

# Pleniglacial Desertization, Large-Animal Mass Extinction and Pleistocene-Holocene Boundary in South America

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## ABSTRACT

*The drastic qualitative and quantitative impoverishment, represented by the extinction of the megafauna biomass constitutes one of the most notable events in the South American Quaternary. Extensive savanna and steppe biomes which today cover 2/3 of the continent are actually in terms of herbivorous megafauna biological deserts (e.g. Fuego-Patagonian, Pampas and Altiplano steppes, Llanos del Orinoco, Cerrados, Gran Chaco, Gran Sabana and Bogotá savannas as well as the Caatinga scrubs).*

*The supraregional scope of this phenomenon and its concurrence with geoscientific data lead for the first time to the hypothesis that it was caused by the radical increase of aridity during the Late Pleistocene (12,000-18,000 y.B.P.), especially in the tropics, and not by cultural reasons which had only a very limited impact. In fact, an area with about  $11.5 \times 10^6$  km<sup>2</sup> suffered long interannual droughts during this period being an unsurmountable physiological barrier for the large mammals. A first extinction wave affected particularly the tropical and subtropical ecosystems of the Atlantic side (regions of the Orinoco, NE of Brazil and the Pampasia of Argentine and Uruguay) between 12,000-18,000 y. B.P. A retarded wave badly affected all the Andean and peri-Andean ecosystems between 10,000-9,000 y. B.P. (regions of the Gran Chaco, western Fuego-Patagonia, Altiplano of Bolivia and the present Atacama Desert). This delay or differential extinction on the South American scale must be associated with the glaciation that affected the Andean Cordillera until the close of the Wisconsin.*

*To the total surface of arid land that included at least the implantation of four continental deserts along the whole tropical and subtropical zone, we must add the marginal deserts of the emerged marine platforms, as well as a discontinuous belt of desert-islands for the megafauna imposed by glaciers and mountains (ca.  $1.2 \times 10^6$  km<sup>2</sup>). In this way, and as indicated by the zoo-and geodata compiled in the last ten years, the transition Pleistocene-Holocene was brutal. In fact, post-glacial fossiliferous beds (less than or equivalent to 10,000 y.B.P.) lack the characteristic giant forms of the last glacial). Mastodons, megatheres, toxodons, palaeolamas, glyptodons, bears, etc. are totally absent. Independent of their biochron, ancestry or geographic origin, only the smaller species survived, leading at the beginning of the Holocene to a clear inversion of the faunal character, —that is the replacement of a dominant megafauna by a micro- and mesofauna. With few exception (Camelidae, Cervidae) the whole megafauna became extinct from the Strait of Magellan up to the Lesser Antilles. This supports the fact that the present zoogeographical arrangement of South America constitutes a modern event. Finally it cannot be disregarded that a similar aridity during the Late Pleistocene was responsible for the large-animal extinctions in other southern continents, such as Australia and Africa.*

## RESUMEN

*Drástico empobrecimiento cualitativo y cuantitativo representado por una extinción a gran escala de la biomasa de megafauna, constituye uno de los eventos más notables del Cuaternario en Sudamérica. Extensos biomas de sabanas y estepas que abarcan hoy más de 2/3 del Continente constituyen en el presente verdaderos desiertos biológicos en términos de megafauna, especialmente herbívora (p. e. estepas de Fuego-Patagonia, Pampas y Altiplano, las sabanas del Orinoco, Gran Sabana, Gran Chaco, Cerrados, Bogotá y la Caatinga).*

*La magnitud suprarregional del fenómeno de extinción y su concurrencia con la data geocientífica llevan a plantear por primera vez que ella ha sido provocada por el radical acentuamiento de la aridez durante el Pleistoceno Tardío (12,000-18,000 años A.P.), especialmente en los trópicos, y no por causas culturales las cuales tuvieron un impacto muy limitado. En efecto, una área cercana a los  $11.5 \times 10^6$  km<sup>2</sup> estuvo durante este período sometida a largas sequías interanuales (drought-trends) —barrera fisiológica esta última infranqueable para los grandes pesos. Una primera fase de extinción afectó particularmente los ecosistemas tropicales y subtropicales de fachada atlántica (regiones de la Cuenca del Orinoco, NE de Brasil y Pampasia argentino-uruguaya) entre los 12.000-18.000 años A.P. Una segunda fase más tardía afectó intensamente a todos los ecosistemas andinos y periandinos entre 10.000-9.000 años A.P. (regiones del Gran Chaco, Fuego-Patagonia occidental, Altiplano de Bolivia y actual Desierto de Atacama). Este retraso o extinción diferencial a escala sudamericana debe ligarse a la glaciación que afectó a la cordillera de los Andes hasta fines del Wisconsin.*

*A la superficie global afectada por los climas secos que incluyó la evolución de por lo menos cuatro desiertos continentales a lo largo de toda la zona tropical y subtropical, deben agregarse los desiertos costeros marginales establecidos sobre las plataformas marinas emergidas, así como un cinturón discontinuo de "desiertos islas" para la fauna sensu lato dispuesto por glaciares y montañas (ca.  $1.2 \times 10^6$  km<sup>2</sup>). De esta manera y, como lo sugiere la zoo- y geodata reunida en los últimos diez años, la transición Pleistoceno-Holoceno fue brutal. En efecto, la mayoría de los yacimientos post-glaciales (edad menor o equivalente a 10.000 años A.P.) carecen de formas gigantes características del último período glacial. Mastodontes, megaterios, toxodontes, paleolamas, glyptodontes, osos, smilodontes, etc. hallanse totalmente ausentes. Independientes de su biocrón, ancestro u origen geográfico sobrevivieron sólo las especies de tamaño menor, dando lugar hacia los comienzos del Holoceno a una clara inversión del carácter de la fauna: es decir, el reemplazo de una megafauna dominante por una micro y mesofauna. Con escasas excepciones (Camelidae, Cervidae) toda la megafauna se extingue desde el Estrecho de Magallanes hasta las Antillas Menores, hecho que permite suponer que la actual organización zoogeográfica de Sudamérica representa un evento moderno. Finalmente, no se descarta el hecho que una aridez similar durante el Pleistoceno Tardío halla sido responsable de extinciones in massa en otros continentes australes tales como Australia y Africa.*



## ZUSAMMENFASSUNG

*Die drastische qualitative und quantitative Verarmung der Biomasse an Megafauna stellt eines der bemerkenswertesten Ereignisse des südamerikanischen Quartär dar. Ausgedehnte Savannen- und Steppenbiome, die heute mehr als 2/3 des Kontinents umfassen, sind gegenwärtig, was die Megafauna, besonders die Pflanzenfresser betrifft, wirkliche biologische Wüsten (z.B. Fuego-Patagonien-, Pampas- und Altiplanosteppen, Llanos del Orinoco, Cerrados, Gran Chaco, Gran Sabana- und Bogotasavannen sowie der Caatinga-Trockenwald).*

