

First gondwanatherian mammal from Antarctica

FRANCISCO J. GOIN¹, MARCELO A. REGUERO¹, ROSENDO PASCUAL¹,
WIGHART VON KOENIGSWALD², MICHAEL O. WOODBURNES³,
JUDD A. CASE⁴, SERGIO A. MARENSSI⁵, CAROLINA VIEYTES¹ &
SERGIO F. VIZCAÍNO¹

¹*División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina (e-mail: fgoin@museo.fcnym.unlp.edu.ar)*

²*Institut für Paläontologie, Universität Bonn, Nussallee 8, D-53115 Bonn, Germany*

³*Department of Earth Sciences, University of California, Riverside, CA 92521, USA*

⁴*Department of Biology, St Mary's College, Moraga, CA 94575, USA*

⁵*Instituto Antártico Argentino, Cerrito 1248, 1010 Buenos Aires, Argentina*

Abstract: Gondwanatherians are an enigmatic group of extinct non-therian mammals apparently restricted to some of the western Gondwanan continents (Late Cretaceous–early Palaeocene of South America, and Late Cretaceous of Madagascar and India). They developed rodent-like incisors and the earliest known hypsodont cheek-teeth among mammals. Recently, a small rodent-like dentary fragment was recovered from middle Eocene beds on the Antarctic Peninsula, preserving part of the incisor; both the incisor enamel structure and the mandibular morphology suggest close affinities with *Sudamerica ameghinoi* from the early Palaeocene of Patagonia, up to now the youngest known Gondwanatheria. Thus, the new specimen becomes the youngest occurrence of a gondwanatherian, adding significant direct and indirect evidence on: (1) the already documented cosmopolitanism of gondwanatherians among Gondwanan mammals; and (2) the crucial biogeographical role of Antarctica during the Cretaceous–Tertiary mammalian transition.

Our knowledge of gondwanatherian mammals is relatively recent. They were first reported in 1984 and were alternatively regarded as edentates (Scillato Yané & Pascual 1985; Mones 1987), paratherians (Scillato Yané & Pascual 1985; Bonaparte 1986), multituberculates (Bonaparte *et al.* 1989; Krause 1990, 1993; Krause & Bonaparte 1990, 1993; Krause *et al.* 1992; Kielan-Jaworowska & Bonaparte 1996) and, recently, as dubious Allotheria (Krause *et al.* 1997); that is, as probably related to the Multituberculata as a sister-group. A study of the most complete gondwanatherian specimen known up to now (a fragmentary dentary with part of the incisor, two cheek-teeth *in situ* and two more alveoli) led Pascual *et al.* (1999) to regard them as *Mammalia incertae sedis*. Their distribution seems to have been restricted to southern continents, as all known taxa come from Upper Cretaceous levels in Patagonia, Madagascar and India, and from Lower Palaeocene levels in Patagonia. With the exception of the more generalized *Ferugliotherium windhauseni* (Family Ferugliotheriidae; Krause *et al.* 1992; Kielan-Jaworowska & Bonaparte 1996), all other gondwanatherians are grouped in the family Sudamericidae, char-

acterized by the possession of high-crowned cheek-teeth, covered with a cementum layer. Among the latter, *Gondwanatherium* and *Sudamerica* at least have the transverse ridges transformed in well-separated lophs/lophids. *Sudamerica* at least has four lower molariforms and the most rodent-like pattern seen among gondwanatherians (Pascual *et al.* 1999). Lower molars of *Ferugliotherium*, *Gondwanatherium* and *Sudamerica* show identical patterns of wear and transverse ridges (Krause & Bonaparte 1993). All three of them are also known to have enlarged, rodent-like incisors, which in *Sudamerica* are followed posteriorly by a large diastema. The remaining gondwanatherians are: (1) *Lavanify miolaka* from Madagascar (Krause *et al.* 1997); (2) an unnamed taxon from India (Krause *et al.* 1997); and (3) an also unnamed ?sudamericid from Tanzania, Africa (Krause *et al.* 2003), all of them known by a few isolated specimens. *Lavanify* and the Indian gondwanatherian have their enamel structure quite derived with respect to the South American taxa (Krause *et al.* 1997; Koenigswald *et al.* 1999).

Here we report the youngest and southernmost discovery of a gondwanatherian mammal,

coming from Middle Eocene levels in Antarctica. One of the specimens consists of a fragmentary dentary bearing part of the rodent-like incisor; an isolated, fragmentary upper incisor is tentatively referred to the same taxon. As shown below, both their general anatomy and the enamel microstructure of the incisors suggest that the Antarctic specimens are closely related to the early Palaeocene sudamericid *Sudamerica ameghinoi*.

All specimens were collected by picking screened sediment concentrate. A preliminary comment on the presence of gondwanatherian mammals in Antarctica was given recently by Reguero *et al.* (2002). This discovery adds a new Gondwanan continent to the distribution of gondwanatherians, extending in time and space the already known extensive distribution of these mammals. In addition, it sheds new light on the biogeographical role of Antarctica in the evolution of Gondwanan mammals.

Stratigraphical setting and terrestrial palaeoenvironment inferred for the *Cucullaea* I allomember

The abbreviations used are: MLP, Departamento Paleontología Vertebrados, Museo de La Plata, Argentina; IAA, fossil Antarctic localities discovered by MLP and Instituto Antártico Argentino researchers. All measurements are in mm.

