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EOCENE HIGH-LATITUDE TERRESTRIAL VERTEBRATES FROM ANTARCTICA AS BIOGEOGRAPHIC EVIDENCE

Marcelo A. REGUERO[1], *Sergio F. VIZCAÍNO*[1], *Francisco J. GOIN*[1], *Sergio A. MARENSSI*[2] *and Sergio N. SANTILLANA*[2]

ABSTRACT. A moderately diverse terrestrial biota is known from the Eocene - ?early Oligocene La Meseta Formation, Seymour Island, Antarctic Peninsula. The La Meseta Formation fills an incised valley and comprises sediments that represent deltaic, estuarine and very shallow marine environments. Forests of both deciduous and evergreen trees were dominated by *Nothofagus*, podocarps, and araucarian conifers. The La Meseta paleoflora is distinctive in having a predominance of Antarctic taxa; this suggests a seasonal, cold-temperate, rainy climate and a latitudinal gradient. Among the terrestrial vertebrates, there are at least nine mammal taxa, predominantly tiny marsupials (mostly endemic and new genera). The presence of these marsupials suggests the existence of some form of isolating barrier (climatic and/or geographic), which must have allowed development of this endemic fauna. Comparisons with faunas assigned to the Itaboraian (late Paleocene), Riochican (late Paleocene), Casamayoran (early Eocene), and Mustersan (tentatively assigned to the middle Eocene) ages of Patagonia were made. The assemblage of terrestrial vertebrates of the La Meseta Formation is unusual in the dominance of several endemic forms. The occurrence of protodidelphid and derorhynine marsupials, that had become extinct elsewhere in the Eocene of South America, on Seymour Island also indicates that isolation may have allowed extended survival of these taxa in the Eocene of Antarctica. The nature, distribution, and composition of the La Meseta fauna firmly suggest a latitudinal differentiation in the middle Eocene. Paleogeographic evidence suggests that the terrestrial mammals of the La Meseta Formation probably lived under crepuscular and even extended nocturnal conditions (assuming that the angle of the earth's spin axis was relatively the same as it is now) during part of the year.

RESUMEN. VERTEBRADOS EOCENOS TERRESTRES DE ALTAS LATITUDES DE ANTÁRTIDA COMO EVIDENCIA BIOGEOGRÁFICA. Una biota moderadamente diversa es conocida en la Formación La Meseta (Eoceno-Oligoceno temprano?), isla Seymour, Península Antártica. La Formación La Meseta rellena un valle incidido y comprende sedimentos que representan ambientes estuáricos y marinos muy someros. Bosques con árboles deciduos y perennes estuvieron dominados por *Nothofagus*, y coníferas podocarpáceas y araucarias. La paleoflora de la Formación La Meseta es distintiva y predominan taxones antárticos que sugieren un clima templado frío, lluvioso, estacional y un gradiente latitudinal. Dentro de los vertebrados terrestres hay 9 taxones de mamíferos, predominantemente pequeños marsupiales, mayormente endémicos y novedosos, que sugieren que alguna forma de barrera de aislamiento, climática y/o geográfica, debió haber permitido el desarrollo de esta fauna endémica. Se realizaron comparaciones con las faunas asignadas a las edades mamífero Itaboraiense (Paleoceno tardío), Riochiquense (Paleoceno tardío), Casamayorense (Eoceno temprano) y Mustersense (tentativamente asignada al Eoceno medio). La fauna de la Fm. La Meseta es particular por el predominio de varias formas endémicas. La presencia de marsupiales protodidélfidos y derorhinchinos, los cuales ya no se registran en ninguna de las faunas del Eoceno de América del Sur, indica que el aislamiento pudo haber permitido la supervivencia de estos taxones en el Eoceno de Antártida. La naturaleza, distribución y composición de la fauna de la Fm. La Meseta firmemente sugiere una diferenciación latitudinal en el Eoceno medio. Finalmente, las evidencias paleogeográficas sugieren que los mamíferos terrestres de la Formación La Meseta probablemente vivieron bajo condiciones crepusculares, aún nocturnas (asumiendo que la oblicuidad del eje de la Tierra fue relativamente la misma que la actual), durante parte del año.

KEY WORDS. Antarctic Peninsula. Eocene. High latitude fauna. Mammals. Palaeobiogeography.

PALABRAS CLAVE. Península Antártica. Eoceno. Fauna de alta latitud. Mamíferos. Paleobiogeografía.

INTRODUCTION

Seymour (Marambio) Island (figure 1) contains the only Eocene land vertebrate fauna known in Antarctica, except for the avian tracks from the 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, middle-late 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, 1984). This was especially true 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; figure 2). Concerted effort between 1988 and 1996 produced terrestrial vertebrates from several different stratigraphic levels (10 localities from 4 different stratigraphic horizons) within the La Meseta Formation (figure 3); these range from the middle Eocene to the ?early Oligocene (Bond *et al.*,

[1]Departamento Científico de Paleontología Vertebrados, Museo de La Plata. Paseo del Bosque s/n, 1900 La Plata, Argentina. E-mail: regui@museo.fcnym.unlp.edu.ar
[2]Instituto Antártico Argentino, Cerrito 1248, 1010 Buenos Aires, Argentina.

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1993; Fordyce, 1989). This biota contains more than 30 taxa of terrestrial plants and vertebrates. Terrestrial vertebrates were recovered by surface prospecting and sieving of the sediment after 5 years of careful fieldwork. These vertebrates, particularly the mammals, have close biogeographical links with Paleogene faunas of Patagonia (Bond *et al.*, 1993).

The La Meseta land vertebrate fauna (here called LMF) is unusual in being dominated by large sparnotheriodontid ungulates and small polydolopine marsupials. This is not the case in the Patagonian fossil record. Moreover, the high proportion of endemic taxa (mainly marsupials) within this fauna, together with relicts such as protodidelphid and derorhinchine marsupials, give it a very distinctive southern appearance, indicating that some form of isolating barrier (climatic, geographic or topographic) was in effect. 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 middle-late Eocene seem to have been matched by the development of a characteristic biota (Marenssi *et al.*, 1994).