*Das überregionale Ausmass dieses Phänomens und seine Übereinstimmung mit geowissenschaftlichen Daten führen zum ersten Mal zu der Hypothese, dass es durch die radikale Zunahme an Aridität, besonders in den Tropen, während dem Spät-Wisconsin (12000 - 18000 Jahre B.P.) hervorgerufen wurde und nicht durch kulturelle Faktoren, die nur eine begrenzte Wirkung hatten. Tatsächlich war ein Gebiet von  $11,5 \times 10^6 \text{ km}^2$  während dieser Zeit langen interannuellen Trockenzeiten (drought-trends) ausgesetzt - eine für die grossen Säugetiere unüberwindliche Barriere. Eine erste Extinktionsphase wirkte sich zwischen 12000-18000 Jahren B.P. besonders auf die tropischen und subtropischen Ökosysteme der atlantischen Seite aus (Gebiete des Orinocos, Nordosten Brasiliens und der Pampasia von Argentinien und Uruguay). Eine zweite Phase wirkte sich später zwischen 10000-9000 Jahre B.P. stark auf alle andinen und periandinen Ökosysteme aus (Gebiete des Gran Chaco, westliches Fuego-Patagonien, Altiplano von Bolivien und die heutige Atacama-Wüste). Diese zeitliche Verschiebung oder differentiale Extinktion im Rahmen Südamerikas muss im Zusammenhang mit der vereisung gesehen werden, die sich auf die Andenkordillern bis zum Ende des Wisconsin auswirkte.*

*Zu der gesamten Trockenfläche, die Evolution von zumindest vier kontinentalen Wüsten in der tropischen und subtropischen Zone umschliesst, müssen die durch den Meeresspiegelrückgang freigelegten Randwüsten sowie ein unterbrochener "Wüsten-Inseln-Gürtel" von Bergen und Gletschern (ca.  $1,2 \times 10^6 \text{ km}^2$ ) hinzugefügt werden. Dies und die in den letzten zehn Jahren zusammengetragenen Geodaten zeigen, dass der Übergang Pleistozän - Holozän brutal war. Tatsächlich fehlen bei der Mehrzahl der postglazialen Fundstellen (jünger oder gleich 10000 Jahre B.P.) die charakteristischen Riesenformen der letzten Eiszeit. Mastodonten, Toxodonten, Palaeolamas, Bären, Glyptodonten, Säbelzahn tiger, Megatherien, etc. fehlen ganz. Unabhängig von Biochron, Abstammung oder geographischer Herkunft überleben nur kleinere Species, was zu Beginn des Holozän zu einer klaren Umkehrung des Faunabildes führt: Die dominierende Megafauna wurde durch eine Meso- und Mikrofauna ersetzt. Abgesehen von wenigen Ausnahmen (Camelidae, Cervidae) stirbt die ganze Megafauna von der Magellanstrasse bis zu den Kleinen Antillen aus, was die Schlussfolgerung erlaubt, dass die gegenwärtige zoogeographische Organisation Südamerikas ein modernes Ereignis darstellt. Schliesslich kann nicht ausgeschlossen werden, dass eine ähnliche Trockenheit während dem Wisconsin für das Aussterben in massa auf anderen südlichen Kontinenten, Besonders Australien und Afrika, verantwortlich war.*

## THE PLEISTOCENE-HOLOCENE BUNDARY

Up to the date, the definition of a Pleistocene-Holocene boundary in the Quarternary chronology of South America has been fruitless, principally due to the poor and uncorrelated geological background. In a recent work, based on paleomastozoological and paleobiogeographical data. Ochsenius (1982) intended to throw light upon this problem establishing that the beginning of the Holocene is clearly characterized by the simultaneous climatic amelioration (Postglacial Savannization) and the spreading of a conspicuous neofauna (micro and meso forms), while the Late Pleistocene times are characterized by the mass-extinction of an impressive megafauna, (see Table 1), the dominance of dry climates over the whole continent, and the evolution of deserts in tropical and subtropical latitudes (Pleniglacial Desertization). This irreversible ecological process that accounts for the drastic change in the South American Biota finds its principal support in the total absence of megafauna in Holocene fossiliferous beds. A few localities with postglacial megafauna (only 0.5% of the total Late Pleistocene localities of about 500) must be interpreted as anomalous datings or as refugial distribution in Holocene times (until 5000 B.P.). In this way, and with high spatial resolution, the zoodata provide a solid alternative while the lithostratigraphical data for an Upper Quaternary

chronology remain speculative. The Holocene neofauna represents rather a typically faunistic succession than the relatively rapid diversification (speciation) of the surviving Pleistocene taxa, enriched by later Holoarctic immigrants. At the present it is undergoing very probably and expansive phase, despite the obvious pressures of the geometric growth in human population since the last 15,000 years (earliest evidence ca. 13,000 B.P. Ochsenius & R. Gruhn, 1979). In accordance with this Holocene spreading (biogeographically verifiable) and the correlative climatic amelioration, takes also place the areal expansion of rain forest refuges (i.e. Amazon) and the return of more humid conditions into the open unforested landscapes like subtropical steppes and tropical savannas, both submitted to the influence of dry climates and deserts during the Late Pleistocene (12,000-18,000 y.B.P.).

As a model to illustrate this faunal change, we can refer to the African megafauna at the arrival of the first Europeans. In fact, if we replace the actual fauna matrix of the intertropical zone of South America with the African equivalent, we would not only get an idea of the South American available biomass during the Last Glaciation, but would also see the great or radical difference between the former fauna stock of grazers and the one of today. The Pleistocene forms resemble without doubt the recent African forms: all need an average of 100-300 kg of vegetal food and about 150 l water per



TABLE 1

Neofauna and Megafauna-component in the Late Pleistocene record

Paleobiome	Neofauna (%)	Megafauna (%)
Coriano Biome	15.90	84.10
Amazon Savanna-Forest Biome	9.70	90.30
Colombia Andes Biome	29.72	70.28
Ecuador Andes Biome	25.94	73.86
Caatinga Biome	2.00	98.00
Cerrado Biome	44.50	55.50
Gran Chaco Biome	35.00	65.00
Tarija Biome	37.00	63.00
Altiplano Biome	13.80	86.20
Atacama Savanna Biome	25.40	74.60
Pampasia Biome	23.20	76.80
Mediterranean Chile Biome	14.60	85.40
Nothofagus Biome	5.30	94.70
Western Fuego-Patagonia Biome	46.40	53.60
$\bar{X}$ (2)	23.47	76.53

(2) From a sample of ca. 500 localities and more than 2500 individuals.

day to drink and for the refreshing and parasite cleansing showers (i.e. 54 m<sup>3</sup> and 73,000 kg/year!). Thus the South American Late Pleistocene megafauna had to provide vast quantities of vegetal food (ca 6% of the body-weight) in not very favorable environments. Was this possible during the Last Glaciation, when open xeromorphic plant formations and dry climates predominated? Reflect the mastodon remains in the present Caatinga, Altiplano, or in the Pampas of Uruguay and Argentina, to mention only some places, a general extinction point as consequence of prolonged drought periods which deteriorated drastically the availability of water and subsequently the life conditions?

