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ANTARCTICA AS BACKGROUND FOR MAMMALIAN EVOLUTION

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ABSTRACT. Since the 1980's, a series of new Cretaceous-Paleogene land mammals has been found in southern continents. They drastically changed the traditional perspective of how mammals evolved all over the world, and particularly, how they evolved in the southern continents. This paper is a preliminary evaluation of how much this new evidence contributes to an understanding of the role Antarctica played both in the evolution of mammals in general, and in the evolution of mammals in southern continents, in particular. The only land mammals thus far recorded in Antarctica come from middle to late Eocene beds of the La Meseta Formation on Seymour Island (Antarctic Peninsula). But the land mammals found in southern South America (Patagonia) and Australia, spanning the Cretaceous-Paleogene, strongly suggest that Antarctica was both an important evolutionary center (at least during the Cretaceous-Eocene), and a "stepping stone" between both continents during the Late Cretaceous-early Paleocene. The taxonomic diversification of monotremes in Australia (represented by at least two Early Cretaceous families, which make four families between that time and the Recent), and the oldest marine barrier between Australia and Antarctica (ca. 64 Ma), indicate that monotremes probably originated and diversified in the Australian/Antarctic sector of Gondwana. The single dispersal (an ornithorhynchid) to the South American sector before or during the early Paleocene, attests to the role of Antarctica as a "stepping stone" between Australia and South America. The immigration of marsupials to the Australian sector of Gondwana must have occurred before 52 Ma. Thus, the "Australian marsupials" probably also diversified in the Australian/Antarctic sector of Gondwana. The available paleontological and biochemical data suggest that species ancestral to some of the present Australian marsupials evolved in Antarctica prior to their entry into Australia. The idea of the Australian/Antarctic sector as the area of origin and diversification of monotremes, and their absence from the Late Cretaceous (Campanian) land-mammal communities of southern South America (otherwise, exclusively composed by other non-tribosphenic and pre-tribosphenic mammals), suggest that by the end of the Mesozoic, there was a regional biogeographical differentiation between the East Gondwanan continents. Thus, Antarctica also might have been an important evolutionary center for non-tribosphenic and pre-tribosphenic mammals throughout the later part of the Mesozoic. The Eocene land mammals from La Meseta Formation pertain to "South American" lineages of marsupials (at least 4 families) and placentals (tardigrades and ungulates). They are characterized by a marked endemism at the specific and generic level. This endemism and the earlier record of certain taxa than in South America suggest both that the diversification of "South American" Tribosphenida mammals occurred in the Antarctic/South American sector of Gondwana, and that after the Paleocene, the Antarctic continent, or part of it, was isolated.

RESUMEN. ANTÁRTIDA COMO OTRO CENTRO DE EVOLUCIÓN DE LOS MAMÍFEROS. A partir de la década de 1980, novedosos hallazgos de mamíferos terrestres cretácicos y paleógenos en los continentes australes cambiaron drásticamente la visión tradicional de cómo evolucionó el grupo, tanto en esos continentes como en el mundo entero. Este trabajo consiste en una evaluación preliminar de cuánto esta nueva evidencia contribuye al entendimiento del papel que le cupo a Antártida en la evolución de los mamíferos, tanto en general como en los continentes australes en particular. Los únicos mamíferos terrestres registrados en Antártida provienen de niveles del Eoceno medio a tardío de la Formación La Meseta de la isla Seymour (Marambio), cerca del extremo de la Península Antártica. Pero mamíferos terrestres del lapso Cretácico-Paleoceno encontrados en el sur de América del Sur (Patagonia) y Australia, sugieren fuertemente que Antártida fue un importante centro evolutivo (al menos durante el período Cretácico-Eoceno) y un "lugar de paso" entre ambos continentes durante el lapso Cretácico Superior-Paleoceno temprano. La diversificación taxonómica de los monotremas en Australia (representados por, al menos, 4 familias desde el Cretácico hasta la actualidad) y la más antigua barrera marina entre Australia y Antártida (ca. 64 Ma), indican que probablemente se originaron y diversificaron en el sector australiano/antártico de Gondwana. La sola dispersión de los ornitorrínquidos al sector sudamericano antes o durante el Paleoceno temprano, propone que Antártida fue también un "lugar de paso". La inmigración de los marsupiales al sector australiano de Gondwana debió haber ocurrido antes de los 52 Ma. Así, probablemente los "marsupiales australianos" se diversificaron en el sector australiano/antártico de Gondwana. De hecho, datos paleontológicos y bioquímicos sugieren que en Antártida se desarrollaron especies ancestrales a algunos de los grupos de marsupiales australianos actuales, antes de su entrada a Australia. La idea del sector australiano/antártico como el área donde los monotremas se originaron y diversificaron y la ausencia del grupo entre las comunidades de mamíferos terrestes del Cretácico Superior (Campaniano) de Patagonia (compuestas exclusivamente por otros mamíferos no tribosfénicos y pre-tribosfénicos), sugieren que a finales del Mesozoico existía una diferenciación biogeográfica regional entre los continentes de Gondwana oriental. Por eso, Antártida pudo haber sido también un importante centro evolutivo para los mamíferos no-tribosfénicos y pre-tribosfénicos durante la última parte del Mesozoico. Los mamíferos eocénicos de la Formación La Meseta pertenecen a linajes "sudamericanos" de marsupiales (al menos cuatro familias) y placentarios (tardígrados y ungulados). En conjunto, muestran un marcado endemismo a nivel específico y genérico. Este endemismo y el registro de ciertos taxones antes que en América del Sur sugiere que la diversificación de los Tribosphenida "sudamericanos" ocurrió en el sector antártico/sudamericano de Gondwana y que después del Paleoceno sufrieron algún tipo de aislamiento en Antártida.

