

The tectonic setting of the Caribbean region and the K/T turnover of the South American land-mammal fauna

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ABSTRACT

According to the fossil record, a biotic interchange of land vertebrates (*e.g.* booid snakes, dinosaurs and mammals) occurred between the Americas during the Late Cretaceous-Early Palaeocene. The arrival of North American immigrants (particularly marsupials and placentals) during the latest Cretaceous-earliest Palaeocene had a profound influence on the composition of the South American mammal communities. During the Late Cretaceous these communities were dominated by native groups of Pangeic lineages, which represented more than 95% of the known genera, but during the Early Palaeocene 70% of South American mammals were derived from North American immigrants that had arrived during the Late Cretaceous-earliest Palaeocene, and by the Late Palaeocene all the South American mammals (with the possible exception of the xenarthrans) were descendants of these North American immigrants. In spite of the fact that no geological evidence is currently available to support the existence of a continuous land connection between the Americas during the Late Cretaceous-early Palaeocene, the fossil record is substantial enough to point to a temporary inter-American connection that permitted the beginning of a land-mammal exchange by the end of the Cretaceous. This interpretation is supported by recent geographic reconstructions of the Caribbean region.

Key words: Cretaceous, extinction, immigration, Palaeocene, palaeogeography

El marco tectónico de la región caribeña y el recambio K/T de la fauna de mamíferos continentales de América del Sur

RESUMEN

De acuerdo con el registro fósil, durante el Cretácico Tardío-Paleoceno Temprano ocurrió un intercambio de vertebrados continentales (e.g., serpientes bóidas, dinosaurios, mamíferos) entre las Américas. El arribo de los inmigrantes norteamericanos (particularmente marsupiales y placentarios) durante el Cretácico más tardío y el Paleoceno más temprano tuvo una influencia crucial en la composición de las comunidades de mamíferos de América del Sur. Durante el Cretácico tardío estas comunidades estuvieron dominadas por grupos nativos de abolengo pangeico, los cuales representaban más del 95% de los géneros conocidos. Sin embargo, durante el Paleoceno Temprano el 70% de los mamíferos derivaba de aquellos inmigrantes norteamericanos arribados durante el Cretácico Tardío-Paleoceno más temprano, y durante el Paleoceno Tardío, todos los mamíferos sudamericanos (con la posible excepción de los xenartros) derivaban de aquellos inmigrantes. A pesar de que ninguna evidencia geológica soporta la existencia de una comunicación continua entre las Américas durante el intervalo Cretácico Tardío-Paleoceno Temprano, el registro fósil elocuentemente sostiene la existencia de una conexión terrestre transitoria entre ambas Américas hacia finales del Cretácico. Esta interpretación es soportada por las recientes reconstrucciones geográficas de la región caribeña.

Palabras clave: Cretácico, extinción, inmigración, Paleoceno, paleogeografía

Introduction

Central America has played a crucial role in the biogeography and evolution of North and South American faunas. The emplacement of the Panamanian isthmus some 3 Ma ago was the essen-

tial geological event that triggered the so-called Great American Biotic Interchange (GABI; see Stehli and Webb, 1985). Today we know that, with the exception of the caviomorph rodents and platyrrhine primates (which arrived from Africa during the Late Eocene-Early Oligocene) and probably the xenarthrans (origi-

nating from South America, Africa, or even Antarctica; see Pascual and Ortiz-Jaureguizar, 2007), the therian mammals recorded in South America before the GABI (*i.e.*, marsupials and “ungulates”) were endemic to South America but had descended from North American immigrants. They arrived from the Late Cretaceous onwards, during the successive stages of the Caribbean and Central American differentiation (see Pascual and Ortiz-Jaureguizar, 2007 and references therein).

The real importance of the Caribbean and Central American differentiation can only be understood if we bear in mind that the oldest land mammals known in South America used to be regarded as the oldest that inhabited the continent (*e.g.*, Ameghino, 1906). The historical knowledge of these supposed oldest (Palaeogene and partially Neogene) mammals were reviewed by Simpson (*e.g.*, 1940, 1950, 1980), but neither Ameghino nor Simpson noticed that they represented just the last third of South American mammal history. Moreover, both of these authors, on the basis of different but purportedly “solid” evidence, wrongly maintained that among those known land mammals were Mesozoic representatives (see Pascual, 2006). In 1982, however, Bonaparte and colleagues discovered in Patagonia, together with hadrosaur remains, the first unquestionable Late Cretaceous mammals, which allowed us to gain a first approximate idea of the compositional status of South American Cretaceous land-mammal communities (see Bonaparte, 1996 and references therein). Furthermore, these discoveries, together with others in Early-Palaeocene Patagonian land-mammal-bearing beds (see Pascual and Ortiz-Jaureguizar, 2007 and references therein), led us to recognise that the whole history of South American mammals can be divided into two quite distinct and unrelated episodes: the “Gondwanan Episode” (?Late Triassic-Late Cretaceous) and the “South American Episode” (Early Palaeocene-Recent). Both episodes were represented by phylogenetically unrelated taxa, which dwelt in similarly distinct ambits. The mammals belonging to the Gondwanan Episode were almost exclusively Gondwanan non- and pre-tribosphenics, while those mammals characterizing the South-American Episode were just Theria, mostly immigrants from North America with a Laurasian history. Both episodes were separated by a critical latest Cretaceous-earliest Palaeocene hiatus, during which South American land-mammal communities underwent a notable evolutionary and biogeographic change: the almost complete extinction of the Gondwanan mammals and the arrival and radiation of North American marsupials and placentals (see

Pascual, 1996, 1998, 2006; Pascual *et al.*, 2001; Pascual and Gelfo, 2004; Pascual and Ortiz-Jaureguizar, 2007).