#### LANDMEGAFAUNA BIOGEOGRAPHY AND PALEOCLIMATE: PALEOMASTOZOOLOGICAL DATA

If we could turn back the time for 16,000 years and fly over the different native landscapes of savannas, steppes, caatingas, tropical deserts, cordilleras, forest refuges, active volcanoes, and emerged shelves of South America we would believe, without exaggeration, to fly over another planet if there would not be the general structural pattern with the geomorphological and botanical features we know today. Where today exists the most impressive cattle-breeding and where the primitive grass steppe has been transformed in an artificial prairie lived a grazer megafauna whose fossil record hardly gives us an approximate idea of its character and

diversity. In fact, on the Pampasia lowlands pastured the most diverse giant beats from edentates like megatheres, scelidodons, mylodons, glyptodons, lestodons to macrauchenias, toxodons, camelids, horses, deers, and mastodons, all of them chased by large carnivores like the saber tooth tiger and bears. However, the Pampasia megafauna was not an exception in South America but only a facet of the continental Biota (9% of the total area). In fact, although the Pampasia fauna has always received special attention by the Quaternary research, it constituted only a regional phenomenon not representative—as we will see in the following—for the whole Late Pleistocene South American Zoogeography.

In a clear geographical triumvirate mastodon herds inhabited and exploited the different savanna and steppe types, from the Caribbean coast up to the northern edge of the Patagonian Desert. *Cuvieronius hyodon*, a form adapted especially to mountainous habitats, spread along the Andes over thousands of kilometers. *Stegomastodon platensis* with its restricted subtropical distribution was the typical form of the Pampasia, although it could not conquer the tropical zone due to the probable competence offered by the *Haplomastodon waringi* herds—the tropical mastodon par excellence. The good adaptative capacity permitted it to inhabit all tropical ecosystems, including the Andes of Ecuador and in a marginal habitat the Pacific Coastal Desert of Atacama (i.e. Talara, La Carolina). The abundance and diversity of mastodons in



South America is supported by 170 paleontological localities, a good evidence for the importance reached by savannas and other open plant formations. It is worth to remember that these three Neotropical forms (taxonomical status for additional forms remains in study) lived 12,000 y. B.P.; as comparison, the last remnants of *Gomphotheriidae* in Africa comprise only one species and one genera (*Loxodonta africana*).

As equivalent of the African rhinoceros *Cerathotherium simon* existed in South America the heavy toxodon (*Toxodon platensis*, *Miotoxodon larensis*), perhaps one of the most hysodont savanna forms. Adapted specially to the herbaceous lowland "Own's Toxodon" was a basically non-oreal animal (steno-orographic) that not inhabited the Andean environments. Furthermore suggests its absence from Pleistocene beds in the cold steppes of Patagonia that the toxodons did not tolerate low temperatures. It was particular common in the tropical zone (Coriano, Amazon, Caatinga, Chaco, and Cerrado biomes) up to the Pampasia. Its supposed amphibian adaptation, long discussed in the literature, can be excluded as 93% of the toxodon findings proceed from ecosystems which partly today and during the Last Glaciation were under semiarid conditions. Very significant is that little less than a fifth of all toxodon rest stem from the actual Amazon rain forest, thus being an argument in favor of the modern areal of the Hyalae. Compatible with its adaptation to tropical environments its migration through the Panama Isthmus and Central America as well as its lacking fossil record in the south of 33°S. Terminal ages for *Toxodontidae* lie between 14,000 and 12,000 y.B.P.

A *sine qua non* megafauna component were the edentates and its most aberrant form, the megatheres (ca. 100 loc.). With a weight of about 3,000 kg and a basically folivore-xylophagous diet (coprolite analyses), herbaceous diet in the Pampasia, the megatheres show a geographic bipolarity as manifest as the mastodons. *Ereotherium rusconi* was a dominant tropical form. Adapted to warm climates, it could not invade the areas south of the Tropic of Capricorn (it crossed however successfully the Isthmus of Panama). In northern South America it reached the Trinidad Island (like *Haplomastodon*) due to the low sea level and the recent sinking of landbridges.

The subtropical zone was inhabited by *Megatherium americanum*, a basically grazing form. From the Atlantic coast of Argentine and Uruguay it spread towards the north through the Gran Chaco, parallel to the tropical line, from where it reached the peri-Andean basins of Tarija and Padcaya. This route was gradually expanded until the vast Altiplano table-land was reached, an area

without relevant topographical elevations. From there, *Megatherium* and close-related forms like *Scelidotherium*, *Scelidodon*, *Glossotherium*, *Nothrotherium* and *Myloodon* continued their way to the Pacific coast, the present Atacama Desert. In biogeographical terms it is important to mention that the whole Late Pleistocene Chilean fauna suggests this wandering route through the Altiplano, given the insurmountable ecological-geomorphological barrier imposed by the Chilean-Argentinian Andes.

The spreading of *Megatherium* and the mentioned close-related forms in direction of Ecuador only took place through the Andean corridors but without surpassing the northern limit of the Puna plant formation (i.e. ca. 7°S, 3,000 m). Undoubtedly it was a more orreal form than *Ereotherium* as is demonstrated by the fossil record in the Andean and peri-Andean ecosystems. My hypothesis that isolated groups of *Megatherium*, *Scelidotherium*, *Myloodon* and other edentates could survive in favorable biotopes (*refugia*) far into the Holocene, receives in the last time more support. According to Ochsenius (1972, 1981) *Megatherium* together with *Nothrotherium* and *Scelidotherium* could have survived in the peri-Andean oases of the Atacama Desert until about 5,000 y.B.P. (4,399 ± 90 y.B.P., WSU-1986). Another example is given by *Myloodon darwini* living at least until 5,000 y.B.P. in the Fuego-Patagonian piedmont, while it generally became extinct 6,000 years earlier in the Pampasia. Astonishing is the long coexistence of *Myloodon* with Paleo-Indian hunters, whereby those hunters had nothing to do with the extinction of *Myloodon*, which died by natural causes (Saxon, 1976). This is a solid evidence of the limited role of Early Man in the whole extinction process.

Perhaps the most typical *Edentata* of the Pleniglacial Biota were constituted by vas populations of armoured glyptodons and armadillos (ca. 200 loc. between 11°N and 33°S). They were giant ambulatory species (up to 300-500 kg) of savannas and grass steppes. Their continuously growing teeth, analogous to the general hysodonty of the other edentates is the obvious answer to their alimentary type: grass, geophyte and terophyte plants. Like the other megafauna, they reached their maximum size during the Upper Quaternary. From the Pampasian plains they spread over the continent; exceptions were the Andean ecosystems from Chile to northern Colombia. In western South America they did not expand over the southern limit of the Pampasia, probably due to the aridity and low temperatures of the Patagonian region (cf. Patagonian Desert, Fig. 4). The physiology of the actual edentates, especially the armadillos, is concurrent with their absence in cold environments



and their nearly absolute restriction to the tropical zone. The apparently anomalous findings in the Late Pleistocene sediments of the Amazon rain forest (Price, *et al.* 1977) contribute, with other savanna fauna rests, to the young age of the Hylaea as biome. The terminal datings are principally based on the *Corianense-Fauna* and correspond to about 10,000 y.B.P. (a similar age is available from the Rancholabrean).

