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Distributional patterns of herbivore megamammals during the Late Pleistocene of South America

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ABSTRACT

The geographic distribution of 27 species of the South American megafauna of herbivore mammals during the Late Pleistocene was analyzed in order to identify their distributional patterns. The distribution of the species was studied using the panbiogeographical method of track analysis. Six generalized tracks (GTs) and two biogeographic nodes were obtained. The GTs did not completely superpose with the areas of open savanna present in Pleistocene, nor with the biotic tracks of some arthropods typical of arid climate, indicating that these animals avoided arid environment. Overall, the GTs coincided with some biogeographic provinces defined on the basis of living taxa, indicating that certain current distributional patterns already existed in Pleistocene. The biogeographic nodes coincided with the borders between the main vegetal formations of the Pleistocene, showing that the type of vegetation had great influence in the distribution of the mammalian megafauna. The node 1 confirmed the existence of contact zones between paleobiogeographic regions near Argentina-Uruguay border. The node 2 connects the Brazilian Intertropical regions.

Key words: Distributional patterns, Historical Biogeography, Panbiogeography, Megafauna, Late Pleistocene, South America.

INTRODUCTION

During the Pleistocene, South America was inhabited by numerous large mammals that became extinct in the Pleistocene-Holocene transition. The causes of the extinction are still debatable, but the most acceptable are the drastic change in the vegetation after the end of the last maximum glacial, direct and indirect human impacts, and the introduction of diseases by humans or by invasive species (Câmara 2006, Koch and Barnosky 2006, Cione et al. 2009).

According to the traditional view, the native South American Pleistocene megafauna was affected by the dispersion of North American species during the biogeographic event known as Great American Biotic Interchange (GABI). In this event, several taxa (not only mammals) expanded their distribution to both continents. It occurred approximately 2.7 Ma, due the emergence of the Isthmus of Panama, and it had a great influence

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in the composition of the extant South American fauna (Webb 2006, Woodburne 2010). However, according to Simpson (1950, 1980) and Webb (2006), the taxa of mammals from North America that participated in the interchange had a higher success in South America than the South American invasive taxa in North America. This asymmetry could be explained by the fact that the northern taxa had a long and wide-ranging history from the time of Eurasia. Only four genera of South American mammals (i.e., *Didelphis*, *Dasypus*, *Erethizon*, and *Trichechus*) survived in the North America (Webb 2006).

The GABI was not the only event of interchange of taxa between North and South America. Remains of some taxa of South American ground sloth were found in North America in more early ages than the emergence of the Isthmus, and remains of some typical Holarctic mammals, such as Carnivora Procyonidae, and a gomphothere and Tayassuidae were found in a Late Miocene locality of Peru (Campbell Jr et al. 2000, 2010, Webb 2006). The groups that expanded their distribution to both continents before this emergence are considered as isolated cases of dispersion, also because of the gap of 6 Ma. Therefore, they did not make part of the GABI (Marshall 1988). Central America was not only a "corridor" during the Interchange, but it has also an important role in this event. Some Holarctic taxa (e.g. *Bison*) were not able to cross Central America (Webb and Rancy 1996), while others (e.g. *Cerdocyon*, *Neochoerus*, *Glossotherium*) spent a longer time in the region before they could expand their distribution, which is called "holding pens", indicating that some of these taxa probably differentiated before crossing Central America (Woodburne et al. 2006, Woodburne 2010).

Except for some groups, several doubts and discussions remain regarding taxonomy and ecology of the American Pleistocene megafauna, as well as how the GABI affected the distribution of that fauna. Although a lot of studies had already been published in order to answer these doubts, these studies are mostly related to ecology and taphonomy (e.g. Sánchez et al. 2004, Mendoza 2007). By contrast, there are few studies accomplished about the distributional patterns of the megafauna, especially with a panbiogeographical approach.

The goal of the present study is to contribute to the knowledge of the South American megafauna, using the panbiogeographical method of track analysis. This is a first attempt to analyze the distributional pattern of the South American Late Pleistocene herbivore megafauna taxa. It shows preliminary results included in R.C.L. Pereira et al. (unpublished data) and R.C.L. Pereira (unpublished data).