Within this context, we presented a few years ago an analysis of the crucial role played by the tectonic settings of the Caribbean region in the evolution of the South American land-mammal fauna at the “4th European Meeting on the Palaeontology and Stratigraphy of Latin America”, published as an expanded abstract (Ortiz-Jaureguizar and Pascual, 2007). Since then, new geological and palaeontological data have been published (*e.g.*, Morán-Zenteno *et al.*, 2008; Somoza, 2008; James *et al.*, 2009; Rich *et al.*, 2009; Rougier *et al.*, 2009) and consequently it has become necessary to revise some of our previous ideas. Thus, on the basis of the most recent palaeontological and geological evidences, we reanalyse in this paper the compositional changes in the Late Cretaceous-Palaeocene South American mammal fauna in the context of the geological and tectonic setting of the Caribbean region.

Palaeogeographic history of South America and the Caribbean region

Within the Pangaea Supercontinent the South American block was situated in a western-central position, so it was in direct contact with those blocks that were to become North America, Africa and Antarctica. By Early Jurassic times Pangaea started its initial rifting and dispersion stages leading to the separation of two supercontinents, Laurasia and Gondwana. Passing through different stages, both supercontinents became separated from each other by a pan-equatorial seaway, the Tethys Sea. At the same time as the separation of Laurasia and Gondwana the latter also began to split up, leading to the formation of a seaway between West Gondwana (*i.e.*, South America and Africa) and East Gondwana (*i.e.*, Antarctica, Australia, New Guinea, India, and New Zealand) (see Rapela and Pankhurst, 1992; Storey *et al.*, 1992; Storey, 1995).

The isolation of the South American continent was heterochronic. Its separation from Africa began about 130 million years ago (Storey *et al.*, 1992) and had finished some 110 million years ago (Sclater *et al.*, 1977; Parrish Totman, 1993). According to common geological features, from as early as the Late Cretaceous and up to the late Eocene or earliest Oligocene, South America and Western Antarctica were part of the same geological province (*e.g.* Woodburne and Case, 1996; Vizcaino *et al.*, 1998; Shen, 1998; Reguero *et al.*, 2002; Pascual and Ortiz-Jaureguizar, 2007). The north-

westward drifting of the South American Plate followed the earlier separation of Tasmania and East Antarctica (initiated ca 50 Ma with a shallow to mid-level seaway, and culminating with a deep seaway ca 33 Ma) and began the separation of the Antarctic continent (Royer and Rollet, 1997; Zachos *et al.*, 2001; Lawver and Gahagan, 2003). Finally, the opening of the Drake Passage ca. 30 Ma (Lawver *et al.*, 1992; Zachos *et al.*, 2001; Lawver and Gahagan, 2003; Livermore *et al.* 2005; Somoza, 2007) led to the isolation of South America, and the final separation of Antarctica, thus allowing the flow of the influential Circumpolar Antarctic Current, which established the preliminary physical conditions leading to the present-day cooler global climate (Ehrmann and Mackensen, 1992; Lawver *et al.*, 1992, Lawver and Gahagan, 2003; Barker *et al.*, 2007).

Among the continental ruptures that led to the isolation of South America, there occurred another geographical event that deeply affected the history of its biota: the formation of the Caribbean Plate, and the first steps leading to the closure of the Caribbean part of the Tethys Sea. The emergence of the Caribbean Plate was probably the most important aspect of a timing sequence for a link between the North and South American land masses (Smith, 1985). Thus, an understanding of the general geological and tectonic setting of the Caribbean region is crucial to an evaluation of the recorded interchange of land vertebrates between North and South America during the Late Cretaceous. Accepting the conclusions of Case *et al.* (2005) about the time of dispersal of the marsupials, as well as the evidence provided by other groups of land vertebrates (*e.g.*, hadrosaurs and booids), the window of dispersal seems to begin in the Campanian, continue throughout the Maastrichtian and wane in the Palaeocene.

