PLEISTOCENE MAMMALS AND PALEOECOLOGY OF THE WESTERN AMAZON

By

ALCEU RANCY

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To Cleusa, Bianca, Tiago, Thomas, and
Nono Saul (Pistolin de Oro).

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KEY TO ABBREVIATIONS

AMNH	American Museum of Natural History, New York
B.P.	Before Present
CNPq	Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil
DNPM	Departamento Nacional da Produção Mineral, Brazil
FZB	Fundação Zoobotanica do Rio Grande do Sul, Porto Alegre, Brazil
ITCZ	Intertropical Convergence Zone
LACM	Los Angeles County Museum of Natural History, Los Angeles, California
LPP	Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Brazil
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MLP	Museo de La Plata, La Plata, Argentina
NALMA	North American Land Mammal Ages
NSF	National Science Foundation, United States
PUC	Pontifícia Universidade Católica de Minas Gerais, Brazil
SALMA	South American Land Mammal Ages
UF	Florida Museum of Natural History, Gainesville
UFAC	Universidade Federal do Acre, Brazil
UFMG	Universidade Federal de Minas Gerais, Brazil
UFPA	Universidade Federal do Pará, Brazil

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

PLEISTOCENE MAMMALS AND PALEOECOLOGY OF THE WESTERN AMAZON

By

Alceu Rancy

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Chair: John F. Eisenberg
Major Department: Forest Resources and Conservation
(Wildlife and Range Sciences)

In recent years, the western Amazon has become the focus of intense scientific interest because of its high biodiversity. During the last two decades, the hypothesized Pleistocene Forest Refugia concept was developed with several of the refugia provisionally located within the western Amazon. This dissertation deals mainly with the Pleistocene mammalian fauna of the western Amazon and its important contribution to the understanding of Amazon biotic history.

An overview is presented of the fundamental environmental factors, including geology, climate, paleoclimate, Pleistocene Refugia, and savanna, that operate within the present rain forest of the region. The history of research on Cenozoic vertebrate faunas and their paleoenvironment is also discussed with a focus on Pleistocene mammals in the western Amazon.

Each major group of Pleistocene mammals from the western Amazon is described, using an ecological perspective, and is compared with members of present-day mammalian communities.

The Pleistocene mammals suggest a complex environmental mosaic in which an open (savanna-like) habitat predominates. Several Pleistocene savanna sites, as interpreted from the mammalian evidence, fall in areas proposed as Pleistocene Forest Refugia.

The last mammal megafauna extinction supposedly occurred at the end of the Pleistocene (approximately 10,000 years Before Present {B.P.}) and provides an approximate time frame for the expansion of the rain forest which now dominates the western Amazon.

The taxa that became extinct were essentially grazers, or animals of predominantly savanna habitat, including *Haplomastodon*, *Pampatherium*, *Toxodon*, *Eremotherium*,

Palaeolama and Mixotoxodon. The survivors are forest mammals, or animals broadly adapted to both forest and savanna habitats.

CHAPTER 1

INTRODUCTION

Statement of Purpose

The rich recent biota of the Amazon region has fascinated scientists and explorers, such as Humboldt, la Condamine, Darwin, Wallace, and Bates, over the centuries (Caufield, 1984; Smith, 1990).

Most early explanations of Amazonian diversity noted the essential feature of stability through a vast period of time. There was no doubt that the hylean forests were "the primeval forests of the equatorial zone" and that "every form of vegetation has become alike adapted to its genial heat and ample moisture, which has probably changed little ever throughout geological periods" (Wallace, 1878:65-66). Also "the paleoecological pedigree of tropical forests has been dominated, in the main, by the phenomenon of environmental stability. With only occasional breaks, there have been millions upon millions of years of ceaseless warmth and moisture; continuity unmatched" (Myers, 1984:79-80).

The past decade has produced a fundamental revision in the paradigm of Amazonian history. It is widely accepted that radical environmental changes transformed the nature of the region during each of the dozen glacial intervals of the Pleistocene. The vast multistrata evergreen forests shrunk into minor refugia, taking with them all obligatory forest adapted taxa. The source of modern diversity is not stability, but rather changeability. And the most important habitat is not rain forest alone, but rather the savanna/forest mosaic (Whitmore & Prance, 1987).

The two purposes of this dissertation are 1) to place on record the late Pleistocene mammals from the western Amazon and 2) to bring this evidence to bear on the history of the Amazon biota. In this introductory chapter I will review the current status of hypotheses about Amazon history. The fossil evidence is presented in Chapter 2. In Chapter 3, the geological background is provided and in Chapter 4, the Pleistocene fauna is described. In Chapter 5, I indicate the ecological significance of the Pleistocene fauna by comparison with modern mammalian faunas. In the final chapter I discuss the ramifications of the new evidence and provide recommendations for further research on Amazon biota history.

To assemble the Pleistocene fossil record of the western Amazon, I used information recorded for other collections and I conducted primary collecting expeditions. I examined relevant fossils stored at the Museu Nacional

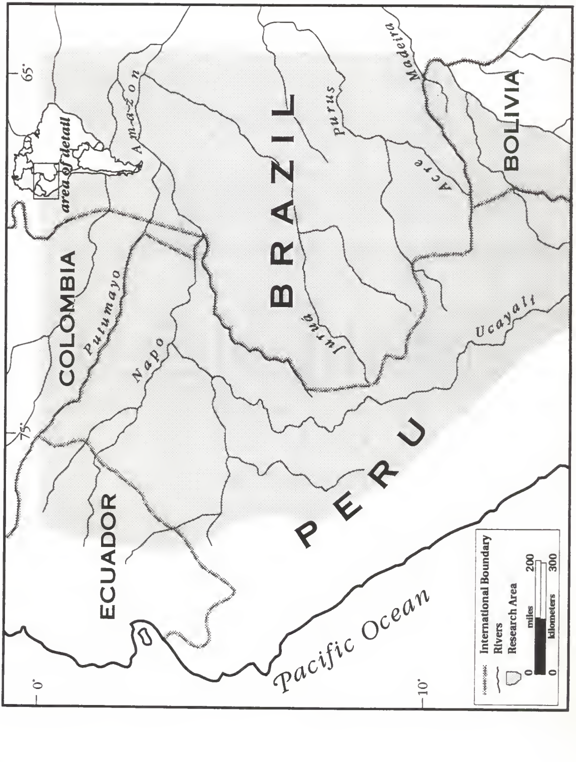
(Rio de Janeiro), Museu Paraense Emilio Goeldi (Belém), American Museum of Natural History (New York), and Los Angeles County Museum of Natural History (Los Angeles). Of particular importance are the collections of the Laboratório de Pesquisas Paleontológicas of the Universidade Federal do Acre (Rio Branco), which were gathered during the past ten years on our seasonal field trips along the upper Juruá River, the upper Acre River, and the Transamazon road in Brazil, and along the Beni River and Madre de Dios River in Bolivia.

Study Area

The western Amazon, as defined here, is bounded by the Caquetá-Japurá River on the north, by the Madeira and Beni rivers on the south, by the Andean chain to the west and by an imaginary line linking the confluence of the Caquetá-Japurá/Solimões rivers to the confluence of the Abunã/Madeira rivers along the east, where this boundary approximates the 65° W meridian. This area includes all of the Peruvian and Ecuadorian Amazon, parts of the Bolivian and Colombian Amazon, and the state of Acre and the western portion of the state of Amazonas in Brazil (Figure 1).

The geography of this region is best understood by reference to the seven great rivers that traverse it on their way to the Amazon River. Five major rivers within

Fig. 1 - General map of the western Amazon.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Putumayo
Napo
Juruá
Purus
Madeira
Acre
Ucayali
International Boundary
Rivers
Research Area
0 miles 200
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this region carry sediments directly from the Andes--the Ucayali, Marañon, Napo, Madre de Dios, and the Putumayo-Içá--. Two major rivers of this region whose headwaters are not in the Andes are the Purus and the Juruá, also called the twin rivers. "Swollen with rich Andean sediment, these rivers--the Putumayo, along with the Juruá and the Purus to the south--make and remake their floodplain with each rainy season, meandering interminably as they open and shut new canals, reinventing the landscape" (Hecht & Cockburn, 1989:20). Even though the Juruá and the Purus do not begin in the Andes chain, they carry white waters, full of sediments very much like the rivers with true Andean sources. The westernmost portion of Brazil is practically surrounded by the Madre de Dios, curving southeast from its origin, and the Ucayali flowing north from its headwaters, thereby cutting off the Juruá and Purus rivers from extending their headwaters into the Andes. The strip of land that separates the headwaters of the Madre de Dios, Purus and Ucayali in the Peruvian Amazon, approximately at 11° S and 72° W, is called the Isthmus of Fitzcarrald. That name was given in honor of a famous "caucho"[1] baron of German origin, who dominated the area at the beginning of this century during the rubber boom.

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[1] Common name for Castilla ulei, one of several rubber trees.

Geology

The geology and stratigraphy of this immense area are not well known because it is largely covered by multistrata equatorial rain forest. Within the western Amazon as delimited above, the following six geological basins[2] are recognized: Acre (Brazil), Madre de Dios (Bolivia/Peru), Ucayali (Peru), Pastaza-Marañon (Peru), Oriente (Ecuador) and Caquetá-Putumayo (Colombia) (Räsänen et al., 1987) (Figure 2). Sedimentary units filling these several geological basins, which spread through five countries (Bolivia, Brazil, Peru, Ecuador and Colombia), have been given a profusion of formational names, with age assignments extending from the Cretaceous through the Holocene (Frailey et al., 1988). A huge effort to understand the geology and geomorphology of the Brazilian portion of the area was made by Radambrasil (1976, 1977). There have been important new contributions by several authors: The latest geological, stratigraphical, and biogeographical study on the area (Frailey et al., 1988) incorporates my own field observations from the Madre de Dios River (Bolivia) in the south to the Juruá River (Brazil) in the north.

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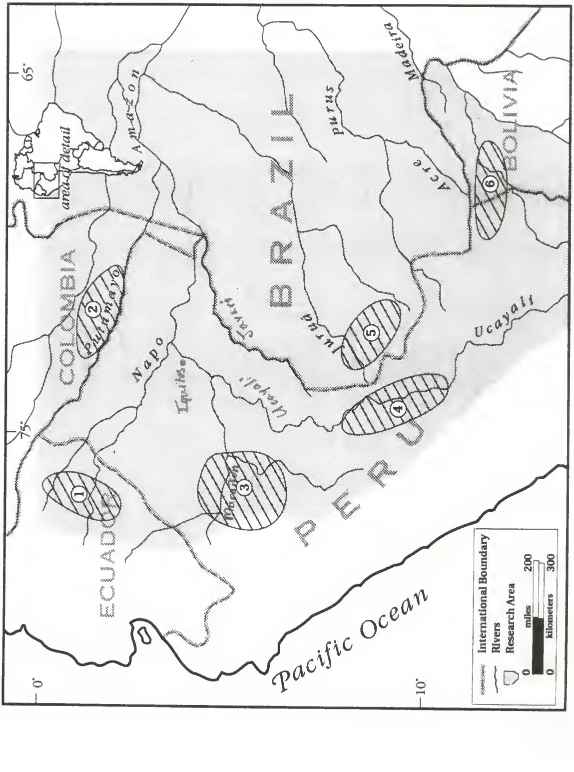
[2] Basins are used here in the geological sense to indicate large structural depressions that tend to accumulate relatively thick sedimentary deposits over long portions of the Cretaceous Period and the Cenozoic Era.

Fig. 2 - Geological basins: 1- Oriente; 2- Caqueta- Putumayo; 3-Pastaza-Maranon; 4- Ucayali; 5- Acre; 6- Madre de Dios (modified after Räsänen et al., 1987).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With the present unresolved status of geological nomenclature in this area it is preferable to abstain from designating any formal formational names. As shown by Campbell et al. (1985), two major sets of late Cenozoic sediments predominate in the region. These are the Miocene Red Beds, several hundred meters thick, and an unconformable overlying set of sediments of Quaternary age that are seldom more than 30 m thick. The Quaternary sediments are composed primarily of clay, with intercalations of silt, fine sand, gypsum veins, and carbonate concretions (Frailey et al., 1988; Kromberg et al., 1989; Radambrasil, 1976, 1977). This Quaternary formation, known as the Solimões formation in Brazil, extends over the entire area from northern Bolivia to southern Colombia. It thus covers more than 1,000,000 sq km (Santos, 1976). Its genesis is clearly traceable to deposition of clastic sediments derived from the active uplift of the Andes.

The history of deposition in the western Amazon was surely complex, just as the structural history of the Andes is complex. For example, Jordan et al. (1983) show that various regions of the Andes have different structural regimes depending upon the subduction geometry of the four major segments of the Nazca plate from 2° S to nearby 40° S. Likewise, the detailed depositional history of each of the six basins in the western Amazon will have to be worked out separately before any broader regional patterns can be securely deduced.

One idea not so novel that has been continually discussed (Haffer, 1981; Irion, 1984; Klammer, 1984; Meggers, 1973; Roberts, 1983; Sioli, 1973), involves one of the most intriguing hypotheses about the Quaternary physiography of the western Amazon region. Lago Amazonas, a concept revived by Frailey et al. (1988), has been described as a huge lake covering a large area of the western Amazon during Pleistocene times, with an outlet shifting alternately from the Orinoco delta to the mouth of the Amazonas, depending on tectonic activity times.

Climate

The climate of the western Amazon is strongly related to the latitudinal position of the area, 0° to 12° S. Athough the region is closer to the Pacific than to the Atlantic Ocean, it is not excluded from the effects of the former because of the Andes Mountains; instead, it is directly influenced by the humid easterly trade winds of the more distant Atlantic Ocean. Salati et al. (1978) provide an excellent account of the origin and distribution of rainfall in the Amazon.

Over most of the western Amazon the rainy season is distributed between October and April, with the remaining months of the year being the dry season. Along the eastern border of the Andes Mountains the precipitation is higher than the regional average because of adiabatic effects, which cause a continuous rain shadow, with precipitation in some places above 5,000 mm per year.

Meteorological observations in Cruzeiro do Sul (7° 38'S-72° 40'W) on the Juruá River for the period of 1931-1960 can be taken as a typical example of the precipitation for the area. From October to April the rainfall is about 240 mm each month, decreasing to 140 mm in May, 100 mm in June, and 45 mm in July, then increasing to 80 mm in August and 140 mm in September (Salati, 1985). The seasonal distribution of the rain is related to the displacement of the Intertropical Convergence Zone (ITCZ).

The average monthly temperature for the rainy season, October to April, is around 26° C, decreasing 3° C or 4° C during the dry season.

Another important aspect of the climate in the area is the so-called "friagem", or "surazo", in Portuguese or Spanish, respectively, a cold front, which moves northward from southern South America. Such climatic episodes occur especially during the months of May, June, and July, corresponding to the southern hemispheric winter, when the temperature can drop more than 15° C in a few hours and last for three to five days (Molion, 1987). The development and advancement of these cold fronts have been registered by satellite observations and field measurements of the wind and temperature (Brinkmann et al. 1971; Parmenter, 1976).

> Every year several of these sweep up the continent, sometimes affecting abrupt and drastic drops in temperature as far north as Iquitos (lat. 3° S). Such frontal systems can arrive any time from May until early September, but are most frequent and pronounced in June and July. The most severe of these storms in our experience came in July 1975, when a low of 8° (46° F) was reached for three nights in succession. . . . Of course, this was an extraordinary, once-in-a-century event. In a more typical year, the minimum temperature is in the range of 14-16° (57-61° F). (Terborgh, 1983:16-17)

The "friagem" related by Terborgh (1983), at the Estación Biológica de Cocha Cashu-Peru, was the same one and strong enough to be registered and accompanied by satellite imagery, as described by Parmenter (1976). An event of such magnitude, occurring several times every year, must be taken into consideration, to understand both the past and the extant biota of the western Amazon. It is clear, that if cold fronts now place severe restraints on the biota of the western Amazon with ecological effects not yet well studied, then the effects of even stronger episodes during glacial intervals of the Quaternary were of great significance. Anecdotal cases are of common knowledge in the western

Amazon regarding the death of large quantities of fish in oxbow lakes, supposedly suffocated by lack of oxygen, due to the inversion of water layers, related to the drop of the temperature on the surface, during cold fronts. Goulding (1990:130-131), during his studies in the central Amazon, reported that, following a friagem "huge numbers of fish and shrimp die and affected floodplain lakes turn into a fetid graveyard."

