although not necessarily connected by land.

Among the tectonic events having an impact on ocean circulation, the opening of Drake Passage is thought to have contributed to the world-wide climatic cooling at the Eocene–Oligocene boundary, and to the subsequent thermal isolation of Antarctica. Today, Drake Passage is the narrowest part of a circum-Antarctic seaway whose presence is necessary for the existence of the Antarctic Circumpolar Current (ACC). The opening of this passage enabled the development of the ACC, which thermally isolated Antarctica through reduced southward heat transport (e.g., Toggweiler and Bjornsson, 2000; Sijp and England, 2004). The existence of a barrier east of the Drake Passage until the late Miocene (10 Ma) had been suggested by Barker (2001), pointing out that its influence on the developing of a deep ACC.

3.1.1. Scotia arc and the opening of Drake Passage

Opening of Drake Passage gateway between the Pacific and Atlantic oceans has been linked in various ways to Cenozoic climate changes. The beginning of the period of extension in Drake Passage region is estimated to have occurred around 50 Ma through crustal stretching followed by sea-floor spreading at the west Scotia Ridge (Livermore et al., 2005). From the oceanic floor of Drake Passage, the largest remaining uncertainties in understanding this process is the timing and mechanism of the opening of the central Scotia Sea.

Geophysical and paleontological data indicate that West Antarctica and southern South America disconnected probably before the end of the Early Eocene and, by the mid–Late Eocene, the continents were already separated by a several hundred kilometer-wide marine gap. Unfortunately, age estimates for the onset of a seaway through Drake Passage between the Antarctic Peninsula and southern South America range from Middle Eocene (Livermore et al., 2005; Scher and Martin, 2006) to Oligocene (Lawver and Gahagan, 2003) or Early Miocene (Barker, 2001), complicating interpretations of the relation between ocean circulation and global cooling. Others have recently argued that the marine connection may have started during the opening of small basins in the embryonic west Scotia Sea, during a period of extension preceding sea-floor spreading (Lawver and Gahagan, 1998, 2003; Eagles et al., 2006; Eagles, 2007). Evidence for the Middle Eocene (?) opening of two of these small depocenters, the Protector and Dove basins, indicates the possible creation of a seaway in the southern part of Drake Passage starting after a major increase in the separation rate between South America and Antarctica ca. 50 m.y. (Livermore et al., 2005; Eagles et al., 2006; Fig. 2).

In contrast to interpretations of latest Paleogene or Early Neogene development of the ACC, several lines of evidence point towards a peak of plate tectonic activity in the Scotia Arc and Drake Passage preceding the Oi-1 glaciation: (1) water-mass provenance data from the Atlantic sector of the Southern Ocean are consistent with Late Eocene penetration of Pacific water through Drake Passage (Scher and Martin, 2006); (2) Lagabrielle et al. (2009) report a phase of rapid deepening of seaways in that region allowing flows of cold, proto-ACC waters, between 37 and 34 m.y.; (3) micropaleontological analysis of a core from Bruce Bank in the Scotia Sea shows that it was lying between 800 m and 2000 m depth around 45 m.y., and that subsidence was active at that time in this region, confirming the early opening of Drake Passage at least to depths greater than 800 m (Eagles et al., 2006); (4) the accumulation of lower Eocene strata in southernmost South America has been interpreted as evidence of coeval crustal thinning (Ghiglione et al.,

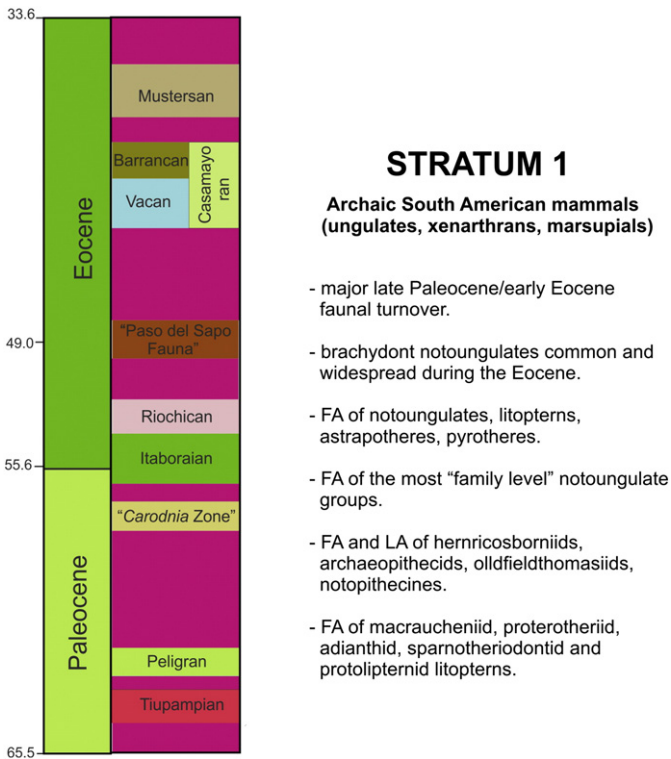


Fig. 4. Simpson's "Stratum 1" (Paleocene–Eocene) of mammalian faunal succession in South America highlighting major events in SAANU evolution. It is calibrated to the time-scale on the left, but the events listed for the stratum are not. FA and LA represent first appearance and last appearance, respectively.

2008); (5) thermochronometric data from the Fuegian Andes of the northern Scotia Arc suggest rapid tectonic exhumation from 60 to 30 m.y. (Barbeau et al., 2009); and (6) the development of deep marine

connection in the proto-Drake Passage region is proposed by Eagles et al. (2006) who suggest the onset of seafloor spreading in the Dove Basin during the period 41–34.7 m.y., moving to Protector Basin between 34 m.y. and 30 m.y.. Therefore, the onset of the period of extension in this region is estimated to have occurred around 50 m.y. (Early Eocene) through crustal stretching before true seafloor spreading between the tips of South America and Antarctica (Livermore et al., 2005; Eagles et al., 2006; Livermore et al., 2007).