The Caribbean Plate, usually referred to as the Caribbean Large Igneous Province (CLIP), is one of the largest oceanic plateaux on Earth. The origin and tectonic evolution of the Caribbean in general and of the CLIP in particular is still under debate. The controversy focuses on two models: (1) autochthonous models; and (2) allochthonous models. Autochthonous models propose an inter-American origin for both the Caribbean oceanic crust and the CLIP (*e.g.* Meschede and Frisch, 1998; James, 2006, 2007; Somoza, 2008). On the contrary, allochthonous models propose a Mesozoic Pacific origin for the Caribbean crust and usually attribute the CLIP to the activity of mantle plumes in the Pacific basin (*e.g.*, Iturralde-Vinent and McPhee, 1999; Kerr *et al.*, 1999; Coates, 2003; Kerr and Tarney, 2005; Pindell *et al.*, 2005, 2006; Mann *et al.*, 2007; Kennan and Pindell,

2009; Pindell and Kennan, 2009). It is not our aim in this paper to discuss the arguments that support one or other of the tectonic models in question, but, to summarise and illustrate the Cretaceous palaeogeography of the Central-American area during Cretaceous-earliest Palaeocene we prefer to follow those authors that accept the allochthonous tectonic models, because: (a) most of the specialists accept this model (a fact also accepted by those authors who are in favour of the autochthonous models; see James, 2006); and (b) most recent papers support the allochthonous models (Kennan and Pindell, 2009; Pindell and Kennan, 2009). It is important to remark that the final consequence of both models is the same from a palaeobiogeographic perspective: during the Late Cretaceous-earliest Palaeocene, some kind of land-corridor or filter located in the Central America area permitted the inter-American exchange of land vertebrates (see below).

Since the latest Triassic, the Caribbean started to form as a system of rift valleys within central-west Pangaea, which later turned into a sort of "Mediterranean" sea, where distinct volcanic and non-volcanic islands evolved. Since the very first steps of its formation this sea had been playing a key role in the control of the historical patterns of ocean water circulation and consequently moderating the world climate. This sea had also been determining the possibilities of biotic exchange of the surrounding terrestrial and marine biotas (Iturralde-Vinent, 2003, 2004, 2006). At the end of the Jurassic, Pangaea slowly began to fracture due to the rising of a central oceanic mountain range. The separation of North America from Europe, North Africa, and South America led to the opening of the Atlantic Ocean, which was connected to the Pacific Ocean through the area now occupied by Central America. On the southern border of the North-American plate, the current Mexican territory formed a peninsula, to which the Mayan and Chortis terranes were connected (Donnelly *et al.*, 1990; Coates, 2003; Ortega-Gutiérrez *et al.*, 2007; Morán-Zenteno *et al.*, 2008). At the same time, the Proto-Caribbean crust began to form between the North and South American plates as a consequence of the seafloor spreading due to the diachronic opening of the North and South Atlantic Ocean (Pindell and Barrett, 1990).

At the beginning of the Cretaceous both the North- and South-American plates continued to separate, giving rise to the proto-Caribbean seaway (Fig. 1A). The opening of the proto-Caribbean gave rise to the eastern Chortis terrane, and also caused a rift in the Juárez terrane in Mexico (Dickinson and Lawton, 2001; Rogers *et al.*, 2007). The oceanic crust of the

proto-Caribbean was later consumed by the eastward and north-eastward advance of the Guerrero-Caribbean arc (Mann *et al.*, 2007). During the Late Cretaceous (Campanian), the Galapagos hot-spot began to issue a vast quantity of basalt, which covered an area of 3,000 km² of the ocean floor. An active central Pacific oceanic mountain range began to separate the eastern Farallon plate from the Pacific one, and the eastern margin of the Farallon plate was transformed into a subduction zone. This subduction zone was accompanied by an active volcanic arc extending along the western margin of the North American plate, the Chortis terrane and the Great Antilles and Aves Ridge Arc (an island arc located in the region now occupied by Central America, see Fig. 1B, and Coates, 2003). Towards the end of the Late Cretaceous, the Great Antilles and Aves Ridge Arc broke up. Consequently, part of this arc, together with the basalt layer produced by the Galapagos hot-spot, moved to the north-west, giving rise to the Caribbean Plate (Coates, 2003).

Taking into account the tectonic and palaeogeographic context of the Caribbean region described above, an uninterrupted land bridge would not appear to be the most plausible Late-Cretaceous route for the dispersal of such huge vertebrates as the Laurasian hadrosaurs and the Gondwanan titanosaurs. For example, Case *et al.* (2005), essentially on the basis of fossil evidence afforded by marsupials, concluded that, "...the dispersal probability is best proposed as having been a sweepstake to a relatively strong filter", as Simpson (1953) proposed. To them, the Aves Ridge could have provided a dry dispersal route for land vertebrates between North and South America during the Campanian-Maastrichtian span. Nevertheless, to Pindell (1994) and Villamil and Pindell (1998), it appears that the existence of a dry dispersal route was only likely during the late Campanian and the Maastrichtian. Additionally, Iturralde-Vinent and MacPhee (1999, 2004) concluded that no permanent landmasses were present in the Caribbean prior to the middle Eocene. As far as these authors are concerned, the north-west margin of the Caribbean plate was the area where emerged islands were aligned between North and South America (Fig. 1B). Notwithstanding this, they admitted that in this area some kind of corridor or filter, possibly of a stepping-stone nature, could have originated during a brief lowstand during the Late Cretaceous, permitting the inter-American exchange of land vertebrates (Iturralde-Vinent and MacPhee, 2004). Iturralde-Vinent and MacPhee (1999) also assessed the possibility of other ephemeral land bridges or stepping-stone islands along the Antillean

