MAMMALS AND STRATIGRAPHY : GEOCHRONOLOGY OF THE CONTINENTAL MAMMAL-BEARING QUATERNARY OF SOUTH AMERICA

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ABSTRACT

Previous chronological arrangements of South American Quaternary land mammal faunas are appraised on the basis of current geological and paleontological data. Three South American late Pliocene-Pleistocene land mammal ages are conventionally recognized, from oldest to youngest, the Uquian, Ensenadan, and Lujanian ; all are defined on Argentine faunas.

The Uquian is based fundamentally and historically on the fauna from the Uquía Formation in Jujuy Province, northwestern Argentina. Important known formations in Argentina yielding Uquian Age faunas include the subsurface Puelche Formation (or *Puelchense*) near the city of Buenos Aires, and the Barranca de Los Lobos and Vorohué Formations between Mar del Plata and Miramar, Buenos Aires Province. A tentative subdivision is proposed for the Uquian into three subages based on knowledge of the Mar del Plata-Miramar sequence, from oldest to youngest, the Barrancalobian, Vorohuean, and Sanandresian. In Argentina the Uquian is presently marked by the first known record of *Scelidodon, Hydrochoeropsis, Ctenomys*, Canidae, Ursidae, Gomphotheriidae, Equidae, Tapiridae, Camelidae, Cervidae, and the last known record of *Thylatheridium, Thylophorops, Dankomys, Eumysops, Pithanotomys, Eucoelophorus*, Hegetotheriidae, Sparassocynidae, and Microtragulidae.

The Ensenadan Age is based on the fauna from the Ensenada Formation near the city of Ensenada, Buenos Aires Province. In Argentina the Ensenadan is marked by the first known record of *Lomaphorus, Neothoracophorus, Plaxhaplous, Cavia, Lyncodon, Lutra, Galera, Smilodon, Dicotyles, Lama, Vicugna*, the last known record of *Orthomyctera*, and the only known record of *Brachynasua*.

Typical beds of late Lujanian Age in Argentina consist of fluvial deposits occupying stream channels, and shallow basins, often incised into beds of early Lujanian (*i.e.* Bonaerian of early workers) and Ensenadan Age. The Lujanian Age is based on a fauna from beds along the Río Luján, about 65 km west of the city of Buenos Aires, Buenos Aires Province. The Lujanian in Argentina is marked by the first record of *Equus, Chlamyphorus*, and *Holochilus*, and the last record of Megatherioidea, Glyptodontoidea, *Arctodus* (= *Arctotherium*), *Smilodon*, Litopterna, Notoungulata, Proboscidea, Equidae, *Morenelaphus*, and *Palaeolama*.

These land mammal ages are often difficult to recognize in other South American countries. The compositions of South American Pleistocene faunas vary with the environment. Some taxa were widely distributed in fossil deposits throughout the continent, but their occurrences need not reflect synchroneity. This is a result of changing climates and habitats in time. Consequently, proposed intracontinental correlations need confirmation based on magnetostratigraphy and a radioisotope time scale. Paleontologic characterizations of these land mammal ages (*i.e.* first and last record, and guide fossils) are useful for much of Argentina, but extensions to most of the other parts of South America are at best tenuous.

The majority of known non-Argentine Pleistocene faunas are believed to be Lujanian in age. Possible non-Argentine early Pleistocene (Uquian) faunas include Ayo Ayo and Anzaldo in Bolivia, and Cocha Verde in southern Columbia. A possible middle Pleistocene (Ensenadan or early Lujanian) fauna is the Chichense of Ecuador. Paleomagnetic and radioisotopic date (MacFadden *et al.*, 1983) clearly indicate that the greater part of the Tarija fauna (Bolivia) is Ensenadan in age.

The end of the Pleistocene and beginning of the Holocene in South America is marked by extinction of nearly all large mammalian herbivores and their specialized large predators. Radiocarbon age determinations suggest that large scale extinctions of megafauna occurred between 15,000 and 8,000 yrs. B.P. (years before present).