3.1.2. Early Paleogene terrestrial faunas from Patagonia related to the final breakup of Gondwana

There are few Paleocene localities in Patagonia with gondwanic terrestrial faunas. Paleocene mammals from Patagonia are represented by a variety of nontherian forms (i.e., no marsupials or placentals) that record a radiation known as the Gondwanan Episode for South America (Pascual, 2006; Pascual and Ortiz-Jaureguizar, 2007). Considering the oldest South American mammalian records and faunas (i.e. *Cocatherium*, Tiupampian and Peligran SALMAs, *Carodnia* Zone) the only groups that are also present in the Antarctic continent are gondwanatherian (Goin et al., 2006a) and a dryolestoid mammal (unpublished data). Dryolestoids are known from several Cretaceous Laurasian and South American outcrops (Rougier et al., 2011, Fig. 5). Gondwanatherians in contrast show a wide Southern Hemisphere distribution during the Late Cretaceous being found in South America (Gurovich, 2005), Madagascar (Krause et al., 1997) and India (Prasad et al., 2007). Considering this previous temporal and geographic distribution, the presence of these lineages in the Eocene of West Antarctica could be interpreted as a relictual ancient distribution (Reguero et al., 2013) and not very informative about the final Gondwana breakup. In contrast, the Eocene Antarctic record of sparnotheriodontids and astrapotheriids, which were not present in the Mesozoic, suggest that they (or their more recent common ancestor) migrated from South America to West Antarctica before the breakup of both land masses. This fact highlights the importance of therian mammals in order to make paleobiogeographic inferences.

The marsupial *Cocatherium* is the oldest therian known in the Cenozoic of South America and comes from marine strata of the Early

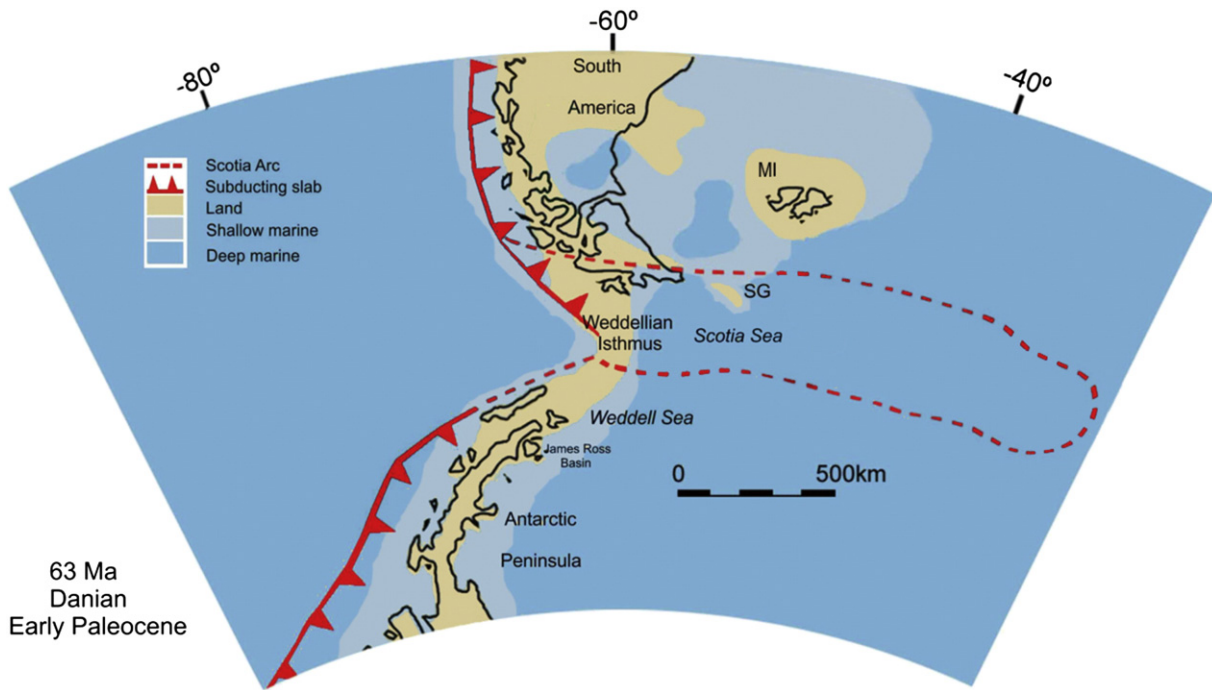


Fig. 5. Polar stereographic plot of the reconstructed land connection (Weddellian Isthmus) between South America and the Antarctic Peninsula at Early Paleocene (Danian), the time of the Punta Peligro fauna. The subduction zone is shown with the teeth pointing in the direction of the down going slab. Abbreviations: MI, Malvinas (= Falkland) Islands; SG, South Georgia Island. Graphic and caption modified from Spalletti and Franzese (2007) and Lawver et al. (2011).