In this paper we present faunistic data, together with

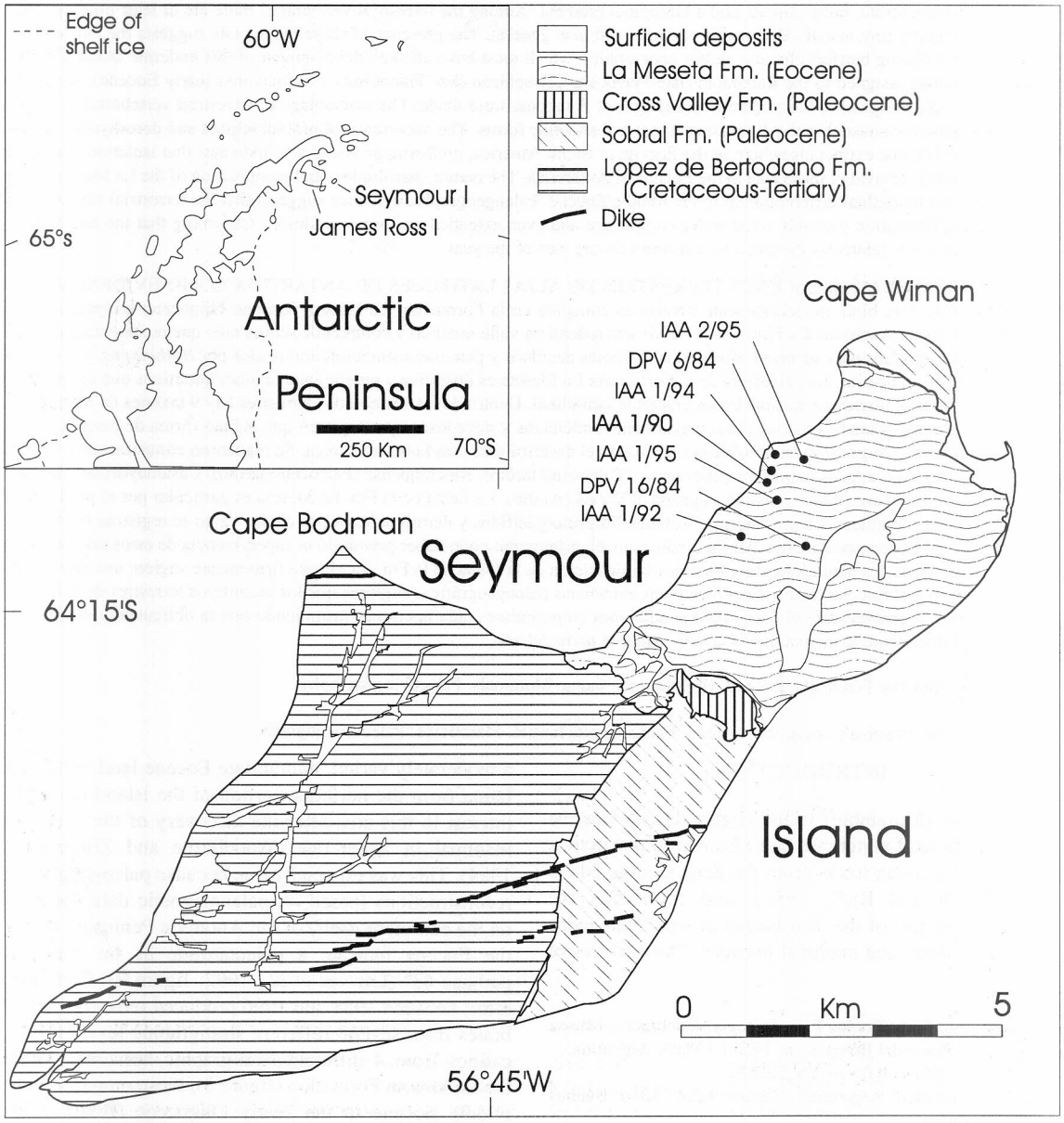

Figure 1. Map showing the location of Seymour Island and the collecting sites. *Mapa de ubicación de la Isla Seymour mostrando los sitios de colección.*

paleofloristic information, supporting the existence of a high latitude land biota with differences from the penecontemporaneous faunas of Patagonia.

ABBREVIATIONS

DPV: Departamento Científico de Paleontología Vertebrados, Museo La Plata. IAA: Instituto Antártico Argentino, Buenos Aires. RV: University of California at Riverside, California. ZPAL: National Academy of Science, Warsaw. TELM: Tertiary Eocene La Meseta (Sadler's stratigraphic nomenclature).

GEOLOGICAL OVERVIEW

Ten terrestrial vertebrate-bearing localities are known in the Eocene of Seymour Island. The stratigraphic positions of these localities are shown in figure 3. Herein we follow the stratigraphic terminology of Sadler (1988), because the newest framework elaborated by Marenssi *et al.* (1998) is not widely accepted yet.

The La Meseta Formation (Elliot and Trautman, 1982) fills an incised valley and comprises deltaic, estuarine, and shallow marine deposits containing both marine and terrestrial fossils (Marenssi, 1995; Marenssi *et al.*, in press). 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.

The location of the incised valley, its temporal persistence, the lenticular nature of the internal units, the thick-

