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Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships

Marcelo A. Reguero[a,*], Sergio A. Marenssi[b], Sergio N. Santillana[b]

[a] *Departamento Científico de Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina*
[b] *Instituto Antártico Argentino, Cerrito 1248, Buenos Aires 1010, Argentina*

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Abstract

The Eocene of Seymour Island contains the only association of Cenozoic plants and land vertebrates known from anywhere in Antarctica and lies at about latitude 63° south. The late Early to latest Eocene La Meseta Formation fills an incised valley and comprises sediments representing deltaic, estuarine and very shallow marine environments. The Paleogene sequence in southern South America (Patagonia) and the Antarctic Peninsula reveals floristically distinct periods (late Paleocene, early and middle Eocene and latest Eocene), based largely on leaf assemblages. The late Paleocene Cross Valley flora (Seymour Island) contains ferns and other elements suggesting a much warmer climate than at this latitude today. The Middle Eocene Fossil Hill (South Shetland Islands) and the Río Turbio (Santa Cruz Province, southern Patagonia) floras have a mixture of both Neotropical and Antarctic elements. The La Meseta paleoflora is distinctive in having a predominance of Antarctic taxa especially *Nothofagus*, podocarps, and araucarian conifers in the Eocene deciduous and evergreen forests. This suggests a cooling trend during the Eocene of Antarctica with mid- to late Eocene seasonal, cool-temperate, rainy climates and latitudinal and altitudinal gradients. The Seymour Island La Meseta Fauna (*Cucullaea* Allomember, middle Eocene) contains at least 10 mammal taxa, predominantly tiny marsupials (mostly endemic and new taxa). The endemism of these marsupials suggests the existence of some form of isolating barrier (climatic and/or geographic) during the Eocene. Faunal similarity between the La Meseta Fauna and the fauna assigned to the Riochican (late Paleocene) South American Land Mammal Age of Patagonia strongly suggests that the former derived from the latter. The occurrence on Seymour Island of sudamericids, that had become extinct in South America in the Paleocene, also indicates that isolation may have allowed extended survival of this Gondwanan group in the Eocene of Antarctica and the factors that caused their extinction did not affect this continent. Global warming and intercontinental dispersal have been major influences on the timing and magnitude of terrestrial biotic change in the late Paleocene and early Eocene epochs. The faunistic evidence indicates that the La Meseta mammalian fauna derived from late Paleocene/early Eocene Riochican/Vacan

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Abbreviations: DPV, Departamento Científico de Paleontología Vertebrados, Museo de La Plata; IAA, Instituto Antártico Argentino, Buenos Aires; RV, University of California at Riverside, CA; SALMA, South American Land Mammal Age; LMF, La Meseta Fauna

* Corresponding author. Fax: +54-21-425-7527.

E-mail addresses: regui@museo.fcnym.unlp.edu.ar (M.A. Reguero), smarenssi@dna.gov.ar (S.A. Marenssi), ssantillana@dna.gov.ar (S.N. Santillana).

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faunas. The dispersal and vicariance events may have occurred during the onset of the climatic optimum of the Cenozoic (late Paleocene–early Eocene) when major regressive events are recorded either in the northern Antarctic Peninsula and southernmost Patagonia (between 58.5 and 56.5 Ma). The absence of notoungulates in the La Meseta fauna is noteworthy. We speculate that the notoungulates could have passed into Antarctica during the latest part of the Paleocene when the environmental conditions were warmer, and then became extinct at the onset of the climatic deterioration during the early Eocene.

Keywords: Cenozoic; Eocene; fauna; flora; Antarctica; Patagonia; biogeography

1. Introduction

Reconstructing the sequence of terrestrial ecosystems through time is frequently frustrated mainly by the inadequacies of the fossil record. Seymour (Marambio) Island (Fig. 1) contains the only Cenozoic land vertebrate fauna known in Antarctica, except for the avian tracks from King George Island (Covacevich and Rich, 1982), and represents the southernmost part of the distribution of some Paleogene South American land mammal lineages. The recovery of a moderately varied, medial Eocene land vertebrate fauna from the northern portion of the island rekindled interest in this area after the discovery of the first land mammal in Antarctica (Woodburne and Zinsmeister, 1982, 1984). This was especially important because paleogeographic reconstructions (based on paleomagnetic data collected on the continent itself) of the Antarctic Peninsula during the Eocene indicate a paleolatitude as far south as perhaps 63° (Lawver et al., 1992) (Fig. 2). Concerted efforts between 1988 and 1996 resulted in the discovery of terrestrial vertebrates and plants from several different stratigraphic levels (10 localities from four different stratigraphic horizons) within the Cross Valley and La Meseta formations (Fig. 2); these range from upper Paleocene to upper Eocene (Marenssi et al., 1994; Dingle et al., 1998). This biota contains more than 30 taxa of terrestrial plants and vertebrates. Surface prospecting and dry sieving of the sediment during 5 yr of careful fieldwork recovered land vertebrates at different localities and horizons. Among these vertebrates, the mammals suggest close biogeographic links with Paleogene faunas of Patagonia (Bond et al., 1993; Marenssi et al., 1994; Reguero et al., 1998; Goin et al., 2000).

The La Meseta Fauna (here termed LMF) from the *Cucullaea* I Allomember of the La Meseta Formation (Fig. 2) is unusual in being dominated by large sparnotheriodontid ungulates and small polydolopine marsupials (Reguero et al., 1998). This is not the case in the Paleogene fossil record of Patagonia. The high proportion of endemic taxa (mainly tiny marsupials) within the Antarctic fauna, together with relicts such as prepidolopid and derorhynchid marsupials, gives it a very distinctive southern appearance, indicating that some form of isolating barrier – climatic, geographic or topographic – existed prior to the deposition of the mammal-bearing horizon. Several types of environmental factors could result from the high latitude, of which temperature may be the most important. The relatively low temperatures of the Antarctic regions during the early Paleocene and again in the late Eocene (Dingle and Lavelle, 1998a,b; Dingle et al., 1998) (Fig. 4) seem to have been matched by the development of a characteristic biota (Marenssi et al., 1994).

In this paper we present paleofloristic and faunistic data supporting the existence of a high-latitude and -altitude land biota with differences from the contemporaneous faunas of Patagonia. The latest possible time for mammal dispersal into Antarctica is also suggested.

2. Paleogene Antarctic Peninsula paleoenvironments: sources of evidence

2.1. Sedimentology

The Antarctic continent now consists of two major parts: East Antarctica, a large stable block that has existed relatively intact for hundreds of

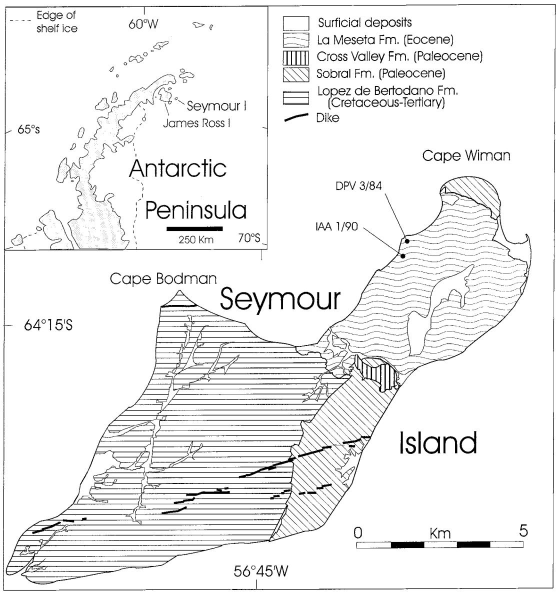


Fig. 1. Map showing fossil localities at Seymour Island, Antarctic Peninsula, with the IAA and DPV mammal-bearing localities cited in the text.

millions of years, and West Antarctica, an assemblage of smaller blocks that have been moving relative to one another and to East Antarctica during the last 230 Myr: Marie Byrd Land, Thurston Island, Ellsworth-Whitmore Mountains, and the Antarctic Peninsula

The Antarctic Peninsula is predominantly an ensialic Mesozoic–Cenozoic magmatic arc related to subduction of the proto-Pacific and Pacific Ocean floors (Pankhurst, 1982; Storey and Garrett, 1985). The Transantarctic Mountains, which separate the West Antarctic rift system from the stable shield of East Antarctica, are the largest mountains developed adjacent to the rift (3500 km long and 4500 m high).

The James Ross Basin (Del Valle et al., 1992) is located in the Weddell Sea, adjacent to the northern part of the Antarctic Peninsula. Paleogene beds of the James Ross Basin are exclusively marine and are only exposed on Seymour and the nearby Cockburn Islands (Fig. 1). They are comprised of shallow marine shelf deposits of the uppermost López de Bertodano and Sobral Formations (early Paleocene) and the incised valley systems of the Cross Valley (late Paleocene) and La Meseta (late Early to late Eocene) formations. Main regressive periods are documented by the unconformities at the base of the Cross Valley and La Meseta Formations. They may be eustatic or tectonic in origin, or a combination of the two (Sadler, 1988; Marenssi, 1995; Marenssi et al., 1998b).

The stratigraphic position of the land mammal bearing localities are shown in Fig. 2. Herein we follow the stratigraphic terminology used by Marenssi et al. (1998b).

The La Meseta Formation (Elliot and Trautman, 1982; Marenssi et al., 1998b) fills an incised valley and is comprised of deltaic, estuarine, and shallow marine deposits containing both marine and terrestrial fossils (Marenssi, 1995; Marenssi et al., 1998a). Paleoenvironmental reconstructions indicate that the La Meseta Formation accumulated at the seaward end of an incised valley during an overall rise in sea level (Marenssi, 1995; Marenssi et al., 1998a). Recent studies of the geometric relationships in the La Meseta Formation

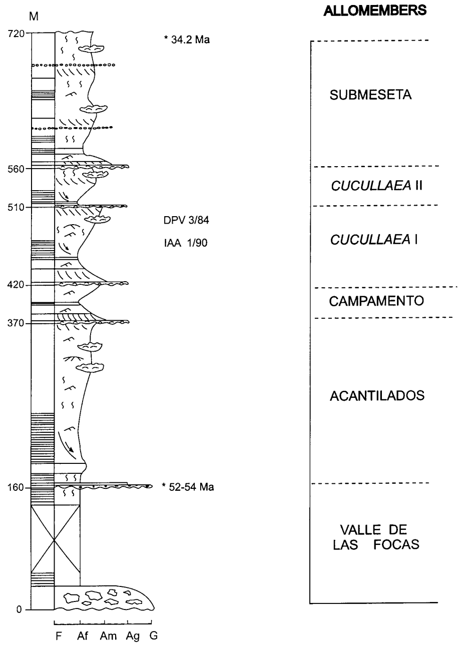


Fig. 2. Stratigraphic section of the La Meseta Formation, Seymour Island showing the mammal-bearing levels and localities.

(Sadler, 1988; Marenssi, 1995; Marenssi et al., 1998b) show that the steep erosional boundaries are the margins of a large channel some 7 km in width that originated farther west. The head of the La Meseta incised valley was placed almost 60 km to the northwest, at the toe of the Antarctic Peninsula (Stilwell and Zinsmeister, 1992).

Sedimentary environments such as tidal channels and flats, an estuary mouth platform, and a mid-estuary (Marenssi, 1995; Marenssi et al., 1998a) formed a coastal area of low relief. In contrast, far inland to the west, the Antarctic Peninsula was a highland, mountainous area characterized by volcanoes sporadically active since the Mesozoic.

Although paleogeographical interpretations indicate that terrestrial facies had to be present nearby to the west, they are not yet known from Seymour Island; hence, all terrestrial fossils reported to date were transported into marine settings.

Land-derived fossils were concentrated in paralic and shallow marine environments after some transport. However, the presence of leaves, tree trunks, and a flower suggest a nearby forested terrain (Gandolfo et al., 1998a,b; Torres et al., 1994; Doktor et al., 1996).