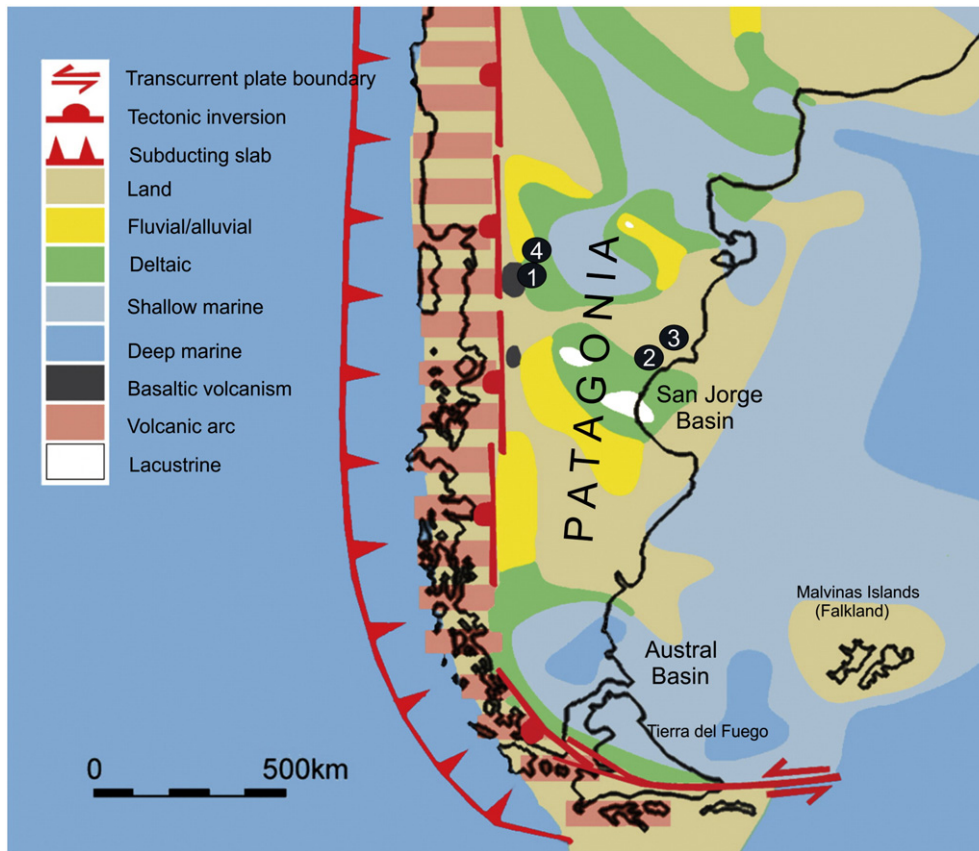


Fig. 6. Reconstruction of Patagonia (Early Paleocene). Modified from Spalletti and Franzese (2007). Black circles numbered indicate the Early Paleogene Gondwanan and post Gondwanan localities in the Chubut province, Argentina with terrestrial fauna discussed in the text: 1. Grenier Farm, Paso del Sapo, 2. Punta Peligro, 3. Bajo Palangana and 4. Laguna Fría, Paso del Sapo.

Paleocene (Danian) Lefipán Formation, Chubut province, Patagonia (Goin et al., 2006b) (Fig. 6). *Cocatherium* is the only terrestrial mammal recovered from this horizon until now to date.

The oldest Paleogene Patagonian terrestrial fauna comes from Punta Peligro, Chubut province (Fig. 6). It was recovered from the Banco Negro Inferior of the Salamanca Formation in the eastern part of the basin, and designated as Peligran SALMA (Bonaparte et al., 1993) which ranges from about 63.2 to 63.8 Ma (Clyde et al., 2014) and is somewhat younger than the Tiupampan SALMA defined in Bolivia (Gelfo et al., 2009a and literature therein).

This fauna includes Anura, Chelonia and Crocodylia (Bonaparte et al., 1993), as well as a unique assemblage of mammals derived from Gondwanan and Laurasian lineages (Bonaparte et al., 1993; Gelfo et al., 2009a). Only 10 mammal taxa are known, and the Gondwanan lineages include the gondwanathere *Sudamerica ameghinoi*; the dryolestoid *Peligrotherium tropicalis*, and *Monotrematum sudamericanum*, a monotreme related to the Australian ornithorhynchid taxa (Pascual et al., 1992a,b). The seven therians comprise four marsupials and three placentals.

Punta Peligro marsupials are represented by two Didelphimorphia?, *Derorhynchus* and *Didelphopsis* and two new genera of Polydolopidae and Bonapartheriidae (Bond et al., 1995; Pascual and Ortiz-Jaureguizar, 2007). Eutherians are represented by the notonychopid *Requisia vidmari*, the oldest known litoptern (Bonaparte and Morales, 1997). Three archaic ungulates, represented by the didlodontid *Escribania chubutensis*, *Escribania talonicuspis* and *Raulvaccia peligrensis*, complete the therian lineages of this fauna.

The “Carodnia faunal zone” (Simpson, 1935a) (~57 m.y.) originally defined for Bajo de La Palangana, in the Chubut coast (Fig. 6) is poorly represented and studied, and includes only the Xenungulata *Carodnia*

feruglioi. Another xenungulate (i.e. *Notoetayoa gargantuai*) probably comes from this biozone (Gelfo et al., 2008). Simpson (1935a) suggests that “Carodnia zone” could be approximately equivalent or probably somewhat older than the lower level from Cerro Redondo. No common taxa were found in this last locality, which contains an undetermined ?borhyaenid, the proterotheriid litoptern *Wainka tshotse* (Bond et al., 1995) and *Amphidolops yapa*, a polydolopid marsupial (see Chornogubsky, 2010). The “Carodnian” fauna is the oldest from Patagonia that was known to Simpson (1935a,b). Vertebrates from these horizons are apparently restricted to the Peñas Coloradas Formation in the San Jorge Basin, but there is no clear evidence that they could represent a new biochronologic unit (Bond et al., 1995; Gelfo et al., 2009a).

Near Laguna del Hunco and the town of Paso del Sapo in the Chubut province, Argentina (Fig. 6) there are local mammalian faunas dated as Early–Middle Eocene (~49–47 m.y.), filling the temporal gap between the faunas of the Río Chico Group and those of the Sarmiento Formation in Patagonia and providing a record of probable rainforest vertebrates (Gosses, 2006; Tejedor et al., 2009). Paleobotanical and palynological evidence from inferred contemporary localities nearby indicate subtropical environments characterized by warm and probably moderately humid climate (Wilf et al., 2005, 2009).