volcanic archipelago during the Aptian-Albian and Santonian-Campanian, but they concluded that there is insufficient evidence to propose actual land connections between North and South America during these periods. Within these time intervals many indications of local uplift are known within the volcanic archipelago (Maurrasse, 1990; Iturralde-Vinent and MacPhee, 1999). Within this context, Horne (1994) suggests that northern Central-American terranes were physically connected to North America at about 85-95 Ma, on the basis of a mid-Cretaceous ornithomimid dinosaur femur found in central Honduras, which formed part of the Chortis Block (see Rogers *et al.*, 2007). According to Iturralde-Vinent (2006), this connection represents a landspan (*i.e.*, a continent-to-island connection) but not a land bridge. But as far as this author is concerned, neither stratigraphic nor palaeontological evidence support that these northern Central American lands extended to South America across the Central American nor the Antillean volcanic arc systems (see Iturralde-Vinent, 2006, and references therein).

Finally, Iturralde-Vinent (2006) maintains that the latest Cretaceous land bridge may have been in place sometime between 75 and 65 Ma, represented by a system of islands and shallow sea-waters, existing when extensive uplifting took place along the Great Antilles and Aves Ridge volcanic-island arc system (Fig. 1B). According to this interpretation, the land-vertebrate exchange between North and South America across this volcanic arc system may have taken place during a time of sea-level drop, probably across a combination of island stepping stones and sweepstake dispersal mechanisms, while this arc collided with the Maya Block and South America near the end of the Cretaceous (Iturralde-Vinent, 2006; Iturralde-Vinent *et al.*, 2006; Pindell *et al.*, 2006).

The South American land-mammal fauna during the Late Cretaceous-Palaeocene

Most of the Mesozoic history of South American mammals is still unknown as we have only a few, enigmatic taxa (*i.e.*, two Jurassic australosphenids, a Jurassic triconodont, and an Early Cretaceous theriiform), which pose more evolutionary and biogeographic questions than they answer (see Kielan-Jaworowska *et al.*, 2004; Macrini *et al.*, 2007; Pascual and Ortiz-Jaureguizar, 2007; Rougier *et al.*, 2007a, 2007b, 2009). The best known South American Mesozoic land-mammals were found in Late Cretaceous (Campanian-Maastrichtian) Patagonian beds. They are represented by several non- and pre-