Known by the Argentinean paleontologists as the 'Ungulate site' (Marensi *et al.* 1994), the locality IAA (Instituto Antártico Argentino) 1/90 is the richest Antarctic mammal-bearing locality known up to now (Bond *et al.* 1990; Goin *et al.* 1994; Case *et al.* 1996; Vizcaíno *et al.* 1998a, b) (Fig. 1), and has also produced the new specimens described here. Locality IAA 1/90 is within the *Cucullaea* I Member of the La Meseta Formation.

The late Early–latest Late Eocene La Meseta Formation (Elliot & Trautman 1982; Marensi *et al.* 1998) crops out in the northern third of Seymour (Marambio) Island, some 100 km off the northern Antarctic Peninsula. This 710 m-thick clastic unit records sedimentation in a deltaic and estuarine setting within an incised valley capped by shallow-marine deposits. The mammal-bearing levels are composed of thick shelly conglomerates, well-sorted sands and interlaminated sand/mud channel fills with thin shelly conglomeratic intervals. The bioclastic fraction comprises mainly gastropods (naticids), but marine and land vertebrate remains, plant fragments and other marine invertebrates also occur. Marensi *et al.* (1994)

considered these beds as reworked, moderate- to high-energy facies of a subtidal shallow-marine environment.

The *Cucullaea* I Allomember, formerly Telm 4 plus 5 of Sadler (1988), is most probably middle Eocene in age (Reguero *et al.* 2002) and it is the richest terrestrial mammal-bearing unit in Antarctica (Reguero *et al.* 1998). This allomember has also provided the largest collection of leaves from the Eocene of Antarctica (locality C/88, Gandolfo *et al.* 1998) and most of the wood remains reported up to now from the La Meseta Formation (Torres *et al.* 1994; Brea 1998). However, all the terrestrial remains were transported and deposited in a shallow-marine setting, being concentrated by means of sedimentological processes and mixed with a normal marine macrofauna (Marensi *et al.* 1998).

Physiognomical analysis of the leaves collected from this interval indicates a temperate–cool temperate, and seasonally moist climate with mean annual temperatures of between 11 and 13°C (locality C/88, Gandolfo *et al.* 1998). Clay mineral and geochemical data show that the northern Antarctic Peninsula (Seymour Island) experienced a climatic deterioration from very warm non-seasonal wet conditions in the Early Eocene to a cold, frost-prone and dry regime at the end of the Late Eocene (Dingle *et al.* 1998). By Middle Eocene times, the Seymour Island climate was experiencing a rapid cooling from very warm to cold through a strongly seasonal period (climatic episodes E2 and E3, Dingle *et al.* 1998).

Fossil wood recovered from the *Cucullaea* I Allomember indicates the presence of a nearby forest mainly composed of Araucariaceae, Podocarpaceae, Cupressaceae and Nothofagaceae trees (Torres *et al.* 1994; Brea 1998), while the leaves attest to the presence of Dilleniaceae, Myricaceae, Myrtaceae and Lauraceae plants. They most closely resemble species of extant plants growing in the Valdivian (Chile and Argentina) and New Zealand forests.

Systematic palaeontology

Class MAMMALIA Linnaeus 1758

Order GONDWANATHERIA Mones 1987

Family SUDAMERICIDAE Scillato-Yané & Pascual 1984

Genus and species indet., cf. *Sudamerica ameghinoi* Scillato-Yané & Pascual 1984

Referred specimen

MLP 95-I-10-5 (Figs 2 A–C & 3A, B), anterior part of a left dentary with the rodent-like incisor partially preserved.