Unlike the glyptodons, the armadillos have been the perhaps most successful edentates occupying actually almost the whole Neotropic realm. Autochthonous of South America the groups of *Dasypodinae*, *Stegotheriinae*, *Chlamyphorinae* and *Pampatheriinae* were the most common grazing Pleistocene elements. With the exception of the first two (smaller forms), all the others (giant forms) became extinct. Another difference is that the surviving forms are omnivore (roots, insects, carcasses, etc.) like the actual *Tamandua tridactyla* (homodont-hypsodont teeth).

As last autochthonous component of this assemblage will be mentioned *Macrauchenia patachonica*, the "South American camel": an indicator for semi-aridity per definition. With a weight of about 600 kg and a folivore-herbaceous diet, it was a dominant browser in tropical scrubs and semiarid savannas. This is indicated by its abundance in the Late Pleistocene deposits of the present Caatinga, the Peri-Caribbean Arid Belt and the steppes of Fuego-Patagonia. Despite its vast areal over 5,000 km from north to south, *Macrauchenia* inhabited the Andes only under exceptional conditions of grass steppe, as it was the case in the Altiplano. Its gradual expansion from southern South America towards the north of the Amazon Basin must be interpreted as indicator of arid environments on all the actual regions of the Brazilian shields. On the other hand, the prevalence of humid environments in the Darien zone could have been a decisive barrier to reach Central America, where it is unknown (Fig. 2).

In this brief paleoecological review rests to mention the allochthonous megafauna component (except, of course, the previously cited mastodons). Among them stand out the horses (*Hippidion*, *Onohippidion*, and *Equus (Amerhippus)*) which experienced after the arrival in South America a fast radiation. Almost all were cosmopolitan and occupied the Andean zone as well as the tropical and subtropical lowlands. The terminal datings for *Equidae* lie at about 10,000 y.B.P. Together with *Camelidae* they constitute one of the best document about the significance reached by the unforested landscapes, especially the steppes.

The fossil record of *Camelidae* (*Lama*, *vicugna*, *Palaeolama* and *Eulamaops*) shows a major range

of the camelids in the past including regions such as Cerrados and Pampas (Fig. 1). With the exception of the giant forms *Palaeolama* and *Eulamaops* which became extinct during the Last Glaciation, the *Lamini* tribe (*Lama*, *Vicugna*) experienced a regional extinction or retreat from western South America.

This disappearance from the La Plata Basin and southern Brazil must be explained with the marked increase of humidity since the beginning of the Holocene, a limiting factor for these stenohydro-pedomorphic animals (steno: low tolerance, hydro-pedomorphism: wet soils) as in the case of *Camelus bactrianus*. This ecological valency is also consistent with their present life-zones in the Arid Diagonal of South America. For this reason I think that the spreading of rich *Camelidae* populations on the Altiplano of Bolivia occurred after the megafauna extinction on the highlands and concurrent dessication of this region in postglacial times.

Among the less heavy forms (mesofauna) stand out the deers as indicator for generally mesophytic environments. Obviously the South American deers suffered less from the extinction than the North American forms where from nine genera and ten species today only three genera and four species live. Thus, South America can be defined as "large refuge" for the *Camelidae* and *Cervidae*, as all the camelids became extinct in North and Central America towards the end of the Wisconsin. *Ozotoceros*, *Blastocerus* and *Morenelaphus* were basically restricted to the Pampasia, while *Agalmaceros*, *Mazama* and *Hippocamelus* showed a clear Andean affinity or temperate zone. The areal of *Hippocamelus*, today restricted to orear biotopes (Andes), demonstrates a retreat from east to west (similar to *Camelidae*) compared with its paleo-areal that include tropical and subtropical ecosystems such as Cerrados, Caatingas and the whole Pampasia. Today only *Odocoileus* inhabits the vast inter-tropical zone (south of 21°S it is unknown). During the earlier Holocene, it was numerous in the Andean forest and savannas of Colombia, where it formed an essential part of the Paleo-Indian diet (e.g. 295 individuals were excavated at El Abra near of Bogota).

The large carnivores, which existed ubiquitous in the different regions of South America, set the character of this fauna even more. Among the outstanding ones are the saber tooth tiger (*Smilodon populator*) and the cave bear (*Arctodus (Pararctotherium)*) which were specialized on large herbivores. Not less important are the still living *Felis puma* and *Panthera onca*, probably in decline since the Holocene. Rich populations of peccaries, tapirs, rodents, birds, and aquatic fauna would have completed this zoogeography; as they lack



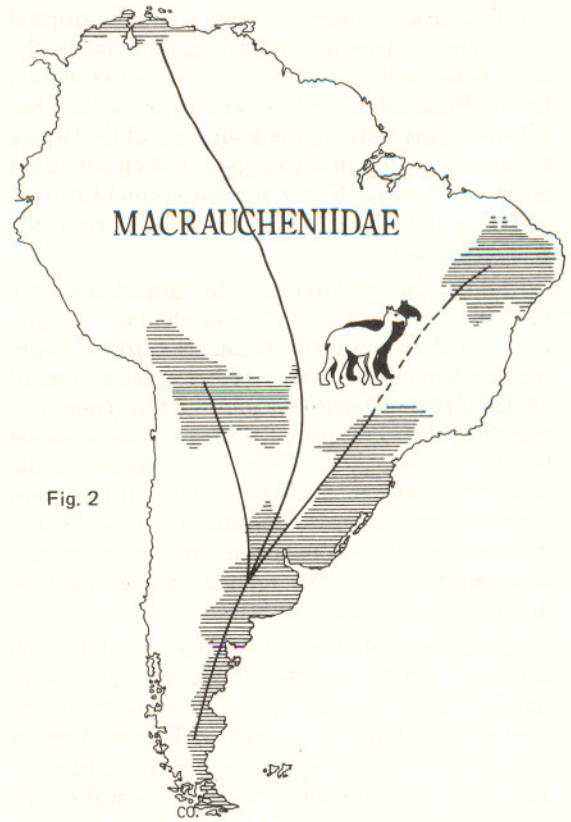
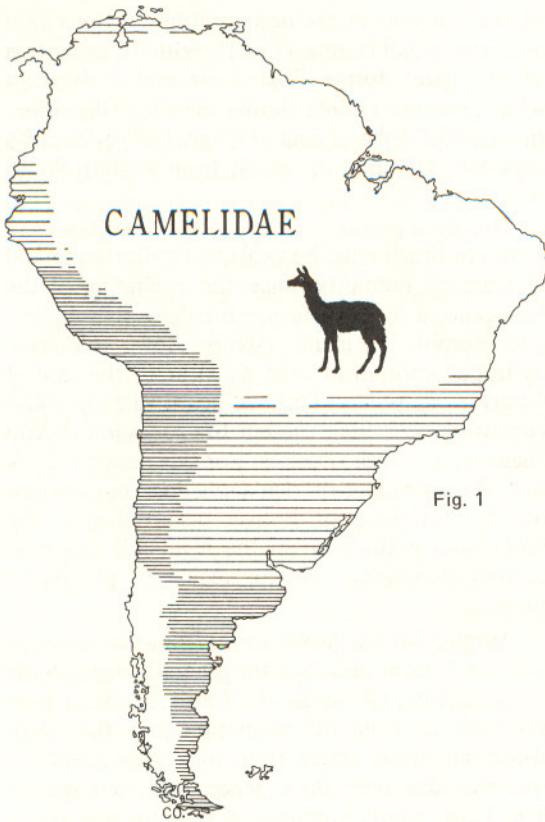


