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# THE HISTORY OF SOUTH AMERICAN LAND MAMMALS: THE SEMINAL CRETACEOUS-PALEOCENE TRANSITION

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ABSTRACT. The last records of Late Cretaceous and early Paleocene (Danian-Selandian) mammals from Patagonia together with those from the early Paleocene of Bolivia, are hard evidence that the whole history of the terrestrial South american mammals followed peculiar evolutionary patterns, very different from those of other regions of the world. We recognize two large episodes, which we call the Gondwanic Stage and the South American Stage. Each results from evolutionary processes which involve genetic isolation, and appear to have been related to the two stages of geographic isolation which happened in the South American continent: as part of the Gondwana supercontinent during most of the Mesozoic, and finally as a discrete and isolated continental unit near the end of the Pliocene. The first one was characterized by communities exclusively composed of no-tribosphenic and pre-tribosphenic mammals. The second one included only tribosphenic mammals (except for one monotremata and one non-tribosphenic from the early Palaeocene, and only from Patagonia). The fisrt stage was a severe isolation from the northern continents which integrated into Laurasia. The second, on the other hand, was characterized by sporadic direct or indirect conexions with the Laurasian continents, or with Africa. For this reason, all mammals belonging to this second stage are regional products which, in isolation, derived from extracontinental immigrants. The drastic compositional changes between these stages should have happened between the Campanian and Danian, but we lack records which would allow the recognition of their *modus operandi*.

RESUMEN. LA HISTORIA DE LOS MAMÍFEROS TERRESTRES SUDAMERICANOS: LA SEMINAL TRANSICIÓN CRETÁCICO-PALEOCENO. Los últimos registros de mamíferos del Cretácico Tardío y del Paleoceno temprano (Daniano-Selandiano) de Patagonia, sumados a aquéllos del Paleoceno Temprano (Daniano tardío?) de Bolivia, son evidencia concreta de que la historia toda de los mamíferos terrestres sudamericanos siguió patrones evolutivos singulares, y muy distintos a aquéllos de otras partes del mundo. Reconocemos dos grandes etapas, que distinguimos como la Etapa Gondwánica y la Etapa Sudamericana. Cada una de ellas resulta de procesos evolutivos sucedidos en aislación genética, y aparecen como causalmente relacionadas, respectivamente, a las dos grandes etapas de aislamiento geográfico por las que pasó lo que devendría el continente sudamericano: como parte del Supercontinente Gondwana durante la mayor parte del Mesozoico, y finalmente como una unidad continental discreta y aislada hasta fines del Plioceno. La primera estuvo caracterizada por comunidades compuestas exclusivamente por mamíferos no-tribosfénicos y pre-tribosfénicos. La segunda, por comunidades compuestas exclusivamente por mamíferos tribosfénicos (salvo un monotremata y otro no-tribosfénico del Paleoceno temprano, y sólo de Patagonia). La primera etapa fue de un más severo aislamiento de los continentes del norte, componentes de Laurasia. La segunda, en cambio, estuvo signada por esporádicas conexiones, directas o indirectas, con los continentes laurásicos, y con África. Así, todos los mamíferos de esta segunda etapa son productos regionales que, en aislación, derivaron de inmigrantes extracontinentales. Los drásticos cambios composicionales entre una y otra etapa debieron ocurrir entre el Campaniano y el Daniano, aunque carecemos de registros que permitan reconocer su *modus operandi*.

KEY WORDS. Land-mammals. South America. Cretaceous-Paleocene transition.

PALABRAS CLAVE. Mamíferos terrestres. Sudamérica. Transición. Cretácico-Paleoceno.

## INTRODUCTION

Strata of continental origin of either the latest Cretaceous or early Paleocene are known in several regions of the world, but there are few areas in which apparently uninterrupted accumulation of continental deposits took place thoughout this entire interval of the Earth history. For this reason, virtually all that is known of the vertebrates that made the transit across the Mesozoic-Cenozoic boundary, particularly the pattern of mammal evolution, comes from continental deposits in the Western Interior of North America. On the basis of this evidence it was claimed (Archibald and Clemens, 1984; Clemens, 1986) that changes in the mammalian fauna from the Cretaceous to the Paleocene, in contrast to those affecting the reptiles, were similar to what is usually seen in any given successsion of North American land-mammal ages. That is to say, that abrupt compositional changes as such occurred in reptiles, did not occurr in North American mammal communities during the Cretaceous-Tertiary transition. Although a similar record of mammals representing the Mesozoic-Cenozoic transition is yet unknown in South America, the present Late Cretaceous and early Tertiary records (Bonaparte and Soria,