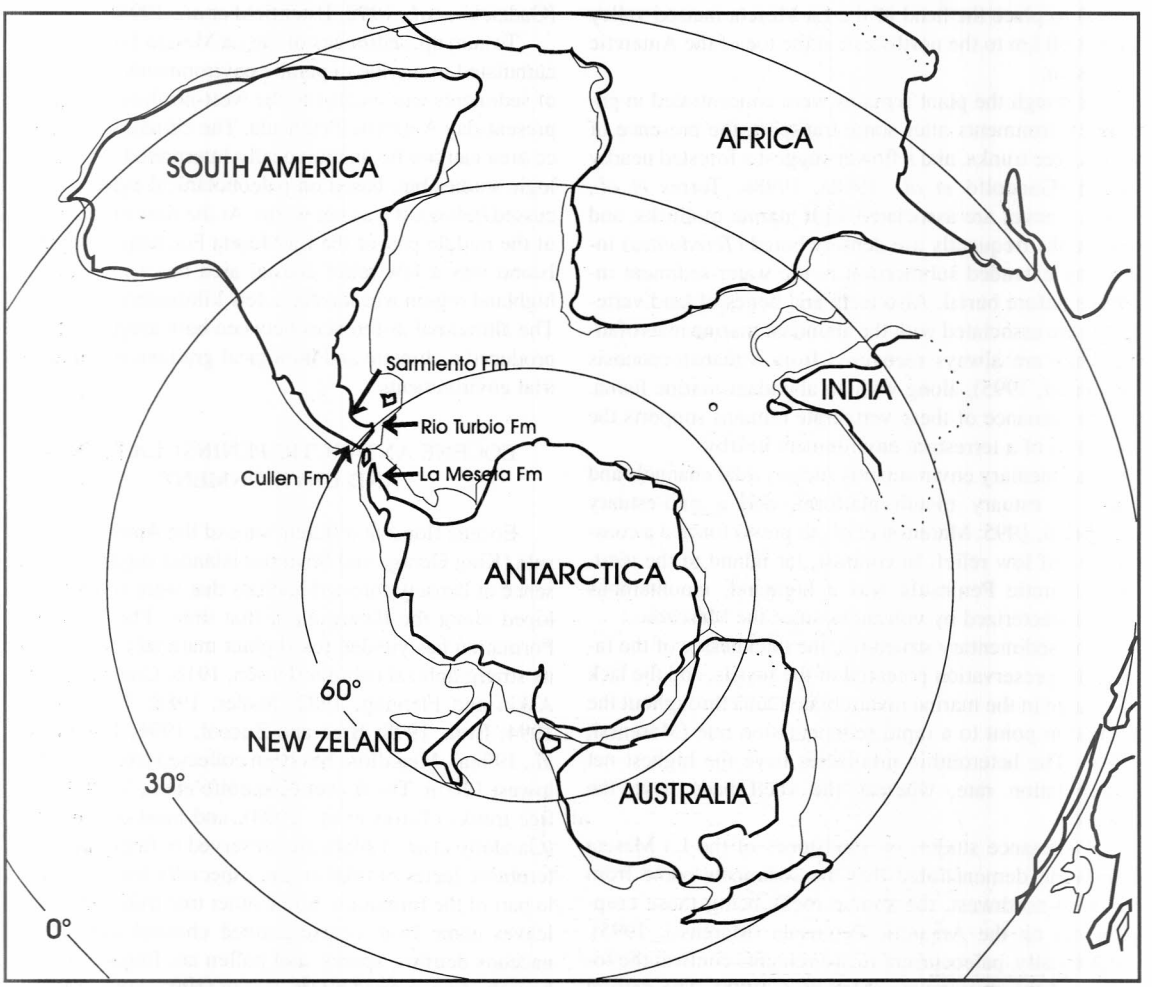

Figure 2. Paleogeographic reconstruction of the southern continents at 50 Ma showing the distribution of the faunal and floristic units at high latitudes. Circles indicate 0°, 30° and 60° S latitude after Lawver *et al.* (1992, fig. 11). Thick line denotes continents; thin lines show continental shelves to present day 200 m isobath. *Reconstrucción paleogeográfica de los continentes del Hemisferio sur a los 50 Ma mostrando las formaciones con elementos faunísticos y florísticas de altas latitudes. Los círculos de 0°, 3° y 60° S están indicados. Modificado de Lawver et al. (1992, fig. 11). La línea gruesa indica los continentes, la línea fina indica los bordes continentales actuales en la isobata de 200 m.*

ness of the sedimentary facies and geometric relationships of the bedding and synsedimentary faults (Sadler, 1988; Marenssi, 1995; Marenssi *et al.*, in press) indicate that sedimentation was strongly controlled by subsidence and tectonics.

Paleoenvironmental restorations 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.*, in press). Recent studies of the geometric relationships in the La Meseta Formation (Sadler, 1988; Marenssi, 1995; Marenssi *et al.*, 1998) show that the steep erosional boundaries are the margins of a large channel some 7 km in width that originated farther west. Outcrops of the La Meseta Formation on Cockburn Island, about 10 km west, and the meandering character of Herbert Sound between James Ross and Vega islands have prompted Stilwell and Zinsmeister (1992) to place the head of the La Meseta incised valley almost 60 km to the northwest, at the toe of the Antarctic Peninsula.

Although the plant remains were concentrated in paralic environments after some transport, the presence of leaves, tree trunks, and a flower suggest a forested nearby terrain (Gandolfo *et al.*, 1998a, 1998b; Torres *et al.*, 1994). Leaves are associated with marine mollusks, and tree trunks frequently are densely bored (*Teredolites*) indicating extended submersion in the water-sediment interface before burial. Also teeth and bones of land vertebrates are associated with the abundant marine macrofauna. They are always recovered from a thanatocoenosis (Marenssi, 1995), along with an abundant marine fauna. The provenance of these vertebrate remains supports the existence of a terrestrial environment nearby.

Sedimentary environments such as tidal channels and flats, an estuary mouth platform, and a mid-estuary (Marenssi, 1995; Marenssi *et al.*, in press) 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 since the Mesozoic.

The sedimentary structures, the thicknesses of the facies, the preservation potential of the fossils, and the lack of change in the marine invertebrate fauna throughout the formation point to a rapid sedimentation rate (Marenssi, 1995). The heterolithic lithofacies have the highest net accumulation rate, whereas the shell beds have the lowest.

Provenance studies on sandstones of the La Meseta Formation demonstrated that the sediments come from the west-northwest, the source rocks being those cropping out on the Antarctic Peninsula (Marenssi, 1995). Additionally, paleocurrent measurements confirm the location of the source area (Marenssi, 1995). The detrital modes of sandstone often are considered to have been influenced by the climate of a source area. Based on the light mineral suite, rock fragments and feldspars are the most sensitive indicators of climate (Suttner and Dutta, 1986), these are quickly destroyed in a warm, humid climate, unless they are rapidly buried. Heavy minerals also may be informative about of climate. Sandstones of the La Meseta Formation are mainly feldspathic and lithic-feldspathic arenites and wackes, containing unstable and metastable heavy minerals (anphiboles, pyroxenes, epidote, garnet); thus, either rapid burial or a low degree of weathering is indicated (Marenssi, 1995). Detrital grains in samples of the La Meseta Formation usually are unaltered, although occasional clasts of feldspars and volcanic rock fragments do exhibit minor to moderate alteration. Historically, feldspars have been considered to be indicative of a humid source area (Folk, 1980) although James *et al.* (1981) determined that the amount of feldspar alteration is similar in wet and arid climates. Furthermore, stable isotope studies of molluscan macrofossils from the La Meseta Formation suggest a cooling trend during the Eocene with water temperatures between 7.9° and 11.7° C (Gadzicki *et al.*, 1992; Ditchfield *et al.*, 1994).

To sum up, sediments of the La Meseta Formation accumulated in marine to paralic environments. The source of sediments was located to the west-northwest along the present-day Antarctic Peninsula. The climate of the source area can not be unequivocally interpreted from petrologic studies but, based on paleobotanical evidence (discussed below), it was not warm. At the time of deposition of the middle part of the La Meseta Formation, Seymour Island was a low-relief coastal area but a mountainous highland region was located a few kilometers to the west. The altitudinal differences between both areas must have produced a climatic and biological gradient in the terrestrial environments.

