

COMMUNITY STRUCTURE OF EOCENE TERRESTRIAL VERTEBRATES FROM ANTARCTIC PENINSULA

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ABSTRACT. The record of Paleogene terrestrial vertebrates from Antarctica is restricted to the shallow marine water sediments of the La Meseta Formation (Eocene) of Seymour Island (56° 43'W 64° 14'S). Mammals are represented by marsupials, edentates and ungulates. Among birds, a falconid and two ground dwellers (a ratite and a ?phorusrhacoid) were recorded. Estimates of body mass and dietary specializations are proposed for these species. Medium- to large-sized carnivorous mammals (greater than 1 kg body mass), such as South American borhyaenid marsupials, are not yet recorded, although their presence is expected. Their absence is interpreted as a consequence of the low proportion of homeothermic carnivorous in all modern vertebrate communities and the relatively small sample recovered to date. The carnivorous role could have been partially fulfilled by some of the birds (falconid and ?phorusrhacoid).

RESUMEN. ESTRUCTURA DE LA COMUNIDAD DE VERTEBRADOS TERRESTRES DEL EOCENO DE LA PENÍNSULA ANTÁRTICA. El registro de vertebrados terrestres del Paleógeno de Antártida está restringido a los sedimentos marinos someros de la Formación La Meseta (Eoceno) de la isla Seymour (Marambio; 56° 43'W 64° 14'S). Los mamíferos están representados por marsupiales, edentados y ungulados. Entre las aves se registraron un falcónido y dos formas no voladoras (una ratite y un probable fororraco). Se estimaron las masas corporales y los hábitos alimenticios de los distintos taxones. Aunque su presencia es esperable, no se registraron mamíferos carnívoros con masa corporal superior a 1 kg, como podrían ser los marsupiales borhiénidos. Su ausencia se explica como una consecuencia de la baja proporción de carnívoros homeotérmicos, tal como lo reflejan las comunidades de vertebrados actuales, y la relativamente pequeña muestra recuperada. El papel de los carnívoros podría haber sido parcialmente cubierto por algunas aves (falcónido y fororraco).

KEY WORDS. Seymour Island. Antarctica. Eocene. Land vertebrates. Palaeoecology.

PALABRAS CLAVE. Isla Seymour (Marambio). Antártida. Eoceno. Vertebrados terrestres. Paleoecología.

INTRODUCTION

The record of Tertiary terrestrial vertebrates from Antarctica is almost completely restricted to the shallow-water marine sediments of the Eocene—?early Oligocene La Meseta Formation of Seymour Island, close to the northern tip of the Antarctic Peninsula (56° 43'W 64° 14'S) (figure 1).

The assemblage comprises several mammals (marsupials, edentates and ungulates) and birds (prey and flightless birds), representing a wide range of body sizes and different ways of life. Up to now, they were mainly studied from the systematic and paleobiogeographic points of view. Herein, we propose a preliminary reconstruction of their paleoecological relationships.

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BACKGROUND

GEOLOGICAL SETTING

All the terrestrial vertebrates from Seymour Island come from the Eocene—?early Oligocene La Meseta Formation, consisting of approximately 650 m of poorly consolidated, shallow-water marine sediments. Elliot and Trautman (1982) divided this formation into three informal members that were thought to represent different parts of a delta system. Sadler (1988) recognized seven major lithofacies units (named TELM 1-7) as shown in figure 2. Finally, Marensi *et al.* (1998) subdivided the La Meseta aloformation into six alomembers. Mammals were recovered from TELMs 3-5 and 7, and birds from TELMs 5 and 7 (table 1). For further description of localities bearing land vertebrates see Marensi *et al.* (1994) and Vizcaíno *et al.* (1997b).

PALEOFLORA

The paleoflora recovered from La Meseta Formation is composed of trunks, leaves, cones (Brea, 1996), and

flowers (Gandolfo *et al.*, 1991). These suggest the presence of nearby forest environment.