This fauna (Laguna Fría, Paso del Sapo) shows several affinities with the Antarctic fauna of La Meseta, since they share several lineages at least at family level (e.g. Polydolopidae, Derorhynchidae, Sparnotheriodontidae; Gelfo et al., 2009b). Tejedor et al. (2009) correlated biochronologically the La Meseta terrestrial fauna with the western Patagonian Paso del Sapo fauna, suggesting a continental extension of the biogeographic Weddellian Province as far north as central western Patagonia.

3.2. Paleobiogeographic implications of the presence of SAANUs in West Antarctica

3.2.1. Evidence from stratigraphically calibrated phylogenetic analyses of *Litopterna* and *Astrapotheria*

Two biogeographic hypotheses about the presence of SAANUs in the Early Eocene of the Antarctic Peninsula can be proposed: 1) as the land connection (Weddellian Isthmus) was maintained between South America and Antarctica until the Late Paleocene, it is quite possible that the Early Eocene record of SAANUs from Antarctica may possibly represent an Early Paleogene dispersal event; and 2) SAANUs had a pan-Gondwanan distribution prior to the fragmentation of Gondwana landmass.

The calibration of the phylogenetic trees which contain fossil taxa with the chronostratigraphic information (geologic age) provides information about the minimal ages of divergence for each node of the tree.

Phylogenies of Sparnotheriodontidae and Astrapotheria are presented here, evaluating the time of diversification of selected nodes. The incompleteness of the fossil record means that minimum divergence times must be established through the calculation of “ghost lineages” (Norell, 1996), which extend the temporal range of a lineage prior to its appearance in the fossil record based on information from its sister lineage.

The stratigraphic calibration of *Litopterna* (Sparnotheriodontidae) and Astrapotheria (Astrapotheriidae) phylogenies here presented evidences the minimum age at which their common ancestor was present on both Antarctica and South America continents.

The Antarctic sparnotheriodontid *Notiolofofos* (Bond et al., 2006), previously referred to *Victorlemoinea* (Bond et al., 1990), is endemic from Antarctica, and has close affinities with an undescribed taxon from Patagonia (Goin et al., 2000). The Patagonian *Victorlemoinea labyrinthica* is a species relatively common in the Riochican (Early Eocene) and Vacan faunas of Patagonia. The oldest known representative of the Sparnotheriodontidae, *Victorlemoinea prototypica*, is from the Late Paleocene/Early Eocene Itaboraia fauna from Brazil, whereas the youngest record in Patagonia is *Sparnotheriodon epsilonoides* from the Vacan age (Middle Eocene). Another species probably of Middle Eocene age is *Phoradiadius divoertensis* from Divisadero Largo Formation, in west Argentina, Mendoza. *Notiolofofos* is known from deposits dating to ~54 m.y. (Acanitlados Allomember; Mörs et al., 2013), whereas the rest of the La Meseta fauna dates between 49 and 52 m.y. (Reguero et al., 2013). The body size of the *Notiolofofos* has been estimated in ca. 395–400 kg indicating that it was the largest herbivore living in Antarctica in the Early Eocene (Vizcaíno et al., 1998). The stratigraphic calibration of litoptern Sparnotheriodontidae phylogeny here presented (Fig. 7), indicates the Late Paleocene as the minimum age at which their common ancestor was present on Antarctica and South America.

The Bond et al. (2011) phylogenetic analysis of Astrapotheria places the Antarctic *Antarctodon* as the sister taxon of a clade including South American species of Astrapotheriidae: *Albertogaudrya* (Eocene, Patagonia), *Scaglia* (Eocene, Patagonia), *Astraponotus* (Late Eocene, Patagonia), *Maddenia* (Oligocene, Patagonia), *Parastrapotherium* (Oligocene to Early Miocene, Patagonia), *Astrapotherium* (Early to Middle Miocene, Patagonia and Chile) and *Granastrapotherium* (Middle Miocene, Colombia).

The oldest known records of Astrapotheria come from Late Paleocene beds of South America. Several taxa are known from this age: *Trigonostylops wortmani* from Patagonia, *Tetragonostylops apthomasi* from Itaboraia, Brazil, *Eoastrapostylops riolorensis* from the Northwest of Argentina and *Shecenia ctirneru* (not included in the analysis of Bond et al., 2011). The relatively limited Paleocene fossil record of South America does not reveal by itself the presence of a radiation during this time. However, when the phylogenetic hypotheses obtained in the parsimony analysis are calibrated against the geological age of fossil taxa, a basal astrapothere radiation is revealed by the presence of two

ghost lineages that must have originated in the Late Paleocene (in addition to *Eoastrapostylops* and *Tetragonostylops* recorded for this age; Fig. 8). These two ghost lineages extend the minimum age of origin of the lineages leading to *Antarctodon sobrali* and the clade formed by advanced astrapotheres (Astrapotheriidae) back to the Late Paleocene. All these forms appear later in the fossil record, in Early Eocene beds. Therefore, the calibrated phylogenies extend the evolutionary origins of these lineages at least 5 m.y. before their first appearance in the fossil record.

The most unexpected circumstance in the Eocene La Meseta Formation is the apparent lack of notoungulates and other ungulate groups such as archaic ungulates (e.g. Kollpaniinae, Didolodontidae) and non-sparnotheriodontid *Litopterna*. Notoungulata were the most diverse (morphologically as well as taxonomically) and successful of the “South American native ungulate” groups. One of the most important radiations of notoungulates in Patagonia occurred during the Late Paleocene–Early Eocene (Itaboraian SALMA).