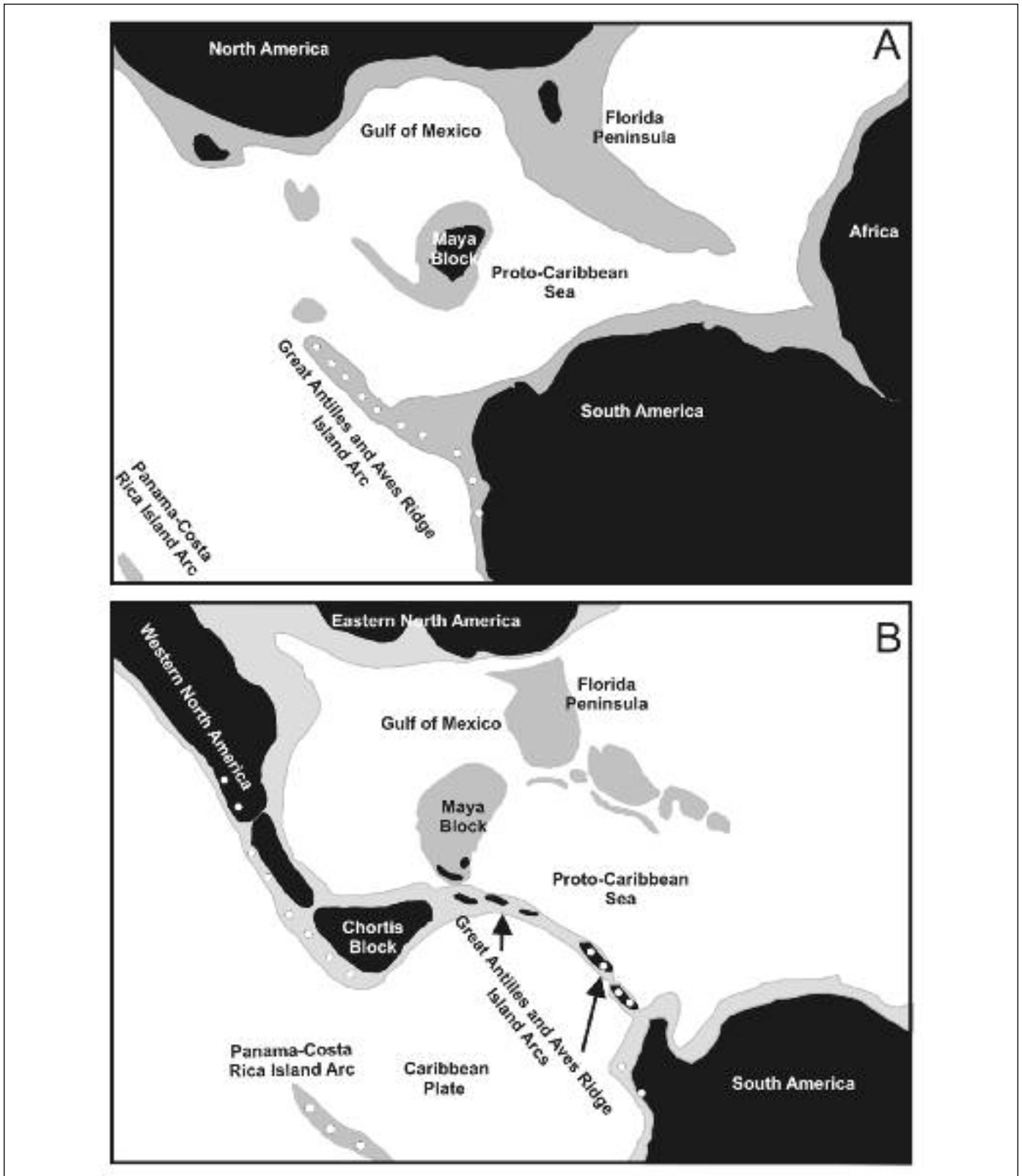


Figure 1. Palaeogeographic reconstruction of the Caribbean region in the Cretaceous. A: Early Cretaceous; B: Late Cretaceous (modified from Iturralde-Vinent, 2006). Black: emerged lands; grey: shallow sea; white: deep sea; white circles: volcanoes
 Figura 1. Reconstrucción paleográfica de la región Caribeña. A: Cretácico Temprano; B: Cretácico Tardío (modificado de Iturralde-Vinent, 2006). Negro: tierras emergidas; gris: mar somero; blanco: mar profundo; círculos blancos: volcanes

tribosphenic genera: one "Plagiaulacida" and one ?Cimolodonta Multituberculata, two Gondwanatheria, one Docodont, one Triconodonta, one "Symmetrodonta" and ten Dryolestida (see Kielan-Jaworowska *et al.*, 2007; Pascual and Ortiz-Jaureguizar, 2007). These mammals were living relicts of Pangeic lineages and were extinct in coeval beds in Laurasia, with the only exception of the cimolodontan multituberculates (see Kielan-Jaworowska *et al.*, 2004).

The total absence of tribosphenic mammals in Late-Cretaceous South American beds, although well diversified in coeval Laurasian beds, and the advanced morphology and endemism of non-tribosphenic and pre-tribosphenic mammals has been interpreted as evidence of the long isolation of South America from the Laurasian land-masses (see Bonaparte, 1996; Ortiz-Jaureguizar, 1996; Kielan-Jaworowska *et al.*, 2004; Pascual, 2006; Pascual and Ortiz-Jaureguizar, 2007). But the recent record of a new genus and species of a probable cimolodontan multituberculate (*Argentodites coloniensis*), the first found in these Late Cretaceous Patagonian beds (Kielan-Jaworowska *et al.*, 2007), could change, at least in part, the classic scenario of an isolated Mesozoic South American land-mammal fauna.

According to Kielan-Jaworowska *et al.* (2007), the new multituberculate is a North-American immigrant that may have arrived in South America at some time during the Cretaceous. The hypothesis of an Early Cretaceous arrival is supported by the presence of some morphological features that are shared with "Plagiaulacida", a multituberculate suborder that did not cross the Early Cretaceous-Late Cretaceous boundary (see Kielan-Jaworowska *et al.*, 2004). But this is not the only cimolodontan multituberculate to show a mosaic of plagiulacidan (plesiomorphic) and cimolodontan (apomorphic) characters. The "Paracimexomys group" (the most plesiomorphic, informal group of Cimolodonta) share some molar features with some "Plagiulacida" (*i.e.* Plagiulacidae and Eobaataridae). Additionally, they have been recorded in the Early Cretaceous (Aptian-Albian) to the Late Cretaceous (Maastrichtian) in North America, as well as in the Late Cretaceous (?Maastrichtian) in Europe (Kielan-Jaworowska *et al.*, 2004). Consequently, it would seem highly likely that *Argentodites* was a South American representative of a clade of basal cimolodontans (not yet recorded in the "classical" Late Cretaceous North American mammal-bearing beds) that arrived in South America during the Late Cretaceous. But very recently Rich *et al.* (2009) have reported the first record of a multituberculate dating to the late Early Cretaceous (Aptian)