Paleoclimate in the Amazon

"The large changes in the earth's climate during the last 18,000 years have altered the vegetation, ice volume, and sea-surface conditions over most of the globe. The nature and timing of these changes have posed many puzzles to scientists studying Quaternary climate" (Cohmap, 1988:1043). As demonstrated by Salati (1985), the rainfall in the Amazon is linked to the easterly winds and moisture originating from the Atlantic Ocean. A drop in average sea surface temperature during the last glacial period of the Pleistocene of about 2.3° C (Climap, 1976) caused less evaporation, and presumably also a concomitant decrease in the level of precipitation, with the consequence that vegetation and hydrology all over the Amazon became more xeric. According to Ab'Saber (1977), stronger cold ocean currents along both coasts of South America--"Corrente

Falkland" along the Atlantic eastern border and "Corrente do Peru" along the Pacific western margin--fundamentally altered the Amazon landscape between 13,000 to 18,000 Before Present (B.P.), with the conspicuous dominance of savanna and cerrado intermingled with gallery forest along the principal rivers of the area.

Studying evidence of Pleistocene glaciers and ice caps in the Peruvian Andes, Mercer and Palacios (1977) concluded that the last glaciation in equatorial South America culminated between 28,000 and 14,000 B.P.. The area under study is situated on the border of the Amazon Basin, suggesting that, during glacial times, the drop in temperature in eastern Peru was about 6° C.

Haffer (1969) and Vuilleumier (1971), reconstructed the South American paleogeography with a major interglacial marine transgression, which produced an enormous lake along the axis of the Amazon River extending almost to the western Amazon region. These advances of the Atlantic Ocean over the Amazon are in accord with the reconstruction of eustatic sea level during the Pleistocene (Savin & Douglas, 1985). Haffer (1981:379) pointed out that "portions of the lowlands were flooded during the height of the interglacial periods, when sea level was approximately 50 to 60 m higher than at present." If this lake was present during each interglacial, then it certainly affected the distribution and evolution of the biota, at least over the central Amazon.

Liu and Colinvaux (1985) demonstrated a depression in the temperature of about 4.5° C, between 33,000 B.P. and 26,000 B.P., during the last glacial. They used evidence from pollen and megafossils of Podocarpus which suggested a disruption of the rain forest of the Napo refuge in the lowland of Ecuador.

Pollen data from studies of lake sediments in the Amazon region, especially from Rondônia (Brazil), suggest "climatic changes during several intervals of the Late Cenozoic (Quaternary)" (Absy, 1985:80), when open vegetation, mainly grasses, covered an area today dominated by tropical rain forest.

Pleistocene Refugia

During the last two decades, the idea of Pleistocene Refugia in the Amazon has attracted the attention of scientists all over the world, especially as a possible explanation of the high biodiversity in the Amazon region. In his seminal paper on aspects of neotropical avifauna, Haffer (1969) proposed the Pleistocene Forest Refugia Model (PFRM) for the Amazon basin (Haffer, 1974). Very soon systematists studying distribution of other taxa recognized similar patterns, e.g. for lizards (Vanzolini & Williams, 1970), woody angiosperms (Prance, 1973, 1982) and butterflies (Brown, 1982).

The concept of forest refugia is linked to the glaciation events that occurred during the Pleistocene epoch, i.e. during the last 1.6 million years. It is possible that each of about two dozen glacial intervals produced a similar pattern of expanded savanna habitats and forest refugia. On the other hand, the single most accessible case, amenable to detailed, multidisciplinary study in many locations, is the last glacial interval (i.e. the Würm-Wisconsin glaciation).

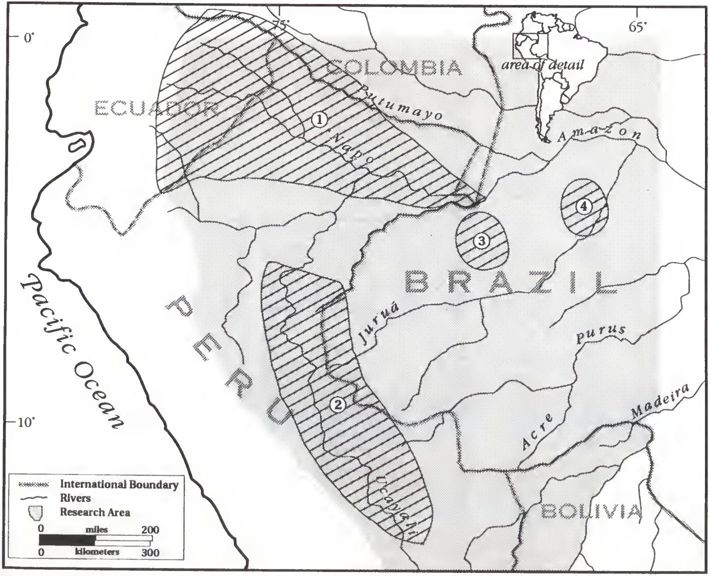
The Pleistocene is distinguished by recurrent glaciation well defined in the northern hemisphere by repeated growths of polar ice caps, which in turn cause a sea-level regression. In areas of tropical forest, ice ages are now believed to produce decreased rainfall, expansion of savanna woodland, and increased fire frequency. At the end of the final glacial period, at about 10,000 years B.P., megafaunal extinctions occurred on most continents although the effects were quite varied in their detail (Owen-Smith, 1988, Fig. 15.1).

The PFRM explains the survival during the glacial ages of the rich tropical fauna and flora in restricted refuge areas, where the climate remained sufficiently humid to support forest biota. Several refugia were proposed within the area defined here as the western Amazon; they are shown in Figure 3. This study focuses special attention on the Napo and the East Peruvian Pleistocene Forest Refugium proposed by Haffer (1969) and Prance (1973).

The idea of PFRM has received strong challenges by several paleoecologists, especially by the group led by P. A. Colinvaux. Their principal arguments are related to evidence from the humid lowland of eastern Ecuador that suggests a temperature decrease of 3° C to 6° C at sea level during glacial times; this decrease is thought to be enough to disrupt the effectiveness of the proposed Napo forest refugium during the Pleistocene. They propose that glacial intervals were characterized not by aridity but only by cooling, and that lowland plant assemblages maintained continuity with the downward retreat of some higher elevation species. Other movements of the forest biota were individualistic with most species surviving along the edges of the rivers (Bush & Colinvaux, 1988; Colinvaux, 1987, 1989; Colinvaux et al., 1985; Liu & Colinvaux, 1985).

Recently Nelson et al. (1990), studying herbarium specimens collected in the Brazilian Amazon, suggested that some proposed centers of endemism and forest refugia may be explained by sampling artefacts.

Fig. 3 - Pleistocene Forest Refugia: 1-River Napo; 2- Eastern Peru; 3- Olivenca; 4- Tefé (Prance, 1973).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Savanna Corridors

The distribution of the extant savanna in South America consists of disjunct habitats, situated to the north, to the south, and within the Amazon rain forest. In times of glacial advance, however, these habitats may have been united by the shrinkage of the forest (Ab'Saber, 1977).

In the paleoamazon context I consider savanna an open-country formation with grass, shrub, and sparse trees.

> In the scientific literature the word savanna has been acquiring an ever broader meaning, to the point that it is used, both in the Americas and in other parts of the world, for any formation that is not a forest or semidesert. (Sarmiento, 1984:6)

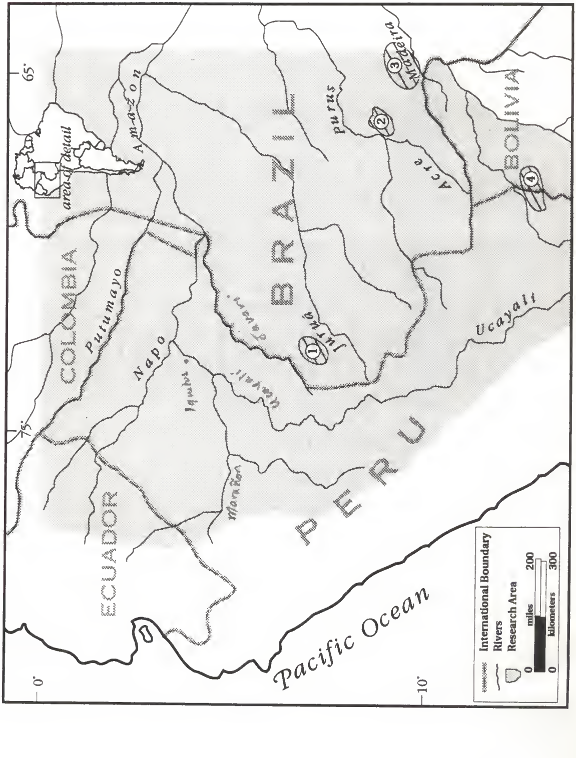
Webb (1978), in the classic study of the Great American Biotic Interchange (GABI), suggested not only a high road or Andean route for savanna biota to extend through South America but also a low road across the Amazon, following the diagonal of open formations of Vanzolini (1974), and thereby linking the northern savannas of Venezuela across the Amazon to the savannas (cerrado) of central Brazil. These corridors provided a north-south route that permitted the dispersal of savanna or open-country biota. In the western Amazon, a savanna corridor can be postulated based on the present existence of the Rio Moa Savanna (Radambrasil, 1977), the Formações Pioneiras de Boca do Acre (Radambrasil, 1976), the

Rio Heath Savanna (Denevan, 1980), and the Campos do Puciarí (Figure 4). Today these savannas are surrounded by tropical rain forest; so the possibility of continuous savanna corridors depends upon the expansion of open formations as the typical feature of the Amazon basin during glacial intervals of the Pleistocene.

Savanna Islands in the Amazon Rain Forest

According to Prance (1978), the forest was reduced to island-like refugia during extreme dry periods. When the rain forest of Amazonia returned to its present-day distribution, the savanna-grassland areas contracted such that those within Amazonia are presently islands. The expanse of the last "savanna maximum" at about 18,000 B.P., during the Würm-Wisconsin glacial advance, may be conservatively indicated by the present relictual distributions of savanna-grassland habitat (Webb, 1978). Prance (1978) noted that the Amazonian savannas are not particularly rich in endemic plant species, a feature which indicated to him that they had been separated only recently. In addition, living species of mammals have populations in northern savanna/grassland areas of Venezuela and Colombia and in the south in Brazil and Bolivia, but no populations in between. Classical examples are the marsupials, *Lutreolina crassicaudata* and *Didelphis albiventris*, present

Fig. 4 - Some of the extant savannas in the western Amazon: 1-Rio Moa Savanna; 2- Formacões Pioneiras de Boca do Acre; 3- Campos de Puciarí; 4- Rio Heath Savanna.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in the open country of southern and northern South America, but absent from the rain forest in between, with a gap of more than 2,000 km. Such disjunct distributions suggest that open-country species were continuously connected during the last glacial epoch when savannas were widespread (Eisenberg, 1989). The same probably should be said about the disjunct distribution of *Euphractus sexcinctus*. This species occurs south of the Amazon in the cerrado, caatinga, chaco, pampas, and gallery forests (Emmons, 1990) and reappears in a cluster of savannas along the border of Surinam and Brazil (Redford & Wetzel, 1985); there is an enormous tract of rain forest in between, although "more data are needed on its distribution in the eastern Amazon basin" (Wetzel, 1985:25). Eisenberg (1989) also observed the same disjunct distribution of *Calomys* and *Cavia*, north and south of the Amazon basin, in areas of open landscape (llanos, cerrado, and campo). Such case studies of modern species distributions are at least strongly suggestive of a radically different distribution of biotopes in the late Pleistocene of tropical South America.

CHAPTER 2
FOSSIL MAMMAL EVIDENCE

For over a century paleontologists and geologists have studied vertebrate fossils from the western Amazon. Chandless (1866) appears to be the first one who made reference to fossil vertebrates from that area of South America. The same fossils collected by Chandless were erroneously referred to as late Cretaceous by Louis Agassiz (1868:409):

> Mr. William Chandless, on his return from a late journey on the Rio Purus, presented me with a series of fossil remains of the highest interest, and undoubtedly belonging to the Cretaceous Period. They were collected by himself on the Rio Aquiry, an affluent of the Rio Purus. Most of them were found in place between the tenth and eleventh degrees of south latitude, and the sixty-seventh and sixty-ninth degrees of west longitude from Greenwich, in localities varying from four hundred and thirty to six hundred and fifty feet above sea-level. There are among them remains of Mosasaurus, and of fishes closely allied to those already represented by Faujas in his description of Maestricht, and characteristic, as is well known to geological students, of the most recent Cretaceous Period.

The Aquiry River mentioned by Agassiz and Chandless is now known as Acre River, and the location of the area is presently between the cities of Rio Branco and Brasiléia in the state of Acre. For more than 80 years, part of the western Amazon, in the state of Acre, was considered Cretaceous in age, based upon the information of Agassiz. Finally Price (1953) rejected this belief, showing that the fossils examined by Agassiz were in fact Miocene Alligatoridae. The Laboratório de Pesquisas Paleontológicas of the Universidade Federal do Acre houses a magnificent collection of huge Crocodylia, which includes a Purussaurus skull that seems to be one of the best and biggest known in the world, thereby confirming the ideas expressed by Price (1953).

Sporadic references to fossils from the western Amazon continued to be published through the turn of the century. Most studies stemmed from material collected during the rubber boom that sent businessmen from Europe and North America to the principal rivers of the area (Barbosa Rodrigues, 1892; Gervais, 1876, 1877; Gurich, 1912; Mook, 1921). At the same time, the Museu Nacional in Rio de Janeiro and the Museu Paraense Emilio Goeldi in Belém also began to receive material sent from the western Amazon by rubber barons and government servants. In Brazil and Argentina, some innovative papers were published by Goeldi (1906), Kraglievich (1930, 1931), Miranda Ribeiro (1938), and, Roxo (1921, 1937).

P. H. Fawcett, explorer of the Brazilian, Bolivian, and Peruvian Amazon during the years 1906-1907, working along the Acre River made reference to fossils in the upper river from Assis Brasil; also he made allusions to the presence of vertebrate fossils along the Igarapé Yaverija, which today serves as the border between Bolivia and Peru (Fawcett, 1909, 1911, 1953).

The first stratigraphical correlation between the western Amazon and the Tertiary of Argentina using vertebrate fossils was made by Patterson (1942). Based on the occurrence of Phoberomys bordasi (Dinomyidae) and Gryphodon peruvianus (Pyrotheriidae), he recognized deposits of Eocene (Mustersan) and Miocene (Huayquerian) ages.

Paula Couto (1944) produced the first of a series of papers about fossil mammals of the state of Acre, followed by a complete revision of the fossil mammals of Amazon and tentatively correlated them with other better known parts of South America, especially in Argentina (Paula Couto, 1956).

Special recognition should be given to the work of Franz Spillmann, who studied mammalian fossils from the Ucayali River region (Peru). He was the first to perceive a different continental environment in an area which is presently rain forest. Spillmann (1949:38) made the following observation:

> El estudio de los restos fósiles del Rio Utoquinea, tributario del Rio Ucayali en su margen derecha, nos ha suministrado conocimientos nuevos sobre la fauna terrestre y acuática del Terciario Superior de la cuenca Amazónica Peruana,

> permitiéndonos la reconstrucción de las condiciones biológicas de un campo viviente, que han predominado todavia en el Pleistoceno inferior en una región donde los vastos campos áridos de una estepa fueron reemplazados más tarde por extensas selvas tropicales con una fauna particular. Estas estepas a lo largo de la falda oriental de la actual Cordillera de los Andes, estuvieron por entonces conectadas hacia el Sur com las imensas pampas de Argentina y Bolívia, prolongándose hacia el Norte muchos centenares de kilómetros más.

A fundamental advance in the study of stratigraphy and paleontology of the western Amazon resulted from the 1956 expedition of G. G. Simpson and L. I. Price. They spent months traveling along the Juruá River and its affluents within the state of Acre. The large collection that they produced was shared between the Departamento Nacional da Produção Mineral (DNPM) in Rio de Janeiro and the American Museum of Natural History (AMNH) in New York (Price, 1957). Carlos de Paula Couto, following up his earlier effort, used these collections to publish a brilliant series of papers on the fossil mammals from the Cenozoic of Acre (Paula Couto, 1976b, 1978, 1981, 1982a, 1982b, 1983a, 1983b; Simpson & Paula Couto, 1981).

Recently, Projeto Radambrasil, using radar imagery covering the entire Brazilian Amazon, provided several volumes of information of special interest about the geology (including paleontology), geomorphology, pedology, and vegetation. The fossils collected by the Projeto Radambrasil were deposited at the DNPM in Rio de Janeiro and were not subjected to detailed study or publication. One of the most intriguing conclusions by the geomorphologists of the Radambrasil team was their recognition in the western Amazon of Pleistocene landforms characteristic of a dry climate an no vegetation cover.

> A esculturação das formas de relevo dissecado nos interflúvios ocorreu na passagem do Pleistoceno para o Holoceno, sob condições de clima agressivo seco e sem cobertura vegetal. (Radambrasil, 1976:149)

This conclusion was based on the form of relief in the area, which was thought to be impossible to develop under the present climatological condition, thereby suggesting that the transition from dry to humid took place rapidly, during the passage from the Pleistocene to the Holocene (Radambrasil, 1976, 1977).