During the Paleocene, there is no evidence of a physical barrier that could prevent dispersal events between Patagonia and the Antarctic Peninsula, or a filter in the Weddellian Isthmus that could limit the dispersion of obligate cursorial mammals. This suggests that the absence of notoungulates in the Antarctic fossil record could be due to their apparently delayed radiation in southern South America. In the Early Paleocene, notoungulates were already present in the lower latitudes of Tiupampa, Bolivia, but not in the higher latitudes of Patagonian (Gelfo et al., 2009a). Their absence from Peligran SALMA records reinforces the idea that their Patagonian radiation occurred after the final breakup of both continents. The stratigraphic calibration of Notoungulata tyotherian phylogeny here presented (Fig. 9), suggests the minimum ages at which their common ancestor were present on South America (Sparnotheriodontidae ~57 to 58 m.y., Astrapotheria ~58 to 59 m.y.).

4. Conclusions

Great insights regarding the extent and duration of the land connection between South America and Antarctica can be obtained from the SAANUs that were medium to large-bodied and inferred to have restricted to terrestrial locomotion, that were the most unlikely to have rafted, swum, or flown across expansive marine barriers. The geological/geophysical evidences for the age of the demise of the terrestrial connection between Antarctica and South America (Weddellian Isthmus) during the Early Paleogene have direct implications for the potential dispersion of terrestrial faunas. The record of Early Eocene terrestrial mammal taxa on Antarctica, i.e., SAANUs and marsupials (Abello et al., 2013; Gelfo et al., 2013) that have sister–taxon relationships to Early Eocene of South America have profound implications for the timing and sequence of Gondwanan fragmentation.

Examination of ghost lineages of astrapotheriid astrapotheres and sparnotheriodontid litopterns currently known to occur in Paleogene rocks of South America and Antarctica indicates that minimum divergence times for these taxa are in the Late Paleocene or even much earlier, thus substantially pre-dating their Early Eocene occurrences. Indeed, the minimum divergence times established from the current fossil record indicate that the lineages of large, terrestrial vertebrates represented in the Early Paleogene of West Antarctica and South America may have evolved in isolation for 5 m.y. A minimum divergence date of the Antarctic and Patagonian litopterns (57–58 m.y.) and astrapotheres (58–59 m.y.) is therefore established as at least Middle Paleocene, approximately 5–6 m.y. earlier than their documented occurrences.

One of the most important radiations of notoungulates, the most diverse (morphologically as well as taxonomically) and successful of the SAANU groups occurred during the Early Eocene in Patagonia. As we suppose that no barrier to dispersal existed between Patagonia and the Antarctic Peninsula during the Paleocene, the absence of this

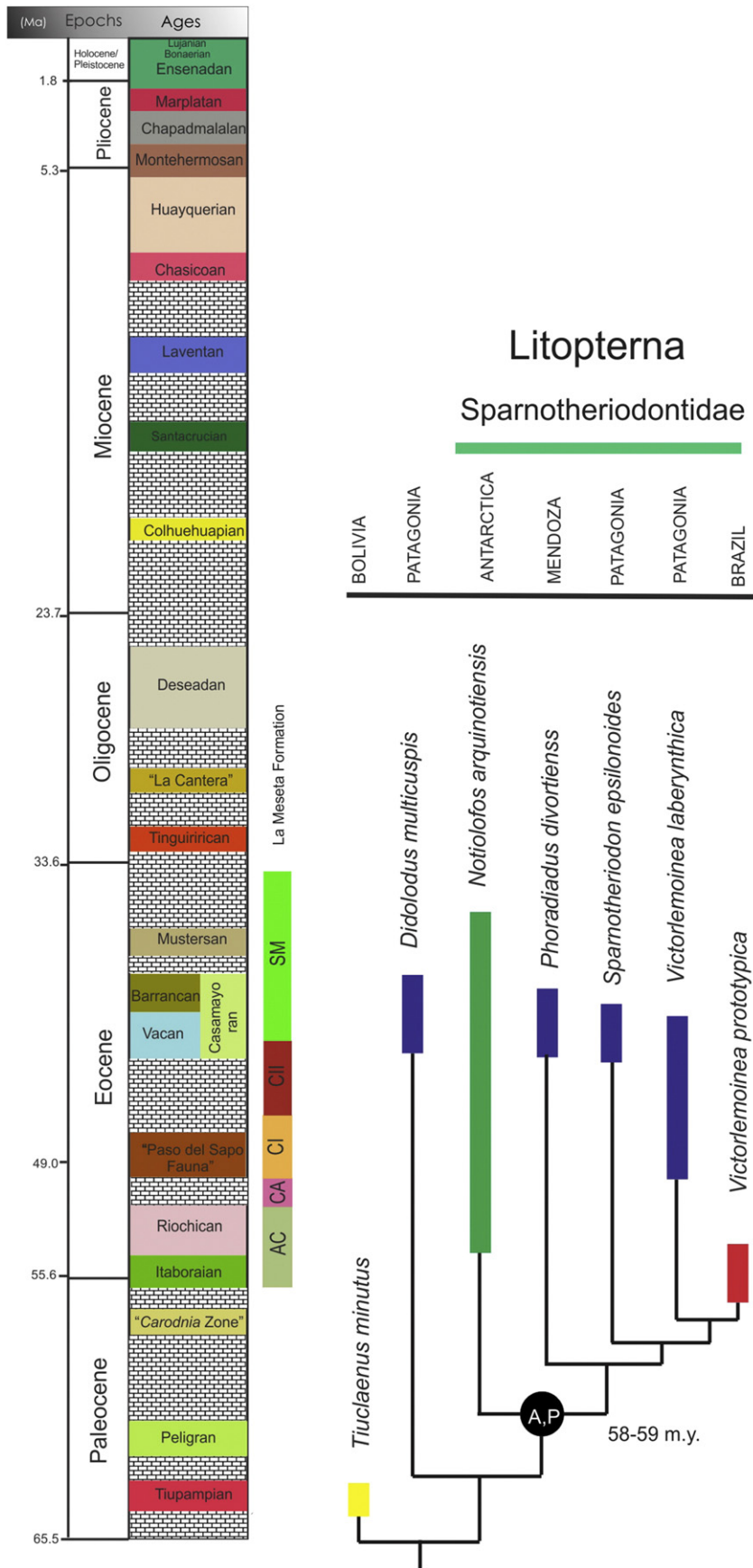


Fig. 7. Stratigraphically calibrated phylogeny and known Paleogene occurrences of Astrapotheria in Antarctica and South America. Geographic area provenance of included taxa is indicated above each terminal taxon name. Minimum estimated times that these taxa diverged from their older sister taxa (black circle) are based on ghost lineages indicated by coloured vertical lines. Phylogeny redrawn from Bond et al. (2011). A, Antarctica; P, Patagonia.