RÉSUMÉ

Les arrangements chronologiques antérieurement proposés pour les faunes mammaliennes terrestres du Quaternaire sud-américain sont évalués sur la base des données géologiques et paléontologiques actuelles. Dans la séquence Pliocène supérieur - Pléistocène de ce continent, trois unités biostratigraphiques (land mammal ages) sont reconnues d'après les faunes de mammifères terrestres ; ce sont, de la plus ancienne à la plus récente : l'Uquien, l'Ensénadien et le Lujanien ; toutes sont définies grâce à des faunes d'Argentine.

L'Uquien est fondamentalement et historiquement basé sur la faune de la Formation Uquia, dans la Province de Jujuy, Argentine Nord-Ouest. Parmi les autres formations argentines qui ont livré des faunes uquiennes, les plus importantes sont la Formation Puelche (ou Puelchense), connue en profondeur près de la ville de Buenos Aires, et les Formations Barranca de los Lobos et Vorohué, entre Mar del Plata et Miramar, Province de Buenos Aires. Un essai de subdivision de l'Uquien en trois «sous-âges» (subages) est proposé, sur la base de la séquence Mar del Plata - Miramar, qui comprend, de bas en haut : le Barrancalobien, le Vorohuéen et le Sanandrésien. En Argentine, l'Uquien est caractérisé par la présence des plus anciens représentants connus des genres ou familles *Scelidodon, Hydrochoeropsis, Ctenomys*, Canidae, Ursidae, Gomphotheriidae, Equidae, Tapiridae, Camelidae et Cervidae, et par celle des derniers *Thylatheridium, Thylophorops, Dankomys, Eumysops, Pithanotomys, Eucoelophorus*, Hegetotheriidae, Sparassocynidae et Microtragulidae.

L'Ensénadien est basé sur la faune de la Formation Ensenada, près de la ville éponyme, Province de Buenos Aires.

En Argentine, l'Ensénadien est caractérisé par la première mention des genres *Lomaphorus, Neothoracophorus, Plaxhaplous, Cavia, Lyncodon, Galera, Smilodon, Dicotyles, Lama, Vicugna*, la dernière mention d'*Orthomyctera*, et la présence de *Brachynasua*, qui semble propre à cette unité.

En Argentine, les couches typiques du Lujanien supérieur consistent en dépôts fluviatiles qui souvent ravinent les sédiments du Lujanien inférieur (= le Bonaérien des anciens auteurs) et de l'Ensénadien. Le Lujanien est basé sur une faune provenant des couches au long du Rio Lujan, environ 65 km à l'ouest de Buenos Aires, Province de Buenos Aires. En Argentine, le Lujanien est caractérisé par les premiers *Equus, Chlamyphorus* et *Holochilus* et par les derniers Megatherioidea, Glyptodontoidea, *Arctodus* (= *Arctotherium*), *Smilodon*, Litopterna, Notoungulata, Proboscidea, Equidae, *Morenelaphus* et *Palaeolama*.

Ces âges définis par des Mammifères terrestres sont souvent difficiles à reconnaître dans les autres pays d'Amérique du Sud. La composition des faunes pléistocènes de ce continent varie avec l'environnement. Quelques taxons étaient largement distribués dans les dépôts fossilifères du continent tout entier, mais leur présence n'indique pas nécessairement un synchronisme ; elle résulte de changements de climats et d'habitats au cours du temps. En conséquence, les propositions de corrélations intracontinentales nécessitent une confirmation basée sur la magnétostratigraphie, et aussi une échelle temporelle radioisotopique... Les caractéristiques paléontologiques de ces âges fondés sur les Mammifères terrestres (c'est-à-dire premières et dernières mentions de taxons, et fossiles guides) sont utilisables pour une grande part de l'Argentine, mais leur extension au reste de l'Amérique du Sud doit être faite avec beaucoup de prudence.

La plupart des faunes pléistocènes observées en Amérique du Sud, hors d'Argentine, semblent correspondre au Lujanien. Cependant, il est possible que des fossiles récoltés à Anzaldo et à Ayo Ayo (Bolivie) et à Cocha Verde (Colombie Sud) appartiennent au Pléistocène inférieur (= Uquien). D'autre part, la faune du Chichéen (Equateur) correspond probablement au Pléistocène moyen (Ensénadien ou Lujanien inférieur). Enfin des données paléomagnétiques et radioisotopiques (MacFadden *et al.*, 1983) démontrent clairement l'âge ensénadien de la majeure partie de la faune de Tarija (Bolivie).