Fig. 1: Recent and Late Pleistocene areal for *Palaeolama* (+) and the *Lamini* tribe (*Lama*, *Vicugna*). Camelids are good paleoclimatological indicators of aridity (stenohydropedomorphism) as is indicated by their present life-zone in Altiplano Hig. Plain and in the Patagonia steppe.

Fig. 2: Areal of the endemic *Macrauchenia patachonica* (*Litopternae*) during the Late Pleistocene and before its extinction at ca. 10,000 y.B.P. The fossil record indicates for this taxa an accentuated affinity with semiarid environments. Its terminal age in northern Venezuela at the beginning of the Holocene shows that the present Amazon Basin was not a barrier in its dispersal.

sufficient paleontological data they are not discussed here.

In sum, the megafauna biogeography of the Late Pleistocene times shows as a whole in the first place the dominance of extense open unforrested landscapes, that is the alternance of tropical savannas with forest refuges, tropical scrubs and tropical continental sand deserts, as well as subtropical steppes associated with vast cold deserts (see Fig. 4).

A typical rainforest megafauna has not been identified. The Andean Cordillera—more humid until the beginning of the Holocene—probably has offered support for a mosaic of refuges for euro-orographic forms such as mastodons, megatheres, horses, mylodons and scelidotheres while it constituted for other taxa not only a barrier in geomorphological terms but also in thermal sense (toxodons, glyptodons, litopternas in part). Despite the general deterioration of temperatures, the megafaunal stock indicates a clear division of

tropical, subtropical and cold-climate zones during the Late Pleistocene. In a parallel way shows the areal—drift of *Camelidae* towards the Andes and Patagonia at the beginning of the Holocene the fast return of humid climatic conditions in the Pampasia semi-desert.

The biostratigraphy of Late Pleistocene deposits have not been sufficient studied in order to explain the effect of droughts on biodynamism. Concrete evidence however has been recovered from the Atacama Desert in northern Chile and Peru (Ochsenius 1974, 1977, 1981), western Bolivia (Ochsenius 1977), Andes of Ecuador (Ochsenius 1984), northern Venezuela and northeast and central Brazil (Ochsenius 1979, 1983). In these regions the polarization of many individuals with adverse ecological valency in smaller areas (fluvial beds, waterholes, sebkhas, ancient lakes, tar-seeps, thermal springs, etc.) suggests by itself the pressures exercised by recurrent droughts and its lethal physiological stress for the megafauna biocenosis.



