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The K-T and Tertiary-Pleistocene South American mammalian turnovers: similar phenomena?

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Abstract. The history of South American mammals has been episodic, apparently "stratified", and the "strata" relatively few in number and, as a rule, sharply and clearly separable. This is a consequence of the physical history of the continent. The fossil record shows that there were two great episodes characterized by drastic turnovers of mammal communities; both appear related to two of the most drastic physical changes withstood by the continent. The oldest episode is related to the separation of Africa from the other Gondwanan continents (shaping the primordial outlines of the eastern cost of the incipient Southern Atlantic Ocean), and to a sporadic connection of the South American plate with the North American plate. This led to the first great turnover: with the exception of two Gondwanan taxa (Monotremes and Gondwanatheres), and probably another one (Dryolestida), all the Gondwanan mammals (all non-tribosphenic taxa) became extinct, and were "replaced" by Laurasian tribosphenic marsupial and placental immigrants. Because of the early extinction (early Paleocene) of the Gondwanan non-tribosphenic survivors, and the subsequent isolation of the continent (including, at least, the Antarctic Peninsula) unique communities solely composed of quite endemic (native) marsupials and placentals were built up. As a consequence of the inter-American connection via the newborn Central America, an increasing biotic interchange began. The second great turnover, involving dispersal, extinction and survival, built up quite peculiar mammalian communities. These are the new basic mammal communities that, after the "Megafaunal Extinction" and the addition of a few and selected immigrants, distinguish the present Neotropical Region. Apparently this second great turnover was accomplished by replacement, not by displacement, as long thought. The failure to find mammals in rocks representing the K-T transition, has no record to analyze the *modus operandi* of the transcendental first turnover.

Key words. South American land-mammals. K-T. Tertiary-Pleistocene. Dispersal. Turnover. Extinction. Survival.

Introduction

The recent record of Patagonian Late Cretaceous land mammals (Bonaparte, 1990, 1996, and literature therein), although not of latest Cretaceous age (see Pascual *et al.*, 2000), compared to the known oldest Paleocene mammals of Patagonia (but not of earliest Paleocene age, see Bond *et al.*,1995), shows not only that during this time interval a distinct evolutionary episode, which we called the Gondwanan Stage (figure 1) (Pascual, 1996), involving mammals not related to those of the Cenozoic, was culminating (cf. Bonaparte, 1996, Appendix, p.130, with Pascual *et al.*, 1996, p. 308-319). Also this event led to a drastic turnover of mammal communities, from exclusively non-tribosphenic to almost exclusively tribosphenic mammals (marsupials and placentals) (see Ortiz-Jaureguizar and Pascual, 1989; Pascual and Ortiz Jaureguizar, 1991, 1992) . This turnover initiated a new episode of the mammalian history which we called the South American Stage (Pascual, 1996) because it was related to the first outlines of the South American continent and isolation, although still including at least the Antarctic Peninsula (figure 2) (see Pascual, 1996, 1998), and characterized by the continental origin of quite endemic taxa. *Prima facie* this turnover appears to be similar to the one which occurred during the late Tertiary-early Pleistocene interval, when the so called "Great American Biotic Interchange" took place (see Stehli and Webb, 1985, and papers therein). Apparently, most of the endemic South American mammalian taxa had became extinct just before the entrance of the new exotic immigrants (see Pascual and Webb, 1989, and papers therein). Subsequently, most the new immigrants replaced the extinct native mammals and formed new communities with the native survivors. A new transcendental change of these communities occurred with the so called Megafaunal Extinction, which, with the incorporation of a few other immigrants (e. gr. insectivores, leporids, Sciuridae, Heteromyidae,