Abundant plant remains characterize TELM 5, with *Nothofagus* being the dominant angiosperm. Other angiosperm families recorded were Dilleniaceae, Hydrangeaceae, Betulaceae, Myrtaceae, Myricaceae, Lauraceae, and Grossulariaceae (Gandolfo *et al.*, 1998). Gymnosperms are represented by Cupressaceae, Podocarpaceae (Brea and Zucol, 1996; Brea, 1998), and Araucariaceae (Askin, 1995). The composition of this

flora resembles those of the Eocene of Southern Argentina, río Guillermo (Santa Cruz Province), and Cullen (Tierra del Fuego Province), which were interpreted as indicating a cool, humid climate (Gandolfo, 1994).

LAND VERTEBRATES

Until now, known land vertebrates from the La Meseta Formation are restricted to birds and mammals, many of which are represented by fragmentary material. Their

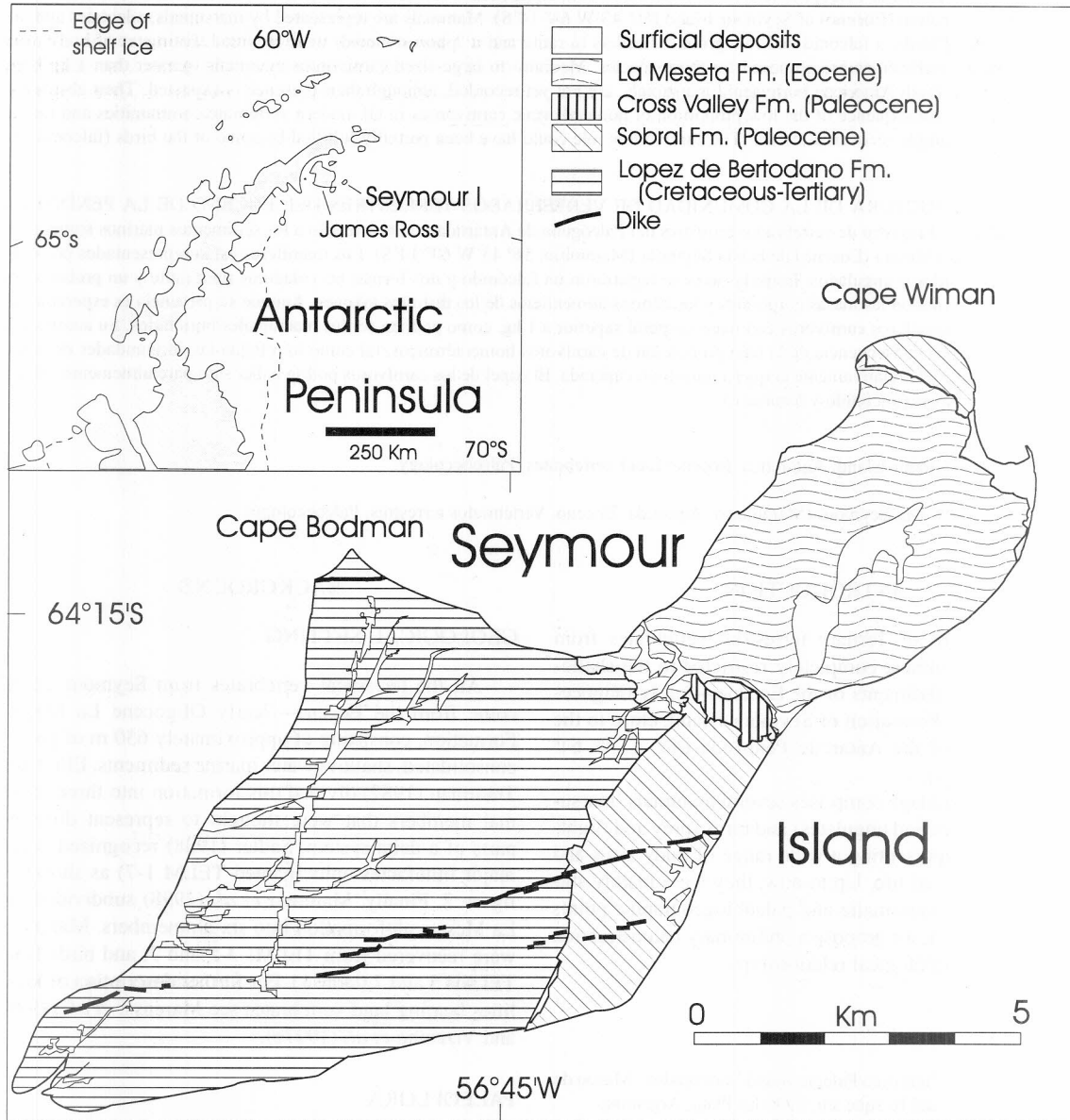


Figure 1. Map of Seymour Island showing the La Meseta Formation distribution. *Mapa de la isla Seymour (Marambio) que muestra la distribución de la Formación La Meseta.*

stratigraphic position is shown in figure 2. Body masses were estimated following equations provided by Campbell and Marcus (1992) and Damuth (1990), and by comparison with related fossil or extant taxa. Dietary specializations were inferred from tooth morphology (when available) or by comparison with related fossil or extant taxa.