Provenance studies on sandstones of the La Meseta Formation demonstrate that the sediments came from the west–northwest, the source rocks being those cropping out on the Antarctic Peninsula (Marenssi, 1995; Marenssi et al., 1999; Net and Marenssi, 1999). Additionally, paleocurrent measurements confirm the location of the source area (Marenssi, 1995). Therefore, the source area of the sediments, leaves and trunks was the northern Antarctic Peninsula, a magmatic arc that underwent uplift during the Cretaceous and Cenozoic (Elliot, 1988). This cordillera supported forests in a range of habitats from coastal to alpine. Seymour Island lies on the eastern (back-arc) margin of the Antarctic Peninsula.

Leaves are associated with marine mollusks, and tree trunks frequently are densely bored by *Teredolites*, indicating extended submersion in the water–sediment interface before burial. Also, teeth and bones of land vertebrates are associated with an abundant marine macrofauna. Consequently, they are always recovered from a thanatocenosis (Marenssi, 1995), along with an abundant marine fauna.

Geochemistry and clay mineralogy of sedimentary rocks from Seymour Island were used to interpret the climatic evolution of the northern Antarctic Peninsula area since the Late Cretaceous (Dingle and Lavelle, 1998a,b). A cool period is indicated during the early Paleocene before the climatic optimum of the Cenozoic (late Paleocene–early Eocene) followed by a climatic deterioration from very warm, non-seasonally wet conditions (early middle Eocene) to a latest Eocene cold, frost-prone and relatively dry stage (Dingle et al., 1998).

In the marine realm, a cool-temperate sea was proposed to exist based on the Paleogene invertebrate fauna (Zinsmeister, 1982). Meanwhile, stable isotope studies carried out on molluscan macrofossils from the La Meseta Formation suggest a cooling trend during the Eocene, with water temperatures between 7.9 and 11.7°C (Gazdzicki et al., 1992; Ditchfield et al., 1994).

2.2. Plant fossils

Eocene floras at different sites of the Antarctic Peninsula (King George and Seymour islands) suggest the presence of densely forested habitats that were widely developed along the Peninsula at that time (Case, 1988; Gandolfo et al., 1998a,b) (Fig. 3).

On the Pacific side of the Antarctic Peninsula, Haomin (1994) described a mixture of Antarctic and Neotropical floral elements in the Fossil Hill Formation (King George Island; Fig. 3), suggesting mean temperatures between 10 and 14°C for the early–middle Eocene of the South Shetland Islands.

The plant megafossils recovered from three Paleogene localities on Seymour Island suggest that the terrestrial environments changed drastically from late Paleocene through late Eocene. The late Paleocene flora recovered from the Cross Valley Formation (Gothan, 1908; Dusén, 1908) has been interpreted to represent a paratropical forest growing in a warm, rainy climate (Gandolfo et al., 1998a). Askin (1992, 1997) reported that the Late

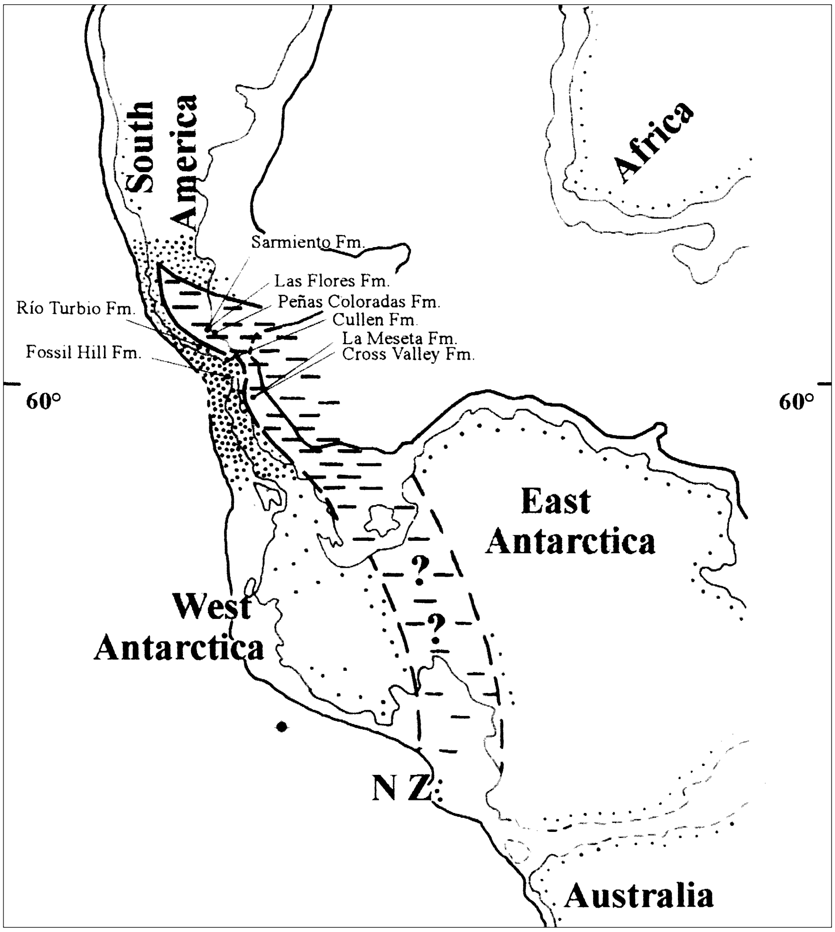


Fig. 3. Late Cretaceous (~75 Ma) paleogeographic reconstruction of southern continents showing the location of the Paleocene and Eocene units discussed in the text. Compiled from distributional data after Zinsmeister (1982); Woodburne and Zinsmeister (1984); Lawver et al. (1992). Abbreviations: NZ, New Zealand.

Cretaceous and Paleocene plant communities were dominated by conifer rainforest in the area of Seymour Island.

The La Meseta Formation (late-early Eocene–late Eocene) has yielded fossil plant material from most of its stratigraphic column (Dusén, 1908; Cranwell, 1959; Askin and Fleming, 1982; Case, 1988; Torres et al., 1994; Brea, 1996; Brea and Zuccol, 1996; Doktor et al., 1996; Askin, 1995, 1997; Gandolfo et al., 1998a,b). Megaflora has been collected from all but the lowest 120 m (Case, 1988; Doktor et al., 1996; Gandolfo et al., 1998a). The flower (Gandolfo et al., 1998b), some tree trunks (Torres et al., 1994; Brea, 1998), and most of the leaves (Gandolfo et al., 1998a) are preserved in fine-grained heterolithic facies of tidal origin, especially from the middle part of the formation (middle Eocene). Some other tree trunks and a few leaves come from coarse-grained channel lags of the underlying late early Eocene Acantilados and medial Eocene Campamento allomembers. Carbonaceous detritus, spores, and pollen are frequent throughout the fine-grained facies.

The late-early Eocene flora of locality University of California at Riverside, CA, USA (RV)-8425 (Acantilados Allomember) is dominated by a large-leafed species of *Nothofagus* suggesting "... a

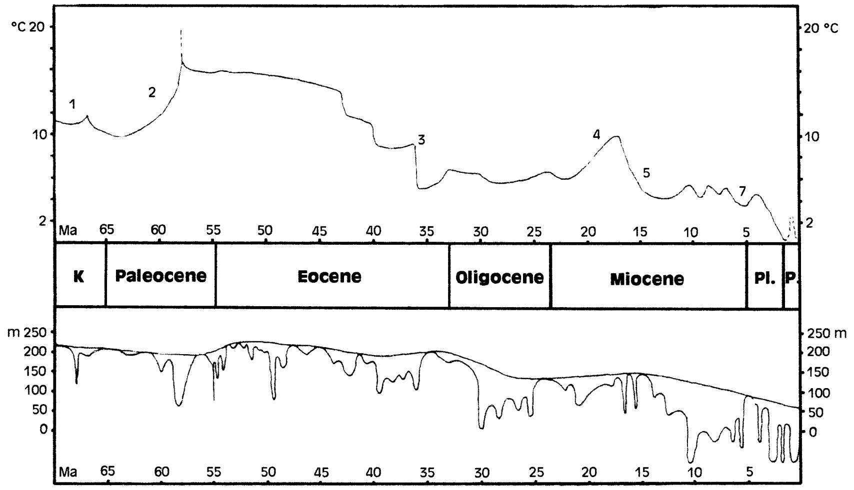


Fig. 4. Temperature and sea level at high southern latitudes during the Cenozoic. The temperature curve is for surface waters. Time scale is according to Berggren et al. (1995). Sea-level pattern is after Haq et al. (1987).

situation of ameliorating climatic conditions...” (Case, 1988: 525). This paleoflora also contains two species of ferns. Doktor et al. (1996) also described a late-early Eocene paleoflora from the La Meseta Formation. Podocarpaceous (*Dacrycarpus? tertiarius*), Araucariaceae (*Araucaria nathorsti*), Nothofagaceae (*Nothofagus* sp.), Proteaceae (*Knightiophyllum andreae*), among others leaves, were found at National Academy of Science, Warsaw, Poland, ZPAL 9 locality (Fig. 2).

Case (1988) described the first megaflora from the La Meseta Formation, indicating a dominance of the genus *Nothofagus*. Gandolfo et al. (1998a,b) recognized this genus and reported the presence of the families Dilleniaceae, Myricaceae, Myrtaceae, Lauraceae, and Grossulariaceae, as well. All but Lauraceae belong to the Antarctic flora of Romero (1986). Based on morphological characters of 88 specimens collected from three localities in the middle part of the La Meseta Formation (*Cucullaea* I Allomember), Gandolfo et al. (1998a) described the forests as mixed mesophytic, indicating a seasonal cool-temperate rainy climate. More than 300 samples representing fossil foliage referred to *Tetracera patagonica* (Dilleniaceae), *Hydrangeiphyllum affine* (Hydrangeaceae), and the families Nothofagaceae, Betulaceae, Myrtaceae, Myricaceae, Lauraceae, and Grossulariaceae were recovered at locality Departamento Científico de Paleontología Vertebrados, Museo de La Plata (DPV) 3/84 (Gandolfo et al., 1998a,b). Based on this flora, the annual mean paleotemperature was calculated to be 11–13°C, whereas the mean of the coldest month might vary between −3 and 2°C. The paleoflora also suggests that spring and summer were rainy, and that the freezing season might last several months. These data agree with the general climatic deterioration that occurred in the rest of Antarctica at the end of the Eocene (Dingle and Lavelle, 1998a,b; Dingle et al., 1998).

Gothan (1908), Torres et al. (1994), and Brea (1996, 1998) studied fossil wood from the La Meseta Formation. Several coniferous and dicotyledonous (*Nothofagus*) woods were identified from the middle part (*Cucullaea* I Allomember) of this unit (Torres et al., 1994), dated as middle Eocene (Marenssi et al., 1994). They have narrow, but regularly spaced and well-marked growth rings, typical of slow-growing trees with vegetative periods corresponding to seasonal climate changes. Torres et al. (1994) described a total of six taxa of fossil woods having affinities with extant trees that grow in cold-temperate rainforest areas of southern South America (the Valdivian and Magellanic forests). Well-defined growth rings within fossil wood samples from Seymour Island indicate that this climate was markedly seasonal.

Temperate to cool-temperate evergreen conifer/broad-leaf forest exists today in southern South America (between 37 and 55°S). Rainfall in this area is very high, mainly in summer and spring seasons, with an average precipitation from 1000–3000 mm/yr and freezing temperatures can prevail during several months of the year. These forests currently contain the richest biota of the sub-Antarctic dominion.