During the last 10 years, the Los Angeles County Museum of Natural History has sent regular expeditions to the western Amazon, under the leadership of Dr. K. Campbell, to gather fossils and to study the geology and geomorphology of the area, particularly northern Bolivia, southeast Peru, and the southwestern part of the state of Acre in Brazil. The principal conclusions of Campbell and his coworkers are related to a possible catastrophic megaflood that drained the altiplano of Bolivia and Peru and disrupted the biota in the lowlands of the Bolivian Amazon and adjacent areas during the late Pleistocene (Campbell et al., 1985; Frailey, 1986). The data suggest that the present richness of the biota of the western Amazon is a temporary condition related to recent geological events, a situation of

> supersaturated disequilibrium, where species adapted to the unstable successional environment existing only a few millennia ago are now in competition with species invading from areas of long-term stability, or Pleistocene tropical forest refugia, on the perimeter of the lowlands. If so, a natural decline in species diversity in lowland Amazonia as equilibrium is achieved can be predicted, in accordance with the MacArthur-Wilson equilibrium model. (Campbell & Frailey, 1984:373)

Recently, two groups have been conducting geological research and producing geochemical analyses in the state of Acre and around the city of Boca do Acre on the Purus River in the state of Amazonas (Brazil). One party is sponsored by the Universidade Federal do Pará (Belém) and the other is a joint effort between the Universidade do Amazonas (Manaus) and Lakehead University (Canada), both with interesting findings about the origin, mineral composition, and age of the sediments. They also have found evidence of Pleistocene aridity in the region, based on the presence of evaporite, calcrete, and carbonate deposition (Benchimol et al., 1987; Costa, 1985; Costa & Costa, 1988; Costa et al., 1989; Kromberg et al., 1989).

In 1983, the Universidade Federal do Acre organized the Laboratório de Pesquisas Paleontológicas (LPP/UFAC) under my leadership. The major purpose of the LPP/UFAC is to collect and curate fossil vertebrates from the Amazon basin in order to understand its geological and paleontological history. During the past seven years our laboratory gathered an impressive collection of paleovertebrates (fishes, birds, reptiles and mammals) of the area, with more than 3,000 specimens catalogued, a significant contribution to the paleobiology of the Amazon. A group of researchers at the Universidade Federal do Acre is working in conjunction with other national and international institutions, including the Florida Museum of Natural History (Gainesville), Museu Paraense Emilio Goeldi (Belém), Museo de La Plata (Argentina), Los Angeles County Museum of Natural History (California), and the Museu de Ciências Naturais of the Fundação Zoobotânica do Rio Grande do Sul (Brazil), and have produced valuable information about the paleoecology of the region (Frailey et al., 1988; Mones & Toledo, 1989; Rancy & Villanueva, 1987; Richter, 1984, 1989; Souza Filho, 1987; Souza Filho & Villanueva, 1989; Villanueva et al., 1989; Villanueva & Rancy, 1987; Villanueva & Santos, 1989).

Among the misconceptions that have arisen during the past century regarding the vertebrate paleontology of the western Amazon, the most egregious concerns the presence of fossils in forested tropical areas. The following two examples will suffice to illustrate the point:

> The fossil record in present-day rain forest areas is notoriously poor because of the paucity of good rock exposures from which collections can be made. Furthermore, the organisms of most interest in this context--land animals, plants and insects--have very low fossilization potentials and thus there are poor geological records, even under good circumstances. (Raup, 1988:56)

Similarly, after a reconnaissance expedition to the western Amazon in 1973, Drs. Bryan Patterson and Paulo Emilio Vanzolini stated that

> it was a fascinating trip . . . but a disappointment from the paleontological standpoint. The (River) Purus in the state of Acre (Brazil) is not an area that can be recommended to the (vertebrate paleontology) profession. (Jenkins, 1974:12)

Clearly, the rapid growth of new collections from the Juruá, Purus, and Acre rivers, housed at the Universidade Federal do Acre, contradicts the reports of these distinguished visiting scientists. We now have the more optimistic view that there is ample evidence to write several major chapters about the prehistory of the Amazon basin.

CHAPTER 3
GEOLOGICAL BACKGROUND

As viewed by a geologist, the western Amazon is the realm of Cenozoic sediments, which were eroded from the Andes and extensively reworked by mature river systems. Geomorphically it can be classified into the white or muddy rivers, according to Sioli's designation (Junk & Furch, 1985). Although ancient Precambrian rocks constitute a major feature of the Amazon basement (Brazilian and Guiana shields) where the rivers are blackwater or clearwater, they are absent from those parts of the western Amazon.

Before the existence of the Atlantic Ocean and prior to the breakup of the supercontinent Gondwanaland, when Africa and South America separated at the end of the Cretaceous, the rivers of equatorial South America flowed into the Pacific Ocean, with an outlet in the present Gulf of Guayaquil (Harrington, 1962).

As South America continued to drift westward, and the Nazca plate was subducted beneath the South American plate along the western border of the continent, the Andes chain began to rise along the margin of the Pacific Ocean. The origin and evolution of the several sedimentary basins of the western Amazon are structurally linked to the eastern flank of the uplifting Andes (Miura, 1972).

The major uplift of the Andean chain is considered to have occurred since the Miocene. Haffer (1981) pointed out that the western Amazon continued to receive marine ingressions from the Pacific even as late as the middle Tertiary, when the Ecuadorian "sea portal" closed.

When the major rivers of the mid-Cenozoic lost their free outlet to the Pacific, the central region of South America formed the "largest lake and swamp ecosystem the planet Earth has ever known" (Goulding, 1990:12). Whether it was just a huge lake, or a series of temporal lakes, with brackish water and successional swamps and savannas, remains an open question. The geological basins of the western Amazon have some marine facies, like the Divisor and Ramon formations in the Acre basin, which are considered to be late Cretaceous to late Tertiary in age (Radambrasil, 1977). The presence of fossil dwarf gastropods in several localities of the western Amazon, from the so-called Pebas Formation (sometimes considered a synonym of Solimões Formation), suggests the prevalence of mixohaline environments during some past time of the middle Tertiary (Costa, 1981).

Vertebrate fossils, generally suggestive of savanna habitats, and ranging in age from the Eocene to the Late

Pleistocene, were described from the western Amazon. The presence of terrestrial vertebrates mixed with dolphin remains, Sirenia, and huge freshwater turtles and the presence of several genera of Crocodylidae (Rancy, 1983) led to a view of temporary environments, or savanna-like habitats, on the edges of brackish and/or freshwater lakes. The recent discovery of bullshark teeth (Carcharhinus), a euryhaline genus noted for becoming landlocked (e.g. Lake Nicaragua), indicates that in the late Miocene the upper Acre River area was still occupied by brackish waters.

Frailey et al. (1988) interpreted the huge expanse of fine-grained sediments in the state of Acre as evidence of a huge lake which they named "Lago Amazonas." Their chronological evidence, surprisingly, indicated that the lake existed from the late Pleistocene until the beginning of the Holocene. They reconciled this idea with that of late Pleistocene forest refugia by postulating that the latter were located on the edges of Lago Amazonas.

> The theories of forest refugia and Lago Amazonas are not incompatible. . . . Grassland could have been present during lake level oscillations, or, if the collapse of Lago Amazonas was as rapid as suggested by the recent age of sediments, normal ecological succession would have produced a vast grassland that then quickly succumbed to the climax forest. (Frailey et al. 1988:136)

Clearly the geology and stratigraphy of the western Amazon remain controversial, poorly known, and open to new approaches to unsolved problems. The vertebrate fossil assemblages and stratigraphy of the late Pleistocene Solimões Formation in Brazil are relatively well studied (e.g. Frailey, 1986; Paula Couto, 1956; Rancy, 1981; Simpson & Paula Couto, 1981) but the overall Cenozoic history of the region is a chapter waiting to be written.

The current status of Cenozoic fossil mammals from the western Amazon is summarized in Table 1, which was based on a complete review of the existing literature. Included among the nominal taxa are 2 marsupials, 24 edentates, 19 rodents, 19 notoungulates, 14 other ungulates, and 4 aquatic mammals.

In Table 2, I grouped these same Cenozoic mammals by age. These determinations were based on the literature, and especially by known ages of analogous taxa from Argentina. The mammals of the western Amazon thus range from the Eocene (? Mustersan) to the late Pleistocene (Lujanian).

Whereas the above tables were compiled based upon information in the literature, in Chapter 4, I describe Pleistocene material recently added to the collections of the Laboratório de Pesquisas Paleontológicas of the Universidade Federal do Acre (LPP/UFAC) and present a catalog of voucher specimens.

Table 1 - Faunal list of Cenozoic fossil mammals from the western Amazon

TAXA	REFERENCE	AGE
MARSUPIALIA		
Caenolestidae		
? *Abderites* Ameghino, 1887	(1)	Huayquerian
Family indeterminate	(2)	Huayquerian
EDENTATA - PILOSA		
Megalonychidae		
Megalonyx Harlan, 1825	(3)	Pleistocene
Pliomorphus Ameghino, 1885	(4)	Pliocene
Genus and species indeterminate	(2)	Huayquerian
Nothrotheriinae		
Genus indeterminate	(12)	? Pleistocene
Nothropus priscus Burmeister, 1882	(2)	Lujanian
Mylodontidae		
Acremylodon campbelli (Frailey, 1986) Mones, 1986	(2) (19)	Huayquerian
Glossotherium (*Oreomylodon*) *wegeneri* (Spillmann, 1931)	(3) (4) (12)	Pleistocene
Lestodon armatus Gervais,1855	(6)	Pleistocene
Scelidotherium Owen, 1840	(3) (6) (12)	Pleistocene
Mylodon Owen, 1840	(11)	Pleistocene
Megatheriidae		
Eremotherium Spillmann, 1948	(3) (4) (6) (23)	Lujanian
Ocnopus Reinhardt, 1875	(4)	Lujanian
EDENTATA - CINGULATA		
Dasypodidae		
Incertae sedis	(5) (11)	
cf. *Euphractus* Wagler, 1830	(5)	Pleistocene
cf. *Propraopus* Ameghino, 1881	(5)	Pleistocene
cf. *Dasypus novemcintus* Linnaeus, 1758	(5)	Pleistocene
Pampatheriidae	(5)	
Pampatherium Ameghino, 1875	(4)	Pleistocene
Genus and species indeterminate	(2)	Huayquerian

Table 1 - Continued

TAXA	REFERENCE	AGE
Glyptodontidae		
Incertae sedis	(5) (11)	
Plohophorus Ameghino, 1887	(4) (5)	Pliocene
Hoplophorus Lund, 1839	(1) (5)	Lujanian
cf. *Neuryurus* Ameghino, 1889	(5)	Pleistocene
cf. *Paraglyptodon* Castellanos, 1932	(5)	Chapadmalalan
? *Panochthus* Burmeister, 1866	(6)	Pleistocene
Glyptodon clavipes Burmeister, 1898	(5) (24)	Pleistocene
NOTOUNGULATA		
Notohippidae		
Purperia cribatidens (Paula Couto, 1981) Paula Couto, 1982	(7) (9)	Santacrucian
cf. *Notohippus* Ameghino, 1891	(8)	Santacrucian
Haplodontheriinae		
Toxodontherium listai Kraglievich, 1932	(4)	Miocene
Abothrodon pricei Paula Couto, 1944	(4) (10)	Huayquerian
Neotrigodon utoquineae Spillmann, 1949	(8) (11)	Huayquerian
Mesotoxodon pricei Paula Couto, 1982	(8)	Pliocene
cf. *Paratrigodon euguii* Cabrera & Kraglievich, 1931	(8)	Chasicoan
cf. *Trigodon* Ameghino, 1882	(8)	Montehermosan
Trigodonops lopesi (Roxo, 1921) Kraglievich, 1930	(4) (8) (20)	Montehermosan
Toxodontinae		
Neotoxodon pascuali Paula Couto, 1982	(8)	Miocene
Minitoxodon acreensis Paula Couto, 1982	(8)	Miocene
Plesiotoxodon amazonensis Paula Couto, 1982	(8)	Miocene
? *Stereotoxodon tehuelche* Ameghino, 1904	(8)	Friasan
Mesenodon juruaensis Paula Couto, 1982	(8)	Miocene
Mixotoxodon Van Frank, 1957	(4)	Lujanian
Gyrinodon quassus Hopwood, 1928	(4) (8)	Montehermosan
Toxodon platensis Owen, 1840	(1) (4) (8)	Pleistocene
Palaeotoxodon Ameghino, 1904	(8)	Montehermosan

Table 1 - Continued

T A X A	REFERENCE	AGE
Nesodontinae		
Nesodon imbricatus Owen, 1846	(7) (8) (12)	Friasan
RODENTIA		
Incertae sedis	(12)	? Tertiary
Erethizontidae		
Genus and species indeterminate	(2)	Huayquerian
Eosteiromys Ameghino, 1902	(25)	Colhuehuapian
Dasyproctidae		
Genus and species indeterminate	(2)	Huayquerian
Caviidae		
Genus and species indeterminate	(2)	Huayquerian
Hydrochoeridae		
Kiutherium orientalis Francis & Mones, 1965	(2)	Huayquerian
Protohydrochoerus schirasakae Spillmann, 1941	(11)	Huayquerian
Protohydrochoerus tahuamanii Spillmann, 1949	(11)	Huayquerian
Echymidae		
Genus and species indeterminate	(2)	Huayquerian
Palaeoechimys peruvianus Spillmann, 1949	(11)	Huayquerian
Neoepiblemidae		
Euphilus Ameghino, 1889	(22)	Huayquerian
Genus and species indeterminate	(2)	Huayquerian
Dinomyidae		
Tetrastylus Ameghino, 1886	(2)	Huayquerian
Telicomys amazonensis Frailey, 1986	(2)	Huayquerian
Potamarchus murinus Burmeister, 1885	(2)	Huayquerian
Phoberomys burmeisteri (Ameghino, 1886) Kraglievich, 1926	(12) (14)	Huayquerian
Phoberomys bordasi Patterson, 1942	(12) (13)	Huayquerian
cf. *Gyriabrus* Ameghino, 1883	(12)	Huayquerian

Table 1 - Continued

T A X A	REFERENCE	AGE
ASTRAPOTHERIA		
Astrapotheriidae	(4) (8)	? Friasan
Synastrapotherium amazonense Paula Couto, 1976	(15)	? Friasan
? *Synastrapotherium* Paula Couto, 1976	(2)	? Friasan
PYROTHERIA		
Pyrotheriidae		
Genus and species indeterminate	(8)	? Mustersan
Gryphodon peruvianus Anthony, 1924	(16)	? Mustersan
LITOPTERNA		
Proterotheriidae		
Genus and species indeterminate	(2)	Huayquerian
Macraucheniidae		
Unnamed new genus	(2)	Huayquerian
cf. *Cullinia* Cabrera & Kraglievich, 1931	(8)	Chasicoan
PROBOSCIDEA		
Gomphotheriidae	(24)	
Haplomastodon waringi (Holland, 1920)	(4) (17) (18) (23)	Lujanian
Cordilleiron Osborn, 1926	(1)	Pleistocene
ARTIODACTYLA		
Tayassuidae		
Dicotyles traunmülleri Spillmann, 1949	(1) (11)	Lujanian
Tayassu pecari Fisher, 1814	(3) (4)	Lujanian
Camelidae		
Vicugna Gray, 1872	(3)	Pleistocene
Palaeolama Gervais, 1867	(4)	Pleistocene
PERISSODACTYLA		
Tapiridae		
Tapirus terrestris (Linnaeus, 1758)	(3) (4) (12)	Pleistocene

Table 1 - Continued

T A X A	REFERENCE	AGE
SIRENIA		
Trichechidade		
Trichechus inunguis (Natterer, 1883)	(3)	Pleistocene
Trichechus manatus Linnaeus, 1758	(6)	Pleistocene
? Ribodon Ameghino, 1883	(2)	Huayquerian
CETACEA		
Platanistidae		
Plicodontinia mourai Miranda Ribeiro, 1935	(21)	Pliocene

References:

(1) Willard, 1966; (2) Frailey, 1986; (3) Simpson & Paula Couto, 1981; (4) Rancy, 1981; (5) Paula Couto, 1983a; (6) Paula Couto, 1956; (7) Paula Couto, 1981; (8) Paula Couto, 1982a; (9) Paula Couto, 1982b; (10) Paula Couto, 1944; (11) Spillmann, 1949; (12) Paula Couto, 1983b; (13) Patterson, 1942; (14) Paula Couto, 1978; (15) Paula Couto, 1976b; (16) Anthony, 1924; (17) Simpson & Paula Couto, 1955; (18) Simpson & Paula Couto, 1957; (19) Mones, 1986; (20) Roxo, 1921; (21) Miranda Ribeiro, 1938; (22) Mones & Toledo, 1989; (23) Hoffstetter, 1952; (24) Roxo, 1937; (25) Stirton, 1953.