The panbiogeographical method of track analysis, developed by Croizat (1958, 1964), and later expanded and quantified by Page (1987), Craw et al. (1999), and Echeverry and Morrone (2010), allows identification of congruent patterns of geographic distribution if phylogenetic information of the studied taxa is not available. This method is especially useful in paleontology, due to phylogenetic data of the most of extinct groups are dubious or even incomplete. Also, it is a tool potentially useful to identify distributional patterns (e.g. Craw 1982, Croizat 1984, Page 1987, Morrone 2001) and some recent studies confirm the validity of the method to be applied to living and extinct species (e.g. Morrone 2006, Gallo et al. 2007, 2010, Alzate et al. 2008, Cavalcanti and Gallo 2008, Arzamendia and Giraudo 2009, Corona et al. 2009, Espinosa-Pérez et al. 2009, Maya-Martínez et al. 2011).

MATERIALS AND METHODS

DATA SET

In this study, the distribution of the following genera was analyzed: *Glossotherium*, *Lestodon*, *Mylodon*, and *Scelidotherium* (Xenarthra, Mylodontidae); *Eremotherium* and *Megatherium* (Xenarthra, Megatheriidae); *Pampatherium* (Xenarthra, Pampatheriidae); *Glyptotherium*, *Glyptodon*, *Hoplophorus*, *Panochthus*, and *Parapanochthus* (Xenarthra, Glyptodontidae); *Cuvieronius* and *Notiomastodon* (Proboscidea, Gomphotheriidae); *Equus* and *Hippidion* (Perissodactyla, Equidae); *Hemiauchenia* and *Palaeolama* (Artiodactyla, Camelidae); and *Macrauchenia* (Litopterna, Macrauchenidae).

The number of localities is based on a comprehensive search in the literature, supplemented by the available records of online databases of several scientific institutions, as well as the website The Paleobiology Database (http://www.paleodb.org/cgi-bin/bridge.pl). We found a total of 549 localities distributed in this decreasing order: *Notiomastodon* (95); *Cuvieronius* (46); *Glossotherium* (46); *Eremotherium* (42); *Equus* (40); *Pampatherium* (33); *Glyptodon* (30); *Hippidion* (27); *Megatherium* (27); *Lestodon* (24); *Glyptotherium* (23); *Hemiauchenia* (23); *Panochthus* (23); *Mylodon* (19); *Palaeolama* (18); *Macrauchenia* (14); *Scelidotherium* (9); *Hoplophorus* (6); *Parapanochthus* (4).

Although some of the fossils and localities analyzed do not have a detailed dating definition, we assume that all included data are from the Late Pleistocene.

TRACK ANALYSIS

The panbiogeographical method of track analysis consists basically of plotting locality records of different taxa on maps and connecting them using lines following a criterion of minimum distance, to constitute individual tracks (distribution areas). These tracks are superimposed and the coincidence of them corresponds to a generalized track (areas of endemism), providing a spatial criterion to biogeographic homology (Morrone 2001) and allowing to infer the existence of an ancestral biota widespread in the past and later fragmented by vicariant events. When two or more generalized tracks converge or superimpose in an area, a biogeographic node is determined, implying that different ancestral biotas interrelated, possibly in different geologic times, and formed a composite or hybrid area. Furthermore, the nodes may represent endemism, high diversity, and distribution boundaries (Craw et al. 1999, Grehan 2001, Heads 2004, Morrone 2004, 2009).

Individual tracks were constructed for each species by plotting the localities on present-day world maps with the help of the software ArcView v3.2 (ESRI 1999) and connecting them by minimum spanning trees (Page 1987) using the Trazos2004 extension (Rojas 2007). Generalized tracks and biogeographic nodes were drawn by hand.