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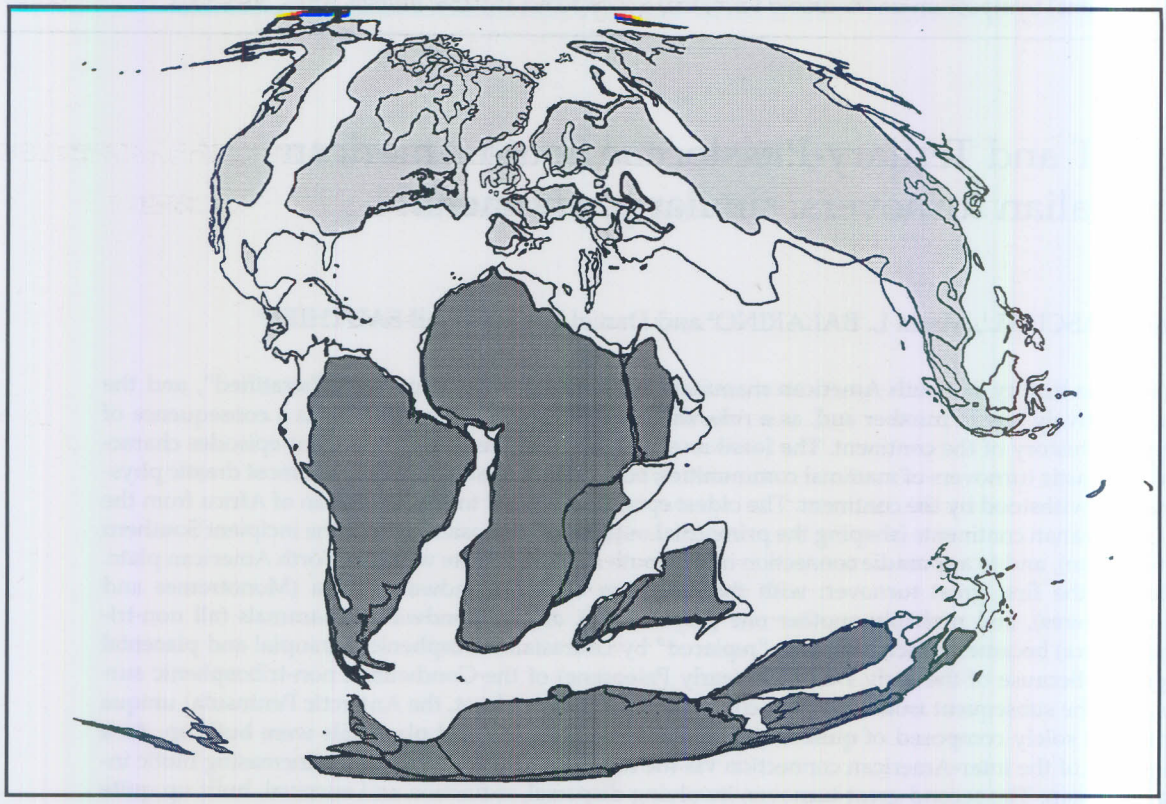

Figure 1. Last steps of the Gondwanan Stage, about 105 Ma.

Geomyidae, and probably new cervids as *Odocoileus*), established the base of what was going to be the present Neotropical mammalian fauna (Neotropical Stage *sensu* Vizcaíno *et al.*, 1998). Both turnovers included intercontinental dispersion, and both dispersal phenomena were closely related to the establishment of new paleogeographical settings. We can compare the Cretaceous-Tertiary and Tertiary-Pleistocene mammal community turnovers within the context of some recently proposed paleogeographical reconstructions.

Results

It is obvious that the fragmentation of the Pangaean mammalian communities occurred well before the origin of the tribosphenidan. According to the South American record (*cf.* list 1), the Gondwanan mammals evolved as vicariants of those of Laurasia [e.g.,+Gondwanatheria as vicariant to the +Multituberculata (Pascual *et al.*, 1993), and among the +Docodonta the Gondwanan +Reigitheriidae as vicariant to the Laurasian +Docodontidae (Pascual *et al.*, 2000). Moreover, the recent records in other Gondwanan continents appear to indicate that "tribosphenidans" differentiated taxa of the same age (Early Cretaceous of northern Africa [Sigogneau-Russell, 1995], and Australia [Rich *et al.*, 1999]), or earlier (Middle Jurassic of Madagascar [Flynn *et al.*, 1999]) than in Laurasia. According to Kielan-Jaworowska *et al.* (1998) the Early Cretaceous Australian *Ausktribosphenos nyktos* Rich *et al.*, 1997 "....appears to have independently acquired dental features functionally analogous to those of tribosphenic mammals". In our opinion, the Gondwanan "tribosphenidans" probably arose as vicariant of the Laurasian tribosphenidans.

In relation with the origin of the Gondwanan mammals we must take into account that neither geographically (Smith *et al.*, 1994) nor biogeographically the Gondwanan supercontinent remained stable throughout its history (Crisci *et al.*, 1993). For example, the record of monotremes suggests that they originated and diversified throughout the Antarctica-Australia sector of eastern Gondwana (Flannery *et al.*, 1995), while the gondwanatheres apparently originated in the Patagonian-Madagascar-Indian sector of Eastern Gondwana (Krause *et al.*, 1997). Even the South American sector of Gondwana was neither geographically nor biogeographically as uniform as currently thought, at least up to the earliest Paleocene (see Pascual *et al.*, 1996, p. 283).