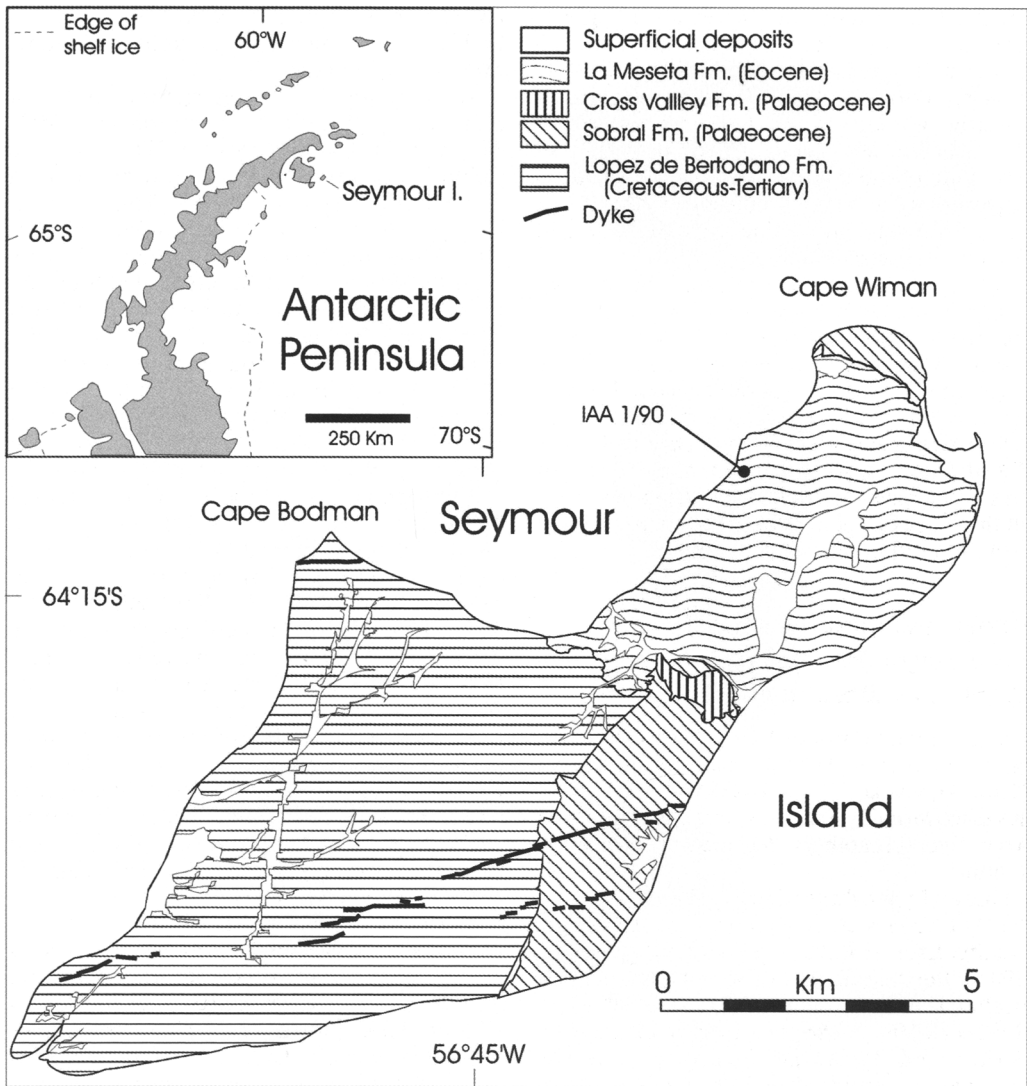


Fig. 1. Map of Seymour (Marambio) Island (Antarctic Peninsula) showing locality IAA 1/90.

Tentatively referred specimen

MLP 96-I-5-47, an isolated ?left upper incisor (Fig. 3A, B) broken at its proximal end. Both specimens were collected by picking screened sediment concentrate matrix worked at locality IAA 1/90.

Measurements

MLP 95-I-10-5: dentary width at the mental foramen 3.49 mm; dentary height at the mental foramen 6.05 mm; height of the lower incisor 3.65 mm; width of the lower incisor

1.53 mm. MLP 96-I-5-47 (isolated upper incisor fragment): mesiodistal width 1.61; buccolingual width 2.29; length 5.37. This last measurement does not reflect the tooth's real length, as it is broken at its proximal end.

Locality

IAA 1/90 (Fig. 1), Seymour (Marambio) Island, Antarctic Peninsula. 64°14' 04.672" S and 56°39' 56.378" W. Elevation is 57.19 m above sea level (Lusky *et al.* 1994). Levels at this locality correspond to the La Meseta Formation, more precisely to the lowest third of Unit II (Elliot &

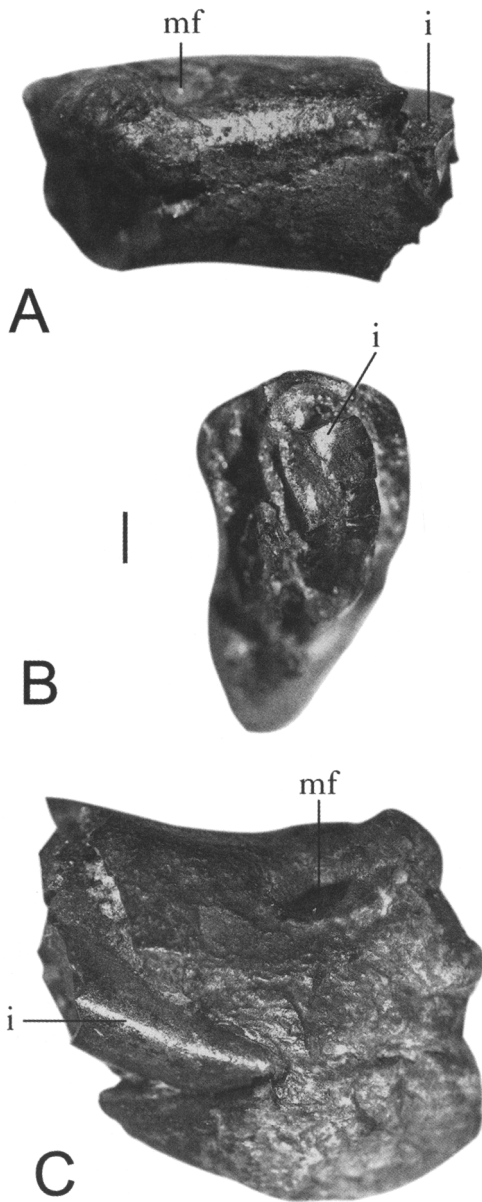


Fig. 2. *Sudamericidae* genus et species indet., cf. *Sudamerica ameghinoi* Scillato Yané & Pascual 1984. Specimen MLP 95-I-10-5, an anterior portion of a left dentary showing the enlarged, rodent-like incisor partially preserved. (A) dorsal, (B) anterior and (C) lateral views. References: i, incisor; mf, mental foramen. The scale bar is 1 mm.

Description

The dentary fragment (MLP 95-I-10-5; Fig. 2A–C) is wider dorsally than ventrally; the symphysis is flat and vertical, while the lateral face is slightly convex. At the lateral face the dentary is broken in such a way that the intra-alveolar portion of the incisor can be seen. In section, this tooth resembles the dentary: medially flat, laterally convex, sharply angled ventromedially and rounded dorsally. A thin enamel layer at the ventral surface covers it. The preserved dorsal surface of the dentary bears no alveoli, indicating that there was a diastema between the incisor and the molariform teeth. The mental foramen is suboval in shape and is placed very high on the lateral face of the dentary, close to the diastema. Immediately behind the mental foramen the horizontal ramus rises sharply. The isolated upper incisor (MLP 96-I-5-47; Fig. 3A, B) is suboval in section, and has the enamel layer restricted to the buccal and distal faces. There is a small, horizontal wear facet at the apex. Even though smaller than the lower incisor, it matches well the size expected for an occlusal antagonist of the lower one.