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1985; Bonaparte, 1986a, 1986b, 1986c, 1987, 1990, 1992; Bonaparte and Rougier, 1987; Bonaparte and Pascual, 1987) suggest that this was not the case on this continent (Pascual and Ortiz Jaureguizar, 1992 and references therein). Herein, I comparatively evaluate these records because they suggest that quite a change occurred throughout this transitional period, probably embracing the whole Maastrichtian and most of the Danian. In addition to the empirical information afforded by these records, they also suggest that the Mesozoic mammal history in South America was quite different from that in northern continents. Actually, this record suggests that the "curious" history of the Cenozoic South American land mammals (*sensu* Simpson, 1980), was related to their "splendid isolation" (*sensu* Simpson, 1980), and was preceded by an even more curious and quite distinctive pre-Cenozoic history, which seems causally related to the likewise long isolation of the Gondwanan Supercontinent. The drastic compositional change recorded between the known Late Cretaceous and early Tertiary mammal communities occurred during most of the Maastrichtian-Danian span. This Cretaceous-Tertiary transition was extremely seminal. During this unrecorded span the most transcendental geobiotic processes that led to the curious history of Cenozoic South American mammals occurred. The data also suggest that the marked episodic history of Cenozoic South American mammals (Simpson, 1950) began in the Mesozoic, which *per se* is distinguished as a distinct main episode, termed the Gondwanic Stage (Pascual, in press). Summing up, from its beginning, the history of the South American land mammals —and probably the whole terrestrial biota— was characterized by relatively few episodes (Simpson's [1950] Faunal Strata), which usually were clearly distinct (Pascual and Ortiz-Jaureguizar, 1992).

## INTERACTION OF THE GEOLOGICAL AND BIOLOGICAL SYSTEMS

### SOUTH AMERICAN MAMMAL PALEOBIOGEOGRAPHY: STATE-OF-THE-ART

By the 1950's, Simpson still maintained that "There were probably sweepstakes routes (but not complete bridges) from Antarctica to Australia and South America...", and that this conclusion "...seems to apply not only to the biogeography of mammals but also to that of all contemporaneous forms of life...". However, he conceded that "...It remains possible that there were transoceanic continents or bridges or that continents drifted in the Triassic or earlier, but there is little good evidence that such was the fact. In any case such remote events would have little or no bearing on the present distribution of living things" (Simpson, 1953: 63). Consequently, at that time his understanding of the history of South American land mammals was cast in the context of this stabilist framework. By the late 1970's Simpson had changed his original stabilist concept, accepting the plate tectonic evidence (Simpson, 1978, 1980). Let us remember that until 1983 (see Bonaparte y Soria, 1985) the record of South American land mammals was almost absolutely restricted to the Cenozoic, and not just from the earliest Cenozoic, but from the medial Paleocene onward (*sensu* Woodburne and Swisher, 1995). Although by the 1980's the evidence supporting continental drifting had been long accepted as unquestionable, explanations of the biogeographic history of the known Cenozoic South American land mammals did not require application of plate tectonic rationale as a *sine qua non* condition. Under Simpson's arguments —basically followed by many other researchers (e.g., Patterson and Pascual, 1972)— his sweepstakes routes could solely account for the biogeographical history of South American land mammals. But the subsequent record of early Paleocene mammals in Bolivia and Patagonia, and Cretaceous mammals in Patagonia drastically challenged Simpson's original concept. It demonstrated that the peculiar history of South American land mammals cannot be explained without using the plate tectonic rationale (see Pascual, in press). Moreover, it demonstrated that the long known Tertiary isolation of the South American continent was preceded by a similar long-standing Gondwanan isolation (Bonaparte, 1986b; Pascual's "Gondwanan Stage" [Pascual, in press]). Actually, these records suggest that during most, if not all, of the Mesozoic the South American continent did not contain the forebearers of any of those mammals known and identified by Simpson (1950) as the "ancient immigrants". Therefore, the designation of "ancient immigrants" was right, since the oldest Cenozoic mammals known at that time originated from immigrants from other continents. He never explicitly denied the existence of "Mesozoic mammals" in South America, but apparently he did not envision that South America was ever inhabited by non-tribosphenic and pre-tribosphenic mammals. The record of supposedly late Cretaceous primitive marsupial and placental mammals in the high Andean plateau of Peru led him to state that "...it would have been expected that mammals like these would occur in the Cretaceous of South America" (Simpson, 1980: 39). These mammals, as well as those from Bolivia, also supposedly Cretaceous in age (e.g., Muizon *et al.*, 1984; Muizon and Marshall, 1985; Marshall and Muizon, 1988), were later demonstrated to be early Palaeocene in age (Gayet *et al.*, 1991; Muizón, 1991). In short, up to the end of the 1970's, Simpson's extremely influential papers on mammalian zoogeography reinforced Matthew's conclusion, i.e., Holarctica was the source of all mammals. For example, it would follow than that the affinity between the South American borhyaenids and the Australian thylacines was considered by Simpson to be the result of parallel evolution from a common stock and not conclusive evidence for a connetion between Soth America and Australia (Simpson, 1941). However, subsequently he abandoned this concept, saying "...that the early dispersal