In recent years, a growing body of information has been accumulated about the Paleogene climate of the Antarctic Peninsula (see Dingle and Lavelle, 1998b) (Fig. 4). Paleofloral data sets show that the middle–late Eocene was warmer than present, but not as warm as the late Paleocene (Cross Valley Formation) through early Eocene (Acantilados Allomember, La Meseta Formation). Paleoflora from the middle part of the La Meseta Formation (RV-8200, Instituto Antártico Argentino, Buenos Aires IAA 1/90, and DPV 3/84 = C/88, from *Cucullaea* I Allomember) indicate a drop in temperature (Case, 1988; Gandolfo et al., 1998a) with respect to lower levels of the sequence.

Nothofagus is considered to be of critical importance as an indicator of paleoclimate. *Nothofagus* is the predominant angiosperm taxon in each of the three paleofloras from the La Meseta Formation mentioned above. Gandolfo et al. (1998a) reported *Nothofagus serrulata* and two indeterminate species of the same genus from the late-early Eocene Acantilados Allomember (A/88). The former species is now restricted to southern South America, where it grows in a cool-temperate climate. *N. serrulata* extends from southern Chile (Carmen Silva, Loreto, and Brush Lake Formations) and Argentina (Río Turbio, Río Guillermo, and Ñirihuau formations) to the southern shores of Tierra del Fuego Province (Cullen Formation), and thus represents a closer geographical approach to Antarctica than is achieved by other South American species (Fig. 3).

Romero (1986), based on a morphological analysis, determined the climate and phytogeography of the Paleogene floras of Patagonia. This author stated that, during the Paleocene and early Eocene, Patagonia's forests were wet and paratropical, with mean temperatures between 20 and 25°C, but in the middle Eocene (Río Turbio Formation) the forests were subtropical with a mixture of Neotropical and Antarctic elements ('Pa-

Table 1
Taxonomic list (families), stratigraphy, and references for the land vertebrates from the Eocene of Seymour Island, Antarctic Peninsula

Taxa	Stratigraphy	References
Marsupialia		
Polydolopidae	A. *Cucullaea* I	Woodburne and Zinsmeister, 1984; Case et al., 1988; Goin et al., 1995; Goin and Carlini, 1995; Goin et al., 1999
Microbiotheriidae	A. *Cucullaea* I	Goin et al., 1999
Derorhynchidae	A. *Cucullaea* I	Goin et al., 1999
Prepidolopidae	A. *Cucullaea* I	Goin et al., 1999
Gondwanatheria		
Sudamericidae	A. *Cucullaea* I	This paper
Xenarthra		
Tardigrada indet	A. *Cucullaea* I	Marenssi et al., 1994; Vizcaíno and Scillato Yané, 1995
?Litopterna		
Sparnotheriodontidae	A.*Cucullaea* I and A. Submeseta	Bond et al., 1990; Marenssi et al., 1994; Vizcaíno et al., 1997
Astrapotheria		
Trigonostylopidae	A. *Cucullaea* I	Bond et al., 1990; Hooker, 1992; Marenssi et al., 1994
Ratitae	A. Submeseta	Tambussi et al., 1994
?Phorusrhacoid	A. Submeseta	Case et al., 1987
Falconidae	A. *Cucullaea* I	Tambussi et al., 1995

A. stands for Allomember

leoflora Mixta'). At the same time, the La Meseta paleoflora had a predominance of Antarctic elements, suggesting a colder climate and a latitudinal gradient with respect to the paleoflora of the Río Turbio Formation (51°35′S, 72°10′W, Santa Cruz Province, Argentina). During the Eocene gramineous phytoliths became more abundant (Spalletti and Mazzoni, 1978), suggesting that grassland environments began to be prominent in middle latitudes (ca. 45°S). The absence of crocodiles and boid snakes after the Casamayoran South American Land Mammal Age (SALMA) suggests a climatic deterioration at that time in Patagonia.

2.3. Mammal fossils

The known diversity of one of the mammal-bearing horizons of the La Meseta Formation (IAA 1/90) can be taken to represent essentially a single fauna (Vizcaíno et al., 1998). There are 13 reported terrestrial vertebrate taxa, 11 of which occur in a single level within the *Cucullaea* I Allomember (IAA 1/90). A taxonomic analysis of the LMF (Table 1) reveals a modest taxonomic diversity that includes three avian and seven mammalian ordinal groups (Table 2). This Eocene mammalian assemblage was probably even more diverse, because the documented diversity of the La Meseta Formation's mammals is, of course, minimal, being derived from a few sites (Fig. 2) and from small samples (less than 60 specimens).

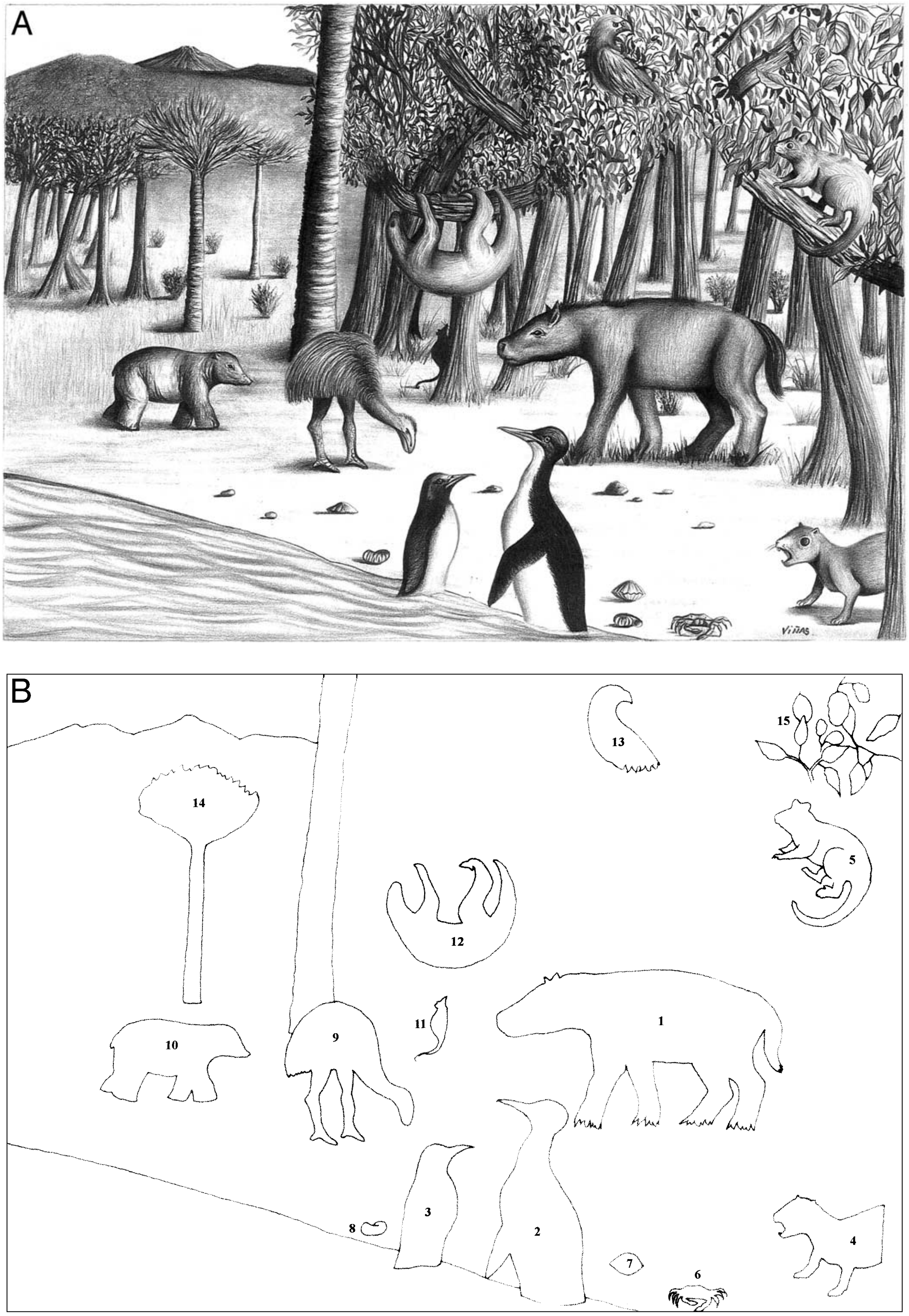
Among the terrestrial mammals, the Sparnotheriodontidae, an extinct South American ungulate group and the marsupial family Polydolopidae were the dominant taxa. They were not usually dominant elements in the much larger Paleogene associations elsewhere in South America (Reguero et al., 1998). The most abundant group in the fauna is a suite of 'opposum-like' marsupials (Goin et al., 1999).

Table 2
Taxonomic list for La Meseta terrestrial mammals, Seymour Island, Antarctica

- Polydolopimorphia
  - Family Prepidolopidae
    - *Perrodelphys coquinense*
  - Family Polydolopidae
    - *Polydolops dailyi*
    - *Polydolops seymouriensis*
    - *Polydolops* sp. nov.
- Didelphimorphia
  - Family Derorhynchidae
    - *Derorhynchus minutus*
    - *Pauladelphys juanjoi*
    - *Xenostylus peninsularis*
- Microbiotheria
  - Family Microbiotheriidae
    - *Marambiotherium glacialis*
- ?Marsupialia
  - Family indet
- Gondwanatheria
  - Family Sudamericidae
    - Gen. et sp. indet

The ungulates are represented by only two taxa (one unnamed genus) in the LMF. The Antarctic sparnotheriodontid (Fig. 5), previously referred to *Victorlemoinea* (= *Sparnotheriodon*) (Bond et al., 1990), is endemic at the generic level, and has close affinity with an undescribed new species from Patagonia (Goin et al., 2000). *Victorlemoinea labyrinthica* is a species relatively common in the Riochican and the early Casamayoran (Vacan 'subage' *sensu* Cifelli, 1985) faunas. The oldest known representative of the Sparnotheriodontidae (*Victorlemoinea prototypica*) is from the medial