in Australia. This multituberculate, *Corriebaatar marywaltersae*, has been tentatively assigned (like the Patagonian Late Cretaceous *Argentodites coloniensis*) to the cimolodontans. According to this hypothesis, Rich *et al.* (2009) conclude that multituberculates had a cosmopolitan distribution during the Mesozoic, with dispersal into eastern Gondwana probably occurring prior to the enforcement of climatic barriers in the Early Cretaceous. They also maintain that the migration of multituberculates between the Australian landmass and elsewhere very probably occurred before the minimum low-temperature period during the Valanginian to Albian. Additionally, if the Mesozoic Gondwanan australosphenid mammals known from the Middle Jurassic in Madagascar (Flynn *et al.*, 1999), late Middle-early Late Jurassic in South America (Rauhut *et al.*, 2002; Rougier *et al.*, 2007a) and late Early Cretaceous in Australia (Rich *et al.*, 1997, 2001) are actually members of a monophyletic group, then the time of interchange between those Gondwanan regions would most probably have been some time during that interval (or perhaps somewhat before) (Rich *et al.*, 2009). Further to this, Gurovich and Beck (2008) suggest that *Argentodites coloniensis* should be removed from the multituberculates and included within the gondwanatherians. We do not agree with this hypothesis, but the papers of Gurovich and Beck (2008) and Rich *et al.* (2009) add new biogeographic scenarios to explain the presence of *Argentodites coloniensis* in Late Cretaceous beds in Patagonia. Thus, it is conceivable that *Argentodites coloniensis* might be: (a) a recently arrived immigrant from North America; (b) another survivor from an old Pangeic lineage (as are triconodonts, dryolestoids and gondwanatherians); or (c) a recently arrived immigrant from Australia-Antarctica. Only new and more complete fossil records in Mesozoic continental beds in southern continents can help us to decide more emphatically upon one of these scenarios.

Leaving aside the taxonomic and biogeographic problem of *Argentodites*, there is no fossil evidence among the South American vertebrates of any arrival of North American immigrants during the Early Cretaceous. Additionally, all the palaeogeographic reconstructions of the Caribbean Central American area (as well as several fossil records of vertebrates of North American lineages in South America during the Late Cretaceous-Palaeocene; see below) are in favour of a Late Cretaceous migration (compare the reconstruction of the Early Cretaceous depicted in Figure 1A with that of the Late Cretaceous depicted in Figure 1B). In fact Late Cretaceous dinosaurs as well as other non-mammalian vertebrates of the Late Cretaceous and

Early Palaeocene (see Rage, 1978, 1981; Estes and Báez, 1985, Bonaparte and Rougier, 1987; Gayet *et al.*, 1992; Case *et al.*, 2005) strongly support the hypothesis that some mechanism of dispersal from the Late Cretaceous via a "terrestrial bridge" existed, as was envisaged by Pindell (1994) and Villamil and Pindell (1998). With regard to this, Iturralde-Vinent and MacPhee (2004) and Iturralde-Vinent (2006) maintained that the fossil evidence of an interchange between the American continents suggests that the elevation that took place during the Campanian-Maastrichtian transition was quite probably that which produced a terrestrial bridge between the American continents, related with a generalized extinction of magmatism throughout some parts of the volcanic-island arc (see above). In summary, the Cretaceous migratory events suggest that there was some kind of temporary inter-American dry-land connection by the end of the Cretaceous and throughout the incipient differentiation of the Caribbean Sea (Fig. 1B).

Changes in the composition of the Late Cretaceous-Palaeocene South American land-mammal fauna

The Late-Cretaceous record of ornithischian dinosaurs in Patagonia and that of saurischian ones in the Late Cretaceous in North America clearly indicate that during this time there occurred a real inter-American exchange of land vertebrates (see Sloan, 1970; Bonaparte *et al.*, 1984; Gayet *et al.*, 1992). Taking into account the mammals, during the Alamitan SALMA (Campanian-Early Maastrichtian) the fauna is composed of only non-tribosphenic and pre-tribosphenic groups, but if we bear in mind the geographic origin of these mammals, only one of them could be a recent immigrant from North America or Australia-Antarctica (see above). These interchanges, which continued into the Early Palaeocene (see below), affected profoundly the composition of the South American land-mammal fauna. During the Late Cretaceous-Palaeocene, all the South American mammal genera (and most of the families) were endemic, but when the biogeographic origin of the lineages and the supposed time of arrival of the immigrants are born in mind, considerable differences are to be found. During the Late Cretaceous (Alamitan SALMA), taking into account two of the three possible scenarios (see above), only one genus (*Argentodites*) could have derived from immigrant ancestors coming recently from North America or Australia-Antarctica; the remainder must have derived from ancestors broadly distributed all over the world during the Jurassic and Early Cretaceous (Pangeic lineages). During the Early (Middle?) Palaeocene

(Peligran SALMA) approximately 75% of the genera derived from immigrants that had arrived during the latest Cretaceous-earliest Palaeocene (differences are due to the uncertain origin of the monotreme *Monotrematum*; see below), and the remaining genera derived from those Pangeic lineages. Finally, during the Late Palaeocene-earliest Eocene (Tiupampan-Riochican SALMAs) all genera, with the probable exception of the xenarthrans (see Pascual and Ortiz-Jaureguizar, 2007) derived from those ancestors that had arrived during the latest Cretaceous-earliest Palaeocene (Fig. 2A; see also Pascual and Ortiz-Jaureguizar, 2007 and references therein). If we add the basic morphologic type of the molars (*i.e.*, non-tri-