of marsupials involved North America, South America, Antarctica, and Australia". He reached this conclusion because he had accepted that "...plate tectonic evidence as usually interpreted at present obviously opens up another possibility for faunal connection between Australia and South America, with Antarctica as the intermediate area" (Simpson, 1978: 323). Although Simpson (1980: 241) admitted that the origins of the oldest ancestral faunas remained enigmatic, he thought that extinct and extant South American land mammals known at that time (with the possible exception of the edentates, discussed below) originated from immigrants from other continents. From these, he selected species to diagnose three "faunal strata" (Simpson, 1950) or "phases" (Simpson, 1980) that characterize the history of Cenozoic South American land mammals: 1) Ancient Immigrants or Old Timers (= first Phase), 2) Old Island-hoppers or Aliens (= second Phase), and 3) Late (Island-hoppers and) Immigrants (= third Phase, The Great American Interchange). All of these mammals were marsupials and placentals. Thus, Simpson (1978, 1980) apparently did not think that South America was populated by mammals other than tribosphenic forms during the Mesozoic.

However, the information available by the 1970's led other researchers to consider South America as the primary source of some of its most peculiar mammal groups, among which are the marsupials and the edentates. For instance, Tedford (1971, 1974) hypothesized a Late Cretaceous, southern continental (specifically South American) origin for the ancestral stock of the Late Cretaceous and Cenozoic marsupials of the Americas (*sic*) and Australia. This hypothesis was based on the incorrect assignment of a Late Cretaceous age to the mammal-bearing sites in Peru (Vilquechico, see Sigé, 1968, 1971, 1972; Grambast *et al.*, 1967) and Bolivia (Tiupampa, Cochabamba); these sites now are known to be early Paleocene in age (See Bonaparte and Pascual, 1987; Pascual and Ortiz-Jaureguizar, 1991; Muizon, 1991). This error led Tedford and many others to think that the mammals of the South American Cretaceous vertebrate faunas shared some of the therian taxa known in the Northern Hemisphere (1974: 119) owing to immigration events from North America. As a result, Tedford (*loc. cit.*) attributed the absence of the allotherian multituberculates in South American Cenozoic strata to the apparent action of biological filtering across the Middle America archipelago. He added that "...had they been present in the south, they surely would have persisted into Tertiary time there, just as they did in Holarctica". Thus, like Simpson, Tedford did not think that the non-tribosphenic and pre-tribosphenic mammals inhabited South America continent in the Mesozoic. With regard to edentates, the relationships of the xenarthrans with the North American Paleogene Palaeanodonta was originally accepted by Simpson and many other workers. However, he later concluded that "...the origin of the Xenarthra, either phylogenetic or geographic, is unknown at present" (Simpson, 1978: 324; see also 1980: 49). Notwithstanding, he was inclined to admit that they originated in South America because this was the simplest hypothesis, "...a group with early members known from one continent only, probably originated there..." (Simpson, 1978: 324). Xenarthras apparently did not originate in South America because they seem to be absent in the Patagonian Cretaceous mammal-bearing stratigraphical units, and they are absent in the early Paleocene mammal-bearing stratigraphical units (both Patagonian and central South American). Moreover, they are scarce in every South American late Paleocene and early Eocene mammal-bearing stratigraphical unit (Pascual, in press). Thus, Storch's (1986) hypothesis that edentates (Edentata = Xenarthra *fide* Storch) were in West Gondwana before (ca. 110 Ma) the South American and African plates drifted apart should be considered a possibility.