Three different orders of birds are known. They include two big ground-dwellers and a flying bird of prey. Case *et al.* (1987: 1280) discovered the anterior part of a beak from a probable phorusrhacoid (Ralliformes), "a gigantic, (?)flightless, predaceous bird", in the upper levels (TELM 6-7). We estimate that its body mass was approximately 40 kg.

A ratite (Palaeognathae Pycraft, Ratitae Wetmore) was also found in TELM 7 (Tambussi *et al.*, 1994). Living representatives of this group include several large

body-sized species (20-130 kg) such as rheas (South America), ostriches (Africa), cassowaries and emus (Australia and New Guinea), and the 1.5-2.5 kg kiwis (New Zealand). Ratites inhabit open grasslands such as steppes and savannas, open areas with scrub forests, as well as humid or swampy forests and scrubs. Usually, they feed on green vegetable matter but also on insects and other animal prey. Estimated body mass of the Antarctic specimen is approximately 60 kg.

Tambussi *et al.* (1995) reported a polyborin falconid (Accipitriformes) from TELM 5. Living polyborines are vulture-like falconids with scavenging habits, but sometimes they include live prey (vertebrates and invertebrates) and plant matter in their diet. Living species of this subfamily occur exclusively in the Americas, mainly in the Neotropical Region. They live in diverse habitats, from dry shrub woodlands to tropical lowland wet