Fig. 5. (A) Reconstruction of the environment and vertebrate assemblage from the middle-late Eocene of Antarctic Peninsula based on the paleontologic evidence from La Meseta Formation (*Cucullaea* I Allomember), Seymour Island. Mammals depicted here were analyzed during this study. In this reconstruction we are exercised a degree of artistic license to assemble these species together. (B) Linear sketch showing the silhouettes of the following vertebrates, invertebrates, and plants: 1: Sparnotheriodontidae gen. et sp. nov., 2: *Anthropornis nordenskjoeldi* (penguin), 3: *Delphinornis larseni* (penguin), 4: Gondwanathere sudamericid, 5: *Polydolops daily*, 6: *Lyreidus antarcticus* (crab), 7: *Cucullaea* (bivalve), 8: *Eutrephoceras* (nautiloid), 9: Ratitae bird, 10: *Trigonostylops* sp., 11: *Marambiotherium glacialis*, 12: Sloth, 13: Polyborinae indet (falconid bird), 14: *Araucaria*, and 15: *Nothofagus* (Southern beech).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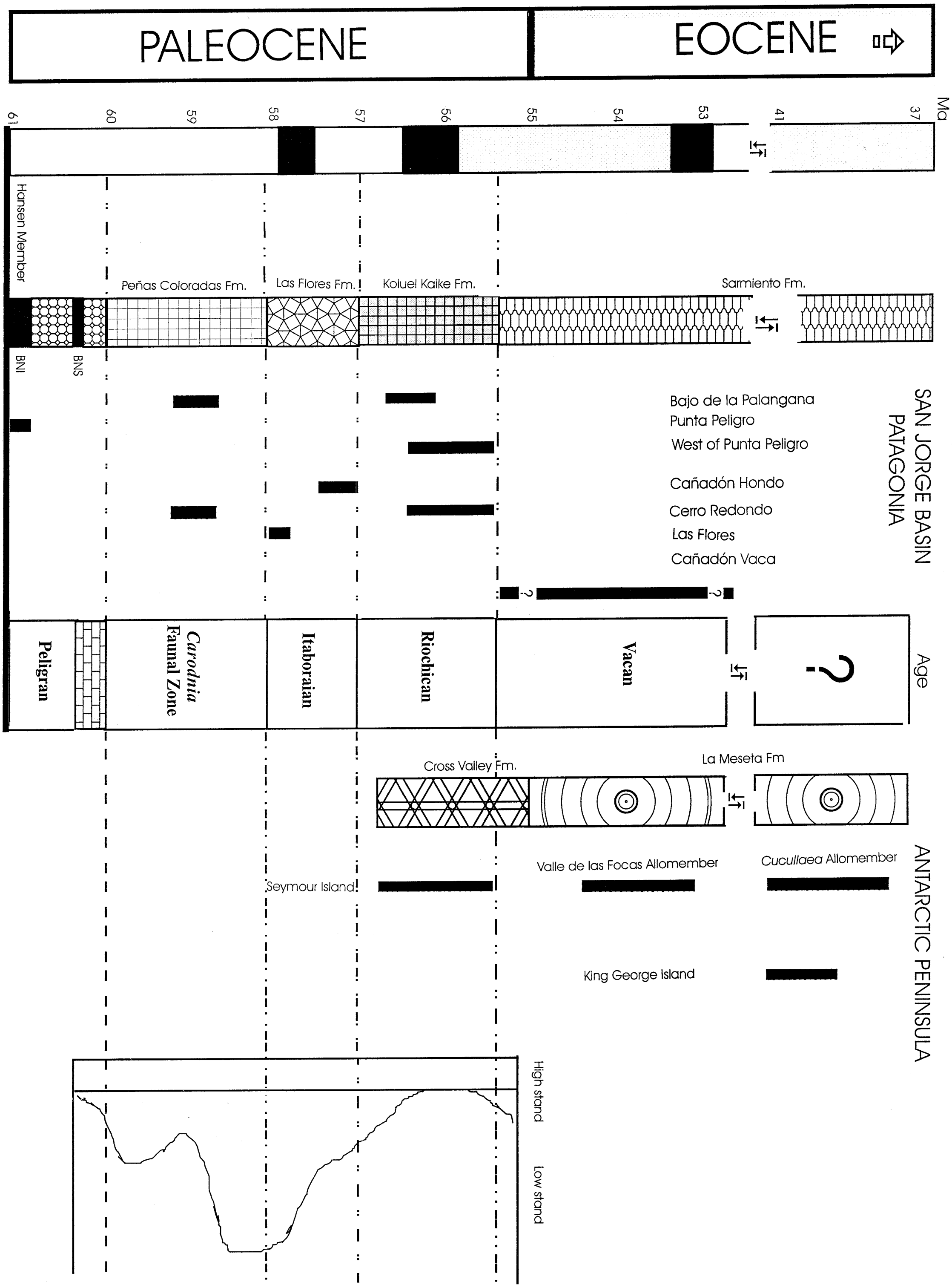
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41
37
Hansen Member
Peñas Coloradas Fm.
Las Flores Fm.
Koluel Kaike Fm.
Sarmiento Fm.
BNI
BNS
Bajo de la Palangana
Punta Peligro
West of Punta Peligro
Cañadón Hondo
Cerro Redondo
Las Flores
Cañadón Vaca
SAN JORGE BASIN
PATAGONIA
?
?
Peligran
Carodnia Faunal Zone
Itaboraian
Riochican
Vacan
?
Age
Cross Valley Fm.
La Meseta Fm
Valle de las Focas Allomember
Cucullaea Allomember
Seymour Island
King George Island
ANTARCTIC PENINSULA
High stand
Low stand

Fig. 6. Paleocene time scale according Berggren et al. (1995), including early–middle Eocene epoch, showing chronology of South American and Antarctic land biotas based on collective data and correlations made by Bond et al. (1995) and Marshall et al. (1997) and discussions in text. Vertical black bars represent timing of fossil accumulation. Abbreviations: BNS, Banco Negro Superior; BNI, Banco Negro Inferior. Sea-level pattern is after Haq et al. (1987).

Paleocene (Itaboraian SALMA) of Brazil, whereas the youngest record in Patagonia is from the Vacan 'subage' (late Paleocene–early Eocene?).

The Antarctic edentate (Fig. 5) represents the earliest unquestionable record of Pilosa in the world (Vizcaíno and Scillato Yané, 1995), and shares plesiomorphic features with the most primitive representative of the group, both Tardigrada and Vermilingua. The earliest records of Tardigrada in South America come from the Deseadan (middle Oligocene) of Patagonia and Bolivia (Hoffstetter, 1982; Engelmann, 1987). The oldest South American vermilinguan was recovered from the Miocene Colhuehuapian beds (Carlini et al., 1992) of Patagonia.

The Antarctic sudamericid (Fig. 5) represents the youngest record of the group and is very closely related to *Sudamerica ameghinoi* from the Paleocene of Punta Peligro in Patagonia, but is more derived than the latter in the microstructure of the enamel (Goin, personal communication, 2000). The Gondwanatheria is a peculiar mammal order with a widespread Gondwanan distribution in the Late Cretaceous of Patagonia (Bonaparte, 1986), Madagascar, and India (Krause et al., 1998) and in the early Paleocene of Patagonia (Scillato Yané and Pascual, 1984). These mammals bear gliriform incisors, and were the earliest South American mammals to develop hypsodont cheek teeth with thick cementum.

3. Discussion and conclusions

3.1. Comparison of LMF with Patagonian faunas

The LMF fauna shows greatest faunal resemblance with older Paleogene faunas of Patagonia (Riochican SALMA and Vacan 'subage'). The oldest faunas of the Paleogene of Patagonia range between (from the oldest to the youngest): early Paleocene Peligran, medial Paleocene '*Carodnia* faunal zone' and '*Kibenikhoria* faunal zone', late Paleocene Riochican, and the late Paleocene–early Eocene Vacan. These faunas in Patagonia are mainly known from the Golfo de San Jorge Basin, Chubut Province at ~45°S (Fig. 6). A summary of the biostratigraphic, biochronologic and faunistic data of these Patagonian faunas is provided below.

The Peligran SALMA ('Banco Negro Inferior', Salamanca Formation, Hansen Member, Tiupampian *sensu* Bond et al., 1995) (~61 Ma, Fig. 6) at Punta Peligro, Chubut, contains only six mammal taxa. Sudamericid gondwanatheres and derorhynchid marsupials are known from these levels.

Simpson's '*Carodnia* faunal zone' (~57 Ma, Fig. 6) is poorly represented and studied, and includes a ?borhyaenid indet, the polydolopid *Seumadia yapa*, the proterotheriid litoptern *Wainka tshotse*, and the pyrothere *Carodnia feruglioi*. Taxa from this horizon are apparently restricted to the Peñas Coloradas Formation in the San Jorge Basin (see Fig. 6), and they appear to represent a new biochronologic unit but present evidence is meager and is not sufficient to warrant erecting a new SALMA (Bond et al., 1995).

Simpson's '*Kibenikhoria* faunal zone' (~58.0 Ma, Itaboraian SALMA *sensu*; Bond et al., 1995; Fig. 6) includes two polydolopines, *Epidolops* and ?*Polydolops*; a primitive ?didelphoid, *Derorhynchus*; several protodidelphid marsupials, and seven families placed in four orders of ungulates. Trigonostylopidae are represented by a primitive genus (*Shecenia*). Four families of Notoungulata are recorded in this age.

The Riochican SALMA (='*Ernestokokenia* faunal zone' Simpson, 1935; ~55.5 to ~57.0 Ma; Table 3; and Fig. 6) records three families of marsupials, the Polydolopidae being one of them. Seven families of Notoungulata are recorded in this age. Sparnotheriodontidae are represented by the genus *Victorlemoinea*. The available record shows that this fauna underwent

Table 3
Taxonomic list for the Riochican mammals (Ernestokokenia faunal zone) from Patagonia, Argentina

- Polydolopimorphia
  - Family Polydolopidae
    - *Polydolops*
  - Family Prepidolopidae
    - aff. *Prepidolops*
- ?Polydolopimorphia
  - Family incertae sedis
    - *Palangania brandmayri*
- Sparassodonta
  - Family Borhyaenidae
    - ?*Nemolestes*
- Edentata
  - Family Dasypodidae
    - Gen. et sp. indet.
- Condylarthra
  - Family Didolodontidae
    - *Enneoconus*
    - *Ernestokokenia*
- Notoungulata
  - Family Henricosborniidae
    - *Henricosbornia*
    - ?*Othnielmarshia*
  - Family Isotemnidae
    - *Isotemnus*
    - ?*Pleurostylodon*
  - Family Interatheriidae
    - *Notopithecus*
  - Family Oldfieldthomasiidae
    - *Oldfieldthomasia*
    - *Maxschlosseria*
  - Family Notostylopidae
    - *Notostylops*
  - Family Archaeopithecidae
    - *Archaeopithecus*
  - Family Archaeohyracidae
    - *Eohyrax*
    - Gen. et sp. nov.
- Notoungulata incertae sedis
  - Family indet
    - *Brandmayria*
- Litopterna
  - Family Proterotheriidae
    - *Ricardolyddekeria*
    - *Anisolambda*
- ?Litopterna
  - Family Sparnotheriodontidae
    - *Victorlemoinea*
- Astrapotheria
  - Family Trigonostylopidae
    - *Trigonostylops*

notable taxonomic reorganization beginning at ~58 Ma (Marshall et al., 1997). This fauna shares four families (Polydolopidae, Prepidolopidae, Sparnotheriodontidae, and Trigonostylopidae) and two genera (*Polydolops* and *Trigonostylops*) with the LMF. During the Riochican the notoungulates became predominant, representing 44% of the taxonomic composition of the fauna (Pascual et al., 1996).

The Vacan fauna (early Casamayoran, Table 4; and Fig. 6) at Cañadón Vaca, Chubut (Sarmiento Formation) comprises archaic notoungulate families (Henricosborniidae, Isotemnidae), and the relative primitiveness of this fauna document a great faunal difference from the subsequent Barrancan 'subage' (Cifelli, 1985).

Concerning age, the Riochican contains species which have been considered to be typically Vacan, and several genera are shared (*Victorlemoinea*, *Asmithwoodwardia*), suggesting that there is almost no time between the latest Riochican (at Bajo Palangana, Chubut) and the Vacan (at Cañadón Vaca, Chubut) faunas. Based on this evidence Marshall et al. (1997) estimated the age of the Riochican/Vacan boundary at ~55.5 Ma (Fig. 6). So, the Vacan 'subage' possibly represents part of the early Eocene. Available K/Ar data from a new Vacan locality near Paso del Sapo, in the west of Chubut Province, from levels (ignimbrites) below and above the vertebrate-bearing horizon shows a great temporal range (~56 and ~43 Ma) that spans the late Paleocene and middle Eocene (Goin et al., 2000). On the other hand, the Casamayoran SALMA (that includes Vacan and Barrancan 'subages') conventionally was regarded as representing early Eocene (55–50 Ma), but recently Kay et al. (1999), on the basis of isotopic age determinations (Ar/Ar), redated the younger Barrancan 'subage' at Gran Barranca, Chubut, as late Eocene (~36 Ma.).