Table 2 - Cenozoic mammals of western Amazon grouped by age

EOCENE ? Mustersan

PYROTHERIA
 Pyrotheriidae
  Genus and species indeterminate
  Gryphodon peruvianus Anthony, 1924

OLIGOCENE ? Colhuehuapian

RODENTIA
 Erethizontidae
  Eosteiromys Ameghino, 1902

MIOCENE ?

NOTOUNGULATA
 Toxodontidae
 Haplodontheriinae
  Toxodontherium listai Kraglievich, 1932
 Toxodontinae
  Neotoxodon pascuali Paula Couto, 1982
  Minitoxodon acreensis Paula Couto, 1982
  Plesiotoxodon amazonensis Paula Couto, 1982
  Mesenodon juruaensis Paula Couto, 1982

MIOCENE Santacrucian

NOTOUNGULATA
 Notohippidae
  Purperia cribatidens (Paula Couto, 1981)
   Paula Couto, 1982
  cf. *Notohippus* Ameghino, 1891

Table 2 - Continued

MIOCENE Friasan

NOTOUNGULATA
 Toxodontidae
 Nesodontinae
  Nesodon imbricatus Owen, 1846
 Toxodontinae
  ? *Stereotoxodon tehuelche* Ameghino, 1904

ASTRAPOTHERIA
 Astrapotheriinae
  Synastrapotherium amazonense Paula Couto, 1976
  ? *Synastrapotherium* Paula Couto, 1976

MIOCENE Chasicoan

NOTOUNGULATA
 Toxodontidae
 Haplodontheriinae
  cf. *Paratrigodon euguii* Cabrera & Kraglievich, 1931

LITOPTERNA
 Macraucheniidae
  cf. *Cullinia* Cabrera & Kraglievich, 1931

MIOCENE Huayquerian

MARSUPIALIA
 Caenolestidae
  ? *Abderites* Ameghino, 1887
 Family indeterminate

EDENTATA - PILOSA
 Megalonychidae
  Genus and species indeterminate
Mylodontidae
  Acremylodon campbelli (Frailey, 1986)
    Mones, 1986

EDENTATA - CINGULATA
 Pampatheriidae
  Genus and species indeterminate

Table 2 - Continued

- NOTOUNGULATA
  - Toxodontidae
  - Haplodontheriinae
    - *Abothrodon pricei* Paula Couto, 1944
    - *Neotrigodon utoquineae* Spillmann, 1949

- RODENTIA
  - Erethizontidae
    - Genus and species indeterminate
  - Dasyproctidae
    - Genus and species indeterminate
  - Caviidae
    - Genus and species indeterminate
  - Hydrochoeridae
    - *Kiutherium orientalis* Francis & Mones, 1965
    - *Protohydrochoerus schirasakae* Spillmann, 1941
    - *Protohydrochoerus tahuamanii* Spillmann, 1949
  - Echymidae
    - *Palaeoechimys peruvianus* Spillmann, 1949
  - Neoepiblemidae
    - *Euphilus* Ameghino, 1889
    - Genus and species indeterminate
  - Dinomyidae
    - *Tetrastylus* Ameghino, 1886
    - *Telicomys amazonensis* Frailey, 1986
    - *Potamarchus murinus* Burmeister, 1885
    - *Phoberomys burmeisteri* (Ameghino, 1886) Kraglievich, 1926
    - *Phoberomys bordasi* Patterson, 1942
    - cf. *Gyriabrus* Ameghino, 1883

- LITOPTERNA
  - Proterotheriidae
    - Genus and species indeterminate
  - Macraucheniidae
    - Unnamed new genus

- SIRENIA
  - Trichechidae
  - ? *Ribodon* Ameghino, 1883

Table 2 - Continued

PLIOCENE

EDENTATA-PILOSA
 Megalonychidae
  Pliomorphus Ameghino, 1885

EDENTATA-CINGULATA
 Glyptodontidae
  Plohophorus Ameghino, 1887

NOTOUNGULATA
 Toxodontidae
 Haplodontheriinae
  Mesotoxodon pricei Paula Couto, 1982

CETACEA
 Platanistidae
  Plicodontinia mourai Miranda Ribeiro, 1935

PLIOCENE Montehermosan

NOTOUNGULATA
 Toxodontidae
 Toxodontinae
  Gyrinodon quassus Hopwood, 1928
  Palaeotoxodon Ameghino, 1904
 Haplodontheriidae
  Trigodonops lopesi (Roxo, 1921) Kraglievich, 1930
  cf. Trigodon Ameghino, 1882

Table 2 - Continued

PLEISTOCENE

EDENTATA-PILOSA
- Megalonychidae
  - Megalonyx Harlan, 1825
- Nothrotheriinae
  - Genus Indeterminate

- Mylodontidae
  - Mylodon Owen 1840
  - Glossotherium (Oreomylodon) wegeneri (Spillmann, 1931)
  - Lestodon armatus Gervais, 1855
  - Scelidotherium Owen, 1840

EDENTATA-CINGULATA
- Dasypodidae
  - cf. Euphractus Wagler, 1830
  - cf. Propraopus Ameghino, 1881
  - cf. Dasypus novemcintus Linnaeus, 1758
- Pampatheriidae
  - Pampatherium Ameghino, 1875
- Glyptodontidae
  - cf. Neuryurus Ameghino, 1889
  - ? Panocthus Burmeister, 1866
  - Glyptodon clavipes Burmeister, 1898

PROBOSCIDEA
- Gomphotheriidae
  - Cuvieronius Osborn, 1923 (= Cordilleiron Osborn, 1926)

ARTIODACTYLA
- Camelidae
  - Vicugna Gray, 1872
  - Palaeolama Gervais, 1867

SIRENIA
- Trichechidae
  - Trichechus inunguis (Natterer, 1883)
  - Trichechus manatus Linnaeus, 1758

PERISSODACTYLA
- Tapiridae
  - Tapirus terrestris (Linnaeus, 1758)

Table 2 - Continued

PLEISTOCENE Lujanian

- EDENTATA - PILOSA
  - Megatheriidade
    - *Eremotherium* Spillmann, 1948
    - *Ocnopus* Reinhardt, 1875

- EDENTATA - CINGULATA
  - Glyptodontidae
    - *Hoplophorus* Lund, 1839

- NOTOUNGULATA
  - Toxodontidae
  - Toxodontinae
    - *Mixotoxodon* Van Frank, 1957

- PROBOSCIDEA
  - Gomphotheriidae
    - *Haplomastodon waringi* (Holland, 1920)

- ARTIODACTYLA
  - Tayassuidade
    - *Dicotyles traunmülleri* Spillmann, 1949
    - *Tayassu pecari* Fisher, 1814

CHAPTER 4
PLEISTOCENE FAUNA

This chapter is to reviews all the information known on the entire late Pleistocene mammalian fauna of the western Amazon. Although some of the information presented here is derived from the early literature, this review is based primarily on specimens in several collections in North and South America, including original new collections at the Universidade Federal do Acre which I assembled during the past seven years.

The first section discusses the localities along the rivers in the western Amazon from which late Pleistocene fossils have been collected. The second section systematically documents the mammalian fauna, especially those in the collections at the Laboratório de Pesquisas Paleontológicas at the Universidade Federal do Acre. It details one new family, Mustelidae, and removes the erroneously included sloth genus Nothropus.

Pleistocene Localities

Even today the best way to travel for paleontological field surveys in the western Amazon is by boat or dugout canoe along the myriads of rivers, small and large, that flow into the Amazon. For this reason, each of the Pleistocene localities is related to a river, as is usually the case in references on the Amazon basin.

Juruá River

The Juruá River is one of the largest tributaries from the right margin of the Amazon. The headwaters of the Juruá lie in eastern Peru, more than 200 km from the Andes, approximately at 73° W and 10° S, where it runs north toward the Amazon River. The Juruá River, in the state of Acre, near the Brazilian/Peruvian border, is the area that has produced the earliest and largest quantity of Pleistocene mammals in the western Amazon region. Fossils from the Juruá are deposited at the Museu Paraense Emilio Goeldi (Belém), Museu Nacional (Rio de Janeiro), Departamento da Produção Mineral (Rio de Janeiro), American Museum of Natural History (New York), and Laboratório de Pesquisas Paleontológicas (Rio Branco). Major studies on these fossils were made by Paula Couto (1956), Rancy (1981), Simpson & Paula Couto (1957, 1981).

References by Schlosser (1925) and Simpson (1940) were the first serious attempts to put the Juruá River on the map of South American Pleistocene paleontology. Roxo (1937) described vertebrate fossils, including two Pleistocene mammals, Glyptododon and Haplomastodon, from

Aquidabã on the Juruá River, which is located downriver from the city of Eirunepé in the state of Amazonas. From that time until the 1980s, no other paleontological field trip was made to the area.

Simpson and Paula Couto (1981) published a series of charts and plotted fossil localities, based on the data gathered by G. G. Simpson during his trip to the Juruá River in 1956.

The upper Juruá River in the state of Acre (Brazil) was considered by Haffer (1969) and Prance (1973) to be part of the East Peruvian Pleistocene Forest Refugium.

Napo River

The Napo River is one of the principal rivers of Ecuador. With its headwaters in the Andes, the Napo River, a tributary of the Amazon River, runs eastward in the direction of the Peruvian border. References to Pleistocene mammals from alluvial deposits of the Napo River in the Amazon region of Ecuador were made by Hoffstetter (1952), Marshall et al., 1984, and Spillmann (1949). The Napo River is an area that deserves special attention by vertebrate paleontologists and paleoecologists, because of the probability, based upon biological evidence, of the existence of the Napo River Pleistocene Forest Refugium (Whitmore & Prance, 1987)

Ucayali River

One of the most important rivers of Peru, the Ucayali River joins the Marañon to form the Amazon River, upriver from the city of Iquitos. Pleistocene mammals from the area were reported primarily by Spillmann (1949) and Willard (1966). The fossils come from near the Peruvian/Brazilian border, especially from the Inuya River a tributary of the Ucayali River. Interestingly, the Inuya and the Juruá rivers have their headwaters in the same geographical area of eastern Peru, and both are rich in vertebrate fossils. This area was included in the East Peruvian Pleistocene Forest Refugium proposed by Haffer (1969), Prance (1973), and Vanzolini and Williams (1970).

Other Localities

The Museu Nacional (Rio de Janeiro) houses material of *Haplomastodon* (MN-310-V), collected from the confluence of the Chandless and Purus rivers in the state of Acre (Paula Couto, 1956).

The vertebrate paleontology collection of the Universidade do Amazonas (Manaus) includes a molar tooth with thick enamel of *Haplomastodon*, from the Purus River, upriver from the city of Boca do Acre, in the state of Amazonas (Prof. Rosalie Benchimol, Universidade do Amazonas, personal communication).

Fossils of <u>Eremotherium</u> and <u>Haplomastodon</u>, from the Madeira River, near the Bolivian border, are housed at the Museu do Estado in Porto Velho, state of Rondônia (Prof. Jonas Pereira de Souza Filho, Universidade Federal do Acre and Prof. Miguel Joaquim Sant'anna Filho, Universidade de Rondônia, personal communication).

Succinct references to Pleistocene vertebrates, including Toxodontidae and mastodont teeth, from the Bolivian Amazon region, were made by Fawcett (1953), Hoffstetter (1968), and Marshall et al. (1984).

The American Museum of Natural History, New York, houses three specimens of Toxodontidae with the following data:

AMNH 107,865--<u>Toxodon</u> <u>platensis</u> Owen, 1840. Left maxilar fragment with P^4 M^1. Eslabón formation, Flora River, Bolivia.

AMNH 22,461--Toxodont tooth, from Tahuamanu River, Peru. An original tag glued on the tooth had the following inscription: "Sr. Victor Salcedo, Diente de Brontosaurio."

AMNH 32,769--Jaw fragment with lower molar of a Toxodont, from middle Ucayali region, Peru.

Table 3 lists the Pleistocene mammalian genera of the western Amazon and their known ranges in South America based on authoritative summaries, such as Patterson and Pascual (1972) and Marshall et al. (1984). The successive South

Table 3 - Ages of Pleistocene mammals of the western Amazon

Taxa \ Ages	Uquian	Ensenadan	Lujanian
EDENTATA-PILOSA			
Eremotherium			++++++++++++
Glossotherium	++++++++++++	++++++++++++	++++++++++++
Lestodon		++++++++++++	++++++++++++
Scelidotherium	++++++++++++	++++++++++++	++++++++++++
Mylodon		++++++++++++	++++++++++++
Megalonyx	++++++++++++	++++++++++++	++++++++++++
Ocnopus			++++++++++++
EDENTATA-CINGULATA			
Pampatherium	++++++++++++	++++++++++++	++++++++++++
Euphractus		++++++++++++	++++++++++++
Propraopus		++++++++++++	++++++++++++
Dasypus		++++++++++++	++++++++++++
Hoplophorus			++++++++++++
Neuryurus		++++++++++++	
Panocthus	++++++++++++	++++++++++++	++++++++++++
Glyptodon	++++++++++++	++++++++++++	++++++++++++
NOTOUNGULATA			
Toxodon	++++++++++++	++++++++++++	++++++++++++
Mixotoxodon			++++++++++++
PROBOSCIDEA			
Cuvieronius	++++++++++++	++++++++++++	++++++++++++
Haplomastodon			++++++++++++
PERISSODACTYLA			
Tapirus	++++++++++++	++++++++++++	++++++++++++
ARTIODACTYLA			
Vicugna			++++++++++++
Palaeolama	++++++++++++	++++++++++++	++++++++++++
Tayassu			++++++++++++
CARNIVORA			
Eira			++++++++++++

American land mammal ages extending from early to late Pleistocene include the Uquian, Ensenadan, and Lujanian (Marshall et al., 1984). Clearly the preponderance of fossil evidence should be assigned to the Lujanian mammal age, the late Pleistocene interval corresponding to the Rancholabrean in North America (Figure 5).

Table 4 lists the same land mammal genera, indicating their rivers of origin. Clearly the most complete record has been collected from the Juruá River. Of the 24 genera known collectively in the western Amazon only the genus Mylodon has not been definitely recognized from the Juruá River. Table 5 presents an inventory of Pleistocene fossil mammals from the western Amazon, which have been catalogued into the collection of the Laboratório de Pesquisas Paleontológicas of the Universidade Federal do Acre.

Among the 24 genera listed in Table 4, only 6 are extant in South America. Particularly striking is the presence of two genera of Camelidae, Palaeolama and Vicugna.

Figure 6 shows a tooth (left P^4) of Palaeolama. Because the Camelidae today are restricted to the Andes and to the Patagonian region (Franklin, 1982) their Pleistocene distribution in the Amazon region requires explanation.

Another impressive feature of the Pleistocene fauna in the western Amazon is the diversity of mammalian species, of very large size, there were two genera each of

Fig. 5 - South American and North American Land Mammal Ages and the late Cenozoic fauna of the western Amazon (after Marshall et al., 1984).