Simpson's theories about the origin and history of South American land mammals generated as much controversy in paleontological circles as those advanced by Ameghino at the beginning of the century (see Simpson, 1948). Apparently, Simpson's last statement "Their origin (the oldest South American Cenozoic mammals) is still largely mysterious" excited revisionist attitudes. Some revisionist hypothesis were rashly advanced by researchers well acquainted with extinct South American mammals. For example, the incorrectly dated Late Cretaceous mammals found in the Bolivian highlands, led Marshall and Muizon (1988) to reverse completely our accepted perspectives; they stated that "The record also suggests that many aspects of the paleobiogeotraphic history of Late Cretaceous and Paleogene mammals of South America can be explained by envisioning dispersal of stocks from, and not to, that continent". Based on this assumption, Marshall and Muizon (1988: 51) advanced a paleobiogeographical hypothesis in too much haste; they suggested "Four Late Cretaceous-Paleocene dispersal events of mammals from South to North America...". To them, these putative Late Cretaceous Bolivian mammals (obviously in reference to marsupials and placentals) "...demonstrate that South America was a major theater for the early cladogenesis of therian mammals". Although Marshall and Muizon subsequently recognized (Gayet *et al.*, 1991; Muizon, 1991) that these mammals were Paleocene (Santa Lucía Formation) instead of Late Cretaceous (El Molino Formation) as previously believed, neither they nor any other vertebrate paleontologist promoted the necessary debate to lead to a complete reversal of perspective on the phylogenetic and geographic origin of many higher therian groups.

## THE GONDWANAN STAGE *VS.* THE SOUTH AMERICAN STAGE. THE EVIDENCE

The first unquestionable records of Cretaceous and early Paleocene Patagonian mammals drastically changed past interpretations and elucidated the history of

South American land mammals. The oldest South American mammals known by the 1980's (middle Paleocene) did not indicate that non-tribosphenic and pre-tribosphenic land mammals could have inhabited this continent during part of the Gondwanan Stage. The first Late Cretaceous records demonstrate that these did live there, and apparently were the only mammals present. These non-tribosphenic and pre-tribosphenic taxa were represented by fully endemic higher taxa (Bonaparte, 1990, 1994, and references therein). This marked endemism may have resulted from macroevolutionary processes during the broader Gondwanan/Laurasian isolation. According to the present paleogeographical evidence, this is the most parsimonious hypothesis among those (otherwise not mutually excluding) recently advanced by Flynn and Swisher (1995: 329). Thus, I agree with Bonaparte (*op. cit.*), and state that the Late Cretaceous Patagonian mammals represent a distinct southern Gondwanan Stage with respect to those coetaneous mammals of the northern Laurasian continents (Bonaparte, 1986b, 1986c, 1987, 1990, 1994; Pascual and Ortiz-Jaureguizar,1992), and those Cenozoic South American mammals (Pascual and Ortiz-Jaureguizar, 1990, 1991; Pascual *et al.*, in press). Given the complex and relatively isolated continental masses integrating Gondwanaland, the endemism of the Patagonian Late Cretaceous mammals might indicates a distinct biogeographic region with respect to other Gondwanan continents, or even biogeographically distinct to other parts conforming the present South American continent. Actually, as pointed out by Crisci *et al.* (1993), Papú and Pascual (1993), Pascual *et al.* (in press); Pascual (1996, in press), the known record of floristic and other faunistic elements of the present South American continent, suggests that by the Late Cretaceous, the Patagonian biota was more closely related to that of the other easterm Gondwanan continents than to the biota of northern South America. Curiously enough, this difference still persists in the present Patagonian biota (Crisci and Morrone, 1990; Crisci *et al.*, 1991) However, comparison of this Late Cretaceous Patagonian land-mammal fauna with the earliest Paleocene Patagonian and Bolivian faunas (Pascual and Ortiz-Jaureguizar, 1992) indicates that the faunas represent quite distinct stages in the history of South American mammals (Pascual, in press). All mammals recorded in the early Paleocene Cochabamban locality (Muizon, 1991), and most of those from the early Paleocene Patagonian locality, pertain to groups of tribosphenic metatherians and eutherians. The exceptions are