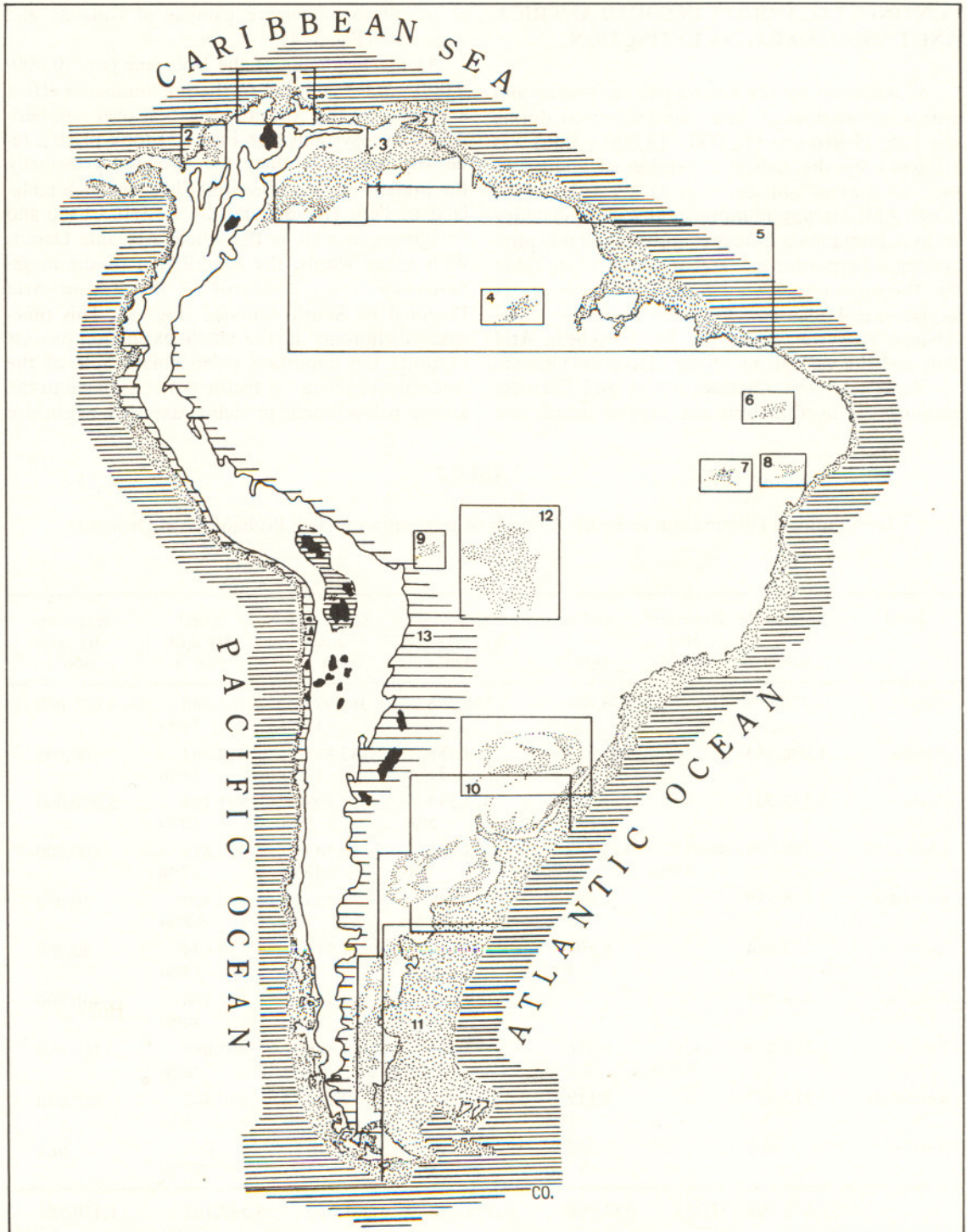


Fig. 3: Ancient dunes and other aeolian accumulations in western South America during the Late Pleistocene (12,000-18,000 y.B.P.) as indicator of full-glacial aridity. (1) Paraganá Penninsula ancient dunes (Peri-Caribbean Arid Belt). (2) Barranquilla ancient dunes (NE Colombia). (3) Great Erg of the Orinoco plains (S Venezuela and E of Colombia). (4) Ancient dunes fields of Obidos (Santarem, Federal Amazon Territory, Brazil). (5) Marajó Island dunes and arkosic sand from the Brazilian Shelf. (6) Xique-Xique dune field (Bahia, Brazil). (7) San Francisco dune field (Bahia, Brazil). (8) Itabainia dune field (Serguipe, Alagoas, Brazil). (9) Northern Chaco dune field (Santa Cruz, Bolivia). (10) Luján Formation (aeolian facies) and Pampa loess (Argentine and Uruguay). (11) Aeolian plains of Patagonia including the marginal shelf-deserts (southern Argentine). (12) Ancient dune fields of the Gran Pantanal (Mato Grosso, Brazil). (13) Altiplano lake-system and predominance effect of the Andean Glaciation over the peri-Andean adjacent areas (former Semi-arid Diagonal of South America).



### CONTINENTAL ARIDITY IN SOUTH AMERICA AND LANDMEGAFUNA EXTINCTION

As indicated by the known paleoecological and paleomastozoological data, the extinction during the Late Pleistocene (12,000 - 18,000 y.B.P.) was triggered by the radical expansion of aridity. In fact, an area of not less than  $11.5 \times 10^6 \text{ km}^2$  of South America was submitted with high probability to long interannual droughts, insurmountable physiological barrier for the large vertebrates (see Table 2). The most representative thanatocentres of this supraregional phenomenon have been the extra-Andean ecosystems like the Peri-Caribbean Arid Belt and the vast plains of the Llanos del Orinoco in Venezuela, the Caatinga-scrubs and Cerrado-savannas of northeastern and central Brazil, and

above all the extensive pampas of Uruguay and Argentina (Fig. 3, 4).

At the beginning of the Holocene (ca. 10,000-9,000 y.B.P.) and due to the predominance effect exercised by the Andean glaciation over and peri-Andean ecosystems (see Fig. 1,3) took place a retarded extinction phase that affected principally the present regions of central Chile, the high tableland of Peru and Bolivia, the western Chaco and Patagonia, as well as the whole Atacama Desert. With other words, the annihilation of the megafauna-biocenosis, recovered in the present Arid Diagonal of South America (Fig. 5). This time-space dichotomy in the whole extinction process supports the important paleoclimatic role of the Andean Cordillera — a factor not considered in the known paleoclimatic models (Damuth & Fairbridge

TABLE 2

Geographical Distribution in South America of Regions with High Probability of Droughts

Land	Total area ( $\text{km}^2$ )	Hyperarid area ( $\text{km}^2$ )	Arid area ( $\text{km}^2$ )	Semi-arid area ( $\text{km}^2$ )	Subhumid area ( $\text{km}^2$ )	Total dry area ( $\text{km}^2$ )	Wisconsin dry area ( $\text{km}^2$ )
Argentina	2,776,899	—	638,686 23%	1,166,298 42%	360,997 13%	2,165,980 78%	c.a. 4,000,000 (3)
Bolivia	1,098,584	—	109,857 10%	164,788 15%	142,815 13%	417,461 38%	100,000
Brazil	8,512,001	—	—	425,599 5%	425,599 5%	851,198 10%	5,950,000
Chile	756,948	90,831 12%	113,543 15%	52,986 7%	136,249 18%	393,612 52%	100,000
Colombia	1,138,918	—	5,695 0.5%	11,388 1%	79,725 7%	96,809 8.5%	50,000
Ecuador	283,444	—	8,508 3%	14,177 5%	17,013 6%	39,699 14%	20,000
Paraguay	406,754	—	—	59,946 14%	130,160 32%	187,106 46%	400,000
Perú	1,285,220	6,426 0.5%	6,426 0.5%	72,112 6%	269,896 21%	359,862 28%	200,000
Venezuela	912,052	—	9,119 1%	18,241 2%	9,119 1%	36,482 4%	650,000
Antilles	961	—	932 97%	10 1%	10 1%	953 99%	961
	17,171,781	97,257	892,766	1,985,545	1,571,583	4,549,162 27%	11,470,961 67%

(3) This area include the extent of emerged shelf in the SW Atlantic. The contraction of the dry area in Chile, Peru, Bolivia, Ecuador and Colombia is due to the predominance effect of the Andean Glaciation. The total dry area during the Late Pleistocene (ca. 11,470,961  $\text{km}^2$ ) does not include the "biological deserts" imposed by glaciers and mountain barriers (ca. 1,200,000  $\text{km}^2$ ) as well as the extense shelf deserts between La Plata Basin and Orinoco Delta. The Venezuelan Wisconsin dry area incorporated the emerged shelf of the Gulf of Venezuela. The Brazilian dry area in the same period was calculated on the base of different cartographical sources, especially the vegetation map of HUECK & SEIBERT (1972) and AB'SABER (1977). The data about the present dry areas partly stem from J. ROGERS (1981. Arid Lands Newsletter 14). The importance of long interannual droughts for the fauna is understood here as the availability of water (plant formations commonly resist longer).