Enamel microstructure

Small enamel fragments belonging to specimens MLP 95-I-10-5 and MLP 96-I-5-47 have been subjected to microstructural investigations carried out at the Institut für Paläontologie, Universität Bonn. For the enamel description we use the terms and abbreviations listed in a recent glossary by Koenigswald & Sander (1997). The enamel of the lower incisor is very thin (about 50 µm). From transverse and longitudinal sections the schmelzmuster was reconstructed (Fig. 4A, B). The enamel structure consists of two well-defined layers of tangential enamel, with prisms rising or descending only very little. Although the prism direction changes, there is no prism decussation, typical for rodent incisors. The tangential enamel is divided into a mesial and a lateral field by a neutral area with straight prism orientation, close to the inflection of the band towards the mesial side. On the lateral side of the neutral area the prisms are laterally oriented in the inner layer, and mesially in the outer layer. In the mesial part, however, the prisms of the inner layer are directed mesially, and laterally in the outer layer. This pattern is seen when the entire length of the section is studied. Between the inner and the outer layers, prisms change direction in a simultaneous prism deviation. The

Trautman 1982), or *Telm* 5 (Sadler 1988) or *Allomember Cucullaea* I (Marenssi & Santillana 1994).

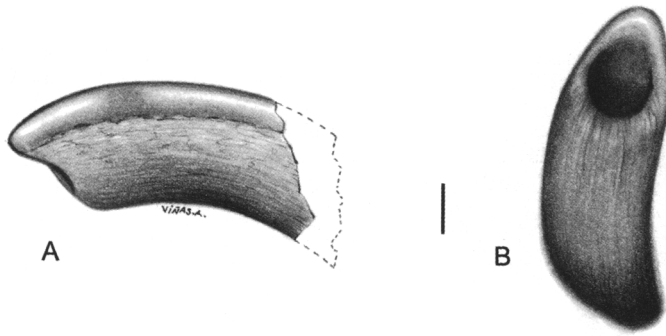


Fig. 3. MLP 96-I-5-47, an isolated ?left upper incisor tentatively referred to the same Sudamericidae genus and species indet cf. *Sudamerica ameghinoi*. (A) Lateral and (B) occlusal view. The scale bar is 1 mm.

prisms are surrounded by a thick interprismatic matrix (IPM), which runs straight from the enamel–dentine junction (EDJ) to the outer enamel surface (OES) without inclination. In the outer layer several prisms disappear so that the IPM becomes dominant, but does not form a continuous prismless outer enamel (PLEX). Prisms are isodiametrical and relatively small (of around 5 μm each), and are surrounded by incomplete prism sheaths. Close to the EDJ several tubules could be seen in the enamel. In the isolated upper incisor (Fig. 3C) the enamel is even thinner (20 μm). The schmelzmuster consists only of one layer of radial enamel. The prisms are straight, but from the sections available we cannot decide how much they are rising. As in the lower incisor, prisms are surrounded by a very thick IPM set at a slight angle in relation to the prisms. The prism cross-section is open and many prisms show a distinct seam. In an almost tangential section prisms seem to be, in some areas, vertically aligned. The IPM between prisms is separated by a discontinuity normally not seen in interrow sheets.

Comments

Although superficially similar, the dentary does not belong to a polydolopine marsupial, the most abundant mammal in the La Meseta Formation: (1) it is very wide dorsally and narrow ventrally, while in polydolopines the cross-section is fusiform, reaching its maximum width at the middle portion of the ramus; (2) in marsupials, the mental foramen is never placed so dorsally on the labial face of the mandible; (3) relative to the symphyseal plane, the plane of the mandible in polydolopines is obliquely oriented, not vertical as seen in anterior view; (4) the lower incisor is proportionally too large compared to any known ‘pseudodiprotodont’

marsupial; and (5) from the preserved material it is clear that the alveolar plane is placed much higher than the diastema, a feature that does not occur in polydolopimorphians. However, all these features agree well with known remains of the gondwanatherian mammal *Sudamerica ameghinoi* (Pascual *et al.* 1999), known only from early Palaeocene levels at Punta Peligro, in Central Patagonia. Additionally, the cross-section of this lower incisor is similar to that of gondwanatherians, and particularly to that of *Sudamerica ameghinoi*: medially flat, laterally convex, angled ventromedially and rounded dorsally (Koenigswald *et al.* 1999). It also agrees well in the presence of a thin, labial enamel layer. Regarding its size, the dentary fragment from the La Meseta Formation is much smaller than that of the only known dentary of *S. ameghinoi* (Pascual *et al.* 1999). Finally, the attribution of the upper incisor is based on its similarity to assigned isolated upper incisors of other gondwanatherians, such as *Ferugliotherium windhauseni* (Krause *et al.* 1992), although no upper incisor is known from *Sudamerica ameghinoi* itself.