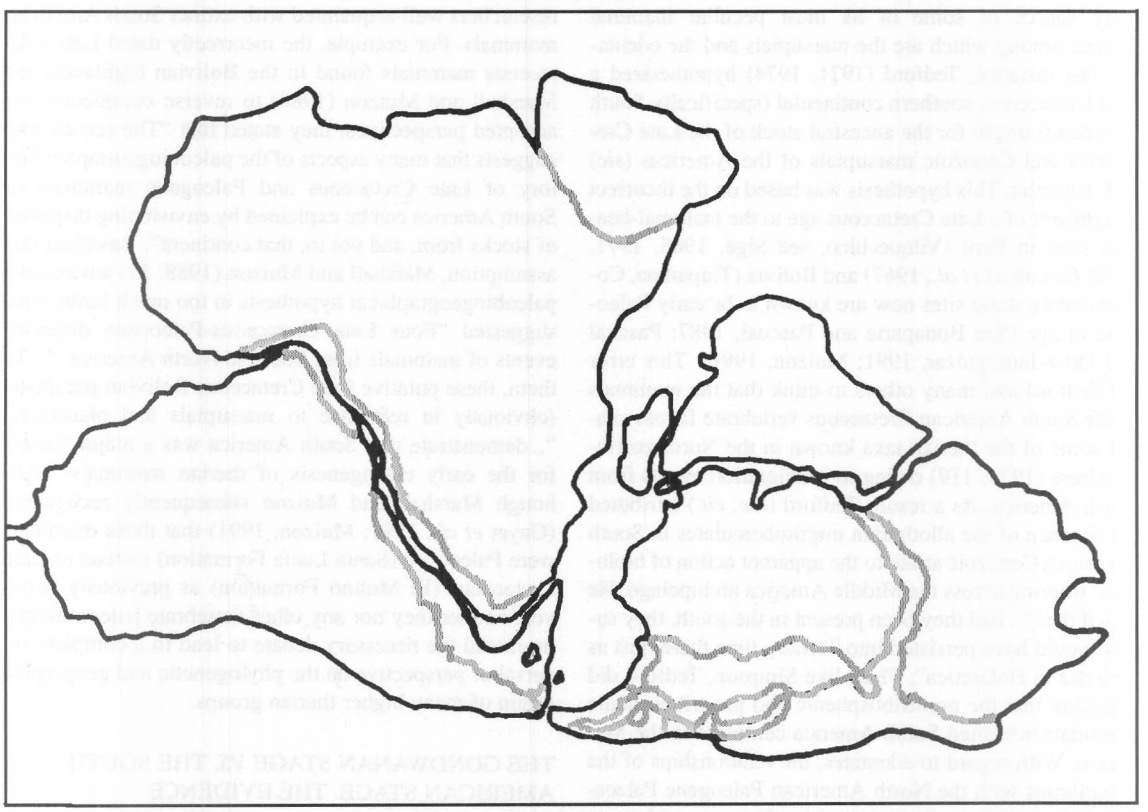

**Figure 1.** Gondwanaland reconstruction for 130 Ma. The South Atlantic opened earlier than the Equatorial Atlantic. Gray line: present coast line; black line: past coast line (modified from Storey, 1995.) / *Reconstrucción del supercontinente de Gondwana a los 130 Ma. El Atlántico sur se abrió antes que el Atlántico ecuatorial. Línea gris: línea de las costas actuales. Línea negra: línea de costas a los 130 Ma (modificado de Storey, 1995).*

the first and only known non-Australian monotreme, and one relictual Gondwanatherian (see Pascual and Ortiz-Jaureguizar, 1991; Pascual *et al.*, 1992a, 1992b, 1993; Bonaparte *et al.*, 1993), These mammals represent a quite distinct stage of evolution that we distinguished as the South American (Isolation) Stage (Pascual, in press). The remaining biotic evidence and, particularly, the abiotic data, also indicate that by the early Paleocene, the South American continent (apparently united to the present Antarctic Peninsula, or part of it) had already become an isolated island continent (Pascual, in press; Vizcaíno *et al.*, 1996).

## THE SUGGESTIVE PART OF THE EVIDENCE

Two quite distinct Mesozoic Gondwanan and Cenozoic South American Isolation stages are clearly indicated by the South American land-mammal record, with both stages separated by long intervals of time. If the Patagonian Late Cretaceous Los Alamitos record is Campanian (Bonaparte, 1990), and both the Bolivian and Patagonian Paleocene records early Paleocene (although not earliest; Gayet *et al.*, 1991; Pascual and Ortiz Jaureguizar, 1991; Bonaparte *et al.*, 1993), there is a gap of about 10 million years. This was a long and seminal transitional span. During this time, South American land mamal communities must have experienced the following main evolutionary phenomena (1) all pre-tribosphenic mammals became extinct ; (2) nearly all the non-tribosphenic taxa became extinct, except the Gondwanatheria; the latter (*Sudamerica ameghinoi* Scillato-Yané and Pascual) apparently survived in Patagonia during the earliest Paleocene (Pascual *et al.*, 1993; Bonaparte *et al.*, 1993; Bond *et al.*, 1995; Pascual *et al.*, in press); (3) the monotreme (*Monotrematum sudamericanum* Pascual *et al.*) emigrated from Australia to Patagonian South America (Pascual *et al.*, 1992a, 1992b) ; (4) metatherians and eutherians emigrated from North America to South America; (5) metatherians emigrate from South America to Australia, via Antarctica. Although less probable, placentals also might have participated (Godthelp *et al.*, 1992). Rather than a dispersalist phenomenon this probably was an extension of the biogeographical range throughout the Weddellian Province; (6) there was a marked cladogenetic radiation of the metatherians, and the first steps of the eutherian radiation.