The Riochican and Vacan faunas (Tables 3 and 4, respectively) are characterized by the dominant presence of browser types including extremely low-crowned ungulates (83%) in several primitive lineages such as henricosborniids (Notioprogonia) and isotemnids (Toxodonta), although a few mesodont types (8%) occur in the Riochican (Pascual and Ortiz Jaureguizar, 1990). This fact supports

Table 4
Taxonomic list for the Vacan (early Casamayoran) mammals from Patagonia, Argentina

- Didelphimorphia
  - Family Didelphidae
    - *Coona*
- Microbiotheria
  - Family Microbiotheriidae
    - *Eomicrobiotherium*
- Sparassodonta
  - Family Proborhyaenidae
    - *Arminiheringia*
- Polydolopimorphia
  - Family Polydolopidae
    - *Amphidolops*
    - *Polydolops*
- Edentata
  - Family Dasypodidae
    - *Astegotherium*
    - *Meteutatus*
    - *Prostegotherium*
    - *Utaetus*
  - Family Pampatheriidae
    - *Machlydotherium*
- Condylarthra
  - Family Didolodontidae
    - *Enneoconus*
    - *Ernestokokenia*
    - *Paulogervaisia*
- Litopterna
  - Family Protolipternidae
    - *Asmithwoodwardia*
  - Family Proterotheriidae
    - *Anisolambda*
    - *Guilielmofloweria*
    - *Ricardolydekkeria*
  - Family Macraucheniidae
    - *Polymorphis*
  - Family Adianthidae
    - *Proectocion*
- ?Litopterna
  - Family Sparnotheriodontidae
    - *Victorlemoinea*
- Notopterna
  - Family Indaleciidae
    - *Adiantoides*
  - Family Amilnedwarsidae
    - *Amilnedwardsia*
    - *Rutimeyeria*
    - *Ernestohaeckelia*
- Notoungulata
  - Family Henricosborniidae
    - *Henricosbornia*
    - *Othnielmarshia*
    - *Peripantostylops*
  - Family Notostylopidae
    - *Eduardotrouessartia*
    - *Homalostylops*
    - *Notostylops*
  - Family Oldfieldthomasiidae
    - *Maxschlosseria*
  - Family Archaeopithecidae
    - *Acropithecus*
    - *Archaeopithecus*
  - Family Isotemnidae
    - *Anisotemnus*
    - *Isotemnus*
    - *Pleurostylodon*
  - Family Notohippidae
    - *Plexotemnus*
- Astrapotheria
  - Family Trigonostylopidae
    - *Trigonostylops*
  - Family Astrapotheriidae
    - *Albertogaudrya*
- Pyrotheria
  - Family Pyrotheriidae
    - *Carolozittelia*

the association of these mammals with warm and humid forested habitats in the late Paleocene. Frenguelli and Parodi (1941) reported the presence of Bambusoideae, the most primitive tribe of Gramineae in the late Paleocene of Patagonia. The paleofloral record suggests that tropical to subtropical coastal mangrove environments alternated with inland sylvan and sclerophyllous forest or savannas (Petriella and Archangelski, 1975).

3.2. Age of the La Meseta terrestrial vertebrate-bearing horizons (Cucullaea I and Submeseta allomembers)

Although the overall age of the La Meseta Formation may span much of the Eocene, the age of the vertebrate-bearing horizons (*Cucullaea* I and Submeseta allomembers) described here can be more tightly constrained. The terrestrial vertebrates recovered from the *Cucullaea* I Allomember, though numerically small, strongly suggest a middle Eocene age (Bartonian, ~37 to ~41 Ma, Woodburne and Case, 1996) or middle Eocene (Goin et al., 1999). This temporal assignment is consistent with the middle Eocene age assigned to the ichthyofauna found in the same depositional horizon (Cione and Reguero, 1994, 1998). Age data from dinoflagellates from the underlying levels (Acantilados Allomember) are consistent with a late-early Eocene age (Coccozza and Clarke, 1992). For our study, one biogenic carbonate sample was collected from shells of *Ostrea antarctica* from the lower part of the Acantilados Allomember (see Fig. 2). This sample with an ^{87}Sr/^{86}Sr ratio of 0.707709 yielded an age between 52.4 and 54.3 Ma. It yields an age consistent with its stratigraphic position and associated fauna. Sr isotope dating from the top of the La Meseta Formation (Submeseta Allomember) yields an age of ~34.2 Ma (Dingle and Lavelle, 1998a,b) and also is consistent with the stratigraphy (see Fig. 2) and the fauna. Based on this temporal determination, the age of the LMF falls in the gap recognized between the Vacan and Barrancan 'subages' (Fig. 7). Therefore, the LMF would partly fill this considerable temporal gap in the Eocene record of the mammalian evolution in South America (converted after Howarth and McArthur, 1997).

The new age assignment for the Barrancan (late Casamayoran) in Patagonia (Kay et al., 1999) and the refined ages for the Paleocene faunas in the San Jorge basin (Bond et al., 1995; Marshall et al., 1997) seem to be more consistent with the observed taxonomic similarities and differences between the land mammal fauna from Seymour Island and those from the Paleocene and Eocene of Patagonia. In summary, reassessment of the age of the taxa from the middle levels of the La

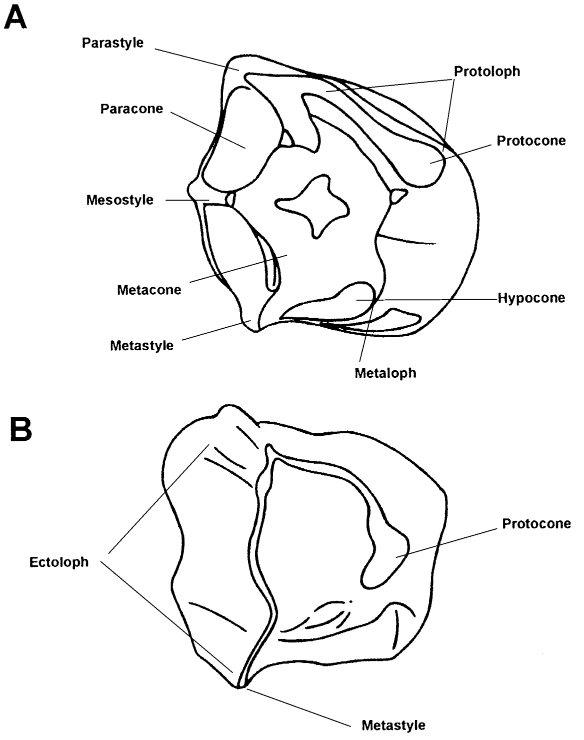

Fig. 7. Antarctic ungulates. Detailed scheme of upper M^1. (A) Sparnotheriodontidae gen. et sp. nov.; (B) *Trigonostylops* sp.

Meseta Formation at Seymour Island shows that they are middle Eocene and not late Eocene as believed earlier by several authors (Zinsmeister, 1978; Wrenn and Hart, 1988; Woodburne and Zinsmeister, 1982). Also, the revised late Eocene age for the Barrancan of Patagonia (Kay et al., 1999) provides indirect evidence for the antiquity of the Seymour Island mammals and for its insertion within a gap in the South American faunal succession. Consequently the LMF from *Cucullaea* I Allomember is a unique fauna that may document the evolution of mammals in the southern area of South America in the Middle Eocene (~49 and 37 Ma.).

3.3. LMF: interactions between plants and plant-eating mammals

Based on the marine invertebrates from Seymour Island, Zinsmeister and Feldmann (1984) stated that high-latitude regions serve as 'holding tanks' for taxa that remain isolated until they disperse towards lower latitudes (heterochroneity). The same authors recognized such high-latitude regions as centers of origin of novel adaptations leading to speciation. Case (1989) expanded the concept of Zinsmeister and Feldmann (1984) to the terrestrial fauna, especially the Seymour Island marsupials ('Weddellian marsupials').

Various climatic and ecological factors influence latitudinal gradients in mammalian diversity and taxonomic composition, and they strongly influence the formation of latitudinal faunal barriers (Flessa, 1975; McCoy and Connor, 1980). One of these factors could be the climatic cooling that occurred in the Antarctic Peninsula during the middle–late Eocene; many aspects of the flora and fauna may have been affected if the temperatures had fallen below certain threshold levels. Compositional differences between Seymour and King George Islands Eocene floras indicate that the climatic conditions were quite different on each side of the Antarctic Peninsula.

Also, at high latitudes, a prolonged period (several months?) of continuous darkness could have had a significant effect on the distribution of some taxa in the fauna. In this regard, the paleolatitude of Seymour Island during the Eocene was high (nearly 63°S), and the terrestrial biota would have routinely experienced several months of almost complete winter darkness as now occurs at these latitudes. Thus, some or all of the terrestrial mammals of Seymour Island probably lived under crepuscular and even extended nocturnal conditions during part of the year (i.e. fall and winter seasons). Direct evidence of crepuscular or nocturnal adaptations of the terrestrial vertebrates from the Eocene of Antarctica is lacking.

Fossil mammalian diet can be inferred from tooth morphology by using modern dental analogues with known diet (Dodd and Stanton, 1990). We are here concerned with fossil plant-eating mammals and thus with deducing frugivory (diet of fruits and seeds) and herbivory (diet of the green part of plants, including bark). In the middle Eocene of Antarctica, the change from podocarp- to *Nothofagus*-dominated closed forests (*Cucullaea* I Allomember) would result in an increase of arboreal habitats facilitating a radiation of arboreal herbivorous/omnivorous mammals. Most of the small-sized mammals recorded in the La Meseta Formation seem to be adapted to this habitat. Marsupials and condylarths appear in South America near the K/T boundary, but here they are divided into different guilds, marsupials becoming frugivorous and insectivorous and condylarths becoming the herbivorous. The browsing guild from the LMF probably consisted of four taxa: sparnotheriodontids, trigonostylopids, sloths, and sudamericids. Antarctic marsupials probably were members of the frugivorous/insectivorous guild (Goin et al., 1999).

The small-sized Antarctic sloth (ca. 10 kg) is considered to have been semi-arboreal and mainly folivorous (Vizcaíno et al., 1998). Also, we can add that the trunk-climbing ability (scansoriality) of this form is difficult to ascertain, but the strong laterally compressed claw recovered at RV-8200 locality (*Cucullaea* I Allomember) suggests this ability.

For the sudamericids, Koenigswald et al. (1999) inferred a semi-aquatic and perhaps a burrowing way of life, similar to that of living beavers. Regarding this, the presence of two Antarctic taxa at Seymour Island (Goin, personal communication, 2000) suggests an important paleoecological constraint related to the dietary preference of this group.

Antarctic ungulates could browse, stripping off twigs and saplings from evergreen trees even during winter months (Vizcaíno et al., 1998). Sparnotheriodontids and trigonostylopids share a number of dental characteristics that may be adaptations to forested habitats (Reguero et al., 1998). As Marenssi et al. (1994) pointed out, the striking features of these mammals are brachyodonty and the particular structure of the enamel (vertically oriented Hunter-Schreger bands). As indicated by Janis (1984) brachyodonty is associated with browsing herbivores that are adapted to forest habitats. No postcranial information is available for the Antarctic ungulates, but information from the nearest relatives (all of them fossils) can be used to infer the locomotor adaptation. Both astrapotheres and sparnotheriodontids were medium to large ground mammals with restrictions in their mobility of limb articulations (presence of wrist and ankle joints that restrict lateral movement), presence of hooves and reduction of digits in related taxa.

Paleobotanical and geological evidence from the Antarctic Peninsula indicates that at this time (middle Eocene), the Antarctic Peninsula was a densely forested high cordillera. These ungulates had a more bilophodont (Fig. 7), also partly selenodont in the case of the sparnotheriodontids, than bunodont dentition and their teeth had strong enamel ridges extending between the cusps. These enamel ridges serve as surfaces of shearing wear, and the formation of dentine ‘lakes’ along the ridges produces a double-edged shearing blade. These performed mainly a shearing action slicing up leaves into quite large pieces like a modern tapir that feeds almost entirely on leaves of forest trees. As Janis (1989) pointed out the bulk food was processed rapidly and inefficiently, a method typically used by perissodactyls to exploit mainly cell contents. In addition, the body size of the Antarctic sparnotheriodontid (395–400 kg) indicates that it was the largest herbivore living in Antarctica at this time (Vizcaíno et al., 1998). Evidently the large size of this herbivore favored the exploitation of leaves because longer residence time in the gut for bacterial fermentation is required to obtain sufficient nutrients from leaves. Also, it is accepted that large herbivores tend to feed more or less continuously on a wide range of plant parts. Low metabolic rate permits large herbivores to derive energy from cellulose by retaining it in the gut for long periods of microbial fermentation (Janis, 1976). Based on dental morphology, astrapotheres and sparnotheriodontids (Fig. 7) probably were hindgut fermenters like non-ruminant artiodactyls and perissodactyls (Fortelius, 1985). Astrapotheres and sparnotheriodontids also have teeth with vertical Hunter-Schreger bands. Fortelius (1985) indicates that a number of lophodont ungulates have evolved vertically oriented Hunter-Schreger bands, a modification that involves the mode of prism decussation and three-dimensional arrangement of the bands. This has been interpreted as an adaptation to resist cracking when the enamel edges are loaded in a direction away from the supporting dentine (Boyde and Fortelius, 1986).