Regarding the enamel structure of the Antarctic specimens, the upper and the lower incisors show a different schmelzmuster. Such a difference is also known in several rodents (Koenigswald 1997), where the lower incisor always shows the more derived state. In our material the lower incisor, with two layers of tangential enamel, is definitely more derived than the upper one. Two-layered schmelzmusters are frequent among enlarged incisors of various mammals, such as primates, rodents, insectivores, etc. (Koenigswald 1996). The absence of Hunter–Schreger bands in the schmelzmuster of the Antarctic specimen, however, rules out its affinities with rodents and most other eutherians. In pilodontoid multituberculates (Sahni 1979)

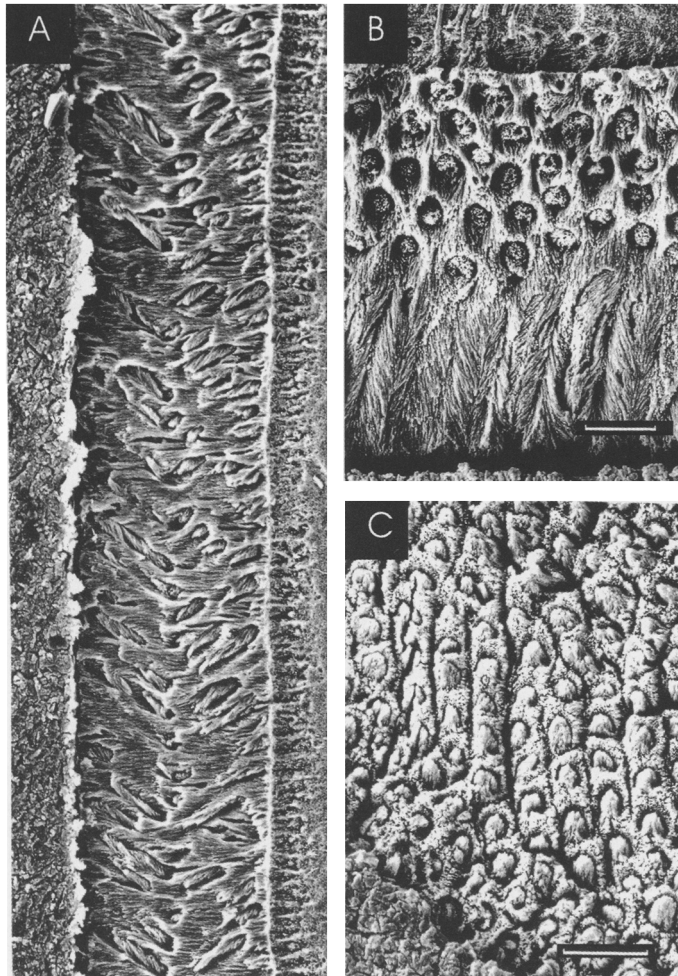


Fig. 4. Enamel of the lower incisor of the Antarctic gondwanatherian (specimen MLP 95-I-10-5) in (A) longitudinal and (B) transverse sections. The longitudinal section shows the two layers and the thick interprismatic matrix (IPM) surrounding the prisms (P). The prism orientation in the two layers of tangential enamel can be seen from the transverse section. In the outer layer the IPM dominates due to the disappearance of several prisms. (C) Semi-tangential section of the upper incisor (specimen MLP 96-I-5-47), showing the incomplete prism sheath surrounding the prisms, and the alignment of prisms with the central discontinuity. The scale bar is 10 μm .

and various South American marsupials such as *Groeberia* and *Argyrolagus*, and most Australian kangaroos, a combination of radial enamel and tangential enamel was found (Koenigswald & Pascual 1990; Koenigswald 1994). This pattern differs distinctly from the schmelzmuster found in the Antarctic specimens, in which the prisms do not show any inclination. Conversely, the enamel structure of the Antarctic specimens shows clear correspondences with *Sudamerica ameghinoi* (Koenigswald *et al.* 1999; Pascual *et al.*

1999). Unfortunately, we cannot compare the schmelzmuster of the Antarctic specimen with gondwanatherians from Madagascar and India as incisors are only known for *Gondwanatherium* and *Sudamerica*. However, judging from their cheek-tooth enamel, both the Madagascan and the Indian forms are substantially more derived than all other gondwanatherians in the possession of continuous inter-row sheets of interprismatic matrix. In turn, the lower incisor enamel of the Antarctic specimen shares with

that of *Sudamerica* almost all characteristics seen in the schmelzmuster: the low inclination of the prisms, the position of the neutral area, the two layers of tangential enamel, the specific prism orientation in each layer, the straight orientation of the crystallites of the IPM and the predominance of the IPM in the outer layer, due to the disappearance of prisms. The similarity of this unique pattern in the two taxa indicates a close relationship. Minor differences, such as the more pronounced angle between the inner and outer tangential layers and the better definition of the prisms, indicate that the schmelzmuster of the Antarctic specimen is somewhat more derived than that of *Sudamerica ameghinoi*. The incisor of the Late Cretaceous *Gondwanatherium patagonicum* shows a quite different schmelzmuster, indicating a more distant relationship compared with *Sudamerica* (Koenigswald *et al.* 1999).

In short, all macro- and microscopic evidence at hand suggests that the Antarctic specimens pertain to a Gondwanatherian mammal, and that they are more closely related to the Early Palaeocene *Sudamerica ameghinoi* than to any other member of this group. While assigning these specimens to the Sudameriidae, owing to their fragmentary nature we do not enter into a formal taxonomy at the generic or specific level.

Discussion

The discovery of Antarctic (this paper), as well as Indian and Madagascan (Krause *et al.* 1997), sudamericid gondwanatherians confirms the broad distribution of this group of mammals in Gondwanan continents during Mesozoic and the earliest Cenozoic times, and gives new insights into our limited knowledge of the history of Gondwanan mammals (Pascual 1997a, b, 1998). It also confirms previous hypotheses on the crucial role of Antarctica in the biogeographical evolution of southern hemisphere mammals (Keast 1972; Elliot & Trautman 1982; Krause *et al.* 1997). The Patagonian Early Palaeocene ornithorhynchid monotreme is yet one more example (Pascual *et al.* 1992a, b). Monotremes and marsupials had to have been active parts of inter-Gondwanan faunal interchanges involving Antarctica as a continental 'crossroad' or 'stepping-stone'. We do not know whether gondwanatheres played a similar role as so far they have not been recorded either in the Antarctic or Australian Cretaceous. Nevertheless, Krause *et al.* (1997) suggested that Antarctica might have served as an important Cretaceous biogeographical link between South America and Indo-Madagascar.