KEY WORDS. Antarctica. Cretaceous-Paleogene. Mammalia. Evolution. Palaeobiogeography.

PALABRAS CLAVE. Antártida. Cretácico-Paleógeno. Mammalia. Evolución. Paleobiogeografía.

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INTRODUCTION

The South American Cretaceous-early Paleocene land mammals found during the last years, along with those newly discovered Early Cretaceous Australian monotremes, and Eocene Antarctic mammals, have opened a new chapter in the study of mammal evolution in general, and of mammal evolution in the southern continents, in particular. In this regard, both direct and indirect evidence indicate that Antarctica played a prominent role in the evolution of land mammals in southern continents. Prior to the breakup of the Gondwana supercontinent in the Early Jurassic (ca. 185 Ma), Antarctica was located at the center of this land mass. Brink *et al.* (1993) pointed out that because of this position, "...Antarctica is the key to an understanding of Gondwana geology and plate reconstruction". By the Early Jurassic, mammals had been evolving for at least 40 m.a. (see Lucas and Hunt, 1990; Lucas and Luo, 1993). As the Early Cretaceous record in the southern tip of South America suggests, land mammals were evolving in the Gondwana supercontinent before and after its breakup. After the breakup of Gondwana, Antarctica retained its original, central position, and for a long time, maintained some kind of contact with some of the other continents (Storey, 1995). Thus, Antarctica is also the key to an understanding of mammalian evolution in southern continents. Considering the current geographical range of *Nothofagus*, the position of Antarctica relative to the other southern continents, was also regarded as critical by Case (1988: 529), as surely it also was for shallow marine invertebrates.

Herein we provide a preliminary evaluation of the degree to which Cretaceous-Paleogene land mammals found during the last few years in southern continents contribute to an understanding of the role of Antarctica in mammalian evolution.

THE SOUTHERN RECORD: A BROADER VIEW

As Keast (1972: 19) pointed out, because of a more or less isolated geographical history, Africa, South America and Australia were supplied (*sic*) with basically different mammalian stocks throughout the Tertiary. He correctly remarked that this provides "... an unusual opportunity for a comparative study of the dynamics of mammalian evolution". In the early 1970's, Africa (see Cooke, 1972), South America (see Patterson and Pascual, 1972), and Australia (see Keast, 1972), were the only three southern continents from which Tertiary mammals had been recovered. However, the Tertiary record of South America and Australia demonstrated that these continents shared the same land mammalian raw material, which from the outset was substantially different than the African mammalian assemblage. This difference is strongly evident if one compares present African and South America-Australian land-mammal faunas. It is thought that this difference is related to the earlier separation of Africa, and to the longer persistent connection between South America and Australia (via Antarctica) along eastern Gondwana (Storey, 1995, figure 1 c-d). The available land-mammal evidence concurs with the abiotic evidence in indicating that, at least up to the early Paleocene, there was some kind of geographical connection that permitted limited interchange of land mammals between southern South America and Australia. This is the "marsupial route" of Schuster (1976); however we now know that interchange occurred only until the early Paleocene (see Woodburne and Case (1996) and not through the Eocene, as originally hypothesized by Case, 1988. Thus, faunal interchange occurred, prior to the separation of Australia from Antarctica; New Zealand, which was separated first (Zinsmeister, 1982) was excluded from this exchange. Owing to its intermediate position, Antarctica obviously had to be part of this faunal interchange.

As recently as the 1970's, Antarctica had not produced fossil land mammals, Tertiary or older. Nevertheless, the well-known fossil record of *Nothofagus* in Upper Cretaceous and Tertiary beds from the tip of the Antarctic Peninsula had been related to modern occurrences of *Nothofagus* in Patagonia. In conjunction with paleoclimatic data, this record was thought to indicate that "... Antarctica was partially vegetated, and hence presumably could have supported mammals in the early Tertiary" (Keast, 1972: 56). This inference was supported by some paleogeographical reconstructions that led Keast (*loc. cit.*) to admit "... the possibility of a continued junction of South America and the Antarctic Peninsula as late as the Late Cretaceous-early Tertiary". Simpson (1978: 323) later stated that the plate tectonic evidence "...opens up another possibility for faunal connection between Australia and South America with Antarctica as the intermediate area"; however he pointed out that "...dispersal to or from Antarctica was not by continuous land connections but by sweepstakes dispersal, probably island hopping...".

Keast and Simpson, writing in the early 1970's on the evolution of mammals in southern continents (see Keast *et al.*, 1972), specifically referred to marsupial and placental mammals, and to a dubious South American Late Cretaceous span, but more unquestionably to the middle Paleocene-Neogene span. Until this time, analyses were based on circumstantial evidence. We must remember that by the Late Cretaceous the continents were approximately delineated as present, and that marsupials and placentals dominated among mammals in northern continents. Also, during the 1970's, the oldest land mammals known in South America were marsupials and placentals; these records are based on a dubious Late Cretaceous Peruvian locality (Grambast *et al.*, 1967; Sigé, 1971, 1972), a late Paleocene Brazilian locality (Paula Couto, 1979), and on various late Paleocene Patagonian localities (Marshall *et al.*, 1983; Bond *et al.*, 1995). Prior to this mobilist scenario, both Keast and Simpson, along with most of their paleontological contemporaries, subscribed the notion that the oldest known mammals in southern continents were immigrants from Laurasia. Hence, the expression the southern continents "were supplied" with basically different mammalian stocks. Matthew's classic study, "Climate and Evolution" (1915), did much to foster the vision that "Holarctica was the source for all mammals". Neither Matthew nor his followers explicitly denied that South America (or the other southern continents) were inhabited by mammals other than marsupials and placentals. They inferred that the beginning of the history of mammals in southern continents was rooted in the oldest known fossil mammals, a suposition that the mammalian fossil record supported for a long time. But now there is new evidence to be considered.