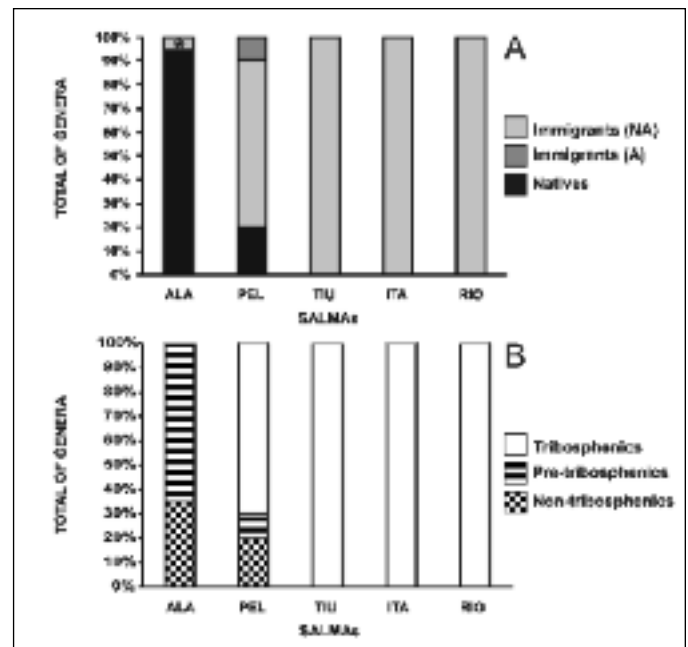


Figure 2. Late Cretaceous-earliest Eocene South American land-mammal faunal changes. A: Mammals grouped according to their biogeographic origin; B: Mammals grouped according to the basic morphologic type of their molars (data from Pascual and Ortiz-Jaureguizar, 2007). ALA: Alamitan; PEL: Peligran; TIU: Tiupampan; ITA: Itaboraian; RIO: Riochican; A: Australia; NA: North America (including primary immigrants as well as secondary immigrants, *i.e.*, native taxa, deriving from immigrant ancestors); *: assuming that *Argentodites* is a North American immigrant (see text for alternative hypotheses)

Figura 2. Cambios en las faunas de mamíferos continentales de América del Sur durante el Cretácico tardío-Eoceno más temprano. A: mamíferos agrupados según su origen biogeográfico; B: mamíferos agrupados según el tipo morfológico básico de sus molares (datos de Pascual y Ortiz-Jaureguizar, 2007). ALA: Alamitense; PEL: Peligrense; TIU: Tiupampense; ITA: Itaboraiense; RIO: Riochiquense; A: Australia. NA= América del Norte (incluyendo tanto inmigrantes primarios como secundarios, *i.e.*, taxones nativos derivados de ancestros inmigrantes); *: asumiendo que *Argentodites* es un inmigrante norteamericano (para hipótesis alternativas, ver el texto)

bosphenics, pre-tribosphenics, and tribosphenics; Fig. 2B), during the Alamitan SALMA 65% of the mammals are pre-tribosphenics and 35% non-tribosphenics and all of them (with the possible exception of the non-tribosphenic *Argentodites*; see above) pertain to Pangeic lineages. During the Peligran SALMA, 10% are pre-tribosphenics, 20% are non-tribosphenics (both deriving from Pangeic ancestors, with the probable exception of *Monotrematum*; see below) and 70% are tribosphenics (placentals and marsupials, both deriving from ancestors that had arrived during the latest Cretaceous-earliest Palaeocene). Finally, from the Late Palaeocene onwards all the mammals are tribosphenics (with the exception of the Gondwanatheria, not recorded anymore in South-American land-mammal-bearing sediments but surviving in the Middle Eocene in the Antarctic Peninsula; see Goin *et al.*, 2006a), and all of them (with the probable exception of the enigmatic xenarthrans, mentioned above) are South-American derivatives of ancestors that had arrived during latest Cretaceous-earliest Palaeocene (Fig. 2B; see also Pascual and Ortiz-Jaureguizar, 2007 and references therein).