Rensberger and Pfretzchner (1992) pointed out that the molars of astrapotheres, especially the uppers, strongly resemble those of rhinocerotoids. In both groups the labial part of the upper molar forms a thin, vertical, blade-like ectoloph (for Sparnotheriodontidae see Fig. 5).

The record of Sparnotheriodontidae on Seymour Island can be traced from the early-middle Eocene to the latest Eocene La Meseta Formation. In the middle Eocene, when the climatic conditions were cool-temperate, this group was common. Its last record occurs in the highest horizon of the Submeseta Allomember, dated by Dingle and Lavelle (1998a,b) at ~34.2 Ma (Fig. 2). This age coincides with the first well-documented formation of the first major sea ice and the initiation of the psychrosphere (Barron et al., 1991).

3.4. *Paleobiogeography: dispersal events*

The dispersal of land mammals supposes several prerequisites. One of them is the existence of a physical link between the start and end points of the route. Another is the availability of food and shelter along with a non-aggressive environment (e.g. climate, topography). Keast (1972) pointed out that Antarctica acted as a "stepping stone" for the dispersal of land mammals between Australia and South America. Simpson (1978) suggested the term "intermediate area" for peninsular Antarctica. Cracraft (1973) envisioned Antarctica "as a faunal dispersal route". Mid- to high-latitude warming has been cited as the key factor permitting interchange of fauna and flora between regions, e.g. Asia and North America, across high-latitude land connections (Woodburne and Swisher, 1995). Currently, Seymour Island land vertebrate-bearing localities are separated from the bulk of the Patagonian localities discussed herein by more than 15° of latitude (i.e. approximately 1600 km). Considering that, on the basis of geologic and paleogeographic data (Lawver et al., 1992), the Drake Passage (about 1000 km wide) started to open at about 36 Ma, then we can assume that, prior to that time, the distance between the Antarctic Peninsula and Patagonia ought to have been shorter (Fig. 3). In fact, they must have been neighbors. We can follow the overland connection between these two major areas at least since the Late Cretaceous. The width of the land connection between South America and West Antarctica is unknown, but it might be assumed that a fairly narrow corridor would have functioned (Fig. 3). The dispersal of dinosaurs into Antarctica from South America in the Late Cretaceous (Gasparini et al., 1987; Olivero et al., 1990; Molnar et al., 1996; Hooker et al., 1991; Case et al., 2000), and monotremes into South America from Australia via Antarctica in the Paleocene (Pascual et al., 1992), implies a connection, either as an island chain or as an isthmus, between Patagonia and the Antarctic Peninsula. By the Late Cretaceous or early Tertiary the Antarctic Peninsula–Andean Cordillera was being fragmented and pushed eastward, and it can be expected that vertebrate dispersal became more of a "sweepstakes" type. Several authors (Macellari, 1988; Askin, 1988) postulated that the regression through the K/T transition might have been largely responsible for changes in marine faunas and floras. This regressive event may also have directly affected land floras by providing newly created lowland areas for new plant species.

The terrestrial mammals of Seymour Island greatly strengthen the hypothesis that the LMF had its origin in times that pre-date the middle Eocene. Various lines of evidence suggesting this are summarized in the following points:

(1) The Antarctic sudamericid probably derived from the Peligran species *Sudamerica ameghinoi* (Goin, personal communication, 2000).

(2) The Antarctic derorhynchids *Derorhynchus minutus* and *Pauladelphys juanjoi* show close similarities with two new, unpublished, species of *Derorhynchus* from the Las Flores locality (Chubut) of Itaboraian age (Goin et al., 1999).

(3) The Antarctic microbiotheriid *Marambiotherium glacialis* closely resembles the Itaboraian species, *Mirandatherium alipioi* of Patagonia (Goin et al., 1999).

(4) The new Antarctic sparnotheriodontid is very close (perhaps representing the same species) to an unpublished new Vacan species from Paso del Sapo (Goin et al., 2000). Some dental features

of the Antarctic species seem to be more advanced than the Riochican and Vacan genus *Victorlemoinea*.

(5) The Antarctic astrapothere belongs to the family Trigonostylopidae and tentatively was referred to the genus *Trigonostylops* by Bond et al. (1990). This genus is recorded in the Riochican, Vacan and Barrancan faunas of Patagonia.

(6) The Antarctic Pilosa shares plesiomorphic features with primitive Tardigrada and Vermilingua. Despite some dubious Eocene records (Simpson, 1948) the Antarctic form represents the earliest unquestionable record of Pilosa (Vizcaíno and Scillato Yané, 1995).

(7) The case of the endemic polydolopine *Polydolops dailyi*, a species closely related to the species *Polydolops thomasi* (Woodburne and Zinsmeister, 1984; Candela and Goin, 1995) present in the Vacan and Barrancan 'subages', is very interesting because their close relationships suggest a short term of differentiation between both species.

The above evidence indicates that the La Meseta mammalian fauna derived from Paleocene, probably Riochican or Vacan faunas.

Put in the simplest terms, we might expect taxa to immigrate into the Antarctic Peninsula during a global warming phase. The late Paleocene–early Eocene was the apogee of Cenozoic warmth. During this interval, the tropics extended between 10 and 15° poleward, and both polar regions were populated with temperate forests (Frakes et al., 1992). The late Paleocene subtropical Cross Valley Flora on Seymour Island documents the warmest climatic conditions in the Paleogene of Antarctica. Based on the record of South American ungulates, one of the most probable dispersal events between Patagonia and the Antarctic Peninsula could have occurred during the late Paleocene and it was probably enhanced by the beginning of the 'climatic optimum' period (late Paleocene/early Eocene) and with the sea-level lowstand identified between 58.5 and 56.5 Ma (Haq et al., 1987). Lowering of the sea level might have increased the extension of low-lying coastal areas, providing an easier route than crossing rough mountainous terrain (Antarctic Peninsula) by leaving a long, continuous coastal region bordered by shallow seas and high mountains. The actual placement of the coastline during the latest Paleocene remains speculative (Fig. 3), but the overall physical consequences are not. The geological record shows a decrease in marine rocks (Cross Valley Formation) before the Paleocene/Eocene boundary.

Some non-mammal groups that may have used the same route at this time include flightless phorusrhacoid and ratite birds. This hypothesis explains the close affinity of the LMF with Paleocene faunas of Patagonia as well as the relict character of some Antarctic taxa, even though a still earlier (Late Cretaceous?) dispersal of Gondwanan vertebrates (gondwanatheres, ratites and monotremes) cannot be ruled out. However, the Gondwanan origin of these groups fits better with vicariance events than with dispersal events. We consider the presence of the family Sudamericidae in Antarctica as reflecting an artifact of a Gondwanan distribution. The first representatives of the family are recorded in the early Paleocene Peligran fauna. The known distribution of gondwanatheres (Argentina, India, Madagascar, and Antarctica) is consistent with at least two major biogeographic hypotheses: (1) the group originated before the major continental fragmentations of the 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.

The most unexpected circumstance in the LMF is the apparent lack of notoungulates and other ungulate groups such as Condylarthra and non-sparnotheriodontid Litopterna. Notoungulata were the most diverse (morphologically as well as taxonomically) and successful of the South American ungulate groups. One of the most important radiations of notoungulates in Patagonia occurred during the late Paleocene–early Eocene. As we suppose that no barrier to dispersal existed between Patagonia and Antarctic Peninsula during the Paleocene, the absence of this group in Antarctica could be explained by suggesting that the LMF is composed only of those taxa that were able to adapt to cooler conditions. However, the evidence of the presence of a high cordillera along the peninsular isthmus could have acted as a strong geographical barrier for the dispersal of terrestrial vertebrates in the late Paleocene. Perhaps only vertebrates adapted to high altitudes were able to migrate further southward. The ungulates so far recorded at Punta Peligro (Peligran SALMA) are the enigmatic *Peligrotherium tropicalis* (?condylarth), the mioclaenid condylarths, and the notonychopid *Requisia vidmari* (?Litopterna) (Bonaparte et al., 1993; Bonaparte and Morales, 1997). They document the existence of primitive ungulate lineages at this time. The most probable progenitors of the notoungulates, the mioclaenid condylarths, are present in this fauna. The first record of representatives of Notoungulata in Patagonia occurs in the late Paleocene '*Kibenikhoria* faunal zone' (Itaboraian SALMA *sensu* Bond et al., 1995) showing a discrete radiation of four families (Henricosborniidae, Isotemnidae, Interatheriidae, Oldfieldthomasiidae). However, the earliest record of this group in South America is in the older Tiupampian beds of Bolivia (Muizon, 1991). Additionally but interestingly, Bond (1999) remarks the noteworthy difference in the geographic distribution between Notoungulata and Litopterna in the late Pleistocene (Lujanian) in Patagonia; whereas the litoptern *Macrauchenia patachonica* has a wide range of distribution southward (Santa Cruz Province) in this age, the notoungulate *Toxodon* reached only Bahia Blanca (38° 45′S). This fact suggests that some factor (geographic or environmental) affected the dispersal of notoungulates to southern latitudes.

If the notoungulates migrated southward into the Antarctic Peninsula during the late Paleocene, they presumably became extinct prior the deposition of the La Meseta Formation (late-early Eocene–late Eocene). In sum, the most plausible hypotheses for the absence of Notoungulata, and other groups, in the LMF are (1) the record of this group is taphonomically biased, or (2) this group could have passed into Antarctica during the latest part of the Paleocene when the environmental conditions were warmer, and then became extinct at the onset of the climatic deterioration (early Eocene), (3) the topography of the Antarctic Peninsula cordillera prevented the dispersal of this group into Antarctica, or (4) the presence of some sort of ecological barrier that prevented the dispersal of this group. Based on the evidence presented above we favor the second choice.

We agree that Seymour Island and the surrounding region (Antarctic Peninsula) started its faunal isolation from South America from the early Eocene and this might suggest that geographic isolation by a physical barrier (seaway) would be among the possible hypotheses available to explain the extinctions and the endemism of the fauna. Although a physical barrier (seaway) might not have developed until the end of the Eocene, the cooling trend that began during the middle Eocene might have acted as an earlier barrier, discouraging new mammal immigrations. Therefore we suggest that regional cooling is the most reliable hypothesis to explain the extinctions, endemism, and relict character of the Eocene LMF. Isolation, that began through temperature decrease during the cooling trend from the middle Eocene onwards, became physical with the development of the seaway between the Antarctic Peninsula and Patagonia at the end of the Eocene.

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References

Askin, R.A., 1988. The Campanian to Paleocene palynological succession of Seymour and adjacent islands, north-eastern Antarctic Peninsula. In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America, Memoir 169, Boulder, pp. 131–153.

Askin, R.A., 1992. Late Cretaceous-early Tertiary Antarctic outcrop evidence for past vegetation and climates. The Antarctic paleoenvironment: a perspective on global change. Antarctic Research Series 56, Washington, pp. 61–73.

Askin, R.A., 1995. Eocene terrestrial palynology of Seymour Island, Antarctica. Abstracts, VII International Symposium on Antarctic Earth Sciences, Siena, Italy, 14.

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

Askin, R.A., Fleming, R.F., 1982. Palynological investigations of Campanian to lower Oligocene sediments on Seymour Island, Antarctic Peninsula. Antarct. J. U. S. 17, 570–571.