The Cretaceous and early Paleocene record in southern South America (Patagonia) suggests that mammals in the southern continents passed through a separated Gondwanan period or Gondwanan Stage (Pascual, 1996, 1998). On a global scale, this was a distinctive epi-

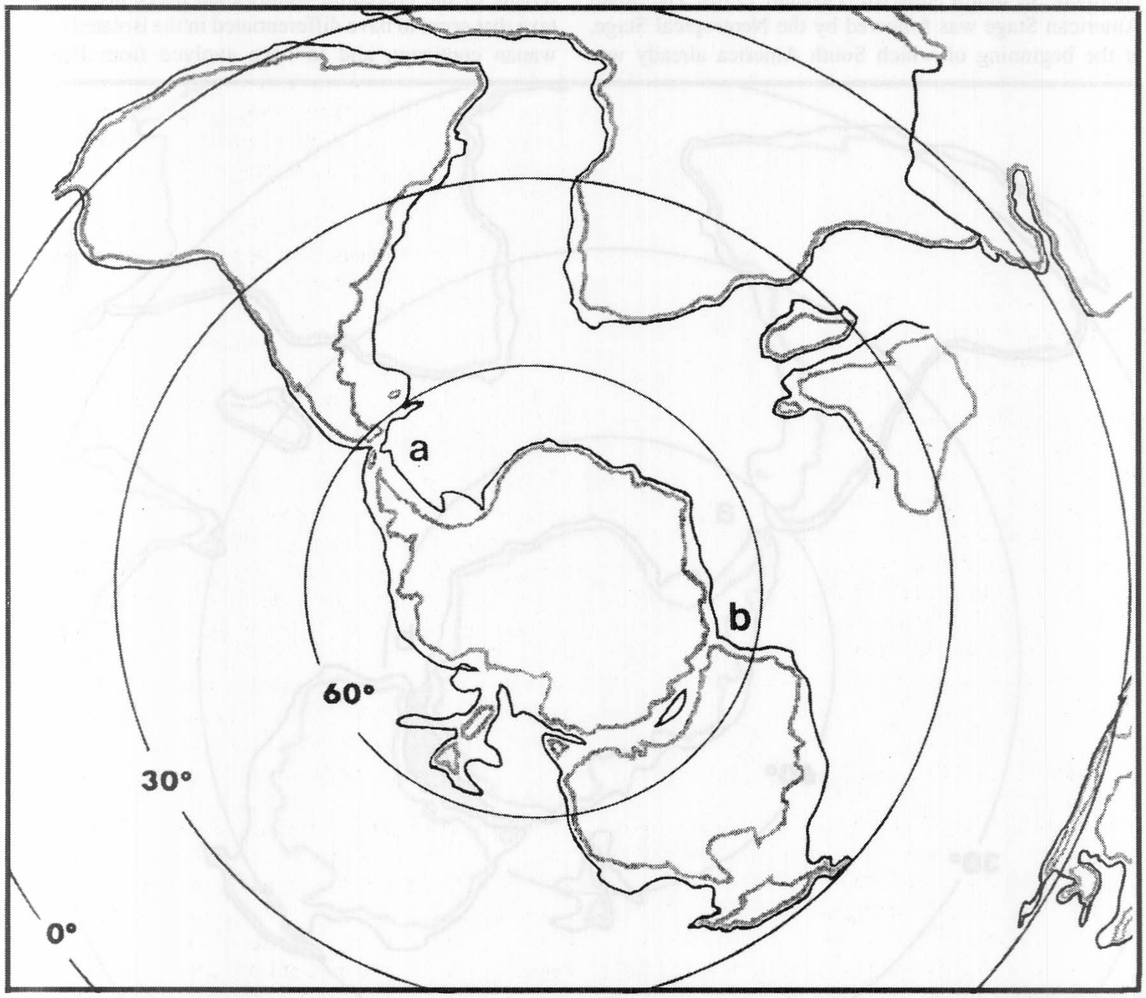

Figure 1. Late Cretaceous (ca. 75 Ma) paleogeographic reconstruction of southern continents. Compiled from distributional data contained in: Zinsmeister, 1982; Woodburne and Zinsmeister, 1984; Lawver *et al.*, 1992. **a.** Antarctic Peninsula-southern South America areas were contiguous. Geologic evidence provided by Grunow (1992) and Shen (1995) suggests that these areas formed part of a continuous geologic province. To Case (1988) both were part of a terrestrial and marine paleobiogeographic province (Weddellian Province). **b.** The crust between Australia and Antarctica began to open about 80 Ma (Veevers and Li, 1991). McGowran (1991) records a series of marine ingressions within the interval 70 to 50 Ma. For Lawver *et al.* (1992) at 64 Ma the Southern Ocean was more widely open. *Reconstrucción paleogeográfica para el Cretácico Tardío (ca. 75 Ma) de los continentes australes. Compilado de datos de distribución contenidos en: Zinsmeister, 1982; Woodburne and Zinsmeister, 1984; Lawver et al., 1992.* ***a.*** *La Península Antártica y el sur de América del Sur eran contiguas. Evidencia geológica provista por Grunow (1992) y Shen (1995) sugiere que todas estas áreas formaban parte de una provincia geológica continua. Para Case (1988) ambas eran parte de una provincia paleobiogeográfica terrestre y marina (Provincia Weddeliana).* ***b.*** *La corteza entre Australia y Antártida comenzó a separarase hace alrededor de 80 Ma (Veevers and Li, 1991). McGowran (1991) registra una serie de ingresiones marinas en del intervalo 70 a 50 Ma. Para Lawver et al. (1992) a los 64 Ma el océano austral estaba más abierto.*