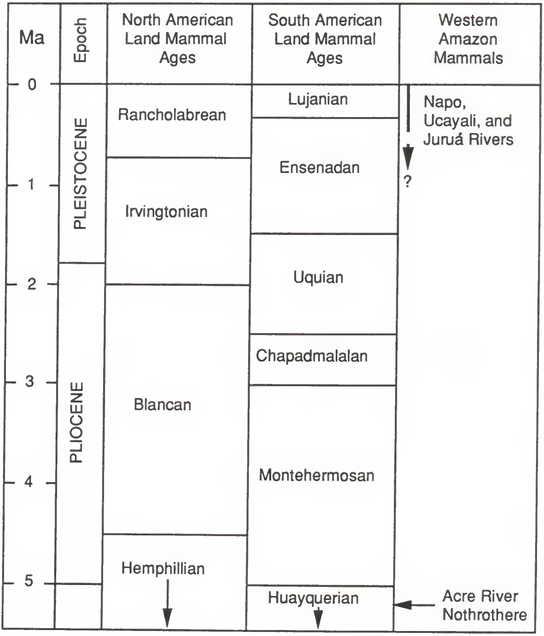
Ma
Epoch
North American Land Mammal Ages
South American Land Mammal Ages
Western Amazon Mammals
0
1
2
3
4
5
PLEISTOCENE
PLIOCENE
Rancholabrean
Irvingtonian
Blancan
Hemphillian
Lujanian
Ensenadan
Uquian
Chapadmalalan
Montehermosan
Huayquerian
Napo, Ucayali, and Juruá Rivers
?
Acre River Nothrothere

Table 4 - Pleistocene mammals in the western Amazon and rivers where they occur

Taxa \ Rivers	Napo River	Juruá River	Ucayali River
A - EDENTATA/PILOSA	x	x	x
Megatheriidae	x	x	x
Ocnopus	-	x	-
Eremotherium	x	x	x
Mylodontidae	x	x	-
Glossotherium	-	x	-
Lestodon	-	x	-
Scelidotherium	-	x	-
Mylodon	x	-	-
Megalonychidae	-	x	-
Megalonyx	-	x	-
B - EDENTATA/CINGULATA	x	x	x
Pampatheriidae	-	x	-
Pampatherium	-	x	-
Dasypodidae	-	x	x
Euphractus	-	x	-
Propraopus	-	x	-
Dasypus	-	x	-
Glyptodontidae	x	x	x
Hoplophorus	-	x	-
Neuryurus	-	x	-
Panocthus	-	x	-
Glyptodon	x	x	x
C - PROBOSCIDEA	x	x	x
Haplomastodon	x	x	x
Cuvieronius	x	x	-
D - ARTIODACTYLA	x	x	x
Camelidae	-	x	-
Vicugna	-	x	-
Palaeolama	-	x	-
Tayassuidae	x	x	x
Tayassu	x	x	x
E - NOTOUNGULATA	x	x	x
Toxodon	-	x	x
Mixotoxodon	-	x	-
F - PERISSODACTYLA	-	x	x
Tapirus	-	x	x
G - CARNIVORA	-	x	-
Eira	-	x	-

Table 5 - Inventory of Pleistocene fossil mammals by family from the western Amazon, housed at the Laboratório de Pesquisas Paleontológicas of the Universidade Federal do Acre, Rio Branco, Acre, Brazil

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EDENTATA/CINGULATA

Glyptodontidae (Osteoderms) - UFAC 022, UFAC 024, UFAC 025, UFAC 026, UFAC 1082, UFAC 1153, UFAC 1199, UFAC 1204 .

Pampatheriidae (Osteoderms) - UFAC 023, UFAC 607, UFAC 861, UFAC 1131.

EDENTATA/PILOSA

Megatheriidae - UFAC 056 (left M^3), UFAC 065 (right M^4), UFAC 068 (right M^5), UFAC 096 (right metacarpus IV), UFAC 098 (left mandibular ramus), UFAC 099 (right tibia), UFAC 100 (eft astragalus), UFAC 101 (distal portion of a left humerus), UFAC 108 (left M^5), UFAC 1118 (right radius).

Megalonychidae - UFAC 067 (molariform tooth), UFAC 074 (right ? M_2), UFAC 077 (molariform tooth).

Mylodontidae - UFAC 063 (left caniniform M^1), UFAC 082 (right M^5) UFAC 091 (left tibia), UFAC 102 (left humerus), UFAC 103 (left humerus).

NOTOUNGULATA

Toxodontidae - UFAC 142 (left I^2), UFAC 052 (right M_2), UFAC 085 (right I^1).

PROBOSCIDEA

Gomphotheriidae - UFAC 095 (right M_3), UFAC 104 (right M_2), UFAC 1212 (right M^2), UFAC 1213 (left mandibular ramus with M_3), UFAC 1214 (left M_2).

PERISSODACTYLA

Tapiridae - UFAC 034 (right mandibular ramus), UFAC 035 (right mandibular ramus - juvenile), UFAC 043 (right femur), UFAC 1150 (fragment of left mandibular ramus with P_3).

ARTIODACTYLA

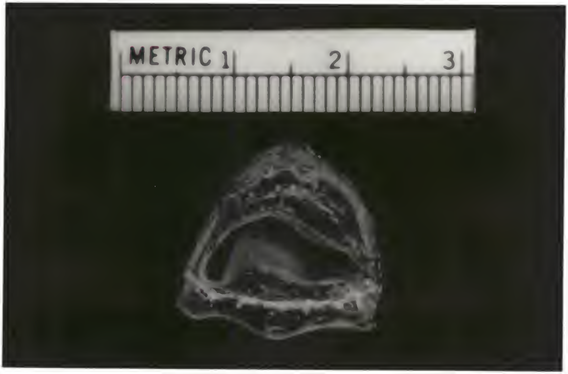
Tayassuidae - UFAC 006 (right tibia), UFAC 008 (right radio-ulna), UFAC 011 (distal portion right femur), UFAC 016 (left tibia), UFAC 031 (left mandibular ramus), UFAC 032 (right mandibular ramus).

Camelidae - UFAC 061 (left P^4).

CARNIVORA

Mustelidae - UFAC 036 (right mandibular ramus with P_3).

Fig. 6 - Left P^4 in occlusal view of *Palaeolama* UFAC 061.


METRIC 1
2
3

megatheriid ground sloths, toxodonts notoungulates, and gomphotheriid proboscidea. Figures 7 and 8 represent Eremotherium and Haplomastodon, respectively. In addition, there was a variety of large edentates including large-shelled glyptodonts and pampatheres. Ground sloths included five genera that were of more moderate size (bear to rhinoceros range) than the megatheriids.

The following sections of this chapter discuss the supposed presence of the Pleistocene sloth, Nothropus, in the Amazon basin and also document a new Pleistocene record of the mustelid genus Eira in South America.

The Supposed Presence of Nothropus in the Late Pleistocene of Western Amazon

Introduction

Among the smallest of the extinct sloths, nothrotheres played a very significant role in the Neogene mammalian faunas of the New World. During the Santacrucian in Argentina (early Miocene), the nothrotheres were dominant and were represented by several genera, including Analcimorphus, Shismotherium, and Xyophorus, although the most common was Hapalops Ameghino, 1887, (Scott, 1904). Nothrotheres similar to Hapalops were present among the La Venta fauna of Colombia, which were considered Friasian (middle Miocene) in age (Hirschfeld, 1985). From Bolivia,

Fig. 7 - Left mandible of <u>Eremotherium</u> lingual view UFAC 098.


0
5
10
20
30cm

Fig. 8 - Right mandible of <u>Haplomastodon</u> with M_2 in labial view UFAC 104.


0
5
10
20
30cm

Frailey (1988) described *Hapalops angustipalatus* among the edentates of Quebrada Honda, which he compared closely with the Santa Cruz fauna of Argentina. The nothrotheres were continuously present among the Cenozoic fauna of South America. During the Pleistocene, when the group became extinct, *Nothrotherium* was well represented in the fossil record of Brazil (Cartelle & Fonseca, 1983). In North America *Nothrotheriops* appeared in the southern United States by the middle Pleistocene (Irvingtonian) (McDonald, 1985).

The main purpose of this section is to clarify the status of the supposed Holocene record of *Nothropus* in the Amazon basin (Frailey, 1986), and to describe a new genus, dating to the late Miocene also from this area.

The fossil described here was collected in 1986 by a joint field team, including Dr. Carl D. Frailey (Midland College, Texas), Professor Jonas Pereira de Souza Filho, and biologist José Carlos Rodrigues dos Santos (Universidade Federal do Acre, Brazil), during an expedition to the upper Acre River on the border between Brazil and Peru.

Frailey (1986) described the skull and mandible of a specimen (LACM 117533) from the same region and assigned it to the genus *Nothropus*.

All the measurements are given in millimeters.

Taxonomy

Order EDENTATA Cuvier, 1798
Suborder XENARTHRA Cope, 1889
Infraorder PILOSA Flower, 1883
Family MEGALONYCHIDAE Zittel, 1892
Subfamily NOTHROTHERIINAE Kraglievich, 1923
New genus and species

Description

Holotype

UFAC 1284 -- Skull and mandible.

Type locality

Upper Acre River, município of Assis Brasil, state of Acre, Brazil.

Age--SALMA (South America Land Mammal Age)

Huayquerian, late Miocene.

Diagnosis of species

Size comparable to *Nothrotheriops*; pterygoid not inflated, similar to *Planops magnus* Scott, 1904:223, plate LVIII). Nasal region flat, not arched as *Pronothrotherium typicum* Ameghino, 1907; predental palate with a V-shaped form. Mandible more robust and horizontal ramus higher than *Senetia* Kraglievich, 1925.

Diagnosis of genus

Same a for species.

Skull

The skull (UFAC 1284) was found complete with the mandible articulated. During the preparation, it was possible to set apart the two pieces.

In dorsal view, when compared to LACM 117533 (Frailey, 1986), the skull has a less bulbous cranium, more tubular shape, and a flatter and wider rostrum (Figure 9). Just behind the suture between the frontal and nasal bones a concavity is present on the medial line. The postorbital process is absent. The supraorbital foramen is present 35 mm behind and is at the same level as the lacrimal foramen.

In lateral view (Figure 10), the skull UFAC 1284 is less domed than LACM 117533. The distance from the highest point of the skull to the superior border of the squamosal measures 50 mm in LACM 117533 but only 39 mm in UFAC 1284.

The base of the squamosal is inflated above the dorsal margin of the external auditory meatus, similar to the condition in Nothrotherium Lydekker, 1889 (=Coelodon Lund, 1839). The jugal notch for the zygomatic process of the squamosal is deeper in UFAC 1284 than in LACM 117533. The buccinator fossa is shallower and smaller than in LACM 117533.

Fig. 9 - Nothrotheriinae new genus and species (UFAC 1284). Skull in dorsal view. Length of the bar 30 mm.

Fig. 10 - Nothrotheriinae new genus and species (UFAC 1284). Skull in lateral view. Length of the bar 30 mm.


JFA-1284

The pterygoid is ventrally expanded, not inflated as it is in Nothrotherium and Nothrotheriops (Hoffstetter, 1954). Its ventral border is stronger than the wall of the bone, which is internally convex and externally concave. Frailey (1986), describing the skull LACM 117533, said that the proximal end of the pterygoid is inflated, but, upon examining the skull, I am unable to see any inflation.

The tympanic is present with a horseshoe-shaped opening that faces dorso-posteriorly and an inclination of roughly 45° . The position of the external auditory meatus relative to the pterygoid differs in the two specimens. In LACM 117533 the inferior border of the tympanic is situated at the same level as the proximal edge of the pterygoid; in UFAC 1284, however, the inferior border of the tympanic is situated at a level about 15 mm superior to the proximal edge of the pterygoid.

The palate is highly convex between the molariform teeth with several pits of vascular foramina. The anterior part of the palate is V-shaped.

The premaxillae are present and are Y-shaped. The lateral branch has two articular surfaces for the maxillae, one posterior (palatal) and the other one medial. The posterior branches of the premaxillae are articulated to the medial sides of the V-shaped anterior part of the palate.

The distal tips of the premaxillae are rounded and dorsally convex. The premaxillae are not fused at the medial line. Apparently they served to support movement of the upper lips (Figure 11).

Five upper teeth are present, M^1 - M^5. The M^1 is caniniform, sub-cylindrical in cross section, separated from M^2 by a (12.4 mm) diastema. The occlusal facet of M^1 is an internal basin opening antero-medially. The four molariform agree with the description given by Frailey (1986). The overall length of the upper dental series (Table 6) is 61.6 mm. Table 7 summarizes the significant differences between the two skulls.

Table 6 - Measurements in mm of upper teeth in nothrothere new genus (UFAC 1284)

	Width	Length
M^1	6.1	5.3
M^2	12.2	8.6
M^3	14.7	11.0
M^4	13.8	9.3
M^5	11.7	5.7

Mandible

The postdental portion of the ramus has a strong coronoid and a fragile angular process. Whereas LACM 117533 has the condylar process that lies midway between the

Fig. 11 - Nothrotheriinae new genus and species (UFAC 1284). Skull in ventral view. Length of the bar 30 mm.

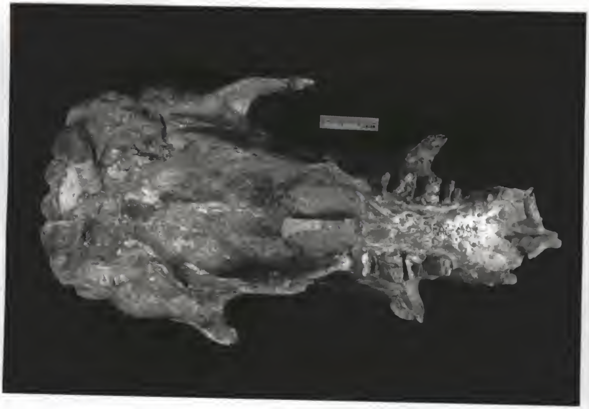


Table 7 - Cranial comparisons between two nothrothere specimens

LACM 11753	UFAC 1284
Pterygoid comparatively small, covered not inflated.	Pterygoid larger, more expanded ventrally, but not inflated.
Predental portion of the the palate long and narrow.	Predental portion of the palate shorter and relatively wider.
Medial line of the palate at the anterior border slightly U-shaped.	Medial line of the palate at the anterior border strongly V-shaped.
Supraorbital foramen situated at a superior level related to the lacrimal foramen.	Supraorbital foramen at same level of the lacrimal foramen.
Notch of the jugal shallow.	Notch of the jugal deep comparatively.
Base of the squamosal not inflated.	Base of squamosal inflated.
Postorbital process weak but present.	Postorbital process absent.
Occlusal surface of caniniform worn in chisel shape.	Occlusal surface of caniniform worn in a rounded internal basin.
Distance from the M^1 to the anterior tip of the palate: 40.3 mm.	Distance from the M^1 to the anterior tip of the palate: 23.3 mm.

coronoid and the angular process, in UFAC 1284 there is a condylar process about 40% nearer to the coronoid.

This proportion is reflected in the following measurements of UFAC 1284: The distance between the condyle and angular process is approximately 50 mm, and the distance between the condyle and coronoid is approximately 30 mm. .

The articular surface of the condyle is convex latero-medially and excavated on the ventral side. The angular process is thin, laterally convex, and medially concave. The ventral margin and the posterior tip of the angular are curved medially.

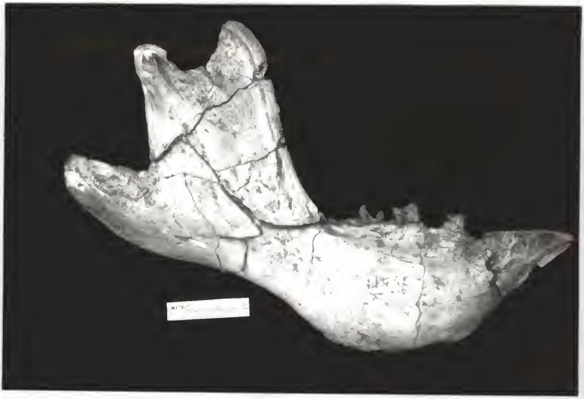
The dentary portion of the ramus is massive, ventrally convex and deep to support the hypsodont teeth. The mandible reaches its maximum depth of about 47 mm beneath the M_{2-3}. The predentary section is about 50% shorter than in LACM 117533. It has a U-shaped spout, a depressed lateral border, and a delicate dorsal border (Figures 12 and 13).

Laterally, near the dorsal border, the anterior segment of the mandible is sculptured with tiny pits. Two more conspicuous, elongate depressions occur on the lateral face just anterior to and posterior to the M_1.

The posterior lateral mandibular foramen is situated at the axis of the ascending ramus and lateral to M_4 . The medial mandibular foramen is placed on the level of the

Fig. 12 - Nothrotheriinae new genus and species (UFAC 1284). Mandible in occlusal view. Length of the bar 30 mm.

Fig. 13 - Nothrotheriinae new genus and species (UFAC 1284). Right mandible in labial view. Length of the bar 30 mm.



teeth approximately 30 mm posterior to M_4. One mental foramen is present in the left ramus, and two mental foramina are present in the right ramus.

Four teeth are present, M_{1-4}. The M_1 is caniniform and subcylindrical in cross section. It is set lower than the M_2, and separated from it by a 9.2 mm diastema. The occlusal surface of the caniniform has a central basin opening labially with anterior and posterior little crests. The M_{2-4} are indistinguishable from the corresponding teeth described by Frailey (1986) for the specimen LACM 117533, and morphologically similar to the molariform of Nothrotheriops. The length of the lower dental series (Table 8) is 57.7mm. Table 9 summarizes the differences between the two mandibles.

Table 8 - Measurements in mm of lower teeth (UFAC-1284)

	Width	Length
M_1	5.1	7.5
M_2	12.8	10.8
M_3	14.6	10.1
M_4	13.0	9.1

Discussion

The subfamily Nothrotheriinae was created (Kraglievich, 1923) as a subfamily of Megalonychidae. This classification is still accepted by most of paleontologists, including

Cartelle and Fonseca (1983), Marshall et al. (1983, 1984), (Paula Couto (1959), and Simpson (1945, 1980). Several researchers, however, favor placing the Nothrotheriinae under the family Megatheriidae rather than Megalonychidae: Carroll (1988), Frailey (1986), Hirschfeld (1985), Patterson & Pascual (1972), Paula Couto (1971, 1979), Perea (1988), Scillato-Yané (1978), Scillato-Yané et al. (1987). Clearly more definitive analysis is needed.