Barron, J., Larsen, B., Baldauf, J.G., 1991. Evidence for late Eocene to early Oligocene Antarctic glaciation, and observations on late Neogene glacial history of Antarctica: results from Leg 119. Proc. Ocean Dril. Prog. Sci. Results 119, 869–891.

Berggren, W.A., Kent, D.V., Swisher III, C.C., Aubry, M-P, 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Berggren, W.A., Kent, D.V., Aubry, M.-P., Hardenbol, J. (Eds.), Geochronology, Time Scales and Global Stratigraphic Correlation. SEPM Special Publication 54, Tulsa, pp. 129–212.

Bonaparte, J.F., 1986. History of the terrestrial Cretaceous vertebrates of Gondwana. Actas IV Congr. Argent. Paleontol. Bioestratigr. 2, 63–95.

Bonaparte, J.F., Morales, J., 1997. Un primitivo Notonychopidae (Litopterna) del Paleoceno inferior de Punta Peligro, Chubut, Argentina. Estud. Geol. 53, 263–274.

Bonaparte, J.F., Van Valen, L.M., Kramartz, A., 1993. La fauna local de Punta Peligro, Paleoceno inferior, de la provincia de Chubut, Patagonia, Argentina. Evol. Monogr. 14, 3–61.

Bond, M., 1999. Quaternary native ungulates of Southern South America. A synthesis. In: Rabassa, J., Salemme, M. (Eds.), Quaternary of South America and Antarctic Peninsula. Rotterdam, pp. 177–205.

Bond, M., Carlini, A.A., Goin, F.J., Legarreta, L., Ortiz Jaureguizar, E., Pascual, R., Uliana, M.A., 1995. Episodes in South American land mammal evolution and sedimentation: testing their apparent concurrence in a Paleocene succession from central Patagonia. Actas VI Congr. Paleontol. Bioestratigr. 47–58.

Bond, M., Pascual, R., Reguero, M.A., Santillana, S.N., Marenssi, S.A., 1990. Los primeros ungulados extinguidos sudamericanos de la Antártida. Ameghiniana 16, 240.

Boyde, A., Fortelius, M., 1986. Development structure and function of rhinoceros enamel. Zool. J. Linn. Soc. 87, 181–214.

Brea, M., 1996. Análisis de los anillos de crecimiento de leños fósiles de coníferas de la Formación La Meseta, isla Seymour, Antártida. Congreso Paleógeno de América del Sur. Resúmenes, Santa Rosa, 28 pp.

Brea, M., 1998. Análisis de los anillos de crecimiento en leños fósiles de coníferas de la Formación La Meseta, Isla Seymour (Marambio), Antártida. In: Casadio, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, Publicación Especial 5, pp. 163–175.

Brea, M., Zuccol, A.F., 1996. Estructura reproductiva femenina de una conífera de la Formación La Meseta, isla Seymour, Antártida. Congreso Paleógeno de América del Sur. Resúmenes, Santa Rosa, 29 pp.

Candela, A., Goin, F.J., 1995. Revisión de las especies antárticas de marsupiales polidolopinos (Polydolopimorphia, Polydolopidae). Terceras Jornadas de Comunicaciones sobre Investigaciones Antárticas. Resúmenes, Buenos Aires, pp. 55–58.

Carlini, A.A., Scillato Yané, G.J., Vizcaíno, S.F., Dozo, M.T., 1992. Un singular Myrmecophagidae (Xenarthra, Vermilingua) de la Edad Colhuehuapense (Oligoceno tardío-Mioceno temprano) de Patagonia, Argentina. Ameghiniana 29, 176.

Case, J.A., 1988. Paleogene floras from Seymour Island, Antarctic Peninsula. In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America, Memoir 169, Boulder, pp. 523–530.

Case, J.A., 1989. Antarctica: the effect of high latitude heterochroneity on the origin of the Australian marsupials. In: Crame, J.A. (Ed.), Origins and Evolution of the Antarctic Biota, Geological Society Special Publication N° 47, Cambridge, pp. 217–226.

Case, J.A., Martin, J.E., Chaney, D.S., Reguero, M., Marenssi, S.A., Santillana, S.M., 2000. The first duck-billed dinosaur (Family Hadrosauridae) from Antarctica. Journal of Vertebrate Paleontology, 20:612–614.

Case, J.A., Woodburne, M.O., Chaney, D.S., 1987. A gigantic phororhacoid(?) bird from Antarctica. J. Paleontol. 61, 1280–1284.

Case, J.A., Woodburne, M.O., Chaney, D.S., 1988. A new genus and species of polydolopid marsupial from the La Meseta Formation, late Eocene, Seymour Island, Antarctic Peninsula. In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America, Memoir 169, Boulder, pp. 505–521.

Cifelli, R.L., 1985. Biostratigraphy of the Casamayoran, early Eocene, of Patagonia. Am. Mus. Novit. 2820, 1–26.

Cione, A.L., Reguero, M.A., 1994. New records of the sharks *Isurus* and *Hexanchus* from the Eocene of Seymour Island, Antarctica. Proc. Geol. Assoc. 105, 1–14.

Cione, A.L., Reguero, M.A., 1998. An Eocene basking shark (Lamniformes, Cetorhinidae) from Antarctica. Antarct. Sci. 10, 83–88.

Coccozza, C., Clarke, C., 1992. Eocene microplankton from La Meseta Formation. Antarct. Sci. 4, 355–362.

Covacevich, V., Rich, P.V., 1982. New birds ichnites from Fildes Peninsula, King George Island, West Antarctica. In: Craddock, C. (Ed.), Antarctic Geoscience. University of Wisconsin Press, Madison, pp. 245–254.

Cracraft, J., 1973. Continental drift, paleoclimatology and the biogeography of birds. Journal of Zoology, London, 169, 455–545.

Cranwell, L.M., 1959. Fossil pollen from Seymour Island, Antarctica. Nature 184, 1782–1785.

Del Valle, R.A., Elliot, D.H., Macdonald, D.I.M., 1992. Sedimentary basins on the east flank of the Antarctic Peninsula: proposed nomenclature. Antarct. Sci. 4, 477–478.

Dingle, R., Lavelle, M., 1998a. Antarctic Peninsula cryosphere: early Oligocene (c. 30 Ma) initiation and a revised glacial chronology. J. Geol. Soc. Lond. 155, 433–437.

Dingle, R., Lavelle, M., 1998b. Late Cretaceous-Cenozoic climatic variations of the northern Antarctic Peninsula: new geochemical evidence and review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 107, 79–101.

Ditchfield, P.W., Marshall, J.D., Pirrie, D., 1994. High latitude palaeotemperature variation: new data from the Tithonian to Eocene of James Ross Island, Antarctica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 107, 79–101.

Dingle, R., Marenssi, S., Lavelle, M., 1998. High latitude Eocene climate deterioration: evidence from the northern Antarctic Peninsula. J. South Am. Earth Sci. 11, 571–579.

Dodd, J.R., Stanton, R.J., 1990. Paleoecology: Concepts and Applications. Wiley, New York.

Doktor, M., Gazdzicki, A., Jerzmanska, A., Porebski, S., Zastawniak, E., 1996. A plant-and-fish assemblage from the Eocene La Meseta Formation of Seymour Island (Antarctic Peninsula) and its environmental implications. Acta Palaeontol. Polonica 55, 127–146.

Dusén, P., 1908. Uber die tertiare Flora der Seymour-Insel. In: Nordenskjold, O. (Ed.), Wissenschaftliche Erbegnesse Schwedischen Sudpolar Expedition 1901–1903, 3, Stockholm, pp. 1–27.

Elliot, D.H., 1988. Tectonic setting and evolution of the James Ross basin, northern Antarctic Peninsula. In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America, Memoir 169, Boulder, pp. 541–555.

Elliot, D.H., Trautman, T.A., 1982. Lower Tertiary strata on Seymour Island, Antarctic Peninsula, In: Craddock, C. (Ed.), Antarctic Geoscience. University of Wisconsin Press, Madison, pp. 287–297.

Engelmann, G.F., 1987. A new Deseadan sloth (Mammalia, Xenarthra) from Salla, Bolivia, and its implications for the primitive conditions of the dentition in edentates. J. Vertebr. Paleontol. 7, 217–223.

Flessa, K.W., 1975. Area, continental drift and mammalian diversity. Palaeobiology 1, 189–194.

Fortelius, M., 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. Acta Zool. Fenn. 180, 1–76.

Frakes, L.A., Francis, J.E., Syktus, J.I., 1992. Climate modes of the Phanerozoic. Cambridge University Press, Cambridge, 274 pp.

Frenguelli, J., Parodi, L.R., 1941. Una chusquea fósil de El Mirador (Chubut). Notas Mus. Plata 6, 235–238.

Gandolfo, M.A., Hoc, P., Santillana, S., Marenssi, S., 1998. Una flor fósil morfológicamente afín a las Grossulariaceae (Orden Rosales) de la Formación La Meseta (Eoceno medio), Isla Marambio, Antártida. In: Casadio, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, Publicación Especial 5, pp. 147–153.

Gandolfo, M.A, Marenssi, S.A., Santillana, S.N., 1998. Flora y paleoclima de la Formación La Meseta (Eoceno medio), isla Marambio (Seymour), Antártida. In: Casadio, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, Publicación Especial 5, pp. 155–162.

Gasparini, Z., Olivero, E., Scasso, R., Rinaldi, C., 1987. Un ankylosaurio (Reptilia, Ornisthichia) campaniano en el continente antártico. Anais X Congresso Brasileiro de Paleontología, Rio de Janeiro, pp. 131–141.

Gazdzicki, A.J., Gruszczynski, M., Hoffman, A., Malkowski, K., Marenssi, S.A., Halas, S., Tatur, A., 1992. Stable carbon and oxygen isotope record in the Paleogene La Meseta Formation, Seymour Island, Antarctica. Antarct. Sci. 4, 461–468.

Goin, F., Carlini, A., 1995. An early Tertiary microbiotheriid marsupial from Antarctica. J. Vertebr. Paleontol. 15, 205–207.

Goin, F.J., Case, J.A., Woodburne, M.O., Vizcaíno, S.F., Reguero, M.A., 1999. New discoveries of 'oppossum-like' marsupials from Antarctica (Seymour Island, Medial Eocene). J. Mamm. Evol. 6, 335–365.

Goin, F.J., Reguero, M.A., Vizcaíno, S.F., 1995. Novedosos hallazgos de 'comadrejas' (Marsupialia) del Eoceno medio de Antártida. III Jornadas de Comunicaciones sobre Investigaciones Antárticas, Resúmenes, Buenos Aires, pp. 59–62.

Goin, F., Tejedor, M., Bond, M., López, G., Reguero, M., 2000. Mamíferos Eocenos de Paso del Sapo, Chubut. Ameghiniana 37, 25R.

Gothan, W., 1908. Die fossilen holzer von der Seymour und Snow Hill Insel. In: Nordenskjold, O. (Ed.), Wissenschaftliche Erbegnesse Schwedischen Sudpolar Expedition 1901–1903, 3, Stockholm, pp. 1–33.

Haomin, L., 1994. Early Tertiary Fossil Hill Flora from Fildes Peninsula of King George Island, Antarctica. In: Yanbin, S. (Ed.), Stratigraphy and Palaeontology of Fildes Peninsula King George Island, Antarctica. Science Press, pp. 165–171.

Haq, B.U., Hardenbol, J., Vail, P.R., 1987. Chronology of fluctuating sea levels since the Triassic. Science 235, 1156–1167.

Hoffstetter, R., 1982. Les édentés xenarthres, un groupe singulier de la faune neotropicale (origines, affinités, radiation adaptative, migrations et extinctions). In: Montanaro Gallitelli, E., (Ed.), Proceedings of the First International Meeting on 'Paleontology, Essential of Historical Geology'. Modena, pp. 385–443.

Hooker, J.J., 1992. An additional record of a placental mammal (Order Astrapotheria) from the Eocene of Western Antarctica. Antarct. Sci. 4, 107–108.