sode in mammal evolution for the exclusively non-tribosphenic and pre-tribosphenic native mammals that were involved; the time period spanned post-Pangean Mesozoic times, and the evolution of the groups took place on the Gondwana supercontinent. Regionally, it was also a quite distinctive episode compared to the two later episodes experienced by Cenozoic South American mammals. The earliest of the latter was the South American Stage, which at first had South America + the Antarctic Peninsula as the substrate, and later, only the isolated island-continent of South America (Pascual, 1998). The South American Stage was followed by the Neotropical Stage, at the beginning of which South America already was connected to North America by Central America (Pascual, 1997). Tribosphenids (i.e. marsupial and placental mammals), were present in both the South American and the Neotropical stages. These mammals immigrated to the southern continents in successive waves from the Laurasian continents, as hypothesized by Matthew and most of later workers. Solely the very first part of the South American Stage in Patagonia (Pascual *et al.*, 1992a) counted with a monotreme and a relictual non-tribosphenic mammal. In contrast, those mammals characteristic of the preceding Gondwanan Stage are endemic taxa that seem to have differentiated in the isolated Gondwanan continent, and to have evolved from Pangean

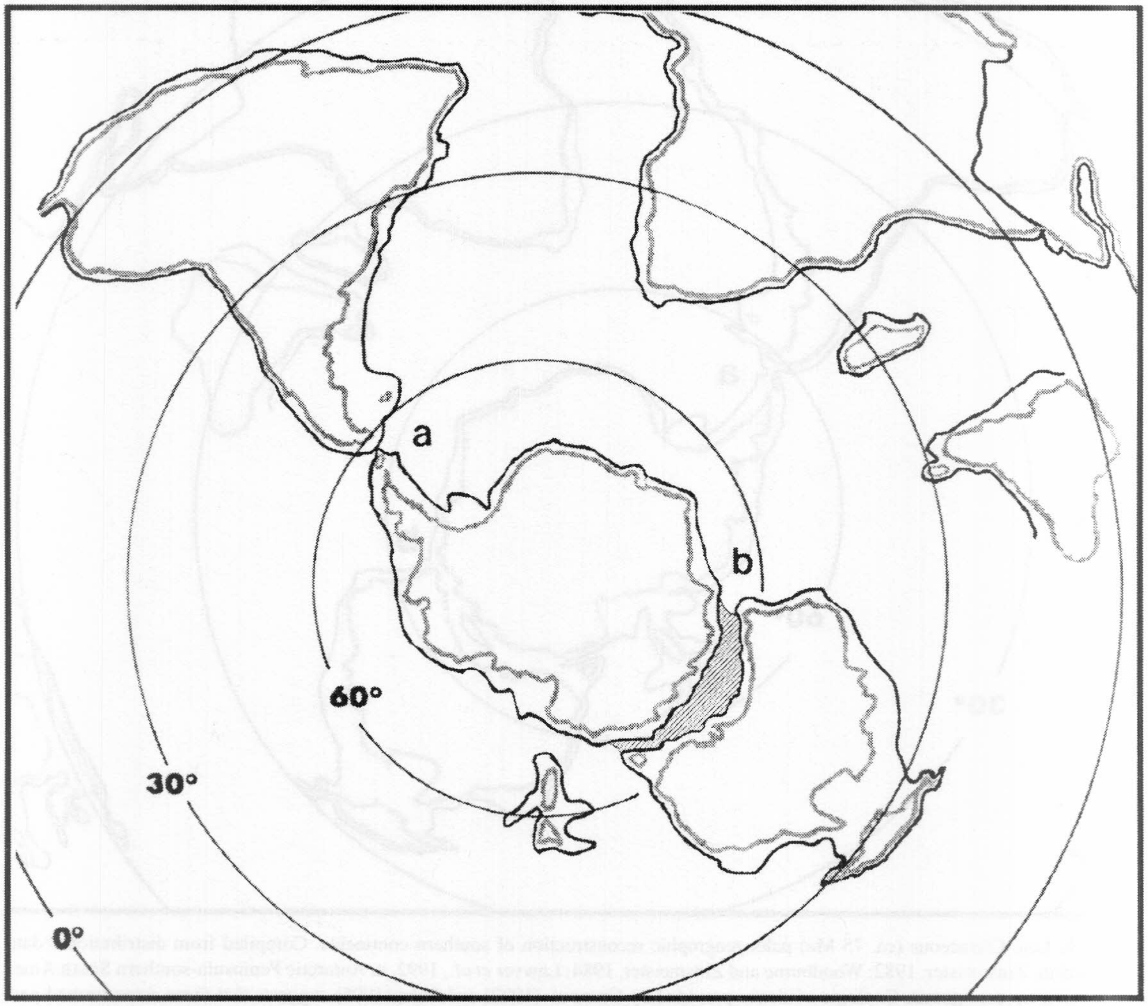

Figure 2. Eocene (ca. 52 Ma) paleogeographic reconstruction of southern continents. Compiled from distributional data contained in: Zinsmeister, 1982; Woodburne and Zinsmeister, 1984; Lawver *et al.*, 1992; Lazarus and Caulet, 1993. **a.** Apparently the same conditions than in the Late Cretaceous prevailed in this area. **b.** Lazarus and Caulet (1993) suggest that shallow marine conditions had developed in this area by the early Eocene (52 Ma). Subsequent rapid spreading and marine subsidence of the Southern Ocean led to the "final" separation of Australia and Antarctica. *Reconstrucción paleogeográfica para el Eoceno (ca. 52 Ma) de los continentes australes. Compilado de datos de distribución contenidos en: Zinsmeister, 1982; Woodburne and Zinsmeister, 1984; Lawver et al., 1992; Lazarus y Caulet, 1993.* ***a.*** *Aparentemente prevalecieron las mismas condiciones que en el Cretácico Tardío.* ***b.*** *Lazarus y Caulet (1993) sugieren que las condiciones de mar somero se habían desarrollado en esta área para el Eoceno temprano (52 Ma). La posterior separación rápida y la subsidencia marina del Océano Austral llevaron a la separación "final" de Australia y Antártida.*

groups. Therefore, there had to be another stage, a Pangean Stage, to date recorded only in Late Triassic beds of southern Africa (Crompton, 1964, 1974; Crompton and Jenkins, 1968, 1978).