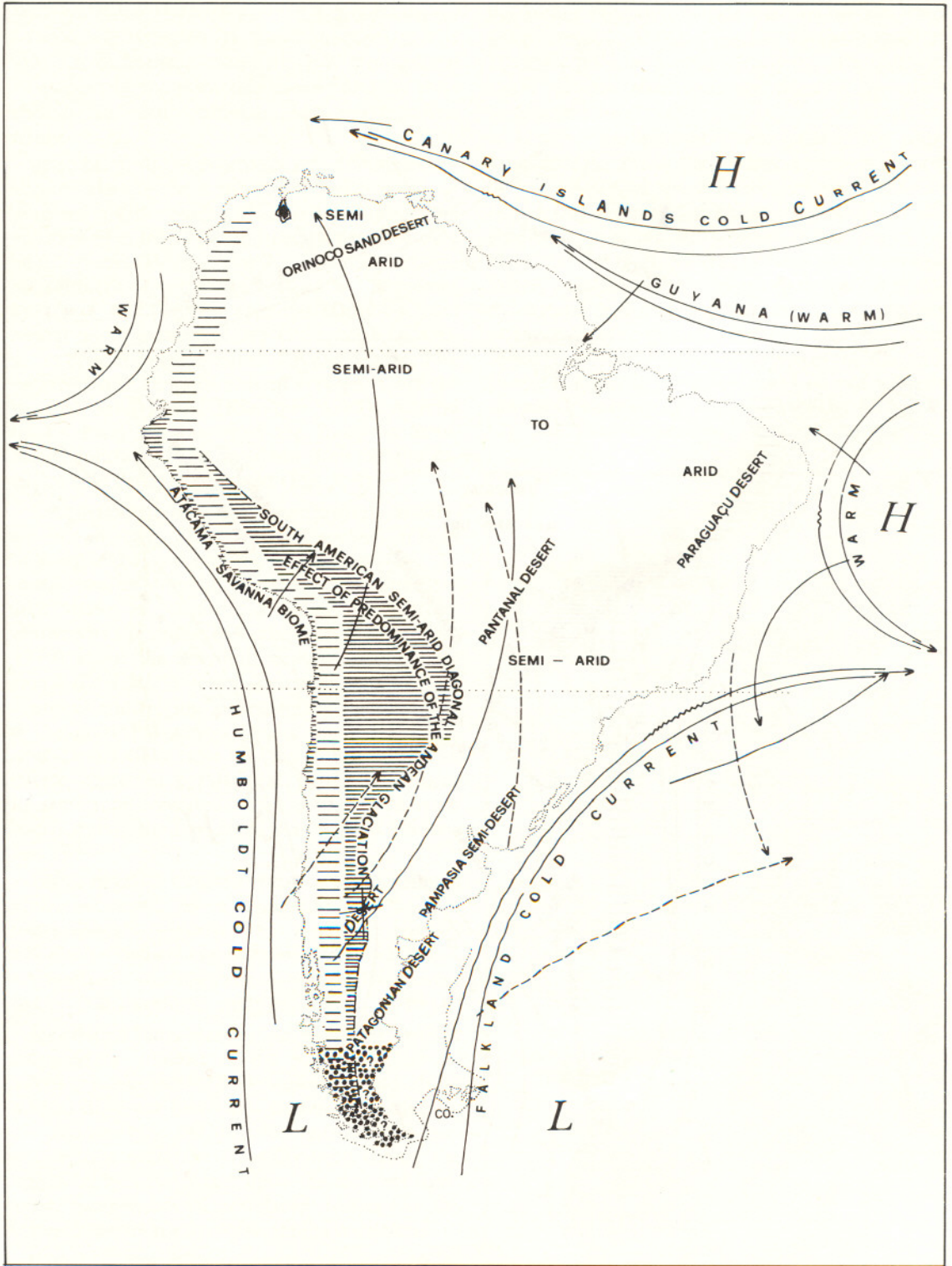


Fig. 4: The paleoclimatic model of South America during the Late Pleistocene (12,000-18,000 y.B.P.) shows the regional division of climatic zones and the most important marine currents around the continent. The dotted lines indicate the dominant winds in January, the continuous lines in July (according to Damuth & Fairbridge 1970). The Andean paleoclimates (Semiarid Diagonal of South America incl. the Atacama Savanna Biome) as well as the data for the tropical, subtropical and cold deserts during the full-glacial (Pleniglacial Desertization) are original. Geodata for the Pantanal Desert stem from Klammer (1982). Paleoeological data do not support a desert (x) in the Andean piedmont of Patagonia, the existence of a Patagonia Ice-Cap (?) remains in study.



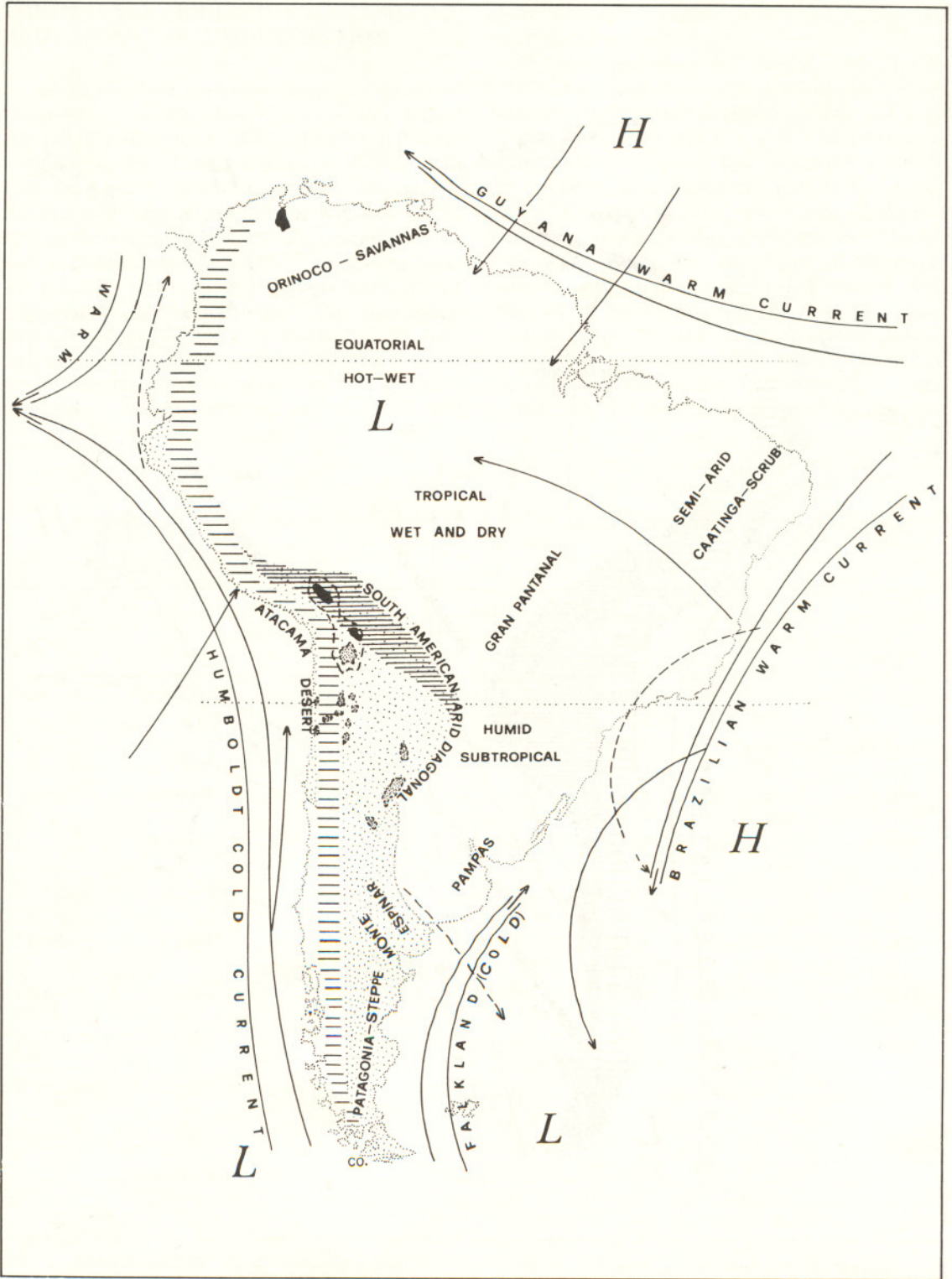


Fig. 5: The Climatic model of South America during the Holocene (since 10,000 y.B.P.) shows the present regional division of climatic zones and the most important marine currents around the continent. The dotted lines indicate the dominant winds in January, the continuous lines in July (according to Damuth & Fairbridge 1970). The Andean climatic context (Arid Diagonal of South America incl. Atacama Desert) as well as the presentecological arrangement of the Late Pleistocene deserts is original and show the climatic amelioration (Postglacial Savannization) in western South America. This model suggests the young age of the Arid Diagonal (ca. 10,000 y.B.P.). According to Ochsenius 1974, 1981, 1982).