Table 9 - Mandible comparison

LACM 117533	UFAC 1284
M_1 with an oblique shear surface, facing anteriorly, higher than M_2.	M_1 with a central basin, lower than M_2.
The posterolateral mandibular foramen laterally placed at the base of the ascending ramus immediately posterior to M_4.	The posterolateral mandibular foramen situated at axis of ascending ramus and lateral to M_4.

In South America, the subfamily Nothrotheriinae includes numerous common genera (Table 10), distributed from the Colhuehuapian (late Oligocene) to the Lujanian (late Pleistocene).

By age and morphology the new genus and species is more closely related to _Pronothrotherium_ and _Senetia_ than to other genera. Perea (1988) and Simpson (1945) considered *Senetia* to be a junior synonym of *Pronothrotherium*.

Table 10 - Nothrotheriine genera in South America distributed by mammal age (SALMA)

Colhuehuapian (late Oligocene)
Hapaloides Ameghino, 1902 and *Proschismotherium* Ameghino, 1902

Santacrucian (early middle Miocene)
Analcimorphus Ameghino, 1891; *Eucholoeops* Ameghino, 1887; *Hapalops* Ameghino, 1887; *Hyperleptus* Ameghino, 1891; *Megalonychotherium* Scott, 1904; *Pelecyodon* Ameghino, 1891; *Pseuhapalops* Ameghino, 1891 *Schismotherium* Ameghino, 1887 and *Xyophorus* Ameghino, 1887.

Friasan (late middle Miocene)
Eucholoeops Ameghino, 1887; *Hapalops* Ameghino, 1887 and *Pseudhapalops* Ameghino, 1891.

Chasicoan (early late Miocene)
Xyophorus Ameghino, 1887 and *Chasicobradys* Scillato-Yané, Carlini and Vizcaino, 1987

Huayquerian (late Miocene)
Pronothrotherium Ameghino, 1907.

Montehermosan (early Pliocene)
Pronothrotherium Ameghino, 1907 and *Senetia* Kraglievich, 1925.

Chapadmalalan (late Pliocene)
Diheterocnus Kraglievich, 1928 (=*Heterocnus* Kraglievich, 1925).

Ensenadan (middle Pleistocene)
Nothrotherium Lyddeker, 1889

Lujanian (late Pleistocene)
Nothrotherium Lyddeker, 1889 and *Nothropus* Burmeister, 1882

In comparing the new skull, in ventral view, to that of Pronothrotherium, the principal distinction is the shorter, broader, V-shaped predental portion of the palate in the new genus. The mandible of the new genus and species is more robust and the horizontal ramus reaches higher than in Senetia.

The inflated pterygoid

A large inflated sinus in the pterygoid is a common trait in Nothrotherium and Nothrotheriops. A good description is given by Reinhardt (1878) for Nothrotherium (=Coelodon) and by Stock (1925) for Nothrotheriops (=Nothrotherium).

Perea (1988), in his description of a skull of a Pronothrotherium Ameghino, 1907, noted the presence of "ampulas auditivas grandes y adelantadas." It is possible that he confused the sinuses of the pterygoid for anteriorly expanded auditory bullae, although I have not seen the original material and am only basing my interpretation on his paper. If my view is correct, this error is the same one that Reinhardt believed Gervais had committed (Reinhardt, 1878), when the French paleontologist suggested the presence of a "caisse auditive considerable" in Nothrotherium (=Coelodon) without mentioning the inflated pterygoid.

If Pronothrotherium shares an inflated pterygoid (Perea, 1988) with Nothrotherium and Nothrotheriops, then the Acre specimen must be assigned to another genus by the lack of this feature. The pterygoid of the new genus has a large ventral expansion but it is flat transversely and lacks an inflated bulla-like structure. In his description of the specimen LACM 117533, Frailey (1986) briefly mentions the presence of an inflated pterygoid, but I am unable to see it when examining that same skull.

Caniniform teeth

Nothrotheriops and Nothrotherium are the only genera of the Nothrotheriinae missing the caniniform teeth. The genus Nothropus created by Burmeister (1882) was based on a right mandibular ramus (MACN 975), which is distinguished from that of Nothrotherium solely by the presence of a small caniniform alveolus. That small alveolous is not comparable to the large caniniform tooth present in LACM 117533 (Frailey, 1986).

Nothropus tarijensis (Burmeister, 1887) Ameghino, 1907, was originally thought by Burmeister to be Nothrotherium (=Coelodon) because of the absence of a caniniform. Ameghino (1907) changed the genus to Nothropus because he observed a minuscule caniniform alveolus. On the other hand, Ameghino suggested in the same paper that Nothropus and Nothrotherium should be combined into one genus, because *Nothropus* was probably the juvenile form, from which the functional caniniform would be lost with increasing age and size of the animal. In his view *Nothrotherium* was the adult form in which the minute caniniform was lost and the alveolus obliterated by growth of the mandibular ramus.

It is important to stress that the principal diagnostic character between *Nothropus* and *Nothrotherium* is the presence or absence, respectively, of the caniniform teeth. It is also noteworthy, that during the past century, despite very productive work by Argentine paleontologists, only one specimen of *Nothropus priscus* (MACN 975) has been found with the alveolus and the root of a caniniform.

Nothropus carcaranensis Bordas, 1942, was based on three pieces, considered to belong to three different individuals: MACN 11300, fragment of a right maxilla with two molariform; MACN 1155, right mandibular ramus with M_3 and MACN 12630, occipital region of a skull. Because *N. carcaranensis* does not have a caniniform, Bordas (1942) compared it to *N. tarijensis* following the ideas presented by Burmeister (1887) but giving the classification proposed by Ameghino (1907). *Nothropus carcaranensis* came from the same locality as *N. priscus*: a railroad bridge over the Carcaranal River near Rosario, thought to be of Lujanian age. Hoffstetter (1954) correctly determined that *N.*

carcaranensis should be referred to as Nothrotherium due to its dental formula 4/3, and the critical absence of the caniniform tooth.

Ameghino (1907 in Obras Completas XVII, page 149), pointed out that the most notable difference between Pronothrotherium and Nothrotherium is the presence in the former of a substantial caniniform tooth. I presume that Ameghino and Hoffstetter were both correct, and that a small caniniform tooth occurred in Nothropus priscus as a rare state of Nothrotherium. In the large sample of Nothrotheriops from Leisey shell pit, dating from the middle Pleistocene (Irvingtonian) of North America, one juvenile maxilla, specimen UF 83700, exhibits a caniniform, whereas in the other nine specimens the caniniform is absent. It is thus a variable character and usually rarely developed.

Conclusions

If the phylogenetic position of Nothropus is correctly interpreted as a rare variant of Nothrotherium, this reopens the question of what taxon to assign the cranium LACM 117533, described and figured by Frailey (1986). It is not Nothropus, because the caniniform is present, strong and functional. Also it is not Pronothrotherium because of the absence of the inflated pterygoid. A second specimen described above shows that Frailey's specimen is a relatively small, probably female, variant of the new genus and species. Further samples may show it to represent a distinct species or even genus. For the present, I regard it as a second representative of the new Miocene taxon.

If this assignment is correct, then the Holocene age determined by Campbell & Frailey (1984) and cited by Frailey (1986) for the site from which the two nothrotheres were collected represents an overprint or contamination by younger carbon. This possibility noted by Frailey (1986) is not surprising in view of the recurrent flooding of the Miocene sediments in this part of the Amazon basin. Furthermore, collections from this area have extensively documented the presence of a rich Miocene vertebrate fauna.

A Mustelidae, *Eira* sp., from the Pleistocene of Western Amazon

Introduction

Worldwide in distribution, the family Mustelidae includes eight Neotropical genera: *Mustela*, *Lyncodon*, *Galictis*, *Eira*, *Mephitis*, *Conepatus*, *Lutra*, and *Pteronura*. Most of these genera clearly originated in the Northern Hemisphere and arrived in South America after the completion of the Panamanian land bridge (Webb, 1985).

Following the Procyonidae during the Huayquerian, Conepatus altiramus from the Chapadmalalan of Argentina (Reig, 1952) has the oldest fossil record of placental carnivores in South America.

The fossil described here was collected in 1977 by a joint field team including Daryl Paul Domning (Instituto Nacional de Pesquisas da Amazônia, Manaus) and Alceu Rancy (Universidade Federal do Acre, Rio Branco) during an expedition to the upper Juruá River.

The following description was made in comparison with the mandible of UF 5644, a skull of Eira barbara. All measurements are given in millimeters (mm).

Taxonomy

Order CARNIVORA Bowdich, 1821
Suborder FISSIPEDIA Blumenbach, 1791
Family MUSTELIDAE Swainson, 1835
Subfamily MUSTELINAE Gill, 1872
Genus Eira Hamilton Smith, 1842
Eira sp.

Material

UFAC 036-Right mandible with P_3.

Locality

Upper Juruá River, Município of Cruzeiro do Sul, State of Acre, Brazil.

Age

Pleistocene

Description

The right mandible is not complete and it lacks the coronoid process. The medial half of the mandibular condyle is broken off. The angular process is less prominent and more rounded than in the recent UF 5644 (Figure 14). The masseteric fossa is smooth and lingually not sculptured. The P_3 is present, worn on the tip of the crown and at the point of contact to M_1; in both places the dentine is exposed. The proximal root of P_2 and alveoli of C_1, $P_{1,2}$ and $M_{1,2}$ are present. The mandible is similar in size to that of _Galictis barbara_ (Lund, 1950:567, plate XLVI, fig. 4). The ventral margin under the masseteric fossa is not arched dorso-laterally. This mandible differs in the symphyseal region from that _Eira_ _barbara_ in having the ventral border under the P_1 well rounded. Measurements given in Table 11.

Table 11 - Measurements (in mm) of _Eira_ sp. mandible (UFAC 036)

Maximum length of P_3........................	7.8
Length from the anterior edge of the alveolus of P_1 to posterior edge of M_2.................	29.9
Length from proximal tip of angular process to ventral border of symphysis..................	58.4

Fig. 14 - *Eira* sp., right mandible with P_3 (UFAC 036), compared to UF 5644.


METRIC
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5644
AK-96

Comments

From the late Pleistocene cave deposits of Lagoa Santa in the State of Minas Gerais, Brazil, Lund reported the presence of Mustelidae as represented in his plate XLVI (Lund, 1950:567). Three species were recognized: *Galictis intermedia*, *G. barbara*, and *G. vittata*. Paula Couto (1979:331) considered that the genus *Eira* (=*Galera*) is "duvidosamente presente no Pleistoceno das cavernas de Minas Gerais," possibly because he believed the material to be Holocene, not Pleistocene. Marshall et al. (1984) recognized the presence of *Eira* (=*Galera*) from the middle Pleistocene badlands of Tarija, Bolivia. This is the first description of any Carnivora from the Pleistocene of the Amazon and also is one of a few references to the fossil representative of *Eira*.

CHAPTER 5
ECOLOGICAL SIGNIFICANCE

Fossil Mammals as Paleoecological Indicators

The Pleistocene Forest Refugia Model was based primarily on the distribution of living plants, reptiles, butterflies, and birds, and is considered the best hypothesis for explaining the high diversity of the Amazonian rain forest biota (Whitmore & Prance, 1987). In this context the obvious advantage of studying fossil mammals is that they directly sample past environments. On the other hand, mammals, particularly extant ones, do not precisely represent the structure of the surrounding vegetation in the sites of their deposition. "Classifying living mammals into categories according to the utilization of certain environmental substrates and according to dietary preferences is fraught with difficulty" (Eisenberg, 1981:247). In order to develop reasonable inferences about mammal habitats in estimating the environments of Pleistocene mammal assemblages, I will apply the following four kinds of evidence for each Pleistocene mammal taxon.

1) Present ecology of living species or closely related living species;

2) Authoritative opinions of other paleontologists based on other sites;

3) Morphological adaptations insofar as they suggest a preferred environment, e.g. "grazing dentition";

4) Analogous taxa and analogous assemblages from other continents.

Edentata/Pilosa

The Megatheriidae are present in the three river sections under study (Table 4). The huge Eremotherium was described from the Juruá River by Paula Couto (1956), Rancy (1981), and Simpson and Paula Couto (1981). Hoffstetter (1952) reported the genus from Napo River and Marshall et al. (1984) recorded the presence of Eremotherium in the area of the Ucayali River. In the collection of the Laboratório de Pesquisas Paleontológicas of the Universidade Federal do Acre, hereafter called LPP collection, Eremotherium is represented by the following: UFAC 096 (right metacarpus IV), UFAC 098 (left mandibular ramus), UFAC 099 (right tibia), UFAC 100 (left astragalus), UFAC 101 (distal portion of a left humerus), UFAC 108 (Left M^5), UFAC 118 (right radius).

Eremotherium ranged from tropical South America to the southern United States (Kurtén & Anderson, 1980; Paula Couto, 1979) and is relatively common in Pleistocene sediments of Central America as well as in the state of Florida as attested by the magnificent collection of the Florida Museum of Natural History, Vertebrate Paleontology Range.

Eremotherium, along with its sister taxon Megatherium, was the largest ground sloth and weighed about four tons. As shown first by Owen (1842), this animal used its strong tail and powerful hind limbs to maintain a bipedal position and grasped tree branches with its robust front claws while browsing. The quadrupedal posture supposedly was used to walk and to forage. Its huge, ever-growing (hypselodont) teeth with two transverse shearing crests per molar clearly provided an effective chopping mill for leaves and other plant matter.

The Mylodontidae are well represented in the Pleistocene American fauna, ranging from Patagonia in South America to the state of Washington in the United States (Kurtén & Anderson, 1980). Of all the ground sloths, this group is considered to be the most adapted to grazing (Coombs, 1983; Salmi, 1955). This is particularly evident in the genus Lestodon, with its wide symphysial area, presumably indicating its ability to take large mouthfuls of grass. Such an adaptation is characteristic of relatively indiscriminate grazers such as the white or square-lipped rhinoceros (Cerathotherium simum) (Owen-Smith, 1988). The

Mylodontidae in the western Amazon are represented by three (possibly four) genera, from Juruá and Napo rivers. Glossotherium was described by Paula Couto (1983b), Rancy (1981), and Simpson and Paula Couto (1981). Lestodon was cited by Paula Couto (1956), although Cartelle (1989) considered the genus restricted to south Brazil. Paula Couto (1956, 1983b) and Simpson and Paula Couto (1981) recorded the presence of Scelidotherium from the Juruá River. Although Mylodon was reported by Spillmann (1949), from Napo River, Hoffstetter (1952) denied its presence in Ecuador and regarded all the materials as Glossotherium. Whether or not this fourth genus is confirmed to occur in the western Amazon, the Mylodontidae were well represented in the area, leading to a strong paleoecological inference that there was extensive open landscape in the region during some significant interval of the late Pleistocene (Webb, 1978). In the LPP collection, the Mylodontidae are represented by UFAC 063 (left caniniform M^1), UFAC 082 (right M^5), UFAC 091 (left tibia), UFAC 102 (left humerus), UFAC 103 (left humerus).

Sloths of the family Megalonychidae were described by Simpson and Paula Couto (1981) on the basis of materials, housed at the American Museum of Natural History from the Juruá River region. Megalonyx "is known mainly from the Pleistocene of North America, where it ranged as far north as Alaska, but it has also been found in the Amazon basin," as noted by Simpson (1980:90). In the LPP collection, the following materials are probably referable to Megalonychidae: UFAC 067 (molariform tooth), UFAC 074 (right M_2), UFAC 077 (molariform tooth).

The fourth family of sloths was recorded from the western Amazon when Frailey (1986) described the skull and related the discovery of a complete skeleton of Nothropus from the Acre River area. The presence of Nothropus, as supposed by Frailey (1986), would have been extremely important because the genus is closely related to Nothrotheriops, a taxon from arid habitats of North America, with direct evidence of its diet from cave dung (Hansen, 1978). Further investigation shows that Frailey (1986) misidentified this genus; instead, as clearly demonstrated in Chapter 4, this nothrothere is a new Miocene taxon related to the genus Pronothrotherium (Figure 15).

Edentata/Cingulata

Shelled edentates are represented in the western Amazon by eight genera (Figure 16). Glyptodon was reported from the Napo and Ucayali rivers by Spillmann (1949) and from Juruá River by Paula Couto (1983a). Rancy (1981) described Pampatherium from the Juruá River, Willard (1966) reported the presence of Hoplophorus in the Ucayali River, and Paula

Fig. 15 - Occurrences of Ground Sloths (Edentata/ Pilosa), during the Pleistocene: 1- Marshall et al., 1984; 2- Spillmann, 1949; 3- Hoffstetter, 1952; 4- Marshall et al., 1984; 5- Rancy, 1981; 6- Simpson & Paula Couto, 1981; 7- Paula Couto, 1983b; 8- Paula Couto, 1956; 9- Paula Couto, 1960; 10- Vertebrate Fossil Collection, Universidade do Amazonas (Manaus); 11- Vertebrate Fossil Collection, Museu do Estado de Rondonia (Porto Velho).