However, by the early 1980's, the first land mammals were found in the Antarctic Peninsula (Woodburne and Zinsmeister, 1982, 1984) (see Marenssi *et al.*, 1994 and Woodburne and Case, 1996 for updated information). These mammals are Eocene in age, and demonstrate that the Antarctic Peninsula was part of the territory where the peculiar evolution of "South American" land mammals occurred the Late Cretaceous?-early Paleogene.

ANTARCTICA DURING THE GONDWANAN STAGE: THE SUGGESTIVE PART OF THE HISTORY

A prerequisite to the dispersal of land mammals between Australia and South America is the use of Antarctica as a "stepping stone", as was pointed out by Keast (1972), or an "intermediate area", as suggested by Simpson (1978). This restricted view of Antarctica's role reflects the paucity of the oldest fossil mammals known at the time -*i.e.*, marsupials in Australia, and marsupials and placentals in South America. Although Keast (1972: 207) recognized that monotremes "...might have enjoyed

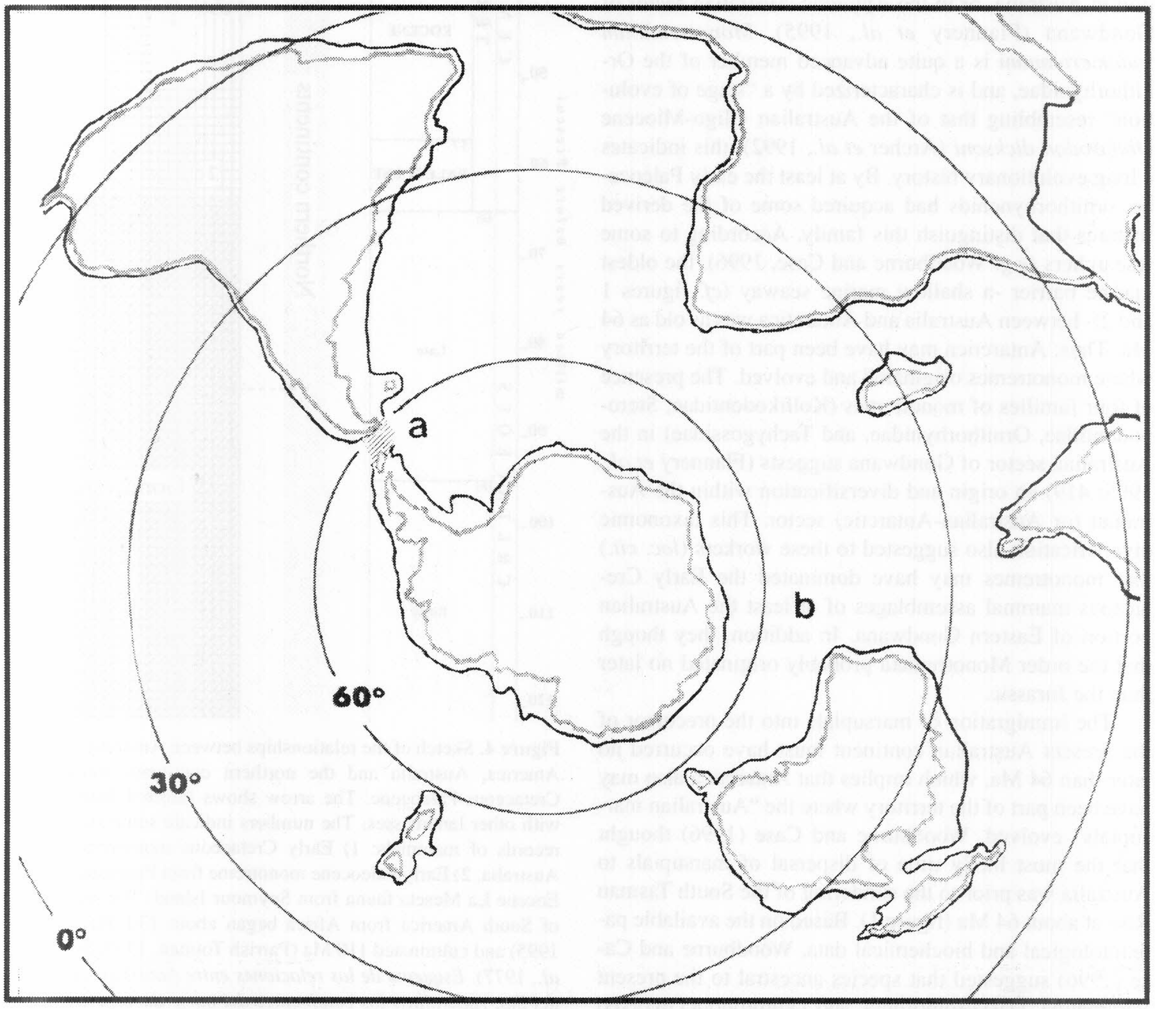

Figure 3. Oligocene (ca. 35 Ma) paleogeographic reconstruction of southern continents. Compiled from distributional data contained in: Zinsmeister, 1982; Woodburne and Zinsmeister, 1984; Lawver *et al*., 1992. **a.** The Drake Passage began to open at about 36 Ma (Woodburne and Zinsmeister, 1984; Lawver *et al*., 1992). The seaways that existed prior to the formation of the Drake Passage involved shallow and intermediate waters (Zinsmeister, 1982). **b.** Australia and Antarctica were separated by oceanic crust. *Reconstrucción paleogeográfica para el Oligoceno (ca. 35 Ma) de los continentes australes. Compilado de datos de distribución contenidos en: Zinsmeister, 1982; Woodburne and Zinsmeister, 1984; Lawver et al., 1992. **a.** El Pasaje de Drake comenzó a abrirse a alrededor de 36 Ma (Woodburne and Zinsmeister, 1984; Lawver et al., 1992). b. Australia y Antártida fueron separadas por corteza oceánica.*

a Cretaceous or early Tertiary radiation (in Australia) prior to the ascendancy of the marsupials...", they were not known as fossils at the time. Currently, the oldest fossil records of monotremes are the primitive Steropodontidae (*Steropodon galmani*; Archer *et al.*, 1985) and the relatively specialized Kollikodontidae (*Kollikodon ritchiei*; Flannery *et al.*, 1995), both from the same Early Cretaceous beds of Australia. They support Keast's suggestion of an early radiation in the Australian sector of Gondwana. The recent record of a monotreme (*Monotrematum sudamericanum*; Pascual *et al.*, 1992a, 1992b) in early Paleocene beds of Patagonia, and it absence in Late Cretaceous land mammal-bearing beds of South America, indirectly add support to an early radiation in Australia, or in the Antarctic-Australian sector of Gondwana (Flannery *et al.