As mentioned in the Introduction, the whole extinction of the endemic South-American non-tribosphenic and pre-tribosphenic mammals by the Late Cretaceous-Early Palaeocene and the apparent contemporary immigration and diversification of the North American tribosphenic ones, distinguish two major moments in the history of the South American mammals: the Gondwanan Episode, and the South-American Episode (Pascual, 2006; Pascual and Ortiz-Jaureguizar, 2007 and references therein). Both episodes are separated by a Late Maastrichtian-earliest Palaeocene span, unfortunately without any good mammal record (the only known record is the polydolopimorphian marsupial *Cocatherium lefipanum*, recovered from Patagonian strata assigned to the Danian; see Goin *et al.*, 2006b), during which the South American land-mammal communities must have undergone notable biogeographic and evolutionary changes. The main events that occurred during this interval, marking the end of the Gondwanan Episode and the beginning of the South-American Episode, were:

- (1) the extinction of most non-tribosphenic and pre-tribosphenic mammals;
- (2) the immigration of monotremes from Australia-Antarctica, although it is equally possible that monotremes were broadly distributed across Australia, Antarctica and southern South America during Cretaceous times. According to this alternative hypothesis, the absence of monotremes in Cretaceous land-mammal-bearing formations

can be put down to an unsound fossil record (see Pascual and Ortiz-Jaureguizar, 2007);

- (3) the emigration from Laurasia (North America) to South America of marsupials and placentals (see Goin *et al.*, 2006b; Pascual and Ortiz-Jaureguizar, 2007);
- (4) the emigration from South America to Australia of marsupials, quite probably following the same Antarctic route at the same time that the monotremes were on their way to South America (although less likely, placentals could also have immigrated to Australia; see Pascual and Ortiz-Jaureguizar, 2007, and references therein); and
- (5) the marked cladogenetic spread of marsupials and the first steps in the spread of placentals (both immigrants from Laurasia, specifically from the rising North American continent). The greater cladogenetic diversification of marsupials than placentals was probably the result of an earlier marsupial migration to South America, to finally populate, via Antarctica, the present Australo-Papuan region (see Pascual and Ortiz-Jaureguizar, 2007 and references therein).

The absolute dominance of tribosphenic mammals in the South-American fauna after the Peligran SALMA (Fig. 2B), when Gondwanan remnant mammals were apparently extinct (except in the Antarctic Peninsula; see above), suggests that there was what appears to be a relatively abrupt turnover, *i.e.*, The First Great Turnover of Pascual *et al.* (2001; but see Rougier *et al.*, 2009) in South American mammal evolution. This phenomenon contrasts with what happened in North America and in the remaining Laurasian continents, in which the extinction at the K/T boundary reduced the total diversity of the mammal fauna (Archibald and Clemens, 1984; Clemens, 2001), but did not produce the almost complete extinction recorded in South America (Pascual and Ortiz-Jaureguizar, 1992; Ortiz-Jaureguizar, 1996; Pascual and Gelfo, 2004; Pascual, 2006). For example, in northeastern Montana (USA), about 60% of its Lancian (latest Cretaceous) lineages became extinct (Clemens, 2001).

Nevertheless, the Laurasian mammal history was comparatively continuous from the oldest Late Triassic onwards, containing only those mammals that had ultimately originated in one or another of the Laurasian continents and showing no significant interchange with Gondwana. The turnover was not so great as that recorded in the South-American sector of Gondwana throughout the Late Cretaceous-Early Palaeocene (Campanian-Danian) interval, which apparently took place over the whole Gondwana continent. Furthermore, the mammals that had originated

ed in Laurasia spread over most of the continents in such a way that today they represent the majority of extant mammals. The almost complete Late Cretaceous-earliest Palaeocene extinction of the Gondwanan mammals and the consequent absence in South America of representatives of The Gondwanan Episode throughout the remaining Cenozoic and Present times (with the probable exception of the *Xenarthra* mentioned above), was related with the tectonic and palaeogeographic changes that occurred in the Caribbean region, and maintained a certain mystery around the history of Gondwanan mammals until comparatively recently. This, however, is not the only event that explains the profound faunal changes recorded during the Late Cretaceous-Early Palaeocene. In fact, Pascual and Ortiz-Jaureguizar (in press) analysed other regional processes and extraterrestrial events that directly or even indirectly may have contributed to the total extinction of the Gondwanan mammals on the South American continent (e.g., the short-term effect of the impact of an extraterrestrial body; the marine regression of the Late Cretaceous-Danian seaway).

Conclusions

All the present-day geological and palaeontological evidence corroborates the essence of our previous conclusions (Ortiz-Jaureguizar and Pascual, 2007): (1) The Caribbean region played a crucial role in the biogeography and evolution of North- and South-American fauna; (2) in the absence of geological evidence to support the existence of a permanent land connection between North and South America during the Late Cretaceous-Early Palaeocene, some kind of corridor or filter, possibly of a stepping-stone type, may have been formed during a brief marine lowstand, which allowed the beginnings of an exchange of land vertebrates between the continental land masses; (3) the arrival of North American immigrants (particularly marsupials and placentals) during the latest Cretaceous-earliest Palaeocene had a profound influence on the South American land-mammal communities. During the Late Cretaceous, these communities were dominated by autochthonous groups, whereas during the Early (Middle?) Palaeocene (Peligran SALMA) 70% of the mammals derived from North American immigrants and from the Late Palaeocene to the Late Eocene all the South American mammals derived from North American immigrants.

Finally, our results accord with others, both astronomical and regional, to explain the biogeographic and evolutionary changes recorded in the South

American land-mammal fauna during the interval that marks the end of the Gondwanan Episode and the beginning of The South American Episode.

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