RESULTS

From the 27 individual tracks (i.e., *Cuvieronius hyodon*, *Equus andium*, *E. insulatus*, *E. neogeus*, *E. santaelenae*, *Eremotherium laurillardii*, *Glossotherium robustum*, *Glyptodon clavipes*, *Glyptotherium* sp., *Hemiauchenia paradoxa*, *Hippidion devillei*, *H. principale*, *H. saldiasi*, *Hoplophorus euphractus*, *Lestodon armatus*, *Macrauchenia patachonica*, *Megatherium americanum*, *M. medinae*, *Mylodon darwini*, *Notiomastodon platensis*, *Palaeolama major*, *Pampatherium humboldti*, *P. typum*, *Panochthus greslebini*, *P. tuberculatus*, *Parapanochthus jaguaribensis*, and *Scelidotherium leptocephalus*) (Figs. 1-21), six generalized tracks (GTs) were obtained (Fig. 22). These are defined as follows: GT1, Transandine Peru (including *Eremotherium laurilardii*, *Equus santaelenae*, *Equus andium*, and *Glossotherium robustum*); GT2, Cisandine Peru/Puna (including *Cuvieronius hyodon* and *Equus insulatus*); GT3, Santiago (including *Hippidion saldiasi* and *Megatherium medinae*); GT4, Chaco/Pampas/Northwest Uruguay (including *Pampatherium typum*, *Panochthus tuberculatus*, *Lestodon armatus*, *Glyptodon clavipes*, *Hemiauchenia paradoxa*, *Mylodon darwini*, *Macrauchenia patachonica*, and *Megatherium americanum*); GT5, Intertropical Region/ Southeastern Brazil (including *Pampatherium humboldtii*, *Notiomastodon platensis*, *Hippidion principale*, and *Equus neogeus*); and GT6, Intertropical Region/Northeastern Brazil) (including *Palaeolama major*, *Glyptotherium* sp., *Panochthus greslebini*, *Parapanochthus jaguaribensis*, and *Hoplophorus euphractus*). *Hippidion devillei* and *Scelidotherium leptocephalus* did not participate in the composition of any generalized track. The GTs regions were recognized and named based on Morrone (2006) biogeographic province definitions.

Two biogeographic nodes were found: node 1, in the intersection of GTs 4 and 5, in the frontier of Uruguay-Brazil (Grassland/Steppe sensu de Vivo and Carmignotto 2004); node 2, in the intersection of GTs 5 and 6, between the Brazilian states of Sergipe and Alagoas, near the São Francisco River.

Fig. 2 - Individual tracks of *Equus* (1 - *Equus andium*; 2 - *E. insulatus*; 3 - *E. neogeus*; 4 - *E. santaelenae*).

Fig. 1 - Individual track of *Cuvieronius hyodon*.

Fig. 3 - Individual track of *Eremotherium laurillardii*.

Fig. 4 - Individual track of *Glossotherium robustum*.

Fig. 6 - Individual track of *Glyptotherium* sp.

Fig. 5 - Individual track of *Glyptodon clavipes*.

Fig. 7 - Individual track of *Hemiauchenia paradoxa*.

Fig. 8 - Individual tracks of *Hippidion* (1 - *Hippidion saldiasi*; 2 - *H. principale*).

Fig. 10 - Individual track of *Hoplophorus euphractus*.

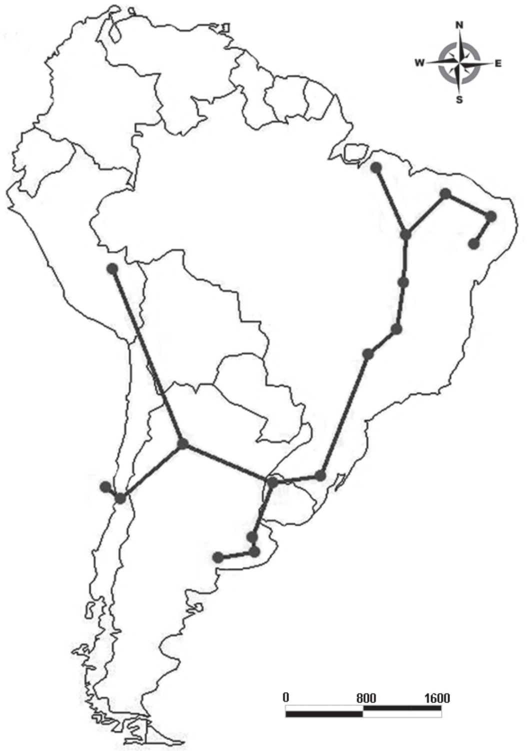

Fig. 9 - Individual track of *Hippidion devillei*.