*, 1995). *Monotrematum sudamericanum* is a quite advanced member of the Ornithorhynidae, and is characterized by a "stage of evolution" resembling that of the Australian Oligo-Miocene *Obdurodon dicksoni* (Archer *et al.*, 1992); this indicates a long evolutionary history. By at least the early Paleocene, ornithorhynchids had acquired some of the derived features that distinguish this family. According to some researchers (*e.g.* Woodburne and Case, 1996), the oldest marine barrier -a shallow marine seaway (*cf.* figures 1 and 2)- between Australia and Antarctica was as old as 64 Ma. Thus, Antarctica may have been part of the territory where monotremes originated and evolved. The presence of four families of monotremes (Kollikodontidae, Steropodontidae, Ornithorhynidae, and Tachygossidae) in the Australian sector of Gondwana suggests (Flannery *et al.*, 1995: 419) an origin and diversification within the Australian (or Australian-Antarctic) sector. This taxonomic diversification also suggested to these workers (*loc. cit.*) that monotremes may have dominated the Early Cretaceous mammal assemblages of at least the Australian portion of Eastern Gondwana. In addition, they though that the order Monotremata probably originated no later than the Jurassic.

The immigration of marsupials into the precursor of the present Australian continent must have occurred no later than 64 Ma, which implies that Antarctica also may have been part of the territory where the "Australian marsupials" evolved. Woodburne and Case (1996) thought that the most likely time of dispersal of marsupials to Australia was prior to the sundering of the South Tasman Rise at about 64 Ma (figure 1). Based on the available paleontological and biochemical data, Woodburne and Case (1996) suggested that species ancestral to the present Peramelina, Dasyuromorphia, and Diprotodonta evolved in Antarctica (at least) prior to their entry into Australia. If we accept that the early Eocene Australian *Tingamarra porterorum* is a placental (?Condylarthra), as suggested by Godthelp *et al.* (1992), then placentals probably were among the mammals that by that time emigrated from South America to Australia. If this is the case, several questions arise - *e.g.*, why were marsupials more successful than the placentals in Australia? Emigration of South American placental mammals to Australia suggests the possibility that -by the latest Cretaceous-earliest Paleocene- the Australia-Antarctica sector of East Gondwana also may have been an important evolutionary center for the immigrant tribosphenid mammals, and perhaps the site of evolution