EOCENE ANTARCTIC PENINSULA FLORA AND ENVIRONMENT

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. The La Meseta Formation has yielded fossil plant material from most of its stratigraphical column (Dusén, 1916; Cranwell, 1959; Askin and Fleming, 1982; Sadler, 1988; Torres *et al.*, 1994; Brea, 1998; Brea and Zuccol, 1996; Gandolfo *et al.*, 1998a). Megaflora has been collected from all but the lowest 120 m. The flower (Gandolfo *et al.*, 1998a), some tree trunks (Torres *et al.*, 1994), and most of the leaves (Gandolfo *et al.*, 1998b) are preserved in fine-grained heterolithic facies of tidal origin, especially from the middle part of the formation. Some other tree trunks and a few leaves come from coarse-grained channel-lags. Carbonaceous detritus, spores, and pollen are frequent throughout the fine grained facies. Askin (1992, 1995) reported that the Late Cretaceous and Paleocene plant community was dominated by conifer rainforest in the area of Seymour Island.

Gothan (1908) and Torres *et al.* (1994), studied fossil wood from the La Meseta Formation. Several coniferous

and dicotyledoneous (*Nothofagus*) woods were identified from the middle part 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 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-leaved forests exist today in southern South America. Rainfall in these areas is very high, mainly in summer and spring seasons, with an average precipitation from 1000-3000 mm/y. These areas currently contain the richest biota of the sub-Antarctic dominion. Freezing temperatures can prevail during several months of the year.

Case (1988) described the first megaflora from La Meseta Formation, indicating a dominance of the genus *Nothofagus*. Gandolfo *et al.* (1998a) recognized this genus and reported the presence of the families Dilleniaceae, Myricaceae, Myrtaceae, Lauraceae, and Grossulareaceae, as well. All but Lauraceae belong to the Antarctic Flora of Romero (1986). Based on morphological characters of 88 specimens collected from three localities of the middle part of the La Meseta Formation, Gandolfo *et al.* (1998a) described the forests as mixed mesofitic indicative of a seasonal cold-temperate rainy climate. In one of these localities, DPV 3/84 (GPS data: 64°13'58" S, 56°39'15" W), more than 300 samples were recovered and represent fossil foliage referred to *Tetracera patagonica* (Dilleniaceae), *Hydrangeiphylum affine* (Hydrangeaceae) and the families Nothofagaceae, Betulaceae, Myrtaceae, Myricaceae, Lauraceae, and Grossulariaceae (represented by a flower, Gandolfo *et al.*, 1998b; 1998a). 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 have lasted several months.

Based on a morphological analysis, Romero (1986) determined the climate and phytogeography of the flora

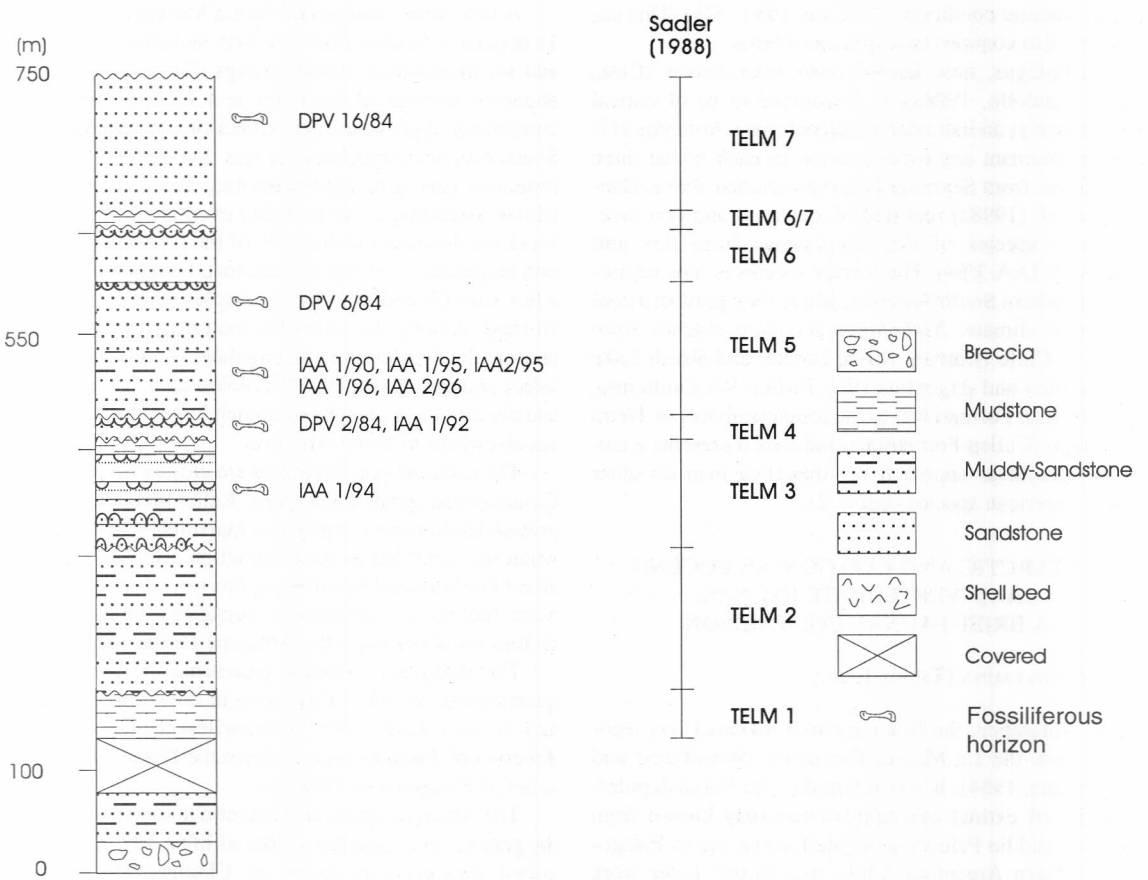

Figure 3. Stratigraphic section of La Meseta Formation (Eocene to ?early Oligocene) showing the land-vertebrate horizons and localities. *Sección estratigráfica de la Formación La Meseta (Eoceno-?Oligoceno temprano) mostrando los horizontes y las localidades con vertebrados terrestres.*

of the middle Eocene. He stated that the forests in Patagonia were wet subtropical with a mixture of Neotropical and Antarctic elements ("Paleoflora Mixta"). At the same time, the La Meseta paleoflora has a predominance of Antarctic elements, this suggests 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, Argentina).