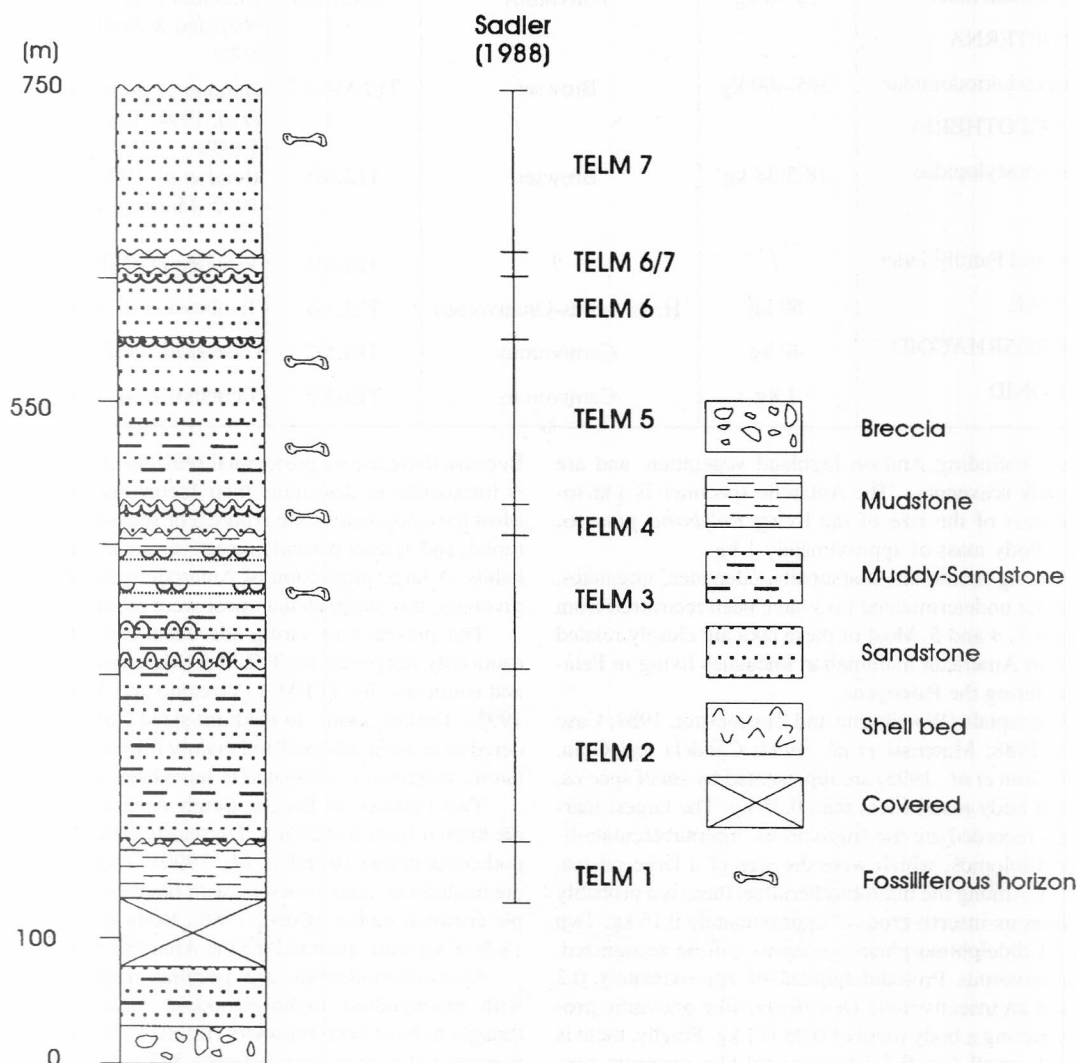


Figure 2. Stratigraphic section of La Meseta Formation after Sadler (1988). *Sección estratigráfica de la Formación La Meseta sensu Sadler (1988).*

Table 1. Synopsis of the land vertebrate taxa recorded in the La Meseta Formation. *Cuadro sinóptico de los vertebrados terrestres registrados en la Formación La Meseta.*