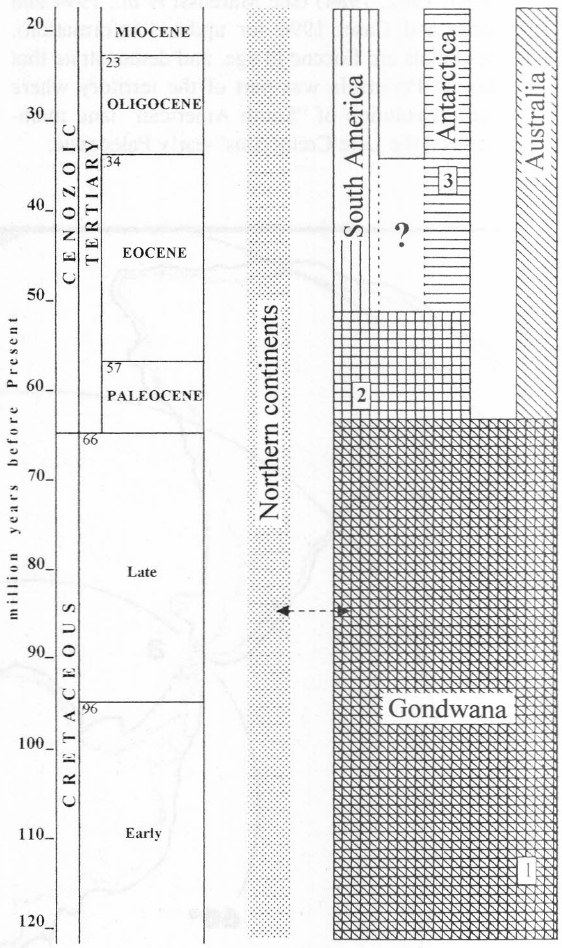

Figure 4. Sketch of the relationships between Antarctica, South America, Australia and the northern continents during the Cretaceous-Paleogene. The arrow shows inferred faunal links with other landmasses. The numbers indicate some significant records of mammals: 1) Early Cretaceous monotremes from Australia, 2) Early Paleocene monotreme from Patagonia and 3) Eocene La Meseta fauna from Seymour Island. The separation of South America from Africa began about 130 Ma (Storey, 1995) and culminated 110 Ma (Parrish Totman, 1993; Sclater *et al.*, 1977). *Esquema de las relaciones entre Antártida, América del Sur, Australia y los continentes del norte durante el Cretácico-Paleoceno. La flecha muestra las relaciones faunísticas inferidas con otros continentes. Los números indican los registros más significativos de mamíferos: 1) monotremas del Cretácico temprano de Australia, 2) monotrema del Paleoceno temprano de Patagonia y 3) fauna de La Meseta, Eoceno de Isla Seymour (Marambio). La separación entre América del Sur y África comenzó alrededor de 130 Ma (Storey, 1995) y culminó a 110 Ma (Parrish Totman, 1993; Sclater et al., 1977).*

for the "South American" tribosphenid mammals. The monotremes and the Tribosphenida (marsupials and eutherians of McKenna, 1975) are two interesting addenda to evidence to be considered in assesing the role of Antarctica in the evolution of mammals in southern continents during the Late Cretaceous-early Paleocene.

The role of Antarctica in the evolution of other non-tribosphenic and pre-tribosphenic mammals is unknown. A non-tribosphenic mammal, the gondwanatherian *Sudamerica ameghinoi* (Scillato Yané and Pascual, 1984, 1985; Krause and Bonaparte, 1993; Pascual *et al.*, 1993) is recorded from Patagonia in the early Paleocene, when a connection persisted between most of the southern continents (the "Weddellian Province"; see Case 1988). Thus, it is obvious that Antarctica had to be part of the territory where the cladogenesis of the southern non-tribosphenic and pre-tribosphenic mammals occurred (Bonaparte, 1990, 1994). The specific evolutionary processes transpiring within what finally became Antarctica is one of the many interesting questions in need of paleontological discoveries from the continent.

ANTARCTICA DURING THE SOUTH AMERICAN STAGE: FACTS AND SUGGESTIONS

The predicted continued junction of southern South America with the Antarctic Peninsula during the Late Cretaceous-early Tertiary (Keast, 1972) was confirmed by subsequent geological, geophysical, and paleontological studies (see papers in Feldmann and Woodburne, 1988; Shen, 1995). Moreover, since 1982 (Woodburne and Zinsmeister, 1982), a series of findings of South American land mammals in strata of middle Eocene age on Seymour Island of the Antarctic Peninsula has supported this conclusion (see Marenssi *et al.*, 1994; Woodburne and Case, 1996, and references therein). These Eocene mammals are related mainly to "South American" marsupial and placental lineages. Marsupials are represented by polydolopids, microbiotheres, protodidelphids, derorhynchids, and one or two as yet indetermined families. The placentals are represented by a tardigrade xenarthran, and a dubious tardigrade or anteater xenarthran, and two "ungulate" families, Sparnotheriodontidae and Trigonostylopidae (see Marenssi *et al.*, 1994; Woodburne and Case, 1996; Goin *et al.*, 1995; Vizcaíno and Scillato Yané, 1995).

Most marsupials resemble South American Paleogene taxa, and most are represented by taxa solely recorded in Paleocene beds (*e.g.*, protodidelphids and derorhynchids). However, at the specific and generic levels they are endemic. Given the middle Eocene age of these beds, this endemism is suggestive. The affinities and the endemic nature of the middle Eocene Seymour Island taxa seem to indicate that they resulted from being isolated in the Antarctic Peninsula subsequent to their derivation from ancestors of Paleocene or earlier age. Among the marsupial remains, there is a peculiar upper molar that resembles the molars of three other groups: (1) North American Late Cretaceous peradectoid-like taxa; (2) Patagonian middle Paleocene didelphimorph taxa; (3) with Australian dasyuromorph taxa (Goin *et al.*, 1995 and in prep.). If we postulate that North America is the primary source of marsupials (Cifelli, 1993), and that both South America and Antarctica acted as early "stepping stones" for the marsupials that eventually reached Australia, the dentitional similarities observed among the four groups seem reasonable. Although South America had to have been an early "stepping stone" for marsupials on their way to Australia, it has been shown that it also was an important center of early evolution for marsupials (Muizon, 1991), as well as for placentals. Moreover, Antarctica also must have been another important center of early evolution for marsupials and for placentals (see figures 1-2, and above). The middle Eocene dasyuromorph-like marsupial from the Antarctic Peninsula could represent a relictual "Australian" taxon differentiated before Australia separated from Antarctica (see figure 1, and above).