In recent years, a growing body of information has been accumulated about the Eocene climate of the Antarctic Peninsula. Paleofloral data sets show that the middle-late Eocene was warmer than present, but not as warm as the Late Cretaceous through early-middle Paleocene. Seymour Island paleofloras RV-8200, IAA 1/90, and DPV 3/84 from TELM 5 seem to indicate a climatic drop that apparently correlates with the general climatic deterioration that occurred in the rest of the world at the end of the Eocene (Case, 1988). The compositions of these paleofloras indicate a cool, humid climate. A different situation characterizes the lower levels of the sequence, where the early-late Eocene flora of the locality RV-8425 (TELM 2) that was dominated by a large-leafed species of *Nothofagus* suggests "... a situation of ameliorating climatic conditions..." (Case, 1988: 525). This paleoflora also contains two species of ferns.

Nothofagus, now known from macrofossils (Case, 1988; Gandolfo, 1998a), 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 Seymour Island mentioned above. Gandolfo *et al.* (1998a) reported *N. serrulata* and two indeterminate species of the same genus from this unit (TELM 5, IAA 3/84). The former species is now restricted to southern South America, where they grow in a cool temperate climate. *Nothofagus 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 (Cullen Formation), and thus represents a closer geographical approach to Antarctica than do other South American species (figure 2).

ANTARCTIC AND PATAGONIAN EOCENE LAND-VERTEBRATE FAUNAS: A BRIEF FAUNAL COMPARISON

La Meseta fauna (Tables 1, 2)

In Antarctica, the first terrestrial mammal was recovered from the La Meseta Formation (Woodburne and Zinsmeister, 1984). It was referred to the Polydolopidae, a family of extinct marsupials previously known from strata of middle Paleocene to late Eocene age in Patagonia, southern Argentina, Chile, and Brazil. Later work within the same unit recorded the first running bird (Case *et al.*, 1987), and, subsequently, new terrestrial mammal remains were reported. A microbiotheriid (Goin and Carlini, 1995) was added to a second polydolopid taxon (Case *et al.*, 1988), and the first terrestrial placental, a Tardigrada or Vermilingua edentate (Carlini *et al.*, 1990). Between 1990 and 1996, new discoveries of cursorial and flying birds (Tambussi *et al.*, 1994, 1995), marsupials (Goin *et al.*, 1995; Candela and Goin, 1995), edentates (Vizcaíno and Scillato Yané, 1995), and South American ungulates (Hooker, 1992; Bond *et al.*, 1990; Vizcaíno *et al.*, 1997) notably increased our knowledge of the Eocene terrestrial Antarctic fauna. The known diversity of one of the mammal-bearing horizons of the La Meseta Formation (TELM 5) can be taken to represent essentially a single fauna (Vizcaíno *et al.*, 1998) and can be compared with Patagonian faunas. There are 12 reported terrestrial vertebrate taxa, 10 of which occur in a single level (Table 1). This land-vertebrate fauna, though numerically small, strongly suggests a middle Eocene age based on cladistic relationships of the sparnotheriodontids and polydolopids (Woodburne and Zinsmeister, 1984; Bond *et al.*, 1993). This age assignment correlates well with the middle Eocene age of the ichtiofauna found in the same depositional horizon (Cione and Reguero, 1994, 1998) and with age data from marine microfossils (Coccozza and Clarke, 1992).

A taxonomic analysis of the La Meseta fauna (Table 1) reveals a modest diversity that includes three avian and six mammalian ordinal groups (Table 2). The most abundant element of the fauna is a suite of marsupials comprising approximately six taxa (4 new genera). The South American ungulates are less diverse with two taxa (one new genus) being represented. This Eocene mammalian assemblage was probably even more diverse, because the documented diversity of the La Meseta Formation mammals is, of course, minimal, being derived from a few sites (9) and from small samples (less than 60 specimens). Among the terrestrial mammals, the dominant taxa are the South American ungulates (Sparnotheriodontidae) and the marsupials (Polydolopidae). They are not usually dominant elements in much larger thanatocoenoses elsewhere in South America.

The endemic polydolopines are closely related to the Casamayoran genus *Polydolops*. Relict taxa in the LMF, protodidelphid and derorhynine marsupials, indicate that whatever factor led to their extinction elsewhere did not affect the Antarctic Peninsula at this time. If these factors were biological, isolation is suggested, in that these factors could not reach the Antarctic Peninsula.

The tardigrade edentate represents the earliest unquestionable record of this group in the world (Vizcaíno and Scillato Yané, 1995). The earliest records in South America of Tardigrada come from the Deseadan (Oligocene) of Patagonia and Bolivia.

The Antarctic sparnotheriodontid taxon is endemic at the generic level, and has a close affinity with one undescribed Casamayoran taxon of Chubut Province (M. Bond, pers. comm., 1996).

Among the terrestrial birds, two flightless taxa were reported (a ?phororhacoid and a ratite). The ratite was

Table 1. Taxonomic list, stratigraphy, and references for the land vertebrates from the Eocene of Seymour Island, Antarctic Peninsula.*Lista taxonómica, estratigrafía y referencias de los vertebrados terrestres del Eoceno de la isla Seymour, Península Antártica.*

TAXA	STRATIGRAPHY	REFERENCES
MARSUPIALIA		
Polydolopidae	TELM 5	Woodburne and Zinsmeister, 1984; Case *et al.*, 1988; Goin *et al.*, 1995
Microbiotheriidae	TELM 5	Goin and Carlini, 1995; Goin *et al.*, 1995
Protodidelphidae	TELM 5	Goin *et al.*, 1995
Derorhynchid-like	TELM 5	Goin *et al.*, 1995
Dasyurid-like	TELM 5	Goin *et al.*, 1995
XENARTHRA		
Tardigrada indet.	TELM 4-5	Marenssi *et al.*, 1994; Vizcaíno and Scillato Yané, 1995
?LITOPTERNA		
Spranotheriodontidae	TELM 4-5-7	Bond *et al.*, 1990; Marenssi *et al.*, 1994; Vizcaíno *et al.*, 1997
ASTRAPOTHERIA		
Trigonostylopidae	TELM 5	Bond *et al.*, 1990; Hooker, 1992; Marenssi *et al.*, 1994
RATITAE		
Family indet.	TELM 7	Tambussi *et al.*, 1994
?PHORUSRHACOID	TELM 7	Case *et al.*, 1987
FALCONID	TELM 5	Tambussi *et al.*, 1995

found in the upper levels of the unit (ZPAL 4, TELM 7). Ratites are mainly distributed in the southern continents and probably have a Gondwanan origin (e.g. Cracraft, 1975). The record of a ?phororhacoid bird is consistent with the previous discovery of avian ichnites (Covacevich and Rich, 1982) on Fildes Peninsula, King George Island. Several of these footprints may belong to phororhacoids.