Fig. 11 - Individual track of *Lestodon armatus*.

Fig. 12 - Individual track of *Macrauchenia patachonica*.

Fig. 13 - Individual tracks of *Megatherium* (1 - *Megatherium medinae*; 2 – *M. americanum*).

Fig. 14 - Individual track of *Mylodon darwini*.

Fig. 15 - Individual track of *Notiomastodon platensis*.

Fig. 16 - Individual track of *Palaeolama major*.

Fig. 17 - Individual track of *Pampatherium humboldti*.

Fig. 18 - Individual track of *P. typum*.

Fig. 19 - Individual tracks of *Panochthus* (1 - *Panochthus tuberculatus*; 2 - *P. greslebini*).

Fig. 20 - Individual track of *Parapanochthus jaguaribensis*.

Fig. 21 - Individual track of *Scelidotherium leptocephalus*.

Fig. 22 - Generalized tracks and nodes.

DISCUSSION

Several studies (e.g. Salgado-Labouriau et al. 1998, Heine 2000, Behling et al. 2002) indicate that climate and vegetation of South America during the Pleistocene were different when compared to the present. Only in the Late Pleistocene the levels of temperature and humidity began to approximate to the present-day levels.

Comparing the GTs map with the one of distributional pattern of vegetation in South America during the Pleistocene (de Vivo and Carmignotto 2004) (Fig. 23), we concluded that herbivore megamammals avoided the two great areas of open savanna present in the Late Pleistocene. Yet, the GTs were not superimposed with the two biotic tracks defined by Roig-Juñent et al. (2003, 2006) for living arthropods typical of xeric natural areas of South America (Fig. 24), confirming that the herbivore megamammals avoid arid or semi-arid ecosystems.

Fig. 23 - Distributional pattern of vegetation during the Pleistocene (modified from de Vivo and Carmignotto 2004).

Fig. 25 - Map of biogeographic provinces (modified from Morrone 2006).

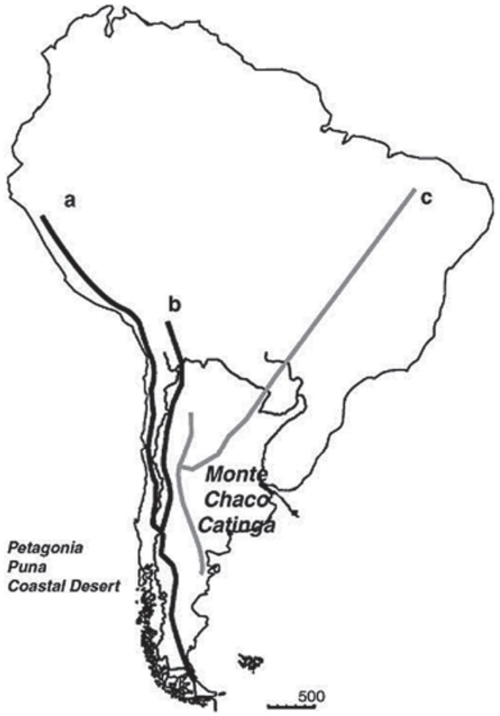

Fig. 24 - South American map with biotic tracks related to the xeric natural areas (modified from Roig-Juñent et al. 2003, 2006).

The biogeographic nodes coincided with the limits between the main plant formations of South America during the Pleistocene: node 1 coincided with the boundary between the grassland and open forest areas; and node 2 coincided with the boundary between the Brazilian open forest and open savanna areas. These patterns confirm the importance of the climate conditions in the distribution of the Late Pleistocene megafauna.

The GT 3 coincided with the transandine "corridor" proposed by Moreno et al. (1994), which could explain the presence of *Hippidion saldiasi* and *Megatherium medinae* in the transandine Chile, as well as in frontier of Chile-Argentina.