TAXA	ESTMATED MASS	INFERRED DIET	STRATIGRAPHY	REFERENCES
MARSUPIALIA				
Polydolopidae	0.3 kg	Frugivorous	TELM5	Woodburne & Zinsmeister 1984; Case <i>et al.</i> 1988
Microbiotheriidae	0.3 kg	Frugivorous-Insectivorous	TELM5	Goin <i>et al.</i> 1995
Protodidelphidae	0.3 kg	Omnivorous	TELM5	Goin <i>et al.</i> 1995
Derorhynchid-like	0.05-0.1 kg	Insectivorous	TELM5	Goin <i>et al.</i> 1995
Dasyurid-like	ca 0.2 kg	Omnivorous-Insectivorous	TELM5	Goin <i>et al.</i> 1995
XENARTHRA				
Tardigrada indet.	ca 10 kg	Folivorous	TELM4-5	Marenssi <i>et al.</i> 1994; Vizcaíno & Scillato Yané 1995
?LITOPTERNA				
Sparnotheriodontidae	395-400 kg	Browser	TELM4-5-7	Bond <i>et al.</i> 1990; Marenssi <i>et al.</i> 1994; Vizcaíno <i>et al.</i> , 1997b
ASTROPOTHERIA				
Trigonostylopidae	18.5-38 kg	Browser	TELM5	Bond <i>et al.</i> 1990; Hooker 1992; Marenssi <i>et al.</i> 1994
Order and Family indet.	?	?	TELM3	Vizcaíno <i>et al.</i> 1997b
RATITAE	60 kg	Herbivorous-Omnivorous	TELM7	Tambussi <i>et al.</i> 1994
?PHOROSRHACOID	40 kg	Carnivorous	TELM7	Case <i>et al.</i> 1987
FALCONID	1 kg	Carnivorous	TELM5	Tambussi <i>et al.</i> 1995

forests, including Andean highland vegetation, and are generally scavengers. The Antarctic specimen is a tarso-metatarsus of the size of the living *Polyborus plancus*, with a body mass of approximately 1 kg.

Among mammals, marsupials, edentates, ungulates, and other undetermined taxa have been recovered from TELMs 3, 4 and 5. Most of these taxa are closely related to South American mammalian lineages living in Patagonia during the Paleogene.

Marsupials (Woodburne and Zinsmeister, 1984; Case *et al.*, 1988; Marenssi *et al.*, 1994; Candela and Goin, 1995; Goin *et al.*, 1995) are represented by small species, all with body masses less than 0.35 kg. The largest marsupials recorded are the frugivorous, multituberculate-like polydolopids, which were the size of a large rat (ca. 0.3 kg). Among the microbiotheriidae, there is a probably frugivorous-insectivorous of approximately 0.15 kg. Two taxa of didelphimorphian opossums can be recognized, an omnivorous Protodidelphidae of approximately 0.2 kg, and an insectivorous *Derorhynchus*-like opossum, probably having a body mass of 0.05-0.1 kg. Finally, there is an odd, small (ca. 0.2 kg) dasyurid-like opossum probably with omnivorous-insectivorous habits that is impossible to place in any of the known South American families.

Because there are no postcranial remains of these taxa, it is impossible to determine their locomotor adaptations. Most living opossums are arboreal or semi-arboreal, nocturnal, and at least partially insectivorous in their feeding habits. A large proportion of Antarctic opossums are frugivorous; this suggests that most were arboreal.

The presence of tardigrade edentates (sloths) was cautiously suggested for TELM 5 (Marenssi *et al.*, 1994) and confirmed for TELM 4 (Vizcaíno and Scillato-Yané, 1995). Tertiary small- to medium-sized sloths are considered to be semi-arboreal and mainly folivorous. The Antarctic specimen is estimated to have been nearly 10 kg.

Two families of Eocene South American ungulates are known from Antarctica; Trigonostylopidae and Sparnotheriodontidae (Bond *et al.*, 1990). Trigonostylopids are medium to large browsers, with brachyodont and simple crowned molars (Bond, 1986). Body mass values of 18.5/38 kg were obtained for the Antarctic specimen.

Sparnotheriodontids are peculiar, large ungulates, with brachyodont lophoselenodont molars; they are thought to have been browsers (Bond, 1986). Body mass is estimated to have been between 395 and 440 kg.

Taxonomic information along with data on body sizes, diets, and the stratigraphic representation of the terrestrial

vertebrates from the La Meseta Formation are presented in table 1.