One of the xenarthran remains was identified as a tardigrade (Vizcaíno and Scillato Yané, 1995). Another one shares plesiomorphic features with primitive Pilosa, both Tardigrada and Vermilingua. Despite some dubious Eocene records (Simpson, 1948), the oldest, unquestionable South American Tardigrada are from Deseadan beds (middle Oligocene) of Patagonia (Hoffstetter, 1982) and Bolivia (Engelmann, 1987). Thus, the Antarctic remains represent the earliest, unquestionable record of Tardigrada. The oldest Vermilingua from South America was unearthed from early Miocene Colhuehuapian beds (Carlini *et al.*, 1992) of Patagonia, and is a myrmecophagid. Thus, the probability of Vermilingua in Antarctica revives the intriguing question of the origin and evolution of Pilosa in general. On the one hand, if *Eurotamandua joresi* Storch from the middle Eocene of Germany is a myrmecophagid that immigrated from Africa across the Tethys Sea, as suggested by Storch (1981, 1984, 1986, 1993), the family occurred earlier in Africa than in South America. Circumstancial evidence could indicate that at least the xenarthran Pilosa did not originate in South America (Pascual, 1996), as has long been thought. The middle Eocene Pilosa from Antarctica seems to reinforce the possibility that they did not originate in South America. On the other hand, it is highly remarkable that during ten field seasons of intensive search for mammals in the Eocene beds of the Antarctic Peninsula (La Meseta Formation), we failed to find a cingulate xenarthran. Cingulates (dasypodids, glypodonts, and pampatheres) usually have more than 1000 bony scutes forming their carapaces, which makes the likelihood of finding their remains highly probable. The oldest record is from the Itaboraian (*circa* 58 Ma; Pascual and Ortiz Jaureguizar, 1991; Flynn and Swisher, 1995) middle Paleocene beds of Brazil (Scillato Yané, 1976, 1986). Therefore, it is noteworthy that cingulates have not yet been found in middle

Paleocene beds of Patagonia (Bond *et al*., 1995), and are relatively scarce in the remaining mammal-bearing Paleogene beds of Patagonia, as well as in all of South America. This is particularly curious because cingulates are quite abundant all over the South American continent from the beginning of the Patagonian Faunistic Cycle onwards *i.e.*, approximately during the last 30 million years (Pascual and Ortiz Jaureguizar, 1990). Thus, their absence in Antarctica during the Eocene could be related to their scarcity during the Paleogene in South American. Apparently, this scarcity was even more marked in Patagonia, because their older record is in late Paleocene beds, and cingulates are extremely rare in the otherwise rich Eocene land mammal-bearing beds. This paleobiogeographical pattern of xenarthran distribution challenges the long-presumed South American origin of the group. At the very least, the record suggests that neither Patagonia nor the remaining East Gondwanan continents were the sites of xenarthran origins.

Ungulates are represented by isolated teeth assigned to two of the most peculiar South American early Paleogene families, Sparnotheriodontidae and Trigonostylopidae. The Sparnotheriodontidae remains are more interesting than those of the Trigonostylopidae, because they have derived features that allow their distinction as a separate genus (Vizcaíno *et al*., 1997). Apparently these dental features are correlated with the younger age and the geographical isolation of the taxon. The oldest known sparnotheriodont is from the middle Paleocene (Itaboraian SALMA) of Brazil and Patagonia, whereas the younger Patagonian record is from early Eocene Casamayoran beds (Soria, 1980). No more recent remains have been found in Patagonia. However, the extra-Patagonian late Eocene Divisaderan beds afforded the last record of Sparnotheriodontidae, *Phoradiadus divortiensis* (Bond, 1986), although apparently, it represents a distinct lineage from that in Patagonia.

The molars of the astrapotherian Trigonostylopoidea (Bond *et al*., 1990; Marenssi *et al*., 1994) cannot be assigned to a lower taxonomic level. The oldest currently known trigonostylopid is from late Paleocene Riochican beds Patagonia (*i.e.,* older than that from the Antarctic La Meseta Formation).

CONCLUSIONS

1. Each of the known post-Pangean Mesozoic land mammals from southern continents indicates that there was a Gondwanan Stage in mammal evolution, solely involving non-tribosphenic and pre-tribosphenic mammals from the middle (?) Jurassic until about the Late Cretaceous. Moreover, these remains suggest that Gondwana (at least East Gondwana) was a major and distinct theater for the evolution of non-tribosphenic mammals.

2. The Patagonian biota from the Late Cretaceous-early Paleocene span was more closely related to that of East Gondwanan continents than to that of West Gondwana.

3. Although meager, the Cretaceous mammal record in Patagonia and Australia suggests that from the beginning (Middle Jurassic?), Gondwana was not an entirely uniform biogeographical region.

4. At present, the role of the Antarctic sector during the Gondwanan Stage of mammal evolution is poorly understood. But given the biotic and abiotic evidence about the fragmentation of Gondwana, cladogenesis of the monotremes must have occurred in what presently is part of Antarctica. The same evidence suggests that Antarctica was also part of the territory where the "Australian" marsupial cladogenesis occurred (figures 1 and 4).

5. During the latest Cretaceous-earliest Paleocene, Antarctica also acted as a "stepping stone" for mammalian dispersal between South America and Australia.

6. The Antarctic Peninsula (at least) was part of the site where early Paleogene evolutionary processes of "South American" Tribosphenida mammals occurred.

7. The latest Antarctic land mammal (?Litopterna, Sparnotheriodontidae) comes from the uppermost level of La Meseta Formation (Unit III of Elliot and Trautman, 1982) exposed in West Antarctica (Seymour Island). It is associated with a molluscan assemblage having an abrupt change with respect to the lower land mammal-bearing beds. To Zinsmeister and Camacho (1982), this change might be related to the abrupt drop in the temperature of deep-sea bottom at the end of Eocene times, as recognized by Shackleton and Kennett (1975). However, to Keller *et al*. (1992) this drop in the temperature was stepwise. In any case, this molluscan faunal change might be related to the well known global climatic-environmental change occurred around the Eocene/Oligocene boundary (Berggren and Prothero, 1992). Regionally, this change might be related to the rupture of the Antarctica-South America connection, to a shift from temperate/temperate-glacial to polar-glacial conditions (in late Oligocene time) (Bartek *et al*., 1992), and to the onset of unfavourable environmental conditions for land mammals in Antarctica (figures 3 and 4).

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