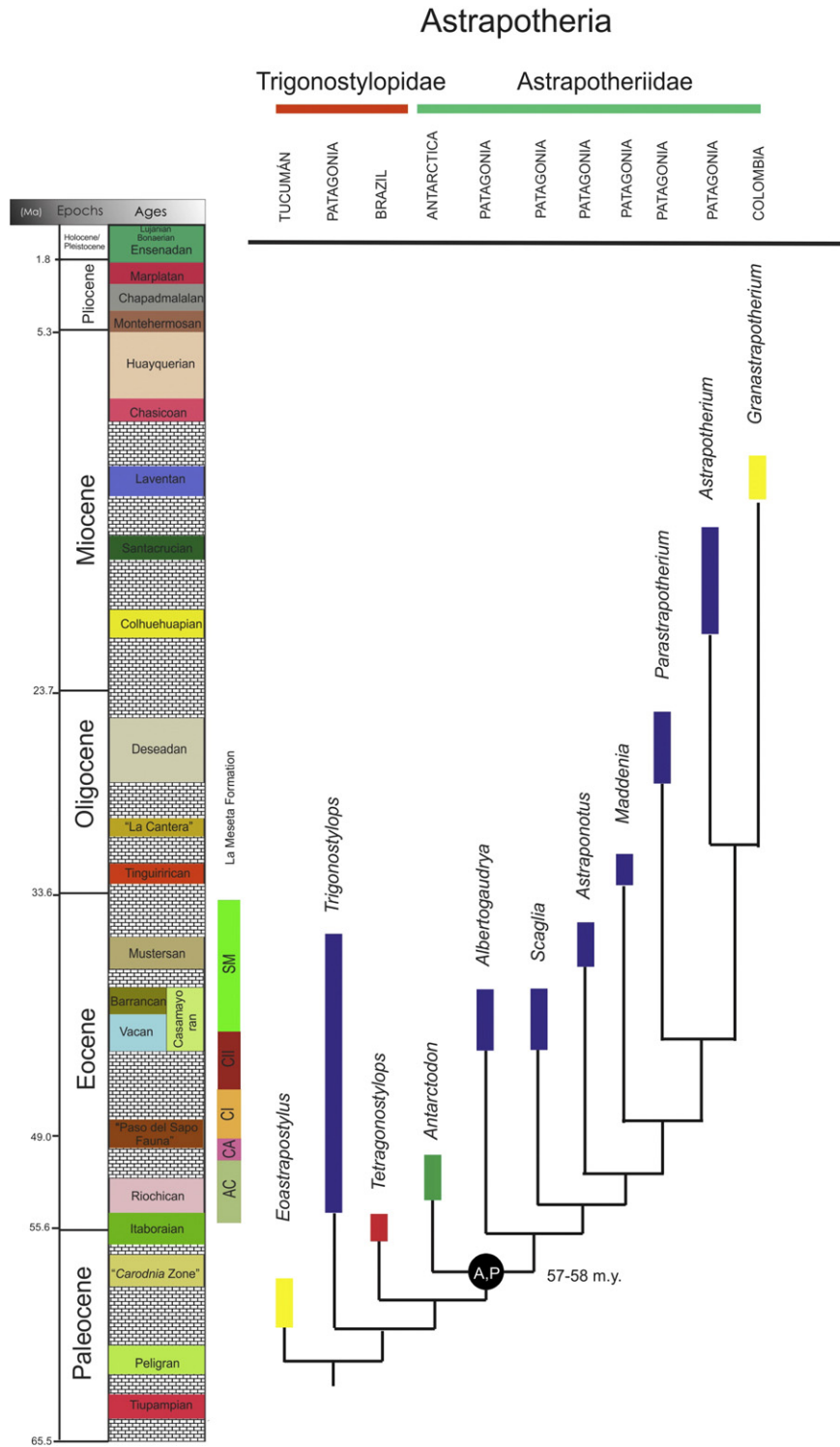


Fig. 8. Stratigraphically calibrated phylogeny and known Paleogene occurrences of Litopterna Sparnotheriodontidae in Antarctica and South America. Geographic area provenience of included taxa is indicated above each terminal taxon name. Minimum estimated times that these taxa diverged from their older sister taxa (black circle) are based on ghost lineages. A, Antarctica; P, Patagonia.

group in Antarctica could be explained by suggesting that the Early Eocene La Meseta fauna is composed only of those taxa that were present in West Antarctica before the disconnection of the Weddellian Isthmus. The stratigraphic calibration of notoungulate (Typotheria) phylogeny evidence a minimum age (~56 m.y.) at which their common ancestor was present only in South America.

Their absence from Antarctic Paleogene and Patagonian Paleocene (Peligran SALMA) records, suggests that their high latitude radiation occurred after the final breakup of both continents (~55 to 56 m.y.).