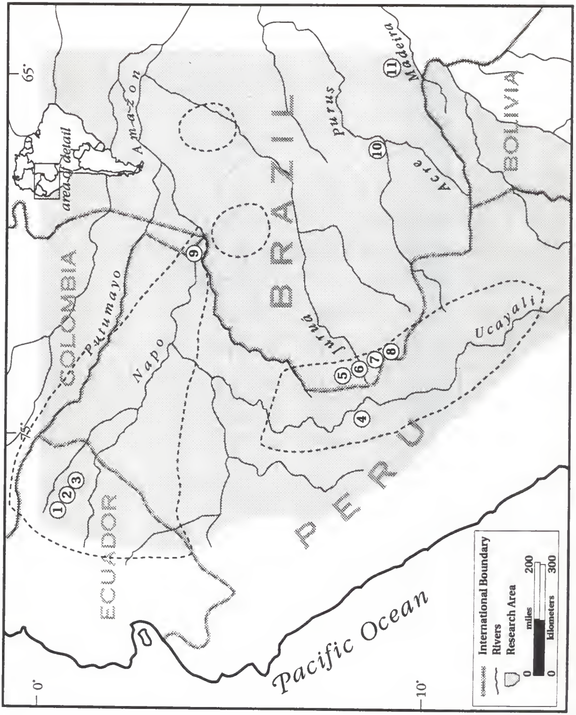
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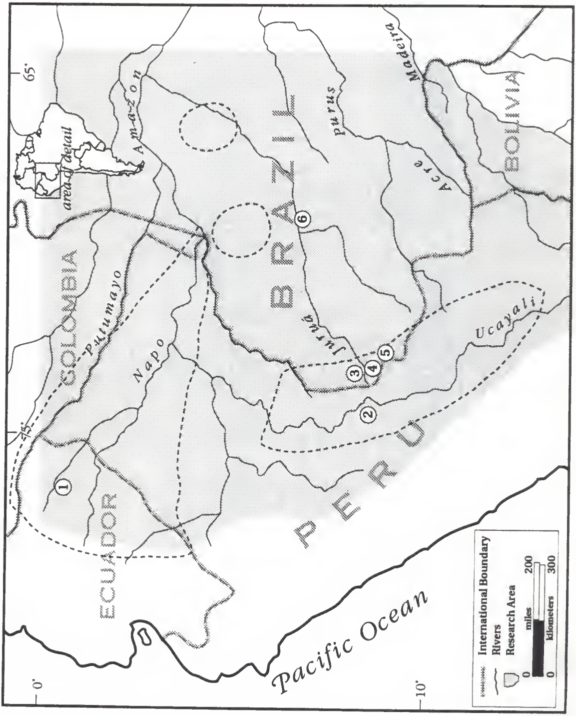
Fig. 16 - Occurrences of Edentata/Cingulata during the Pleistocene;
1- Spillmann, 1949; 2- Willard, 1966; 3- Paula Couto, 1956;
4- Rancy, 1981; 5- Paula Couto, 1983a; 6- Roxo, 1937.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Couto (1983a) recognized that genus from the Juruá River. Euphractus, Propraopus, Dasypus, Neuryurus and Panocthus were described from the Juruá River by Paula Couto (1956, 1983a).

As noted by Simpson (1980:87), the Glyptodontidae were characterized by

> uniformly deep and short skulls and jaws, the presence of a descending spikelike process from the cheekbone below the eye, the strong, heavily muscled legs, longer behind than in front, and the stout, blunt, almost hooflike claws. All were herbivorous and probably ate coarse, abrasive plants such as siliceous pampa grasses.

The LPP collection includes the following osteoderms of Glyptodontidae UFAC 022, UFAC 024, UFAC 025, UFAC 026, UFAC 1082, UFAC 1153, UFAC 1199, UFAC 1204.

Pampatherium (Pampatheriidae) is a well-known extinct South American genus, represented in Florida by its sister taxon Holmesina (Edmund, 1987). It has a long cranium, at least eight bilobate molariform teeth in each jaw quadrant. These teeth have flat occlusal surfaces, suggesting that it was a consumer of coarse vegetation and was probably associated with savanna habitats.

The LPP collection includes the following osteoderms of Pampatheriidae: UFAC 023, UFAC 607, UFAC 861, and UFAC 1131. Dasypus is extant in the western Amazon with two species, D. kappleri and D. novemcinctus. Dasypus novemcinctus is broadly adapted to diverse habitats from thorn scrub and savanna to wet forest, with an enormous geographical range from the southeastern United States to central Argentina (Wetzel, 1985). On the other hand, *Dasypus kappleri* is a lowland rain forest animal (Emmons, 1990). The presence of *Dasypus* in the western Amazon during the Pleistocene (Paula Couto, 1983a) is not a good paleoecological indicator because the genus is adapted to a wide range of environments, from savanna to forest (Emmons, 1990; Wetzel, 1985).

Euphractus was described by Paula Couto (1983a), based on material from the Juruá River. Wetzel (1985:25) considered its optimal habitats to be "savanna, parkland, forest edge and steppe." The presence of *Euphractus* in the western Amazon, as proposed by Paula Couto (1983a), suggests a synchronous occurrence of savanna in that region during the late Pleistocene.

The distribution and ecology of the extant Dasypodidae are presented in Montgomery (1985). In the western Amazon, the group is represented today by four species: *Dasypus kappleri*, *Dasypus novemcinctus*, *Priodontes maximus* and *Cabassous unicinctus* (Emmons, 1990).

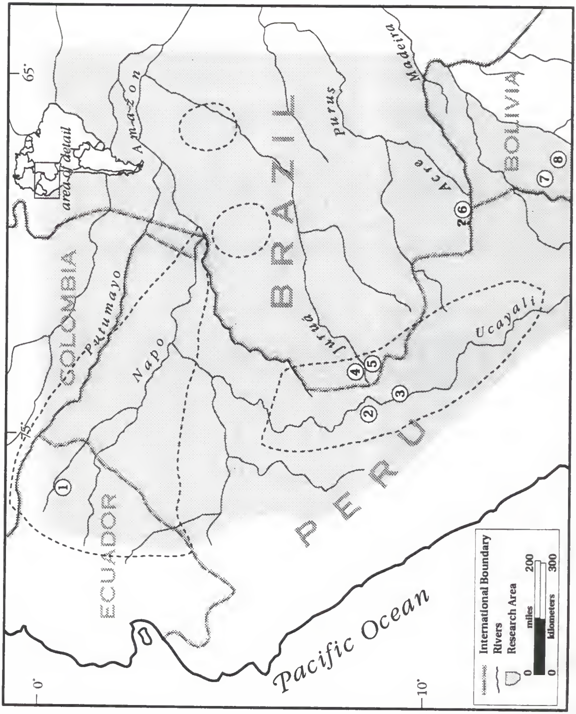
Notoungulata

The Toxodontidae were large mammals and were widely and abundantly represented in South America. The name of the family refers to the strong curvature of their ever-growing (hypselodont) upper cheek teeth. They "may have been partly amphibious, and they seem to have converged adaptively to a limited extent toward both rhinoceroses and hippopotamuses" (Simpson, 1980:131).

Toxodon, a common Pleistocene genus in the Pampas of Argentina, was reported from Ucayali River by Marshall et al. (1984) and Willard (1966), and was also described from the Juruá River by Paula Couto (1982) and Rancy (1981) .

Mixotoxodon was reported from the Juruá River by Paula Couto (1982a) and Rancy (1981). The identification of Mixotoxodon, a typical Pleistocene genus, by Radambrasil (1986:68), along the Acre River, needs to be carefully reexamined because our work in the area has revealed only fossils of Miocene age, and other Notoungulata were common at that time (Figure 17). It is important to note that Mixotoxodon was described from Pleistocene sites in Argentina, Venezuela, El Salvador, and Honduras by Marshall et al. (1984), Van Frank (1957), and Webb & Perrigo (1984), respectively. The presence of Mixotoxodon with large ever-growing (hypselodont) teeth is evidence that it was adapted to consuming abrasive grasses and suggests a continuum of

Fig. 17 - Occurrences of Notoungulata/Toxodontidae, during the Pleistocene: 1-Spillmann, 1949; 2- Marshall et al., 1984; 3- Willard, 1966; 4- Rancy, 1981; 5- Paula Couto, 1982b; 6- Radambrasil, 1976; 7- Marshall et al., 1984; 8- Marshall et al., 1984.



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open habitat during the late Pleistocene from Argentina to Central America along the eastern side of the Andes (Webb, 1978; Webb & Perrigo, 1984).

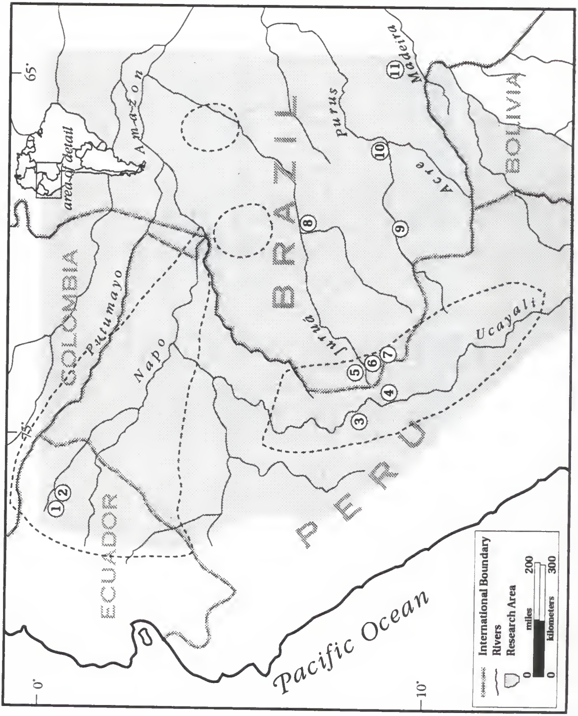
Although the LPP collection of Notoungulata is outstanding, most specimens represent the Miocene epoch. The following specimens, however, are assigned to Mixotoxodon and are therefore considered to be Pleistocene in age: UFAC 142 (left I^1), UFAC 052 (right M_2), UFAC 085 (right I^1).

Proboscidea/Gomphotheriidae

The family Gomphotheriidae dispersed from North America during the time of the Great American Biotic Interchange and then became abundant in the Pleistocene of South America, where it is represented by three genera, namely Stegomastodon, Haplomastodon, and Cuvieronius (Patterson & Pascual, 1972; Stehli & Webb, 1985). The latter two genera occur in the western Amazon (Figure 18). Haplomastodon is known from three rivers (Juruá, Napo, and Ucayali), and Cuvieronius (=Cordillerion Osborn, 1926) occurs in the Napo River (Hoffstetter, 1952; Marshall et al., 1984; Rancy, 1981; Simpson & Paula Couto, 1957, 1981; Spillmann, 1949; Willard, 1966).

As the name implies, mastodonts have mammary gland-like cusps on their molar teeth. Their large size and broadly adapted masticatory apparatus indicate a wide-ranging

Fig. 18 - Occurrences of mastodonts (Proboscidea/Gomphoteriidae) during the Pleistocene: 1- Spillmann, 1949; 2- Hoffstetter, 1952; 3- Willard, 1966; 4- Marshall et al., 1984; 5- Simpson & Paula Couto, 1957; 6- Rancy, 1981; 7- Paula Couto, 1956; 8- Roxo, 1937; 9- Paula Couto, 1956; 10- Vertebrate Fossil Collection, Universidade do Amazonas (Manaus); 11- Vertebrate Fossil Collection, Museu do Estado de Rondonia (Porto Velho).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association with forest and savanna-like habitats. On the other hand, Owen-Smith (1988:99) pointed out that "the extinct mammoths and grazing gomphotheres such as Stegomastodon, which from their dentition were adapted for a diet of fine grass leaves, most probably resembled the grazing rhinos in having a relatively efficient hindgut fermentation." Janzen and Martin (1982) noted their possible important role in dispersing the seeds of tropical palms such as Sheelea.

Simpson and Paula Couto (1957) reviewed the abundant and widespread material of gomphotheres from Brazil and concluded that only a single taxon, Haplomastodon waringi, lived in the tropical part of Brazil, including the western Amazon. On the other hand, one molar (DGM-541-M) in the collection of DNPM in Rio de Janeiro suggests the presence of Cuvieronius in the upper Juruá River as observed by Llewellyn Ivor Price's field notes (Paula Couto, 1976b). The most diagnostic difference between the two genera is the spiral distribution of enamel along the tusks of Cuverionius; in the absence of tusk material, positive identification of the latter genus remains dubious.

The LPP collection of Gomphotheriidae includes UFAC 093 (atlas), UFAC 095 (right M_3), UFAC 104 (right M_2), UFAC 1212 (right M^2), UFAC 1213 (left mandibular ramus with M_3), UFAC 1214 (left M_2).

Artiodactyla

During the Pleistocene in South America, the Camelidae were more widespread than today (Paula Couto, 1979). Abundant material of Palaeolama, recovered from caves of the Caatinga realm of northeast Brazil, is housed in very well preserved condition, at the Museu de Paleontologia of the Pontifícia Universidade Católica de Minas Gerais (PUC--MG). Extant relatives of this genus, Lama and Vicugna, extended in historic times along the Andean chain from Colombia southward and onto the plains of Patagonia in the southern extremity of South America; Lama guanicoe extended into the Pampas of Argentina as far eastward as Buenos Aires (Franklin, 1982; Mares et al., 1989).

Simpson and Paula Couto (1981) and Rancy (1981) reported both Vicugna and Palaeolama along the Juruá River. Both genera constitute the strongest evidence of drier conditions and savanna-like vegetation with Gramineae in the region during the late Pleistocene. Hershkovitz (1972:392) pointed out that "the American camelids are hardy and thrive in pastures and climates where introduced domestic cattle cannot live." The Camelidae are represented in the LPP collection by a single left P^4 (UFAC 061).

Two species of Tayassuidae, Tayassu pecari and Tayassu tajacu, live at present in the Amazon basin. The family has a modern geographical range from the southwest United States to northern Argentina (Eisenberg, 1989), almost comparable to the distribution of Dasypus. The presence of the genus Tayassu, with relatively brachydont dentition, in the Pleistocene of the western Amazon was reported by Rancy (1981), Simpson and Paula Couto (1981), Spillmann (1949), and Willard (1966). There may be an environmental resemblance between the Pleistocene of the western Amazon and the Chaco of Argentina and Paraguay where the surviving genera Tayassu and Catagonus, with its more lophodont dentition, are both important elements of the Chacoan biota.

Fossils of Tayassu in the LPP collection are represented by UFAC 006 (right tibia), UFAC 008 (right radio-ulna), UFAC 011 (distal portion of right femur), UFAC 016 (left tibia), UFAC 031 (left mandibular ramus), and UFAC 032 (right mandibular ramus).

Perissodactyla

The family Tapiridae survives today in the western Amazon. Tapirs are well represented as fossils in the Pleistocene of the Ucayali and Juruá River areas (Marshall et al., 1984; Rancy, 1981; Simpson & Paula Couto, 1981).

All of the extant forms seem to be browsers and frugivores. All are tropical but may range to high elevations. Tapirus pinchaque habitually is found at elevations exceeding 1,000 m. On the other hand, Tapirus indicus is a lowland species, associated with streams and lacustrine environments in southeast Asian forested habitats. Gallery forests may allow Tapirus terrestris to penetrate seasonally arid areas in South America, such as the Chaco and Cerrado (John Eisenberg, personal communication). Emmons (1990:156) pointed out that Tapirus terrestris is "found in rain forest, gallery forest, and more open grassy habitats with water and thick vegetation for refuge." Kent Redford (personal communication) found evidence of the presence of Tapirus terrestris in a dry (500 mm per year) area of the Chaco in Paraguay.

The presence of Tapirus in the western Amazon during the Pleistocene fits, in a broad sense, with indications of savanna with riparian vegetation along water courses in the area. The LPP collection of Tapirus is composed of UFAC 034 (right mandibular ramus), UFAC 035 (right mandibular ramus-juvenile), UFAC 043 (right femur), and UFAC 1150 (left mandibular ramus with P_3).

Summary

The presence of such extinct mammals as Toxodontidae, Camelidae, Gomphotheriidae, Megatheriidae, and Glyptodontidae in the western Amazon constitutes strong evidence suggesting an open landscape and/or a savanna-like habitat at least during some interval of the Pleistocene.

Table 12 lists the genera of Pleistocene mammals presently known from the western Amazon region. Many of these same genera range into south temperate parts of Argentina including Patagonia.