Patagonian faunas (Tables 3, 6)

Paleocene continental Patagonian mammal faunas include the middle Paleocene Tiupampian, the middle Paleocene Itaboraian and the late Paleocene Riochican (see tables 3 and 4). Only the Itaboraian and Riochican faunas share familial and generic taxa with LMF. Two polydolopines, *Eudolops* and ?*Polydolops*, a primitive ?didelphoid, *Derorhynchus*, and several protodidelphid marsupials (table 3) are present in the Itaboraian Fauna. Within the ungulates, Trigonostylopidae is present with one genus, *Shecenia*. The South American ungulates are represented by seven families placed in four orders. Four families of Notoungulata are recorded in this age. The Riochican Fauna records three families of marsupials, the Polydolopidae being one of them. Polydolops is the only genus of this family present in the Riochican Age (Bond *et al.*, 1995).

These ages are characterized by the dominant presence of brachyodont ungulates (92% of the fauna), although a few mesodont types (8%) occur in the Riochican (Pascual and Ortiz Jaureguizar, 1990). This fact suggests the existence of a forested habitat in the middle to late Paleocene. Additionally, the presence of crocodiles, alligators, boid snakes, and ?pelomedusid turtles indicate at least warm temperatures. The paleofloral record suggests that tropical to subtropical coastal mangrove environments alternated with inland sylvan and sclerophylic forest or savannahs (Petriella and Archangelski, 1975).

The mammal faunas of the Eocene of Patagonia include the early Eocene Casamayoran, the relatively poorly known middle Eocene Mustersan (both known almost exclusively from Argentine Patagonia), the ?late Eocene Divisaderan (very incompletely known), and the late Eocene "Tinguiririan" from central Chile. Only the Casamayoran and Mustersan (included in the Pancasamayoran Subcycle of Pascual and Jaureguizar, 1990) have taxonomic similarities (in age and taxonomic composition) with LMF. The Patagonian mammal-bearing horizons are included in the Sarmiento Formation composed of pyroclastic-derived sediments (Spalletti and Mazzoni, 1978). The Casamayoran (early Eocene) is perhaps the best known and best sampled of the South American Cenozoic ages (Simpson, 1967). The best representative localities yielding Casamayoran mammals cluster around 45°, 48° S (Gran Barranca –45°42' S, 68°42' W–, Cañadón Vaca, Cañadón Hondo, and Valle Hermoso from Chubut Province). Mammals from these localities are listed in table 5. A striking feature of the Casamayoran fauna is its domination by extremely low-crowned ungulates (83%), including several primitive lineages such as henricosborniids and isotemnids. The South American ungulates are represented by 20 families

Table 2. Taxonomic list for La Meseta terrestrial mammals, Seymour Island, Antarctica.*Lista taxonómica de los mamíferos terrestres de la Formación La Meseta, Isla Seymour, Antártida.*

Polydolopimorphia	
	Family Polydolopidae
	Polydolops dailyi
	Polydolops seymouriensis
	Polydolops sp. nov.
Didelphimorphia	
	Family Protodidelphidae
	gen. et sp. nov. 1
	Family indet.
	gen. et sp. nov. 2
Microbiotheria	
	Family Microbiotheriidae
	gen. et sp. nov. 3
	gen. et sp. indet.
?Dasyurida	
	Family indet.
	gen. et sp. nov. 4
Order indet.	
	Family *incertae sedis*
	gen. et sp. nov. 5
Edentata	
	Tardigrada or Vermilingua
	Tardigrada indet.
?Litopterna	
	Family Sparnotheriodontidae
	gen. et sp. nov.
Astrapotheria	
	Family Trigonostylopidae
	Trigonostylops
Mammalia *incertae sedis*	
	Family indet.

placed in four orders. Notoungulates dominate, with seven families present in this age. In contrast, litoptern diversity during the Casamayoran is surprisingly low in view of the earlier diversity of the group. Sparnotheriodontids and trigonostylopids were part of this fauna. Within the Sparnotheriodontidae, *Victorlemoinea* (= *Sparnotheriodon*, junior synonym) is the best represented genus. A modest radiation of trigonostylopids occurred during the Casamayoran. Only seven marsupial families with nine genera are present in the Casamayoran. The polydolopines had a southern distribution and in the Casamayoran, three genera were present, including *Polydolops*. The polydolopines were small, rodent-like marsupials that appeared last in the "Tinguiririca" (late Eocene) of Chile (Wyss *et al.*, 1990). Coincidently, Tinguiririca (34°59' S, 70°26' W) represents the northernmost distribution of this subfamily. The Mustersan Age (tentatively assigned to the middle Eocene) is known almost exclusively from Patagonia. The best representative localities yielding Mustersan mammals are Gran Barranca, Cerro del Humo and La Gran Hondonada from Chubut Province. Mammals from these localities are listed in table 6. Notoungulates are the dominant group among the ungulates, with six families present in this age. The lower diversity among Mustersan ungulates (4 orders and 10 families) almost certainly reflects the relatively short duration of the Mustersan and the fact that it is poorly sampled. No sparnotheriodontids are recorded in this fauna. The diversity of the marsupials is low, consisting of two families with two genera.

Environmental and climatic data are provided by the "Paleoflora Mixta" ("cold temperate flora" + subtropical flora") of Romero (1978) from Río Turbio Formation (Eocene), Santa Cruz Province. Throughout the Casamayoran and Mustersan gramineous phytoliths became more abundant (Spalletti and Mazzoni, 1978) suggesting that grassland environments began to be prominent in middle latitudes (ca. 45°S). In addition, the dental features of some marsupials with "plagiaulacoid" specializations (e.g. Polydolopidae) suggest the presence of scansorial and probably arboreal types that one would expect to occupy forested habitats (Pascual, 1980). The absence of crocodiles and boid snakes after the Casamayoran age suggests a climatic deterioration at that time.

HIGH LATITUDE EFFECT

Increasing latitudinal separation yields decreases in faunal similarities between localities (Flyn, 1984). Today, the Seymour Island land vertebrate-bearing localities are separated from the bulk of the Casamayoran-Mustersan localities by more than 15°. If we consider, on the basis of geologic and paleogeographic data (Lawver *et al.*, 1992; Shen, 1995), that the Drake Passage (about 1000 km wide) started to open at about 36 Ma, we can assume that, prior that time, the distance between Antarctic Peninsula and Patagonia ought to have been shorter.