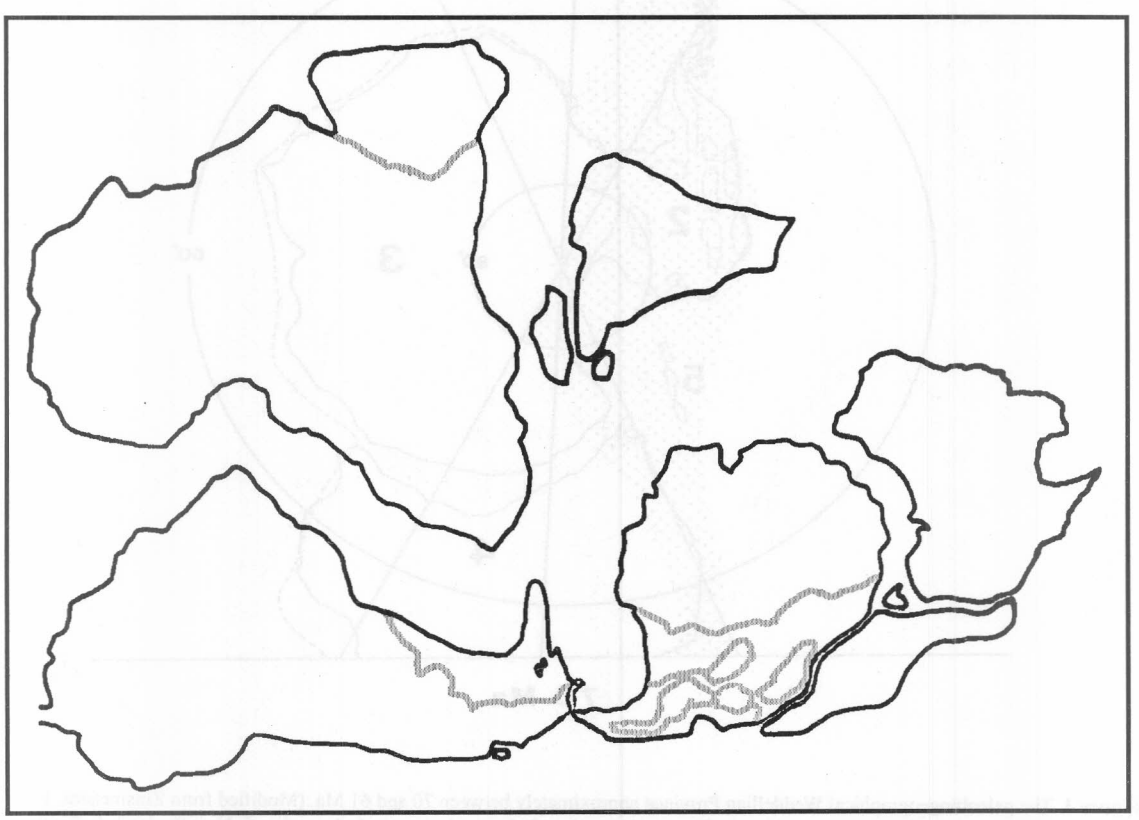

**Figure 2.** Gondwanaland reconstruction for 100 Ma. The present African Atlantic configuration had already been created. Gray line: present coast line; black line: past coast line (modified from Storey, 1995.) / *Reconstrucción del supercontinente de Gondwana a los 100 Ma. La actual configuración atlántica de África habíase creado ya. Línea gris: línea de costas actuales. Línea negra: línea de costas a los 100 Ma (modificado de Storey, 1995).*

## THE PALEOGEOGRAPHICAL BACKGROUND

According to Sclater *et al.* (1977), initiation of equatorial Atlantic rifting occurred in the Albian, about 110 Ma, by which time these researchers suggested that the Brazil-Angola and Argentine-Cape basins had already subsided below 3000 m. Agreement with Sclater *et al.* on timing of the opening of the equatorial Atlantic is widespread (Parrish, 1993). If we accept Pindell and Dewey's (1982) and Storey's (1995) interpretation that the South Atlantic opened first (ca. 130 Ma, figure 1), followed by the opening of the equatorial sector, we must coincide that by at least 100 Ma, the present configuration of the Atlantic margins of Africa had been created (figure 2). If the marine-continental palebiogeographical Weddellian Province was established by the latest Cretaceous (figure 3), and by late Paleogene deep marine conditions had not developed in the Drake Passage (Marenssi *et al.*, 1994; Woodburne, 1996), it is obvious that at least up to the late Paleogene, the present South American Atlantic configuration did not exist. In short, during the unrecorded South American Cretaceous-Paleocene transition,