1970; Ab'Saber 1977; cf. Fig. 1, 2, 3. See discussion in Ochsnius 1979, 1981). From another point of view this dichotomy shows the E-W geographical component of the extinction process and the close relation between zoogeography and climatic change.

In addition to the enormous area dominated by the dry climates and the local development of forest refugia, the paleoecological data support the evolution of at least four continental deserts during the full-glacial. The first two were situated northern and southern of the Amazon Basin in the present regions of the Orinoco savannas (Orinoco Sand Desert) and Caatinga scrubs (Paraguaçu Desert). In the present tropical zone of Brazil occupied by the wet Great Pantanal existed very probably the Pantanal Sand Desert (Klammer 1982). Around the La Plata Basin evolved the Pampasia Semi-Desert, followed in its southern limit by the extensive cold Patagonian Desert (Fig. 3, 4).

Concurrent with this continental aridity, marginal deserts (Shelf Deserts) evolved around the continent favored by the low sea level (Fig. 3). Former studies about arkosic sands in the Brazilian Shelf made by Damuth & Fairbridge (1970), followed by the studies of Kolla, Biscaye & Handley (1979) about the distribution patterns of quartz grain in the Atlantic Ocean, support this continental record of aridity (Fig. 6), especially the existence of the great Patagonian Desert and the Orinoco Sand Desert. The area of the South American deserts, suggested in this work, is tentative but at the same time consistent with the data for African deserts during the full-glacial (Sarnthein & Diester-Hass 1977).

Other negative environments for the megafauna were constituted by a discontinuous "belt of desert-islands" originated by mountain barriers and glaciers which reached an area of ca.  $1.2 \times 10^6$  km<sup>2</sup> (this area does not include the Patagonian Ice-Cap that remains in study).

Megafauna biogeography, taxonomical profiles and geodata of most of the paleontological localities—more than 2,500 individual findings in ca. 500 different biotopes—support in great part this paleoecology and its paleoclimatological context. Furthermore the areas occupied during the full-glacial by deserts lack up to the moment fossil fauna, compared with postglacial deserts like the Atacama, where the fossil megafauna is well-known.

With the climatic amelioration since the Holocene in western South America, these deserts (including here the Pampasia Semi-Desert) were replaced by the Atacama Desert, the cold high-desert of the dry Puna, the western dry Chaco, the Monte, the Espinal, and the cold steppe of Fuego-Patagonia. This aridity-drift supports in great part

the author's hypothesis that the present Arid Diagonal of South America reaches not much beyond 10,000 y.B.P.; with other words the principal arid zones of the Neotropic are modern in paleoecological terms.

Finally, the present study contributes with valuable data about the paleoecological evolution of the aridity in the Neotropic, amplifying and completing Damuth/Fairbridge's model about the generative systems of aridity during the Late Pleistocene (Fig. 4, 5). At the same time it recommends a revision of Ab'Saber's map (1977) about the natural landscapes during the Last Glaciation in the following points: (1) The author's studies about the paleoecological evolution of the Atacama Desert (including the megafauna) do not support the pre-Quaternary age attributed to it by Ab'Saber. (2) The Late Pleistocene areal of the Cerrado

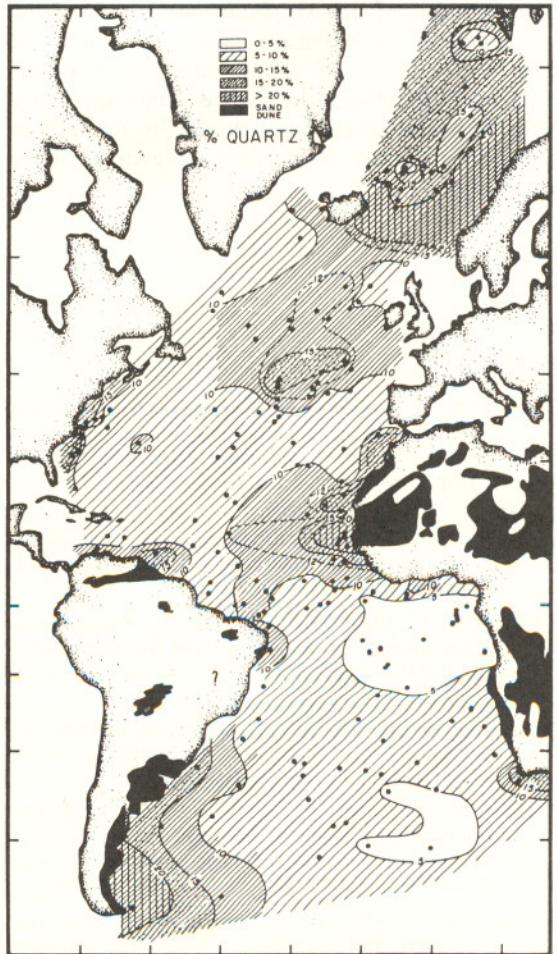


Fig. 6: Late Pleistocene distribution (18,000 y.B.P.) of weight percent quartz (carbonate-free) in the sediments of the Atlantic Ocean as indicator of continental aridity (according to Kolla, Biscaye & Handley 1979). Late Pleistocene sand deserts of Africa (according to Sarnthein & Diester-Hass 1977). Late Pleistocene desert of South America (according to Ochsnius 1982).



would have been much more extended than that of the Caatinga, as is demonstrated by the grazer fauna recovered in the actual rain forest. (3) The areal of the Caatinga scrubs would have been more restricted and the desert environments more spread (Paraguçu Desert). (4) The large Orinoco Sand Desert is not consistent with a landscape of wet savannas. (5) Undetermined areas in Ab'Saber's map, such as the Peri-Caribbean Arid Belt, suggest a ecoconstancy of the present thorn and bush savannas where long droughts have been more frequent. (6) The peri-Andean fauna between Chaco and Patagonia indicates less arid environments than at the present (western component of the former semiarid Diagonal of South America). (7) The map nomenclature for the former Great Pantanal's ecological conditions remains imprecise. (8) Desert conditions in the extense tableland of Peru and Bolivia are not consistent with the trophic requirements of the Altiplano megafauna and the evolution of an extensive lacustrine system of Late Pleistocene age. These and many others interrogatives about the native landscapes (too long to be discussed here) should be resolved in the future by the Quaternary research in South America.

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