Consequently, dispersal, extinction and survival of some selected groups occurred during the interval between ca. 85 m.y.b.P. and ca. 63 m.y.b.P. (figure. 2) when the first Great Turnover occurred, as well as

Figure 2. The South American Stage, *ca.* 30 Ma.

between ca. 9 m.y.b.P. and the Holocene when the second Great Turnover took place.

The first Great Turnover

Dispersal. 1- Apparently, the hadrosaurid dinosaurs are among the first immigrants from Laurasia (North America) into southern South America (Casamiquela, 1964; Brett-Surman, 1979; Bonaparte, 1984a, 1984b, 1986, in literature therein; Powell, 1987.
2- Although it still remains unsettled, the place and time of origin of the xenarthrans, as well as the time and direction of the dubious migration between Africa and South America, we included them provisionally (see Pascual, 1996, and Storch, 1984, 1986, but see Szalay and Schrenk, 1998). If such a migration occurred, either to or from South America, it anticipated the Paleogene emigration of Rodentia and Primates from Africa to South America (Wyss *et al.*, 1993; Pascual *et al.*, 1996).
3- Marsupial and placentals dispersed from Laurasia (North America) to South America (Bonaparte *et al.*, 1993; Bonaparte, 1994).
4- According to Bonaparte (1999), some holotherian Dryolestidae probably emigrated from South America into North America.
5- From Australia to South America, via Antarctica, dispersed ornithorhynchids (Monotremata), just before the early Paleocene, becoming extinct by that time in South America (Pascual *et al.*, 1992a, 1992b; Pascual, 1996).

Extinction and survival. Most of the non-Tribosphenida became extinct. The only survivors were the Gondwanatherian, represented by *Sudamerica ameghinoi* Scillato-Yané and Pascual, 1985, and probably the Dryolestida? represented by *Peligrotherium tropicalis* Bonaparte *et al.*, 1993, in Patagonia and just up to the early Paleocene. The Patagonian ornithorhynchid (*Monotrematum sudamericanum* Pascual *et al.*, 1992a) apparently emigrated only to Patagonia during the latest Cretaceous or earliest Paleocene and became extinct there during the early Paleocene.

The increasing proximity and biogeographical connection by islands between North America and South America (Smith, 1985; Donnelly, 1990), directly of indirectly led to dispersal, extinction and survival, gradually changing the unique endemic mammalian communities that characterized the end of the long interval of South American geobiotic isolation. The rupture of this transcendental isolation had its first steps by 9 m.y.b.P. by mean of what Simpson called the "island hoppers" migration (Simpson, 1950, 1953, 1980), heralds of Webb (1985), initiating the "Great American Biotic Interchange" (GABI) (Stehli and Webb, 1985), which we call the Second Great Turnover. The end of this period was marked by transcendental phenomena, such as the latest Pleistocene "Megafaunal Extinction" (Martin and Klein, 1984), and the subsequent immigration of some mammals (see below). These two events shaped the last stage of the South American mammal evolution, which we have called the Neotropical Stage (Vizcaíno *et al.*, 1998)

The second Great Turnover

Dispersal. From South America to North America: Xenarthra, Notoungulata, Caviomorpha rodents and didelphid marsupials.

Form North America to South America: cricetid rodents, Carnivora, some Perissodactyla (Equidae, Tapiridae), some Artiodactyla (Tayassuidae, Camelidae, Cervidae), Proboscidea, Hominidae. During, or more probably later and once the Late Pleistocene Megafaunal Extinction was over, were added insectivore, sciurid, heteromyidae and geomyidae rodents, and lagomorphs.

Extinction. Notoungulata, mega-Xenarthra, Litopterna and peculiarly specialized marsupials (*e.g.*, Borhyenidae, Thylacosmilidae, and Argyrolagidae), some Carnivora (*e.g.*, Machairodontinae), and Proboscidea.

Survival. The present Neotropical mammalian fauna is composed of the survivors of the Late Pleistocene Megafaunal Extinction and man, to which later were added immigrants as insectivores, sciurid, heteromyid, geomyid rodents and lagomorphs.