In recognition of the derived enamel structure of the Antarctic sudamericid and the endemism of the contemporaneous ungulate mammals with respect to South American relatives (Bond *et al.* 1995), the most parsimonious hypothesis is that the La Meseta Formation mammal fauna was relictual in the Antarctic Peninsula relative to a biota shared between the Antarctic Peninsula and South America in the Early Palaeocene. This vicariant hypothesis appears to reflect the subsequent separation of the Antarctic and South American continents. The remarkably good fossil record of late Palaeocene (Itaboraian Age) South American mammals, both in Patagonia and Brazil (see, for example, Pascual *et al.* 1996), adds support to this hypothesis: no gondwanatheres have been recorded in Itaboraian beds, or in the subsequent Tertiary land mammal-bearing beds.

Up to now, the Middle Eocene mammals recovered from the Antarctic La Meseta Formation included frugivorous polydolopimorphian and insectivorous didelphimorphian marsupials (Goin *et al.* 1994, 1999), tardigrade xenarthrans (which are likely to have been folivorous) and ungulate browsers, such as a trigonostyloid astrapothere (Vizcaíno *et al.* 1998b). As indicated elsewhere, hypsodonty cannot be related only to grazing as it also occurs in burrowing and semi-aquatic mammals such as the ctenomyids (Pascual *et al.* 1965) and the castorid rodents, respectively.

It is evident that the record of a sudamericid gondwanatherian in the Eocene Antarctic beds does not contribute to our understanding of the presence of this group in Madagascar and India during the Late Cretaceous. First, the Antarctic record is geologically too young; second, the La Meseta Formation taxon seems more closely allied to the Early Palaeocene *Sudamerica ameghinoi* than to any other gondwanatherian. The hypothesis of Krause *et al.* (1997) that Antarctica may have served as an important Cretaceous biogeographical link between South America and Indo-Madagascar requires the record of a gondwanatherian in Cretaceous Antarctic beds. The apparent absence of gondwanatheres during this time in Antarctica, and in Late Cretaceous and younger beds in Australia, is probably due to lack of discoveries. Such remains should be diligently sought.

We thank the personnel and authorities of the Instituto Antártico Argentino, and especially to S. Santillana for their logistic support during field work at locality IAA 1/90 in the Antarctic Peninsula; Mr J. J. Moly, for his fieldwork in Antarctica and picking efforts at the Museo de la Plata that led to the

discovery of the specimens studied here; A. Sahni, from Panjab University, for loaning to us the indeterminate Indian gondwanatherian mentioned in the text for examination at the Institut für Paläontologie in Bonn; M. Tomeo, A. Viñas, G. Oleschinski and D. Kranz for their contributions to the artwork; D. Kalthof, who helped F. J. Goin use the SEM facilities at the Institut für Paläontologie in Bonn; the 'Alexander von Humboldt Stiftung', who generously provided F. J. Goin with a fellowship in order to study in Bonn during 1998, and with the stereomicroscope equipment and software used in the making of Figure 2; the 'Deutsche Forschungs Gemeinschaft', who supported the background of the work of W. v. Koenigswald in the form of several grants to study the structure of mammalian enamel; and J. J. Hooker and D. W. Krause for their very useful critical comments on the original manuscript. Financial support to R. Pascual and F. J. Goin was derived from the Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (PMT-PICT 0227) and National Geographic Society, USA (grant 5905-97).