Highly distinctive Late Cretaceous and Eocene high latitude terrestrial vertebrate faunas have been described (Brouwers *et al.*, 1987; McKenna, 1980; Hickey *et al.*, 1983; Rich *et al.*, 1988) and each is characterized by special attributes related to the highly distinctive paleoenvironment in which each fauna developed at different times. It is accepted that several types of environmental factors could effect latitudinal zonation (Hallam, 1984). 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 from the region ("high latitude heterochroneity" = differential appearance of taxa between high and mid- to low latitudes). The same authors recognized such high-latitude regions as centers of origin of novel adaptations leading to speciation. Case (1989) expanded Zinsmeister and Feldmann's (1984) concept to the terrestrial fauna, especially the marsupials ("Weddellian marsupials"), from Seymour Island.

Lewin (1983) hypothesized that the high-latitude regions seem more suitable for the origin of new taxa than areas of low latitude, such as the tropics. Also, it is apparent that many austral biotas (high-latitude biotas) have demonstrably lower taxonomic diversities than their lower-

Table 3. Taxonomic list for the Itaboraian mammals from Patagonia, Argentina. *Lista taxonómica de los mamíferos itaboraianos de Patagonia, Argentina.*

- Polydolopimorphia
  - Family Polydolopidae
    - *Epidolops*
    - *?Polydolops*
- Didelphimorphia
  - Family Protodidelphidae
    - *Bobbscaefferia*
    - *Guggenheimia*
    - *Protodidelphis*
  - ?Didelphoidea
    - aff. *Itaboraidelphys*
    - aff. *Didelphopsis*
    - *Derorhynchus*
    - *Minusculodelphis*
    - *Marmosopsis*
    - *Monodelphopsis*
- Peradectida
  - Family Caroloameghiniidae
    - *Procaroloameghinia*
- Microbiotheria
  - Family Microbiotheriidae
    - *Mirandatherium*
- Sparassodonta
  - Family Borhyaenidae
    - *Patene*
- ?Metatheria
  - Family indet.
    - *Gashternia*
- Condylarthra
  - Family Didilodontidae
    - *Ernestokokenia*
- Notoungulata
  - Family Henricosborniidae
    - *Henricosbornia*
    - *?Peripantostylops*
  - Family Isotemnidae
    - *?Isotemnus*
  - Family Interatheriidae
    - *?Transpithecus*
  - Family Oldfielthomasiidae
    - *Kibenikhoria*
    - *Colbertia*
    - *Camargomendesia*
    - *Itaboraitherium*
- ?Litopterna
  - gen. indet.
- Astrapotheria
  - Family Trigonostylopidae
    - *Shecenia*

Table 4. Taxonomic list for the Riochican mammals from Patagonia, Argentina.

- Polydolopimorphia
  - Family Polydolopidae
    - *Polydolops*
  - Family Prepidolopidae
    - aff. *Prepidolops*
- 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*

latitude counterparts (Sheehan, 1986). Various climatic and ecological factors influence latitudinal gradients in mammalian diversity and taxonomic composition, and they strongly influence the formation of latitudinal faunal barriers, as well (Simpson, 1964; Flessa, 1975; McCoy and Connor, 1980). One of these factors could be a cooling of the climate in the Antarctic Peninsula during the Eocene; many aspects of the flora and fauna may have been affected if the temperatures fell below certain threshold levels. Also, at high latitudes, a prolonged period (several months?) of continuous darkness (assuming that the position of the earth's rotational pole with regard to Seymour Island was not signicantly different than at present) could have had an important effect on the distribution of some taxa of the fauna. In this regard, the paleolatitude of the Antarctic Peninsula during the Eocene was high (nearly 63° S). Although the terrestrial biota was living far from the Polar Circle (85° S), it could have routinely experienced 1 to 3 months of complete winter darkness as

Table 5. Taxonomic list for the Casamayoran mammals from Patagonia, Argentina. *Lista taxonómica de los mamíferos casamayorenses de Patagonia, Argentina.*

- Didelphimorphia
  - Family Didelphidae
    - *Coona*
- Microbiotheria
  - Family Microbiotheriidae
    - *Eomicrobiotherium*
- Peradectida
  - Family Caroloameghiniidae
    - *Caroloameghinia*
- Sparassodonta
  - Family Proborhyanidae
    - *Arminiheringia*
  - Family Borhyaenidae
    - *Nemolestes*
  - Family Hathliacynidae
    - *Patene*
- Polydolopimorphia
  - Family Polydolopidae
    - *Amphidolops*
    - *Eudolops*
    - *Polydolops*
- Edentata
  - Family Dasypodidae
    - *Astegotherium*
    - *Meteutatus*
    - *Prostegotherium*
    - *Utaetus*
  - Family Pampatheriidae
    - *Machlydotherium*
- Condylarthra
  - Family Didolodontidae
    - *Didolodus*
    - *Enneoconus*
    - *Ernestokokenia*
    - *Paulogervaisia*
    - *Proectocion*
- Litopterna
  - Family Protolipternidae
    - *Asmithwoodwardia*
  - Family Proterotheriidae
    - *Anisolambda*
    - *Guilielmofloweria*
    - *Josepholeidya*
    - *Ricardolydekkeria*
  - Family Macraucheniidae
    - *Polymorphis*
  - Family Adianthidae
    - *Proectocion*
- Notopterna
  - Family Indaleciidae
    - *Adiantoides*
  - Family Amilnedwarsidae
    - *Amilnedwarsia*
    - *Rutimeyeria*
    - *Ernestohaeckelia*
- ?Litopterna
  - Family Sparnotheriodontidae
    - *Victorlemoinea*
    - *Sparnotheriodon*
- Notoungulata
  - Family Henricosborniidae
    - *Henricosbornia*
    - *Othnielmarshia*
    - *Peripantostylops*
  - Family Notostylopidae
    - *Eduardotrouessartia*
    - *Homalostylops*
    - *Notostylops*
  - Family Oldfieldthomasiidae
    - *Maxschlosseria*
    - *Oldfieldthomasia*
    - *Paginula*
    - *Ultrapithecus*
  - Family Archaeopithecidae
    - *Acropithecus*
    - *Archaeopithecus*
  - Family Interatheriidae
    - *Antepithecus*
    - *Notopithecus*
    - *Transpithecus*
  - Family Archaeohyracidae
    - *Eohyrax*
  - Family Isotemnidae
    - *Anisotemnus*
    - *Isotemnus*
    - *Pleurostylodon*
    - *Thomashuxleya*
  - Family Notohippidae
    - *Plexotemnus*
- Astrapotheria
  - Family Trigonostylopidae
    - *Trigonostylops*
  - Family Astrapotheriidae
    - *Albertogaudrya*
    - *Scaglia*
- Pyrotheria
  - Family Pyrotheriidae
    - *Carolozittelia*

now occurs. Thus, 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). Most forest trees, such as some *Nothofagus* spp. and araucarians, are evergreen; therefore, they would have retained green foliage even during several months of darkness, as is evident in extant taiga floras. Hence, Antarctic ungulates could continue to browse, stripping off twigs and saplings from evergreen trees (Vizcaíno *et al.*, 1998). Unfortunately, there is no direct evidence that the terrestrial vertebrates from the Eocene of Antarctica were adapted to crepuscular or nocturnal conditions. We could speculate that seasonal migration of medium- and large-sized mammals (trigonostylopids and sparnotheriodontids) might have occurred, as it does in many modern, large, polar mammals, which move over great distances annually. Nevertheless, by the Eocene, the Antarctic Peninsula was separated from the