DISCUSSION

Body size provides a rough indication of the niche diversity (Van Valen, 1971). This descriptor was applied to early Tertiary ungulates from Patagonian by Cifelli (1985). The distribution of body sizes among land vertebrates of the La Meseta Formation varies from 0.1-0.3 to 200-300 kg (figure 3a). Two distinct increments characterize mammals; one separates small marsupials from eutherians, and the other distinguished medium-sized tardigrades and trigonostilopids from large sparnotheriodontids. Birds occur in both groups; the falconid is associated with the marsupials, and the ground dwellers with the medium-sized mammals. It is remarkable that the most abundant ungulate remains from Antarctica are large sparnotheriodontids, which are only sparsely represented in Patagonia. If they were gregarious, this might account for their relative abundance with respect to the trigonostilopids.

From another point of view, mammalian dietary specializations seem not to have been very diverse. Most were herbivorous, and a few were partially or fully insectivorous. Polydolopids and protodidelphids were frugivorous, and microbiotheriids (and Family *inc. sedis*) were frugivorous/insectivorous. The *Derorhynchus*-like opossum was insectivorous, whereas tardigrades and ungulates were folivorous and browsers, respectively. Among the birds, the ratite was herbivorous, and the falconid and the phorusrhacoid carnivorous scavengers or predators.

The herbivorous mammals are closely associated with forested habitats. Frugivorous marsupials, such as polydolopids, presumably were well adapted for the consumption of relatively hard food items, such as seeds,

some fruits, and insects with a hard exoskeleton. A forested environment seems to be appropriate for large browsers at high latitudes, such as moose in North America, where they manage to survive through the dark winters by feeding on twigs and saplings.

Insectivorous opossums are invariably small, whereas the omnivorous opossum is the largest didelphimorphian recorded.

The absence of medium to large carnivorous mammals, such as those belonging to some South American lineages, is remarkable, because contemporaneously in Patagonia, carnivorous marsupials (Sparassodonta) were well differentiated. The range includes small taxa (Hathlyacinidae) to the medium-sized Borhyeanidae and the large and highly specialized Proborhyaenidae (Marshall, 1978).

The absence of carnivorous marsupials in Antarctica may be an artifact of the limited number of specimens (approximately 50 specimens housed at the Museo de La Plata). It is useful to recall that in modern mammalian predator/prey systems, the prey/predator ratio usually reaches about 50:1 (Farlow, 1993). As mentioned above, the carnivore role would have been partially fulfilled by some birds -the falconids and phorusrhacoids.

Some restrictions to the model proposed must be considered. The sample is not taphonomically biased because the largest sparnotheriodontid teeth were recovered while sieving in the same sites that yielded the tiny marsupials. Moreover, the analysis is predicated solely on the presence of taxa, not on their abundance.

The stratigraphic provenance may be also discussed. All mammals and the falconid were recorded in the same horizon of TELM 5 (except for the sloths). The two ground-dwelling birds were recovered from the uppermost level TELM 7 together with sparnotheriodontids, already mentioned as relatively abundant in TELM 5. Because the