References

- BONAPARTE, J.F. 1986. A new and unusual late Cretaceous mammal from Patagonia. *Journal of Vertebrate Paleontology*, **6**, 264–270.
- BONAPARTE, J.F., KRAUSE, D.W. & KIELAN-JWOROWSKA, Z. 1989. *Ferugliotherium windhauseni* Bonaparte, the first known multituberculate from Gondwanaland. *Journal of Vertebrate Paleontology*, **10**, 14A.
- 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 Palaeocene succession from central Patagonia. In: *IV Congreso Argentino de Paleontología y Bioestratigrafía, Trelew, Actas*, Asociación Paleontológica Argentina, Trelew, 47–58.
- BOND, M., PASCUAL, R., REGUERO, M.A., SANTILLANA, S.H. & MARENSSI, S.A. 1990. Los primeros ungulados extinguidos sudamericanos de la Antártida. *Ameghiniana*, **26**, 240.
- BREA, M. 1998. Análisis de los anillos de crecimiento en leños fósiles de coníferas de la Formación La Meseta, Isla Seymour (Marambio), Antártida. In: CASADÍO, S. (ed.) *Paleógeno de América del Sur y de la Península Antártica*. Asociación Paleontológica Argentina, Publicación Especial, **5**, 163–175.
- CASE, J.A., GOIN, F.J. & WOODBURNE, M.O. 1996. Eocene Antarctic ameridelphian marsupials with tribosphenic molars: implications upon marsupial biogeography. *Journal of Vertebrate Paleontology*, **16**, (3 Suppl.), 26A.
- DINGLE, R., MARENSSI, S. & LAVELLE, M. 1998. High latitude Eocene climate deterioration: evidence from the northern Antarctic Peninsula. *Journal of South American Earth Sciences*, **11**, 571–579.
- ELLIOT, D.H. & TRAUTMAN, T. 1982. Lower Tertiary strata on Seymour Island. In: CRADDOCK, C. (ed.) *Antarctic Geoscience*. University of Wisconsin Press, Madison, WI, 287–297.
- 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: CASADÍO, S. (ed.) *Paleógeno de América del Sur y de la Península Antártica*. Asociación Paleontológica Argentina, Publicación Especial, **5**, 155–162.
- GOIN, F.J., CASE, J.A., WOODBURNE, M.O., VIZCAÍNO, S.F. & REGUERO, M.A. 1999. New Discoveries of 'Opossum-like' Marsupials from Antarctica (Seymour Island, Middle Eocene). *Journal of Mammalian Evolution*, **6**, 335–365.
- GOIN, F.J., REGUERO, M.A. & VIZCAÍNO, S.F. 1994. Novedosos hallazgos de 'comadrejas' (Marsupialia) del Eoceno Medio de Antártida. In: *III Jornadas de Comunicaciones sobre Investigaciones Antárticas*. Dirección Nacional del Antártico-Instituto Antártico Argentino, Buenos Aires, Abstracts, 59–61.
- 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, NY, 19–22.
- KIELAN-JWOROWSKA, Z. & BONAPARTE, J.F. 1996. Partial dentary of a multituberculate mammal from the late Cretaceous of Argentina and its taxonomic implications. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' Nueva Serie*, **145**, 1–9.
- KOENIGSWALD, W.V. 1994. Differenzierungen im Zahnschmelz der Marsupialia im Vergleich zu den Verhältnissen bei den Placentalia (Mammalia). *Berliner Geowissenschaftliche Abhandlungen (Bernard Krebs Festschrift)*, **E13**, 45–81.
- KOENIGSWALD, W.V. 1996. Die Zahl der Schmelzschichten in den Inzisiven bei den Lagomorpha und ihre systematische Bedeutung. *Bonner Zoologische Beiträge (Festschrift J. Niethammer)*, **46**, 33–57.
- KOENIGSWALD, W.V. 1997. The variability of the enamel at the dentition level. In: KOENIGSWALD, W.V. & SANDER, P.M. (eds) *Tooth Enamel Microstructure*. Balkema, Rotterdam, 193–201.
- KOENIGSWALD, W.V. & PASCUAL, R. 1990. The Schmelzmuster of the Paleogene South American rodentlike marsupials *Groeberia* and *Patagonia* compared to rodents and other Marsupialia. *Paläontologische Zeitschrift*, **64**, 345–358.
- KOENIGSWALD, W.V. & SANDER, M.P. 1997. Glossary. In: KOENIGSWALD, W.V. & SANDER, P.M. (eds) *Tooth Enamel Microstructure*. Balkema, Rotterdam, 267–280.
- KOENIGSWALD, W.V., GOIN, F.J. & PASCUAL, R. 1999. Hypsodonty and enamel microstructure in the Palaeocene gondwanatherian mammal *Sudamerica ameghinoi*. *Acta Palaeontologica Polonica*, **44**, 263–300.
- KRAUSE, D.W. 1990. The Gondwanatheria, a new suborder of Multituberculata from South America. *Journal of Vertebrate Paleontology*, **10**, (3 Suppl.), 1S.
- KRAUSE, D.W. 1993. *Vucetichia* (Gondwanatheria) is a junior synonym of *Ferugliotherium* (Multituberculata). *Journal of Paleontology*, **67**, 321–324.