Conclusion

Already Simpson (1950: 368) observed that the Cenozoic history of South American mammals was clearly episodic, and apparently stratified, and that the "strata" were relatively few in number and, as a rule, sharply and clearly separable. He added that these facts are the result of the physical history of the continent. However, earliest Paleocene and Cretaceous mammals were unknown at that time. Recent discoveries have filled these hiatuses partially, supporting and corroborating his inferences. In this sense, both the Late Cretaceous and early Paleocene mammal record, and the late Miocene and early Pleistocene one, have established the sharper and clearly separable "strata" between the "episodes" than mark the whole history of South

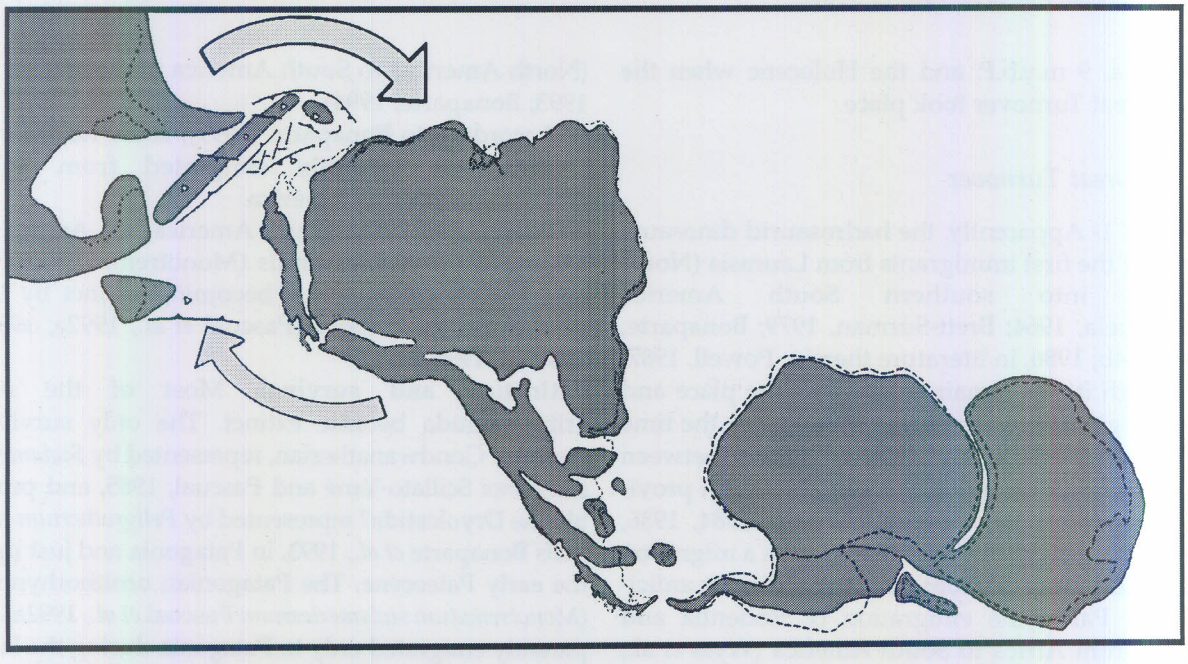

Figure 3. First steps of the South American Stage (first inter-American exchange), between 85-63 Ma.

Figure 4. First steps of the Neotropical Stage (the beginning of the "Great American Biotic Interchange". (G.A.B.I.), from *ca.* 9 Ma.

American mammals, i.e. the Gondwanan Stage and the South American Stage, respectively. And this is because they are respectively related to two of the most drastic physical changes experienced by what was going to be the present South American continent: (1) rifting and separation of the South American primordium from Africa, rifting and separation of northern eastern Gondwana, including Patagonia and Antarctic Peninsula, and rifting and separation of South America from the Antarctic Peninsula; and (2) northward rifting of South America and gradual connection to Laurasia, involving linking of the various tectonic components (blocks) that formed Central America. The model of Londsdale and Klitgord (1978), and Pindell and Dewey (1982), appears to favor a closure of the Caribbean sector of the Tethys Sea around the Miocene-Pliocene boundary, by 5 m.y.b.P., initiating in such a way the present Neotropical Stage (Vizcaíno *et al.*, 1998). More accurate dating of the mammal-bearing formations related with the Second Great Turnover (Cione and Tonni, 1995) suggests that this faunal change was not accomplished by displacement (see Pascual and Webb, 1989), as long thought (Simpson, 1980), but by replacement. The lack of fossil mammals that represented the K-T transition hinders understanding of the *modus operandi* of the significant mammal turnover that occurred during this interval.

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