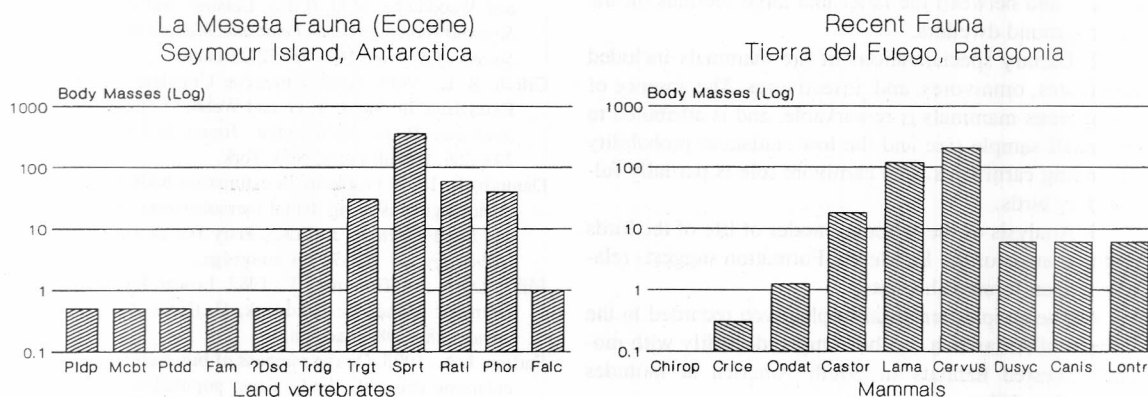


Figure 3. Distribution of body masses of terrestrial vertebrates of the La Meseta Formation (left), and Recent land mammals of Tierra del Fuego (right). Pldp: Polydolopidae, Mcbt: Microbiotheriidae, Ptdd: Protodidelphidae, Fam: derorhynchid-like, Dsd: dasyurid-like, Trdg: Tardigrada, Trgt: Trigonostylopidae, Sprt: Sparnotheriodontidae, Rati: Ratitae, Phor: ?Phorusrhacoid, Falc: Falconidae, Chirop: Chiroptera, Crice: Cricetidae, Ondat: *Ondatra*, Castor: *Castor*, Lama: *Lama*, Cervus: *Cervus*, Dusyc: *Dusycion*, Canis: *Canis*, Lontra: *Lontra*. / Distribución de masas corporales de los vertebrados terrestres de la Formación La Meseta (izquierda) y de los mamíferos terrestres actuales de Tierra del Fuego (derecha).

ratite could be regarded as an artifact of a widespread Gondwanan distribution (Woodburne and Case, 1995), it could be anticipated to occur in the lower levels. Land vertebrates of the La Meseta Formation can be regarded to represent mainly a single fauna.

Finally, the modern land vertebrate community from the southern extreme of South America (Tierra del Fuego, 52°S - 55°S), can be compared with that of the Eocene of Seymour Island (figure 3). Average temperatures at sea level in Tierra del Fuego do not exceed 10°C in the summer and 0 - 2°C in the winter. Forests are dominated by the southern beech *Nothofagus pumilus*. Massoia and Chébez (1993) provided a list of mammals living in the forests of Tierra del Fuego and adjacent islands. Average masses were taken from Nowak and Paradiso (1991) and Redford and Eisenberg (1989). There are two genera of granivorous-insectivorous cricetid rodents with a body mass less than 0.1 kg (*Oligoryzomys*, *Abrothrix*) and two aquatic herbivorous rodents -*Ondatra* (0.7 - 1.8 kg) and the exotic *Castor* (12 - 25 kg). There are two genera of insectivorous vesperilionid chiropterans with body masses of about 0.01 kg (*Myotis*, *Histiotus*). Among artiodactyls, there is a camelid (*Lama*, 120 kg) and a cervid (*Cervus*, 210 kg). Carnivores are represented by two small canid species (*Dusicyon*, 6 kg), wild dogs (*Canis* spp.) of a similar size, and an aquatic mustelid (*Lontra*, 6 kg), which feeds mainly on fishes and crustaceans.

SUMMARY

1. The distribution of body sizes among land mammals of the La Meseta Formation is described by three groups. The smallest are marsupials, with body masses of few grams. The medium-sized are the sloths and trigonostylopids. The largest are sparnotheriodontids, which reached as much as 300 kg. Birds are intermediate between the marsupials and medium therians on one side -falconids- and between the latter and large therians on the other -ground dwellers.

2. Dietary specializations of the mammals included herbivores, omnivores, and insectivores. The absence of carnivorous mammals is remarkable, and is attributed to the small sample size and the low statistical probability of finding carnivores. The carnivore role is partially fulfilled by birds.

3. Analysis of the different modes of life of the birds and mammals of the La Meseta Formation suggests relatively open forested habitats.

4. The simple terrestrial trophic web recorded in the Eocene of Antarctica can be compared readily with modern forested habitats in South America at latitudes higher than 50°.

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