- KRAUSE, D.W. & BONAPARTE, J.F. 1990. The Gondwanatheria, a new suborder of Multituberculata from South America. *Journal of Vertebrate Paleontology*, **10**, 13A.
- KRAUSE, D.W. & BONAPARTE, J.F. 1993. Superfamily Gondwanatherioidea: A previously unrecognized radiation of multituberculate mammals in South America. *Proceedings of the National Academy of Science*, **90**, 9379–9383.
- KRAUSE, D.W., KIELAN-JAWOROWSKA, Z. & BONAPARTE, J.F. 1992. *Ferugliotherium* Bonaparte, the first known multituberculate from South America. *Journal of Vertebrate Paleontology*, **12**, 351–376.
- KRAUSE, D.W., GOTTFRIED, M.D., O'CONNOR, P.M. & ROBERTS, E.M. 2003. A Cretaceous mammal from Tanzania. *Acta Palaeontologica Polonica*, **48**, 321–330.
- KRAUSE, D.W., PRASAD, G.V.R., KOENIGSWALD, W.V., SAHNI, A. & GRINE, F.E. 1997. Cosmopolitanism among Gondwana Late Cretaceous mammals. *Nature*, **390**, 504–507.
- LINNAEUS, C. 1758. *Systema Naturae*, X edn. (*Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.*) Holmiae (Laurentii Salvii), [1–4], 1–824.
- LUSKY, J.C., REGUERO, M.A. & VIZCAÍNO, S.F. 1994. Geographical position applying Global Position System (GPS) in the Eocene land-vertebrate bearing localities from Seymour (Marambio) Island, Antarctic Peninsula. In: *III Jornadas de Comunicaciones sobre Investigaciones Antárticas*. Dirección Nacional del Antártico–Instituto Antártico Argentino, Buenos Aires, Abstracts, 53–54.
- MARENSSI, S.A. & SANTILLANA, S.N. 1994. Unconformity bounded units within La Meseta Formation, Seymour Island, Antarctica: a preliminary approach. In: ZALEWSKI, M. (ed.) *XXI Polar Symposium*, Institute of Geophysics, Warsaw, 33–37.
- MARENSSI, S.A., REGUERO, M.A., SANTILLANA, S.N. & VIZCAÍNO, S.F. 1994. Eocene land mammals from Seymour Island, Antarctica: palaeobiological implications. *Antarctic Science*, **6**, 3–15.
- MARENSSI, S.A., SANTILLANA, S.N. & RINALDI, C.A. 1998. Stratigraphy of the La Meseta Formation (Eocene), Marambio (Seymour) Island, Antarctica. In: CASADÍO, S. (ed.) *Paleógeno de América del Sur y de la Península Antártica*. Asociación Paleontológica Argentina, Publicación Especial, **5**, 137–146.
- MONES, A. 1987. Gondwanatheria, un Nuevo Orden de Mamíferos Sudamericanos (Mammalia: Edentata: ?Xenarthra). *Comunicaciones Paleontológicas del Museo de Historia Natural de Montevideo*, **1**, 237–240.
- PASCUAL, R. 1997a. Fossil land mammals and the geobiotic history of Southern South America. In: *II Southern Connection Congress. Noticiero de Biología*, **5**, 59.
- PASCUAL, R. 1997b. The Gondwanan history of mammals, the other history. In: *7th International Theriological Congress, Universidad Nacional Autónoma de México, Acapulco, México*, Abstracts, 278–279.
- PASCUAL, R. 1998. The history of South American Land Mammals: the seminal Cretaceous–Paleocene transition. In: CASADÍO, S. (ed.) *Paleógeno de América del Sur y de la Península Antártica*. Asociación Paleontológica Argentina, Publicación Especial, **5**, 9–18.
- PASCUAL, R., ARCHER, M., ORTIZ-JAUREGUIZAR, E., PRADO, J.L., GODTHEL, H. & HAND, S.H. 1992a. First discovery of monotremes in South America. *Nature*, **356**, 704–705.
- PASCUAL, R., ARCHER, M., ORTIZ-JAUREGUIZAR, E., PRADO, J.L., GODTHEL, H. & HAND, S.H. 1992b. The first non-Australian monotreme: an early Palaeocene South American Platypus (Monotremata, Ornitorhynchidae). In: AUGÉE, M.L. (ed.) *Platypus and Echidnas*. Royal Zoological Society of New South Wales, Sydney, 1–14.
- PASCUAL, R., GOIN, F.J., KRAUSE, D.W., ORTIZ-JAUREGUIZAR, E. & CARLINI, A.A. 1999. The first gnathic remains of *Sudamerica*: implications for Gondwanathere relationships. *Journal of Vertebrate Paleontology*, **19**, 373–382.
- PASCUAL, R., ORTEGA HINOJOSA, E.J. & PISANO, J. 1965. Un nuevo Octodontidae (Rodentia, Caviomorpha) de la Formación Epecuén, Plioceno medio de Hidalgo (Provincia de La Pampa). *Ameghiniana*, **4**, 19–30.
- PASCUAL, R., ORTIZ-JAUREGUIZAR, E. & PRADO, J.L. 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. *Münchener Geowissenschaftlich Abhandlungen (A)*, **30**, 265–319.
- REGUERO, M.A., MARENSSI, S.A. & SANTILLANA, S.N. 2002. Antarctic Peninsula and Patagonia Paleogene terrestrial environments: biotic and biogeographic relationships. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **276**, 1–22.
- 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: CASADÍO, S. (ed.) *Paleógeno de América del Sur y de la Península Antártica*. Asociación Paleontológica Argentina, Publicación Especial, **5**, 185–198.
- SADLER, P.M. 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. In: FELDMANN, M. & WOODBURN, M.O. (eds) *Geology and Paleontology of Seymour Island, Antarctic Peninsula*. Geological Society of America, Memoirs, **169**, 303–320.
- SAHNI, A. 1979. Enamel ultrastructure of certain North American Cretaceous Mammals. *Palaeontographica Abteilung A*, **166**, 37–49.
- SCILLATO YANÉ, G.J. & PASCUAL, R. 1984. *Un peculiar Paratheria, Edentata (Mammalia) del Paleoceno de Patagonia (Argentina)*. Primeras Jornadas Argentinas de Paleontología de Vertebrados, Resúmenes, **15**.
- SCILLATO YANÉ, G.J. & PASCUAL, R. 1985. Un peculiar Xenarthra del Paleoceno medio de Patagonia (Argentina). Su importancia en la sistemática de los Paratheria. *Ameghiniana*, **21**, 173–176.
- TORRES, T., MARENSSI, S.A. & SANTILLANA, S.N. 1994. Maderas fósiles de la isla Seymour, Formación La

- Meseta, Antártica. *Serie Científica del INACH, Santiago de Chile*, **44**, 17–38.
- VIZCAÍNO, S.F., PASCUAL, R., REGUERO, M.A. & GOIN, F.J. 1998a. Antarctica as a background for mammalian evolution. *In*: CASADÍO, S. (ed.) *Paleógeno de América del Sur y de la Península Antártica*. Asociación Paleontológica Argentina, Publicación Especial, **5**, 199–209.
- VIZCAÍNO, S.F., REGUERO, M.A., GOIN, F.J., TAMBUSI, C.P. & NORIEGA, J.I. 1998b. An approach to the structure of the Eocene terrestrial vertebrate community from Antarctic Peninsula. *In*: CASADÍO, S. (ed.) *Paleógeno de América del Sur y de la Península Antártica*. Asociación Paleontológica Argentina, Publicación Especial, **5**, 177–183.