We interpret that this faunistic isolation between Antarctica and South America (Patagonia) is documented at least 25 m.y. before

Notoungulata (Typotheria)

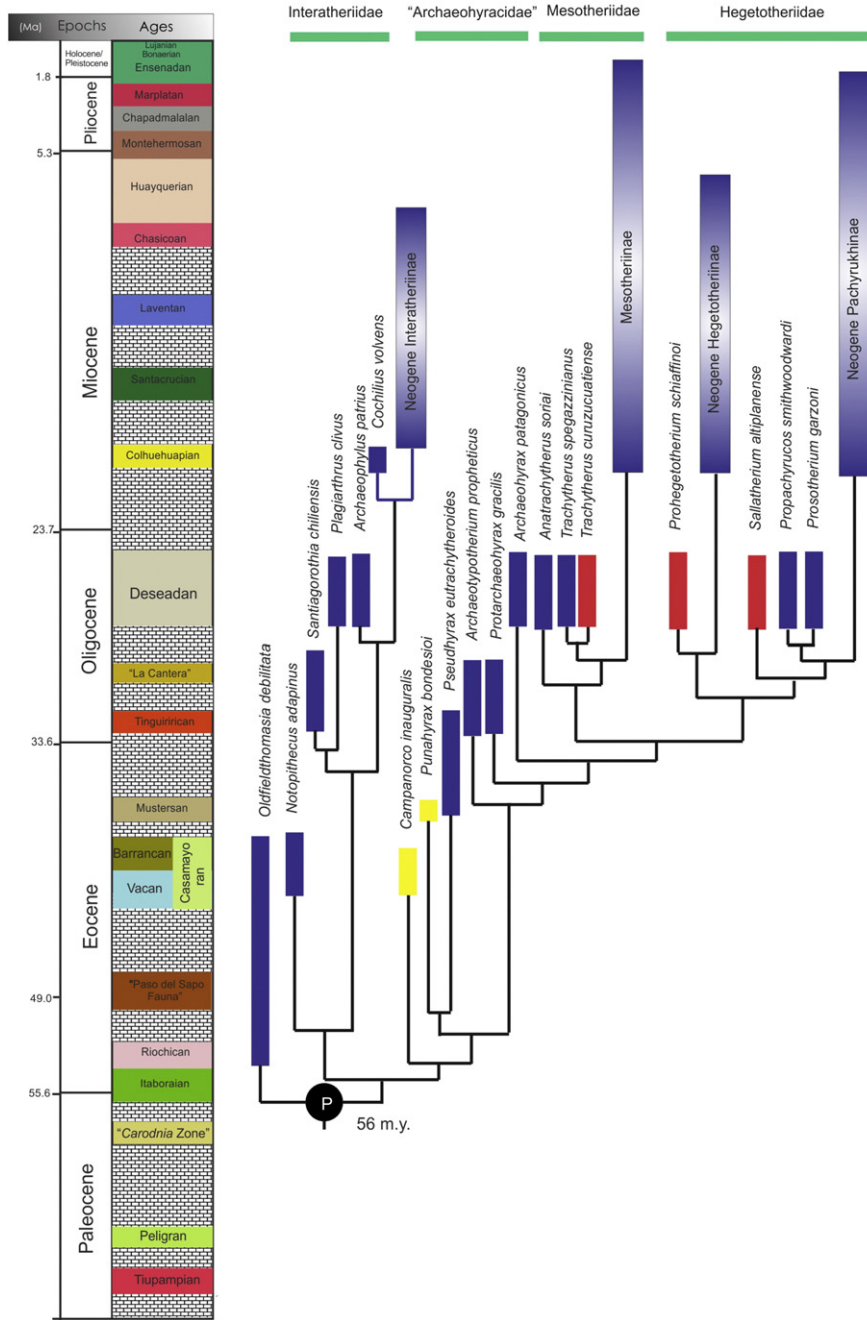


Fig. 9. Stratigraphically calibrated phylogeny and known Paleogene occurrences of Notoungulata Typotheria in South America. Geographic area provenance of included taxa is indicated above each terminal taxon name. Minimum estimated times that these taxa diverged from their older sister taxa (black circle) are based on ghost lineages. Phylogeny redrawn from Reguero and Prevosti (2010). P, Patagonia.

the existence of deep-water circulation conditions in Drake Passage (~30 m.y.) based on the onset of seafloor spreading in the west Scotia Sea region.

The conclusions drawn from the analyses of fossil SAANUs indicate that the overland dispersal route between South America and the West Antarctica through the Antarctic Peninsula closed by Late Paleocene times, many million years before the reported existence of sea-floor on Drake Passage and at least 5 m.y. before the presumed initiation of the extensional regime of that area. Considering that as a

whole, the Late Paleocene–Early Eocene was a period of warm climates and global sea-level low-stands, our hypothesis is that at the early stages of extension a wide and relatively shallow epicontinental sea developed between the Antarctic Peninsula and South America drowning the former Weddellian Isthmus and preventing the faunal interchange for the cursorial terrestrial forms.

If this is correct, then an early stage of rifting produced stretching crustal thinning and widespread subsidence during the Paleocene leading to the development of a shallow although wide

epicontinental sea. It was followed by an Eocene drifting stage with the development of discrete deep-marine basins along the southern Scotia Sea which eventually led to the opening of Drake Passage and the initiation of the ACC which in turn caused the thermal isolation of Antarctica.

By now, there are several phylogenetic inferences and fossil remains that could be used to analyze the timing of the Antarctic breakup. The presence of a late Danian monotreme in Patagonia (Pascual et al., 1992a,b) is indicative from a dispersal event from Australia through Antarctica. Considering the origin of Australian marsupials, the molecular evidence strongly support a South American origin (Nilsson et al., 2010), and, at least, Sigé et al. (2009) proposed a ~ 55-m.y. trans-Antarctic dispersal between the fauna of Chulpas, Peru, and Tingamarra fauna, Australia. Even though, this last proposal was not completely accepted because of the doubtful dating of Tingamarra and the scarcity of the remains studied (Wilf et al., 2013).