Table 6. Taxonomic list for the Mustersan mammals from Patagonia, Argentina. *Lista taxonómica de los mamíferos mustersenses de Patagonia, Argentina.*

Sparassodonta		
	Family Borhyaenidae	
		Plesiofelis
		Procladosictis
Polydolopimorphia		
	Family Polydolopidae	
		Polydolops
Edentata		
	Family Dasypodidae	
		Meteutatus
Condylarthra		
	Family Didolodontidae	
		Xesmodon sp.
Litopterna		
	Family Proterotheriidae	
		Heteroglyphis
		Polyacrodon
Notoungulata		
	Family Notostylopidae	
		Otronia
	Family Oldfieldthomasiidae	
		Tsamnichoria
	Family Interatheriidae	
		Guilielmoscottia
		?Notopithecus
	Family Archaeohyracidae	
		Pseudhyrax
		?Eohyrax
	Family Isotemnidae	
		Distylophorus
		Periphragnis
		Rhypodon
	Family Notohippidae	
		Puelia
Astrapotheria		
	Family Trigonostylopidae	
		Trigonostylops
	Family Astrapotheriidae	
		Astraponotus

southernmost part of South America; therefore, it was not possible for large mammals to migrate to the distant north. At present, we cannot resolve whether these mammals (mainly the large ones) occupied the area only seasonally or whether they were permanent residents of these high latitudes. Small marsupials might have survived such a regime by seeking natural shelters (e.g., by burrowing). Extant South American marsupials have several adaptations (e.g. incrassated tail, daily torpor and/or hibernation) that may have been present in the Antarctic taxa.

The LMF is important paleoecologically because it documents the coexistence of two ecologically similar, primitive groups of South American ungulates. sparnotheriodontids and trigonostylopids share a number of dental characteristics that may be adaptations to Antarctic habitats (*Nothofagus* forests). As Marenssi *et al.* (1994) pointed out, the striking features of these mammals are brachyodoncy and the particular structure of the enamel. Brachyodoncy is associated with browsing herbivores that are adaptated to forest habitats (Janis, 1984). In Patagonia, the latest community dominated by low-crowned (brachyodont) herbivores is the middle Eocene Mustersan fauna. The appearance of hypsodoncy is documented in the late Eocene Tinguiririca fauna (Wyss *et al.*, 1994), and the fauna from the presumably coeval localities of Cañadón Blanco and Lomas Blancas (Reguero, 1993) in Chubut Province. Hypsodoncy probably is related to climatic changes, the establishment of seasonally drier, more open habitats, and more abrasive diets (Janis, 1984). The numerical dominance of the sparnotheriodontids among the ungulates on Seymour Island could reflect adaptation of these animals to high-latitude climates.

Our interpretation of the structure of the La Meseta land-vertebrate community (Vizcaíno *et al.*, 1995a, 1995b, 1998) is in accordance with presumably analogous, present-day environments, such as those at the austral end of Patagonia (Tierra del Fuego Province).

SUMMARY OF SIGNIFICANCE OF TERRESTRIAL FAUNA OF SEYMOUR ISLAND

1. The far south was occupied during the Eocene by a terrestrial biota composed of plants and vertebrates having at least temperate climatic adaptations. During a period of global cooling, such as the one that occurred during the middle-late Eocene, a distinctive, high-latitude flora was present on Seymour Island, Antarctica. Striking differences in the composition of this flora with respect to other paleofloras of southern distribution are evident. The Eocene Seymour Island flora was dominated by Antarctic taxa, whereas the Eocene Patagonian paleofloras were dominated by a mixture of Neotropical and Antarctic taxa (Río Turbio Formation).

2. The LMF shares important similarities with the Riochican, Casamayoran, and Mustersan faunas; however, this does not necessarily indicate an assignment of this fauna to one of these ages. The phylogenetic relationships of the Antarctic sparnotheriodontid and polydolopine taxa suggest that they could have been derived from Casamayoran taxa, and thus, suggest a younger age for the La Meseta Formation.

3. The numerical dominance of the sparnotheriodontids among the ungulates and the polydolopids among the marsupials in the LMF could have resulted from adaptations of these groups to high-latitude paleoenvironments in combination with isolation in Antarctica.

4. In Patagonia, the notoungulates were the most diverse (morphologically as well as taxonomically) and successful South American ungulate group. Four families are represented in the Itaboraian, seven in the Riochican and the Casamayoran, and 10 in the Mustersan of Patagonia. Nevertheless, this group is notably absent in the La Meseta fauna.

5. No species are shared between Antarctic and Patagonian assemblages in the middle Eocene. Only two genera, *Polydolops* and *Trigonostylops*, are common taxa between the LMF and the Casamayoran, and Mustersan faunas of Patagonia. This supports differentation of two distinct biogeographic regions.

6. Among marsupials, six species only known from the LMF fauna demonstrate significant endemism. The diversity of the tiny Antarctic marsupials is greater than those of the Pancasamayoran.

7. The occurrences of protodidelphids and derorhynchines are thought to represent temporal relicts and to indicate isolation of this part of Antarctica during the early Eocene.

8. The presence of hoofed, medium-sized herbivore taxa having low-crowned teeth in peninsular Antarctica during the Eocene to ?early Oligocene suggests a persistence of archaic forms that lived in Patagonia prior to the climatic deterioration in this region.

9. The geological and biological evidence discussed here suggests that peninsular Antarctica was located at a high latitude during the early-middle Eocene, just as it is today. Peninsular Antarctica contained a distinctive terrestrial fauna, the high-latitude position of this fauna suggests that climate and isolation were the most important factors affecting the distribution of these mammals.

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