Comparing the generalized tracks (Fig. 22) with the regions and biogeographic provinces defined by Morrone (2006) on the basis of living taxa (Fig. 25), we verified that: GT 1 is delimited by Tumbes-Piura (area 34) and Coastal Peruvian Desert (area 57); GT 2, by Napo (area 35), Ucayali (area 42), Yungas (area 47), and Puna (area 58); GT 3, by Santiago (area 62); GT 4, by Pampa (area 51), Chaco (area 50), and Parana Forest (area 54); GT 5, by *Araucaria angustifolia* Forest (area 55), Parana Forest (area 54), Cerrado (area 49), and Caatinga (area 48); and GT 6, by Caatinga (area 48). This coincidence between tracks of living and fossil taxa suggests that certain recent biogeographic patterns were also present during the Late Pleistocene.

When we compared our results to other studies related to Pleistocene biogeography, we verified that the GTs 5 and 6 coincided with the Intertropical Region proposed by Cartelle (1999). According to this study, this region would house some megafauna taxa of pampean origin (e.g. *Equus neogeus*, *Hippidion devillei*, *H. principale*), but also present some endemic taxa (e.g. *Parapanochthus* and *Hoplophorus*) confirmed by the composition of GTs. However, the generalized tracks indicate the division of this region in two parts, with the node 2 showing the area where this division occurred.

The GTs 5 and 6 are partially in agreement with Costa et al. (2000), which point to an Atlantic Forest divided in two areas, and also coincided with the results of Carnaval and Moritz (2008), who defined two stable areas in the Atlantic Forest that remained unfragmented during the Pleistocene climatic changes.

The GT 2 coincided partly with some refugium areas proposed by Haffer (1969) and Prance (1982), situated in Bolivia and Peru. Although these areas possess some biogeographic meaning, the existence of refugia is debatable, because there are some evidences that Amazonia was never fragmented (Colinvaux et al. 2000).

The biogeographic node 1 is related to the contact between tropical and more temperate taxa and coincides with an area today composed by south Brazil, northwest Uruguay and Argentinian Mesopotamia (Missiones, Corrientes and Entre Rios provinces). According to Carlini et al. (2004) and Oliveira and Pereira (2009) it could be a contact zone between paleobiogeographic regions, with high biological diversity, supported by the presence of this node.

Overall, the generalized tracks and biogeographic nodes coincided with the limits between the main vegetal formations of South America during the Pleistocene (de Vivo and Carmignotto 2004). GT 3 coincided with the limit between the Argentinean desert and the Chilean open forest; part of the GT 4 coincided with the limits between the desert and steppe formations; node 1 coincided with the limit between the steppe and open forest formations; GTs 5 and 6 and node 2 coincided with limits between the great open savanna area in Brazil and the open forest formation. These data confirm the importance that vegetation and climate conditions had in the distributional patterns of herbivore megamammals during the Pleistocene in South America, and probably the changing on those conditions were the main cause for their extinctions.

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RESUMO

A distribuição geográfica de 27 espécies da megafauna de mamíferos herbívoros sul-americanos durante o Pleistoceno Superior foi analisada, visando à identificação de seus padrões de distribuição. A distribuição das espécies foi estudada com o uso do método pan-biogeográfico de análise de traços. Seis traços generalizados (TGs) e dois nós biogeográficos foram obtidos. Os TGs não superpõem completamente com as áreas de savana aberta presentes no Pleistoceno, nem com os traços bióticos de alguns artrópodes típicos de clima árido, indicando que estes animais evitavam ambiente árido. De um modo geral, os TGs coincidiram com algumas das províncias biogeográficas definidas com base em táxons viventes, indicando que certos padrões de distribuição atuais já existiam no Pleistoceno. Os nós biogeográficos coincidiram com as bordas entre as principais formações vegetais do Pleistoceno, mostrando que o tipo de vegetação teve grande influência na distribuição da megafauna mamaliana. O nó 1 confirmou a existência de zonas de contato entre regiões paleobiogeográficas próximo à borda Argentina-Uruguai. O nó 2 conecta as regiões intertropicais brasileiras.

Palavras-chave: Padrões de distribuição, Biogeografia Histórica, Pan-biogeografia, Megafauna, Pleistoceno Superior, América do Sul.

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