Hooker, J.J., Milner, A.C., Sequeira, S., 1991. An ornithopod dinosaur from the Late Cretaceous of West Antarctica. Antarct. Sci. 3, 331–332.

Howarth, R.J., McArthur, J.M., 1997. Statistics for strontium isotope stratigraphy. A robust LOWESS fit to the marine Sr-isotope curve for 0–206 Ma, with look-up table for the derivation of numerical age. J. Geol. 105, 441–456.

Janis, C.M., 1976. The evolutionary strategy of the Equidae, and the origins of the rumen and cecal digestion. Evolution 30, 757–774.

Janis, C.M., 1984. The use of fossil ungulate communities as indicators of climate and environment. In: Brenchley, P. (Ed.), Fossils and Climates. John Wiley and Sons, New York, pp. 85–104.

Janis, C.M., 1989. A climatic explanation for patterns of evolutionary diversity in ungulates mammals. Palaeontology 32, 463–481.

Kay, R.F., Madden, R.H., Vucetich, M.G., Carlini, A.A., Mazzoni, M.M., Re, G.H., Heisler, M., Sandeman, H., 1999. Revised geochronology of the Casamayoran South American Land Mammal Age: Climatic and biotic implications. Proc. Nat. Acad. Sci. U. S. A. 96, 13235–13240.

Keast, A., 1972. Introduction: The southern continents as backgrounds for mammalian evolution. In: Keast, A., Erk, F.C., Glass, B. (Eds.), Evolution, Mammals, and Southern Continents. State University of New York Press, Albany, pp. 19–22.

Koenigswald von, W., Goin, F., Pascual, R., 1999. Hypsodonty and enamel microstructure in the Paleocene gondwanatherian mammal *Sudamerica ameghinoi*. Acta Palaeontol. Polonica 44, 263–300.

Krause, D., Prasad, G.V., Koenigsvald, W. von, Sahni, A., Grine, F.E., 1998. Cosmopolitanism among Gondwanan Late Cretaceous mammals. Nature, 390:504–507.

Lawver, L.A., Gahagan, L.M., and Coffin, F.M., 1992. The development of palaeoseaway around Antarctica. In: Kennett, J.P., Warnke, D.A. (Eds.), The Antarctic Paleoenvironment: A Perspective on Global Change. Antarctic Research Series 65, Washington, pp. 7–30.

Macellari, C.E., 1988. Stratigraphy, sedimentology and paleoecology of Upper Cretaceous-Paleocene shelf-deltaic sediments of Seymour Island (Antarctic Peninsula). In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America, Memoir 169, Boulder, pp. 25–53.

Marenssi, S.A., 1995. Sedimentología y paleoambientes de sedimentación de la Formación La Meseta, isla Marambio, Antártida. Tomo I: 330 pp., Tomo II: 172 pp. Tesis Doctoral, Universidad de Buenos Aires. Unpublished.

Marenssi, S.A., Reguero, M.A., Santillana, S.N., Vizcaíno, S.F., 1994. Eocene land mammals from Seymour Island, Antarctica: Palaeobiogeographical implications. Antarct. Sci. 6, 3–15.

Marenssi, S.A., Santillana, S.N., Net, L.I., Rinaldi, C.A., 1999. Heavy mineral suites as provenance indicator: La Meseta Formation (Eocene), Antarctic Peninsula. Asoc. Sedimentol. Argent. 5, 9–19.

Marenssi, S.A., Santillana, S.N., Rinaldi, C.A. 1998. Paleoambientes Sedimentarios de la Aloformación La Meseta (Eoceno), Isla Marambio (Seymour), Antártida. Instituto Antártico Argentino, Contribución 464, 51 pp.

Marenssi, S.A., Santillana, S.N., Rinaldi, C.A. 1998. Stratigraphy of the La Meseta Formation (Eocene), Marambio (Seymour) Island, Antarctica. In: Casadio, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, Publicación Especial 5, Buenos Aires, pp. 137–146.

Marshall, L.G., Sempere, T., Butler, R.F., 1997. Chronostratigraphy of the mammal-bearing Paleocene of South America. J. South Am. Earth Sci. 10, 49–70.

McCoy, E.D., Connor, E.F., 1980. Latitudinal gradients in the species diversity of North American mammals. Evolution 34, 193–203.

Molnar, R.E., López Angriman, A., Gasparini, Z., 1996. An Antarctic Cretaceous theropod. Mem. Qld. Mus. 39, 669–674.

Muizon, C. de, 1991. La Fauna de mamíferos de Tiupampa (Paleoceno inferior, Formación Santa Lucía), Bolivia. In: Suárez-Soruco, R. (Ed.), Fósiles y Facies de Bolivia. Vol. I, Vertebrados. Revista Técnica de YPFB (Yacimientos Petrolíferos Fiscales Bolivianos) 12, pp. 575–624.

Net, L.I., Marenssi, S.A., 1999. Petrografía de las areniscas de la Formación La Meseta (Eoceno), isla Marambio, Antártida. IV Jornadas sobre Investigaciones Antárticas, Buenos Aires 1 al 5 de septiembre de 1997, 2, pp. 343–347.

Olivero, E., Gasparini, Z., Rinaldi, C., Scasso, R., 1990. First record of dinosaurs in Antarctica (Upper Cretaceous, James Ross Island): palaeogeographical implications. In: Thomson, M.R.A., Crame, J.A., Thomson, J.W. (Eds.), Geological Evolution of Antarctica. Cambridge University Press, Cambridge, pp. 617–622.

Pankhurst, R.J., 1982. Rb-Sr geochronology of Graham Land, Antarctica. J. Geol. Soc. Lond. 139, 701–712.

Pascual, R., Ortiz Jaureguizar, E., 1990. Evolving climates and mammal faunas in Cenozoic South America. J. Hum. Evol. 19, 23–60.

Pascual, R., Archer, M., Ortiz Jaureguizar, E., Prado, J.L., Godthelp, H., Hand, S.H., 1992. First discovery of monotremes in South America. Nature 356, 704–705.

Pascual, R., Ortiz Jaureguizar, E., Prado, J.L., 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. Münch. Geowiss.liche Abh. A 30, 265–319.

Petriella, B.T.P., Archangelski, S., 1975. Vegetación y ambiente en el Paleoceno de Chubut. Actas I Cong. Argent. Paleontol. Bioestratigr. 2, 257–270.

Reguero, M.A., Vizcaíno, S.F., Goin, F.J., Marenssi, S.A., Santillana, S.N., 1998. Eocene high-latitude terrestrial vertebrates from Antarctica as biogeographic evidence. In: Casadio, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, Publicación Especial 5, pp. 185–198.

Rensberger, J.M., Pfretzchner, H.U., 1992. Enamel structure in astrapotheres and its functional implications. Scanning Microsc. 6, 495–510.

Romero, E.J., 1986. Paleogene phytogeography and climatology of South America. Ann. Mo. Bot. Garden 73, 449–461.

Sadler, P., 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula, Geological Society of America, Memoir 169, Boulder, pp. 303–320.

Scillato Yané, G.J. and Pascual, R., 1984. Un peculiar Paratheria, Edentata (Mammalia) del Paleoceno medio de Patagonia. 1° Jornadas Argentinas de Paleontología de Vertebrados, Resúmenes, 15. La Plata.

Simpson, G.G., 1935. Occurrence and relationships of the Río Chico fauna of Patagonia. Am. Mus. Novit. 818, 1–21.

Simpson, G.G., 1948. The beginning of the age of the mammals in South America. Part I. Introduction. Systematics Marsupialia, Edentata, Condylarthra, Litopterna, and Notioprogonia. Bull. Am. Mus. Nat. Hist. 91, 1–232.

Simpson, G.G., 1978. Early mammals in South America: fact, controversy, and mistery. Proc. Am. Phylos. Soc. 122, 318–328.

Spalletti, L.A., Mazzoni, M.M., 1978. Sedimentología del Grupo Sarmiento en un perfil ubicado al sudeste del lago Colhué-Huapi, provincia de Chubut. Obra Centenario Mus. Plata 4, 261–283.

Stilwell, J.D., Zinsmeister, W.J., 1992. Molluscan Systematics and Biostratigraphy. Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. Antarctic Research Series. American Geophysical Union. Vol. 55, Washington, 192 pp.

Storey, B.C., Garrett, S.W., 1985. Crustal growth of the Antarctic Peninsula by accretion, magmatism and extension. Geol. Mag. 122, 5–14.

Tambussi, C.P., Noriega, J.I., Gazdzicki, A., Tatur, A., Reguero, M.A., Vizcaíno, S.F., 1994. Ratite bird from the Paleogene La Meseta Formation, Seymour Island, Antarctica. Pol. Polar Res. 15, 15–20.

Tambussi, C.P., Noriega, J.I., Santillana, S.N., Marenssi, S.A., 1995. Falconid bird from the middle Eocene La Meseta Formation, Seymour Island, West Antarctica. J. Vertebr. Paleontol. Abstr. 15, 55A.

Torres, T., Marenssi, S.A., Santillana, S.N., 1994. Maderas fósiles de la isla Seymour, Formación La Meseta, Antártica. Serie Científica del INACH, 44, Santiago de Chile, pp. 17–38.

Vizcaíno, S.F., Bond, M., Reguero, M.A., Pascual, R., 1997. The youngest record of fossil land mammals from Antarctica, its significance on the evolution of the terrestrial environment of the Antarctic Peninsula during the late Eocene. J. Paleontol. 71, 348–350.

Vizcaíno, S.F., Reguero, M.A., Goin, F.J., Tambussi, C.P. and Noriega, J.I. 1998. Community structure of Eocene terrestrial vertebrates from Antarctic Peninsula. In: Casadio, S. (Ed.), Paleógeno de América del Sur y de la Peninsula Antártica. Asociación Paleontológica Argentina, Publicación Especial 5, pp. 177–183.

Vizcaíno, S.F., Scillato Yané, G.J., 1995. An Eocene tardigrade (Mammalia, Xenarthra) from Seymour Island, West Antarctica. Antarct. Sci. 7, 407–408.

Woodburne, M.O., Case, J.A., 1996. Dispersal, vicariance, and the post-Gondwana Late Cretaceous to early Tertiary biogeography from South America to Australia. J. Mamm. Evol. 3, 121–161.

Woodburne, M.O., Swisher III, C.C., 1995. Land-mammal high resolution, geochronology, intercontinental overland dispersals, sea-level, climatic and vicariance, pp. 335–364. In: W.A. Berggren, D.V. Kent, M.P. Aubry and J. Handerbol (Eds): Geochronology, time-scales, and global stratigraphic correlations: a unified framework for an historical geology. Society of Stratigraphy Geology, Special Publication 54.

Woodburne, M.O., Zinsmeister, W.J., 1982. Fossil land mammal from Antarctica. Science 218, 284–286.

Woodburne, M.O., Zinsmeister, W.J., 1984. The first land mammal from Antarctica and its biogeographic implications. J. Paleontol. 58, 913–948.

Wrenn, J.H., Hart, G.F., 1988. Paleogene dinoflagellates cyst biostratigraphy of Seymour Island, Antarctica. In: Feldmann, R.M., Woodburne, M.O. (Eds.), Geology and Paleontology of Seymour Island, Antarctic Peninsula, Geological Society of America, Memoir 169, Boulder, pp. 321–447.

Zinsmeister, W.J., 1978. Eocene nautiloid fauna from the La Meseta Formation of Seymour Island, Antarctic Peninsula. Antarct. J. U. S. 13, 24–25.

Zinsmeister, W.J., 1982. Late Cretaceous-Early Tertiary molluscan biogeography of the southern circum-Pacific. Journal of Paleontology, 56:84–102.

Zinsmeister, W.J., Feldmann, R.M., 1984. Cenozoic high latitude heterochroneity of southern hemisphere marine faunas. Science 224, 281–283.