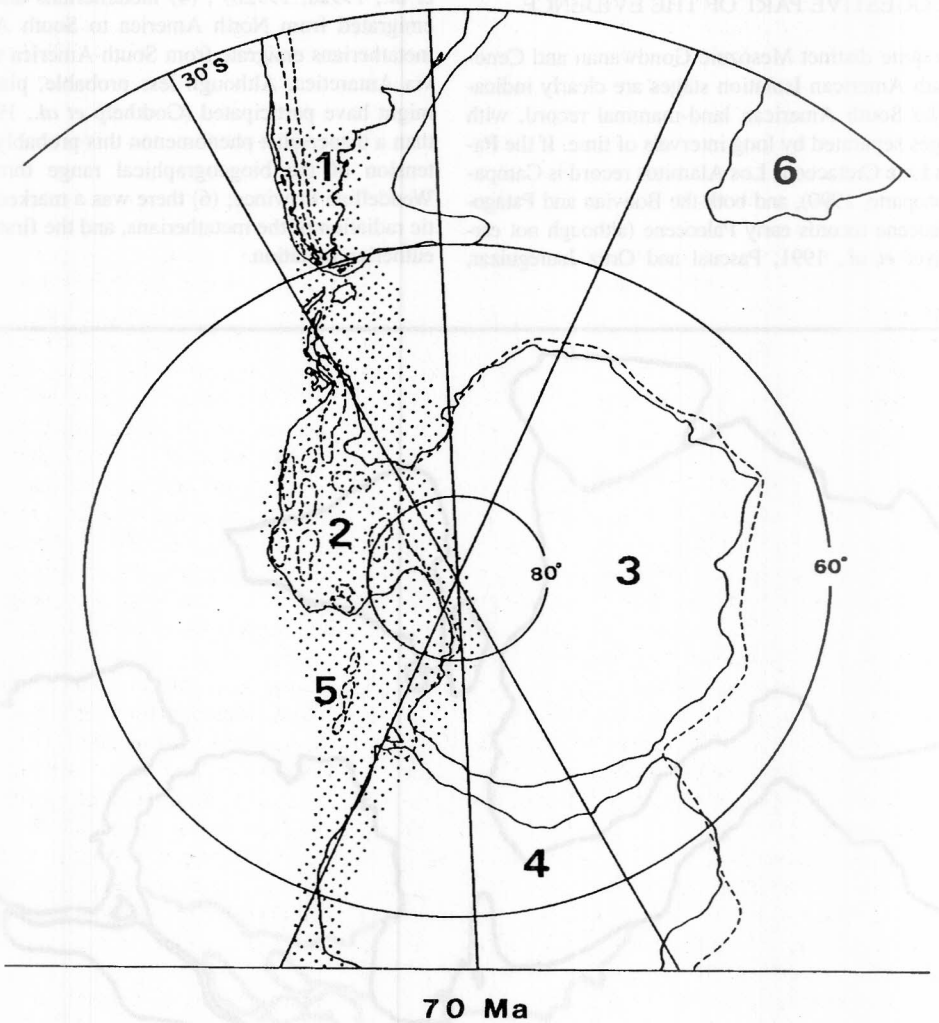


**Figure 3.** The paleobiogeographical Weddellian Province approximately between 70 and 61 Ma. (Modified from Zinsmeister, 1982, and Case, 1988). 1. Southern South America; 2. Western Antarctica; 3. Antarctic craton; 4. Australia; 5. New Zealand; 6. Southern Africa. The present South American Atlantic configuration was created later than the African, approximately by the late Paleogene. / *La Provinca Weddelliana (biogeográfica) aproximadamente entre 70 y 61 Ma (Modificado de Zinsmeister, 1982 y de Case, 1988). 1. Sur de Sudamérica: 2. Antártida Occidental. 3. Cratón Antártico. 4. Australia. 5. Nueva Zelanda. 6. Africa del Sur. La configuración atlántica de Sudamérica fue creada más tarde que la de África, aproximadamente por el Paleógeno tardío.*