The pollen and macrofossil evidence of Eucalypteae is Early to Middle Eocene in Australia, and early Eocene in South America, which are indicative of a broader distribution that encompassed Antarctica and southern Patagonia. As for *Nothofagus*, it was suggested a Late Cretaceous origin of eucalyptes (Ladiges et al., 2003) and a later vicariance event. But, the calibrated molecular phylogenies indicate the origin of the crown group Eucalypteae is in the Paleocene to earliest Eocene (Hermsen et al., 2012 and literature therein). Thus, a post-Cretaceous origin of this group and/or range expansion of Eucalypteae over the three continents could not be discarded (Hermsen et al., 2012).

Developing a more complete floristic and faunistic fossil record from other intervals and areas (e.g., Paleocene–Eocene of Australia) will provide critical information for reconstructing the biogeographical history of the final breakup of Gondwana.

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Appendix 1. Character–taxon data matrix used for the phylogenetic analysis of Sparnotheriodontidae, the results of which are shown in Fig. 7.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
<i>Tiuclaenus minutus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	?	0	0	0	0	0	0	3	0	0	0	0
<i>Didolodus multicuspis</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1
<i>Notiolofofus arquinotiensis</i>	?	0	1	1	1	0	2	1	1	2	1	1	2	2	2	2	2	0	0	2	2	?	?	?	2	1	1	1	2	1	3	2	1	2	2
<i>Sparnotheriodon epsilonoides</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	1	1	?	1	3	1	1	2	
<i>Victorlemoinea prototypica</i>	2	1	1	1	1	1	2	1	1	1	1	2	1	2	2	2	2	0	3	3	2	2	2	2	2	1	1	1	2	1	2	1	1	2	
<i>Victorlemoinea labyrinthica</i>	2	?	1	1	1	0	1	?	1	?	1	1	2	1	2	2	2	0	?	?	2	?	?	?	1	1	1	?	1	2	?	1	2	2	
<i>Phoradiadus divortiensis</i>	2	0	1	1	1	0	1	2	1	0	1	1	2	1	2	2	2	0	3	3	2	1	1	2	1	1	1	2	1	0	0	1	2	2	

Appendix 2. Character state scores for Sparnotheriodontidae used in phylogenetic analyses.

Characters:

- M1-2 hypocone: (0) absent; (1) present distal to the protocone; (2) present distolabial to the protocone.
- M3 hypocone: (0) absent; (1) present.
- M1-2 metaconule: (0) bunoid; (1) lofoid.
- M3 metaconule: (0) bunoid; (1) lofoid.
- M1-2 entocrist: (0) absent; (1) present.
- M3 entocrist: (0) absent; (1) present.
- M1-2 paraconule: (0) bunoid; (1) reduced as part of the anterolophid; (2) absent.
- M3 paraconule: (0) bunoid; (1) absent; (2) reduced as part of the anterolophid.
- M1-2 protocone: (0) preprotocristid and postprotocristid pointing to the paracone and metacone; (1) with entocristida contacting the hypocone and without postprotocrista.
- M3 protocone: (0) preprotocristid and postprotocristid pointing to the paracone and metacone; (1) with entocristida contacting the hypocone and without postprotocrista; (2) projected to the anterolophid without entocristida or postprotocrista.
- Paracone and metacone molars: (0) bunodont; (1) selenodont.
- Linguo-metaconular crista: (0) absent; (1) present.
- M1-2 protostile: (0) absent; (1) bunoid interrupting the continuity of the anterior cingula; (2) high and in continuity with the anterior cingula.
- M3 Protostile: (0) absent; (1) lofoid, high and in continuity with the anterior cingula lofoid; (2) join to the protocone.
- Mesostile: (0) absent; (1) bunoid; (2) as part of the ectoloph.
- Parastile: (0) absent; (1) bunoid; (2) as part of the ectoloph.
- Metastile: (0) absent; (1) bunoid; (2) as part of the ectoloph.
- Preparaconular crista: (0) absent; (1) present and distinguish from the paraconule but as part of the anterolophid.
- Posparaconular crista: (0) absent; (1) present.
- Premetaconular crista: (0) absent; (1) present; (2) unified with the lophoid metaconule and non-differentiable; (3) unified with the lophid metaconule but differentiable.
- Postmetaconular crista: (0) absent; (1) present; (2) unified with the lophoid metaconule and non-differentiable; (3) unified with the lophid metaconule but differentiable.
- Metacone of the P4: (0) absent; (1) bunoid and almost fused with paraconid; (2) separated from the paracone and lophoid.
- Metaconule of P4: (0) absent; (1) bunoid; (2) lofoid.
- Paraconule of P4: (0) absent; (1) bunoid; (2) lofoid.
- m1-3 paraconid: (0) present; (1) almost fused with the metaconid; (2) separated from the metaconid but integrated to a paralophid.
- m1-3 paracristid: (0) present and concave distally; (1) part of the paralophid.
- Lingual side of the trigonid in m1-3: (0) close; (1) with metaflexid.
- Protocristid in m1-3: (0) almost transversal with V shape; (1) integrated to an oblique lophid.
- Metaconid in m1-3: (0) well differentiated, bunoid; (1) integrated to a lophid; (2) integrated to a lophid with their distal part rounded.
- Hypoconid in m1-3: (0) well differentiated, bunoid; (1) integrated to a lophid.

31. Entonconid in m1-2: (0) well differentiated, bunoid; (1) small and integrated to the hypolophid; (2) large and integrated to the hypolophid; (3) reduced and associated to the postcrisid and entocristid.
32. Entoconid in m3: (0) well differentiated, bunoid; (1) small and integrated to a lophid; (2) large and integrated to a lophid.
33. Hipoconulid in m1-3: (0) well differentiated, bunoid; (1) absent and fused to a lophid.
34. Cristid obliqua: (0) well differentiated; (1) well differentiated with mesoconid; (2) forming part of a lophid.

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