In a review of the Pleistocene mammals and climate of South America, Pascual and Jaureguizar (1990) recognized the strong relationship between mammal megafauna and environment during the late Pleistocene. A similar conclusion can be drawn for the late Pleistocene of the western Amazon, based on the abundance of pastoral mammals. The contrast with present conditions, however, is far more extreme in the Amazon than in the open landscape of Brazil and Argentina.

The Paleo-Mammal Community Contrasted with the Present Community

Table 13 is a list of extant species in the western Amazon (body mass more than 1 kg) and it is based on the geographical distribution given by Emmons (1990). The dietary specialization is based on Robinson and Redford (1989). Aquatic and semiaquatic forms, such as *Inia*, *Trichechus*, *Sotalia*, *Lutra*, and *Pteronura* are excluded from this list. Table 13 is useful for contrasting present-day species with the actual state of knowledge of Pleistocene mammalian fauna of the western Amazon, as presented in the Table 12.

Table 12 - Known Pleistocene mammals of western Amazon
Body mass more than 1 kg

Genera	Habitat	Diet
EDENTATA-PILOSA		
Eremotherium	Forest edge/savanna	Grass/browse
Ocnopus	Forest edge/savanna	Grass/browse
Glossotherium	Savanna	Grass/browse
Lestodon	Savanna	Grass/browse
Scelidotherium	Savanna	Grass/browse
Mylodon	Savanna	Grass/browse
Megalonyx	Savanna	Grass/browse
EDENTATA-CINGULATA		
Propraopus	Forest edge/savanna	Omnivore
Dasypus	Forest/savanna	Insectivore
Euphractus	Savanna	Omnivore
Pampatherium	Savanna	Grass
Hoplophorus	Savanna	Grass
Neuryurus	Savanna	Grass
Panocthus	Savanna	Grass
Glyptodon	Savanna	Grass
NOTOUNGULATA		
Toxodon	Savanna	Grass/low browse
Mixotoxodon	Savanna	Grass/low browse
PROBOSCIDEA		
Cuvieronius	Savanna	Grass/browse/fruit
Haplomastodon	Savanna	Grass/browse/fruit
PERISSODACTYLA		
Tapirus	Forest/savanna	Browse/fruit
ARTIODACTYLA		
Vicugna	Savanna	Grass/low browse
Palaeolama	Savanna	Grass/low browse
Tayassu	Forest/savanna	Omnivore/frugivore
CARNIVORA		
Eira	Forest	Carnivore

Table 13 - Extant mammalian species from the western Amazon
Body mass more than 1 kg

Taxa	Habitat	Diet
DIDELPHIDAE		
Didelphis marsupialis	Forest/savanna	Frugivore/omnivore
DASYPODIDAE		
Cabassous unicintus	Forest/savanna	Myrmecophage
Priodontes maximus	Forest/savanna	Myrmecophage
Dasypus novemcinctus	Forest/savanna	Insectivore-omnivore
Dasypus kappleri	Rain forest	Insectivore-omnivore
BRADYPODIDAE		
Choloepus didactylus	Forest	Herbivore-browser
Choloepus hoffmanni	Forest	Herbivore-browser
Bradypus variegatus	Forest/savanna	Herbivore-browser
MYRMECOPHAGIDAE		
Myrmecophaga tridactyla	Forest/savanna	Myrmecophage
Tamandua tetradactyla	Forest/savanna	Myrmecophage
CEBIDAE		
Alouatta seniculus	Forest	Frugivore-herbivore
Aotus trivirgatus	Forest	Frugivore-omnivore
Callicebus moloch	Forest	Frugivore-omnivore
Cebus apella	Forest	Frugivore-omnivore
Cebus albifrons	Forest	Frugivore-omnivore
Pithecia monachus	Forest	Frugivore-omnivore
Ateles paniscus	Forest	Frugivore-herbivore
Ateles belzebuth	Forest	Frugivore-herbivore
Lagothrix lagothricha	Forest	Frugivore-herbivore
Saimiri sciureus	Forest	Frugivore-omnivore
Cacajao calvus	Forest	Frugivore-omnivore
ERETHIZONTIDAE		
Coendou prehensilis	Forest/savanna	Frugivore-granivore
Coendou bicolor	Rain forest	Frugivore-granivore
DASYPROCTIDAE		
Dasyprocta fuliginosa	Forest/savanna	Frugivore-granivore
Myopocta pratti	Rain forest	Frugivore-granivore
Agouti paca	Forest/savanna	Frugivore-granivore
HYDROCHAERIDAE		
Hydrochaeris hydrochaeris	Savanna/forest	Herbivore-browser
DINOMYDAE		
Dinomys branickii	Forest	Frugivore-granivore

Table 13 - Continued

Taxa	Habitat	Diet
PROCYONIDAE		
Procyon cancrivorous	Forest/savanna	Frugivore-omnivore
Potos flavus	Forest	Frugivore-omnivore
Nasua nasua	Forest/savanna	Frugivore-omnivore
Bassaricyon gabbi	Forest	Frugivore-omnivore
CANIDAE		
Atelocynus microtis	Forest	Carnivore
Speothos venaticus	Forest/savanna	Carnivore
MUSTELIDAE		
Galictis vittata	Forest/savanna	Carnivore
Eira barbara	Forest	Carnivore
FELIDAE		
Felis pardalis	Forest/savanna	Carnivore
Felis wiedii	Forest/savanna	Carnivore
Felis yagouaroundi	Forest/savanna	Carnivore
Felis concolor	Forest/savanna	Carnivore
Panthera onca	Forest/savanna	Carnivore
TAPIRIDAE		
Tapirus terrestris	Forest/savanna	Frugivore-herbivore
TAYASUIDAE		
Tayassu tajacu	Forest/savanna	Frugivore-herbivore
Tayassu pecari	Forest/savanna	Frugivore-herbivore
CERVIDAE		
Mazama americana	Forest/savanna	Frugivore-herbivore
Mazama gouazoubira	Forest/savanna	Frugivore-herbivore
LEPORIDAE		
Sylvilagus brasiliensis	Forest/savanna	Herbivore-grazer

Arboreal mammals, such as Cebidae, Bradypodidae, Erethizontidae, and Procyonidae, represent the group with the maximum adaptation to living in the forest realm. The scansorial group, in the western Amazon, is composed of *Didelphis*, *Tamandua*, *Eira*, and *Felis wiedii*.

The Dasypodidae, Dasyproctidae, Canidae, Tapiridae, Tayassuidae, Cervidae, and Leporidae are strictly terrestrial. On the other hand, Myrmecophagidae, Mustelidae, and Felidae represent adaptations for both terrestrial and scansorial behavior. The scansorial and terrestrial groups are as successful in the savanna as in the forest habitat (August, 1983; Fonseca & Redford, 1984).

During the Pleistocene, the western Amazon was dominated by large and extremely large edentates and ungulates, such as *Toxodon*, *Haplomastodon*, *Eremotherium*, *Mixotoxodon*, *Pampatherium*, *Glyptodon*, and *Palaeolama*. These genera are characteristic of a savanna habitat, and according to their dental morphology as compared to analogous forms in extant and extinct faunas in other parts of the American continents they are recognized as browsers and grazers. These megaherbivores vanished at the end of the Pleistocene.

Some of the mammals described as fossils in the western Amazon continue to live in the area as survivors of the late Pleistocene extinction. Examples are *Tapirus*, *Tayassu*, Dasypus, and Eira. All of these taxa are widely adapted, ranging from rain forest to deciduous forest, cerrado, chaco and caatinga.

The last extinction supposedly occurred in the western Amazon during the transition from the late Pleistocene to the early Holocene epochs approximately 10,000 years B.P. Radambrasil (1976, 1977) documented Pleistocene landforms in the area of the state of Acre that are characteristic of a dry climate with little or no vegetative cover. Damuth and Fairbridge (1970) independently arrived at a similar conclusion (semi arid climate in the Amazon) based on their studies of sediments in the Amazon River delta, which consisted of extensive eolian sands. If these observations are correct, the most probable place to support relictual forest vegetation and refuges for forest fauna, at low elevation up to 160 m above sea level, was the riparian or gallery forest along the edges of rivers.

CHAPTER 6
DISCUSSION AND CONCLUSIONS

Discussion

Most of the fauna described from the late Pleistocene of the western Amazon belong to groups related to an open-country habitat, which could be referred as savanna grazers (Table 12). This finding supports the general hypothesis of the retreat of the forest at least during glacial times of the Pleistocene (Ab'Saber, 1977). In his study of the paleofauna of the state of Acre, Paula Couto (1982a:7) stated that "the Hylaea seems to be of relatively recent origin, for that fauna was not adapted to the life in so dense forest. It was perhaps a fauna of savanna."

Most of the Pleistocne taxa that became extinct were essentially grazers or animals predominantly of savanna habitat (Table 12). On the other hand, the extant survivors are forest mammals or animals with the ability to thrive in both forested and savanna habitats alike (Table 13).

The geographic distribution of the postulated Pleistocene Forest Refugia, in light of this fossil evidence, needs to be reconsidered carefully. To illustrate the Napo River paleofauna is composed of Glyptodon, Eremotherium, Mylodon, Haplomastodon, Cuvieronius, and

Tayassu, a set of large mammals well adapted for a predominantly open-country, savanna, or savanna-like habitat. This same area has been postulated as a Pleistocene refugium for a biota ecologically adapted to a tropical rain forest (Haffer, 1969; Prance, 1973, 1978).

The Juruá River in the state of Acre contributed the largest sample of fossil mammalian taxa (23 genera), the majority of which were large and characteristic of an open habitat; the Camelidae, Palaeolama and Vicugna, provide particularly strong evidence of savanna-adapted genera. The primary reason for this apparent abundance of large mammals in this region is that it has received more paleontological attention than other parts of the Amazon. This section of the upper Juruá also is situated in a proposed forest refugium, the East Peruvian Pleistocene Refugium of Prance (1973), and is supposedly a center of endemism for numerous tropical rain forest species (Whitmore & Prance, 1987).

The Pleistocene fauna of the Ucayali River, also in the area of the proposed East Peruvian Pleistocene Refugium, is composed of probable open-country grazers and browsers, such as Eremotherium, Haplomastodon, Glyptodon, and Toxodon. The presence of Tayassu, Tapirus, and a Dasypodidae, animals of forest and savanna environments, however, does not weaken the idea of a partly forested (or mixed) habitat with the possibility of strips of gallery forest.

The application of the Pleistocene Forest Refugia Model as a fundamental basis for planning and demarcating units for conservation in South America (Lovejoy, 1982), on the other hand, is not totally invalid, but needs to be taken with some caution, at least in the western Amazon. The high biodiversity of the so-called Pleistocene Forest Refugia in the lowland rain forest may be explained as a temporary condition of supersaturated disequilibrium following recent mingling of forest biota. Recent geological events may have drastically altered environments and their exact positions in the western Amazon (Campbell & Frailey, 1984; Räsänen et al., 1987), just as post-Pleistocene shifts have followed the retreating glaciers and altered climatic zones in North America. As examples, the paleofauna of the Napo River and the East Peruvian Refugia (encompassing the middle Ucayali River and the upper Juruá in the state of Acre) tends to discredit the Pleistocene Forest Refugia Model. The vertebrate fauna of these two supposed refugia during the Pleistocene was more predominantly adapted to savanna habitats.

The persistent presence of gallery forests along many of the Amazonian rivers is probably more important than the supposed Pleistocene Forest Refugia as an explanation for the high diversity of flora and fauna in the western Amazon. Murça Pires (1984:599) pointed out that "if forest contractions occurred due to climatic changes in the past, the residual areas would not take the shape of round islands as they are commonly figured in the literature, rather, they would accommodate themselves to the dendritic pattern of river drainage." This point of view is in accordance with the observations of August (1983) and Fonseca and Redford (1984), who postulated that ribbons of gallery forest support much of the mammalian fauna in the llanos of Venezuela and in the cerrado of central Brazil, respectively. The current treatise is not the final word on the Pleistocene mammals of the western Amazon but, instead, is a contribution from a new set of data that should be considered in conjunction with other complementary geological and biological evidence. The integration of many approaches, including fossils mammals, palynology, soils, and sediments will be required to reconstruct the complex history of the Amazon paleoenvironment. As stated by Webb (1977:356), "The present is surely the key to the past, but one may assert also with good reason, that the past is the key to the present."

Conclusions

This treatise represents the first scientific effort to summarize and review the Pleistocene vertebrate paleofauna of the western Amazon for the purpose of empirically testing the Pleistocene Forest Refugia Model. The presence of a rich grazer/browser paleofauna in the western Amazon supports the hypothesis of expanded savanna during glacial phases of the Pleistocene (Ab'Saber, 1977). Some fossil occurrences directly contravene some of the supposed rain forest refugia, particularly the East Peruvian and Napo River refugia of Haffer (1969) and Prance (1973).

These new data suggest that a savanna-type domain extended across most of the lowlands of the western Amazon and linked the llanos of the Orinoco to the llanos of Moxos (Bolivia) and south to the Gran Chaco and pampas of Argentina during at least some intervals of the Pleistocene. This hypothesis rests on the evidence of an open-country-adapted mammalian paleofauna, including *Eremotherium*, *Toxodon*, *Palaeolama*, *Vicugna*, *Glyptodon*, *Pampatherium*, *Mixotoxodon* and *Haplomastodon*.

These conclusions are in harmony with the view that "forest and nonforest refugia should not be identified only on the basis of biological data such as centers of endemism, but rather on the basis of geoscientific data" (Haffer, 1981:411).

If, as suggested by Colinvaux (1989) and Haffer (1981), the temperature in the tropical lowlands of South America during glacial times was 3° C to 6° C lower than today, its effect was strong enough to result in some physiological constraints on both flora and fauna. Notably even today, the "friagem" can result in a temperature decrease to 10° C for two or three days several times a year during the winter season in the western Amazon. Mercer and Palacios (1977) suggested a decrease in temperature of about 6° C in the Peruvian Amazon during glacial intervals based on the study of Andean glaciers and ice caps. Bush et al. (1990) pointed out that the lowland western Amazon (Napo Refugium) during the late Pleistocene would therefore have been submitted to freezing temperatures. Speculatively, if one subtracts the 4.5° C temperature projected for glacial times from the present minimum cold front temperature of 10° C, the temperature could have dropped to about 5° C for short intervals several times a year over the entire Amazon.

If these inferences regarding temperature drops are accurate, the presence of a savanna woodland biota in the Amazon during episodes of cold, dry climates associated with glacial phases of the Pleistocene appears quite probable.

Near future will undoubtedly yeld more information about the Cenozoic paleovertebrates of the Amazon. The screen-washing technique should prove valuable for recovering small rodents, which are considered the best paleoenvironmental indicators for mammals. The task of gathering data to fill in some of the pieces of this huge puzzle is in its infancy. Vertebrate paleontologists will have an opportunity to contribute to the discussion and to help advance our understanding of the evolution of tropical lowland rain forest biota of South America. In the meantime, it appears most plausible, as reflected by mammalian fossil evidence, that the Pleistocene fauna of the western Amazon was an admixture of forest and savanna species, a factor leading to the high diversity of the mammals in this region of the Neotropics.

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BIOGRAPHICAL SKETCH

Alceu Rancy was born on December 12, 1949, in Espumoso, state of Rio Grande do Sul, Brazil. He is married to Cleusa Maria Damo Rancy and is the father of three children, Bianca (born in Rio Branco in 1978), Tiago Juruá (born in Porto Alegre in 1980), and Thomas Augusto (born in Rio Branco in 1984).

In August 1978, Alceu graduated as a Licenciado in geography from the Universidade Federal do Acre. In August 1981, he received a master's degree in geosciences from the Universidade Federal do Rio Grande do Sul under the orientation of the late Professor Carlos de Paula Couto. From 1981 to 1986, he taught vertebrate zoology and paleontology at the Universidade Federal do Acre and organized the paleontological research laboratory. In 1987, he was granted a scholarship for graduate studies at the University of Florida by the National Research Council of Brazil--CNPq. He is a member of the Brazilian Society for the Progress of Science, the Brazilian Society of Zoology, the Brazilian Association of Geographers, the Brazilian Society of Paleontology, the American Society of

Mammalogists, and the Society of Vertebrate Paleontology. He also is affiliated with the Los Angeles County Museum of Natural History as an Associate Researcher in Vertebrate Paleontology.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg

John F. Eisenberg, Chair
Katharine Ordway Professor of
Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

S. David Webb

S. David Webb
Professor of Zoology and Geology

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Kent H Redford

Kent H. Redford
Assistant Professor of Latin
American Studies

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Bruce J MacFadden

Bruce J. MacFadden
Professor of Zoology and Geology

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Ronald F. Labisky

Ronald F. Labisky
Professor of Forest Resources and
Conservation

This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Director, Forest Resources and
Conservation

Dean, Graduate School