estimated to range between the latest Campanian (ca. 71,3 Ma *fide* Gradstein *et al.*, 1995) and the latest Danian (ca. 61 Ma *fide* Berggren *et al.*, 1995), Africa and South America were separated by an already wide Atlantic Ocean. However, the present southern tip of South America maintained some kind of connection with Antarctica approximately up to the late Paleogene. Shen (1995) interpreted this as a narrow, continuous land mass during the Late Cretaceous through Eocene, which he called "Isthmus of Scotia", rather than shallow water or a chain of islands. Geological features indicate to researchers such as Grunow (1993), Lawver *et al.* (1992), and Shen (1995) that from as early as the Late Cretaceous and up to the late Eocene or earliest Oligocene, both the Antarctic Peninsula and the southernmost part of South America were part of the same geological province. Opening of the Drake Passage about 36 Ma (Ehrmann and Mackensen, 1992; Lawver *et al.*, 1992) led to the differentiation of Antarctica and the influential Circum-Antarctic Current. These geographical readjustments established the basic physical conditions leading to the present cooler global climate. They also led to the isolation of South America, which, and for the first time, became a discrete continent, a huge island-continent. The separation of the continental microplate of the South Tasmanian Rise occurred early, at least by 50 mybp, but it was submerged as early as 64 mybp (Veevers *et al.*, 1991). In this manner, the isolation of Australia began, and with it rupture of the Australia connection with South America via Antarctica.

As Smith pointed out (1985: 17), "The most important aspect of a timing sequence for a link between the North and South America land masses is apparently the creation of the Caribbean Plate". But, he cautiously added that "...details (of) a tectonic evolution of the Caribbean Plate and its margins is so enigmatic that many critical questions remain unresolved, and every developed model is couched in some incompatibilities" (Smith, 1985). Likewise, Donnelly (1985: 89) stated that each worker has turned to the task of the reconstruction of Caribbean Plate history influenced by a particular set of experiences or a special approach, and the results have varied accordingly. However, Donnelly afforded a Late Cretaceous reconstruction that is relevant to what appears to be the very first biogeographical connection between the North and South America continents. To him (1985: 105), the first steps leading to the closing of the Caribbean part of the Tethyan Sea were related to the compressional environment that by 85 Ma supplanted the formerly tensional regime. Consequently, the movement of South America relative to North America shifted northward. Compressional features (both subduction and obduction) surrounded the Caribbean, and calc-alkaline magmatism became important for the first time, creating island arc volcanism that could have created an archipelago between both American plates. According to Donnelly (1985: 112), by the end of the Eocene (about 38 Ma) the "...isthmus of Central America forms a continuous structural and morphological unit...not yet emergent..." because shallow-water pelagic and coastal faunas of both sides were similar. As Donnelly pointed out, the model of a Caribbean "Plate" as a very plastic unit, instead of a rigid plate with a conservative geometry, opens the possibiliity that up to emergence of the Panamanian land bridge within the Caribbean region, there probably was a series of second order phenomena of greater importance to biogeography. The formation of topographic blocks are among them, and can account for the immigratory events recorded by the South American vertebrates of the Campanian-early Paleocene span (Bonaparte, 1986a; Bonaparte and Rougier, 1987; Bonaparte and Kielan-Jaworowska, 1987; Bonaparte *et al.*, 1993; Pascual and Ortiz Jaureguizar, 1990, 1991, 1992). These topographic blocks would "...govern species distributions far more effectively than would blocks moving here and there like cars" (Donnelly, 1985: 118).

## CONCLUSIONS

Taking into account only the evidence afforded by the fossil vertebrate record, specifically that of mammals, the following general conclusions emerge.

1. Between the Campanian (the Patagonian Los Alamitos Formation [Bonaparte, 1987]) and the Danian (the Bolivian Santa Lucía Formation [Muizon, 1991] and the Patagonian Hansen Member of the Salamanca Formation [= "Punta Peligro"; Bond *et al.*, 1995]) there was a marked turnover in land mammal communities. Exclusively non-tribosphenic and pre-tribosphenic taxa (Gondwanan Stage) were replaced by tribosphenic taxa (South American Stage *fide* Pascual, in press) everywhere, except in Patagonia. Here two non-tribosphenic mammals, a gondwanathere allotherian and a monotreme, have been recorded.

2. The changes in South American mammal communities followed a different pattern than those recorded in coeval North American communities. The Albian Paluxian NALMA (North American Land Mammal Age) yielded records of the first theria of metatherian-eutherian grade, and later on marsupials (middle Cenomanian) and then eutherians (Campanian Aquilan NALMA). These different scenarios were related to quite different geological histories and, consequently, to quite different biogeographical histories (Pascual and Ortiz-Jaureguizar, 1992).

3. If the Patagonian Late Cretaceous record of land mammals represents a valid standard for the entire continent during the Campanian-Danian interval, South America should have had some kind of connection/s with both North America and Australia, the latter including Antarctica as an "intermediate" continent (see Vizcaíno *et al.*, 1996). Both connections appear to have been discontinuous, in space or time, since the interchange was selective.

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