En Amérique du Sud, la fin du Pléistocène et le début de l'Holocène sont marqués par l'extinction de presque tous les grands Mammifères herbivores et aussi de leurs grands prédateurs spécialisés. Des datations par le radiocarbone suggèrent que des extinctions massives de mégafaune ont eu lieu entre 15000 et 8000 ans avant l'Actuel.

RESUMEN

Las ordenaciones cronológicas ya propuestas para las faunas de mamíferos terrestres del Cuaternario sudamericano, se evalúan basándose en datos geológicos y paleontológicos actuales. En la secuencia Plioceno tardío-Pleistoceno de Sudamérica, se reconocen tres unidades bioestratigráficas (land mammal ages) basadas en faunas de mamíferos terrestres; éstas son, de abajo hacia arriba : Uquiense, Ensenadense y Lujanense, todas definidas por faunas argentinas.

El Uquiense está basado, fundamental e históricamente, en la fauna de la Formación Uquía, en la Provincia de Jujuy, Argentina noroeste. Entre las otras formaciones argentinas que contienen faunas de edad uquiense, las más importantes son la Formación Puelche (o Puelchense) conocida en el subsuelo cerca de la ciudad de Buenos Aires, y las Formaciones Barranca de los Lobos y Vorohué, entre Mar del Plata y Miramar, Provincia de Buenos Aires. Se propone una subdivisión tentativa del Uquiense en tres «sub-edades» (subages), basándose en la secuencia Mar del Plata - Miramar, que incluye, de abajo hacia arriba : Barrancalobense, Vorohuense y Sanandresense ; en Argentina, el Uquiense se caracteriza por la primera aparición conocida de *Scelidodon, Hydrochoeropsis, Ctenomys*, Canidae, Ursidae, Gomphotheriidae, Equidae, Tapiridae, Camelidae, Cervidae, y la última observación de *Thylatheridium, Thylophoros, Dankomys, Eumysops, Pithanotomys, Eucoelophorus*, Hegetotheriidae, Sparassocynidae y Microtragulidae.

El Ensenadense está basado en la fauna de la Formación Ensenada, cerca de la ciudad epónima, Provincia de Buenos Aires. En Argentina el Ensenadense se caracteriza por la primera aparición conocida de *Lomaphorus, Neothoracophorus, Plaxhaplous, Cavia, Lyncodon, Lutra, Galera, Smilodon, Dicotyles, Lama, Vicugna*, por la última mención de *Orthomyctera*, y por la presencia del género *Brachynasua*, aparentemente confinado en esta unidad.

En Argentina, las capas típicas del Lujanense tardío consisten en depósitos fluviátiles que frecuentemente rellenan canales de erosión o cuencas poco profundas, dentro de estratos pertenecientes al Lujanense temprano (o sea el Bonaerense de los autores antiguos) o al Ensenadense. El Lujanense está basado en una fauna procedente de capas situadas a lo largo del Río Luján, unos 65 km al oeste de la ciudad de Buenos Aires, en la Provincia homónima. En Argentina, el Lujanense está marcado por la primera aparición conocida de *Equus, Chlamyphorus y Holochilus* y por la última mención de Megatherioidea, Glyptodontoidea, *Arctodus* (=*Arctotherium*), *Smilodon*, Litopterna, Notoungulata, Proboscidea, Equidae, *Morenelaphus* y *Palaeolama*.

Frecuentemente resulta difícil reconocer en otros países sudamericanos estas Edades definidas por faunas de mamíferos terrestres. La composición de las faunas pleistocenas de Sudamérica varía con el medio ambiente. Algunos taxa están ampliamente repartidos en depósitos fosilíferos de todo el continente ; pero eso no implica necesariamente un sincronismo ; puede resultar de cambios de climas y habitats con el tiempo. Consecuentemente las proposiciones de correlaciones intracontinentales requieren confirmación basada en magnetoestratigrafía y en una escala temporal radioisotópica. Las características paleontológicas de estas Edades basadas en mamíferos terrestres (es decir primeras y últimas menciones de taxa, así como fósiles guías) son utilizables en casi toda Argentina, pero su extensión en los demás países sudamericanos exige bastante prudencia.

La mayor parte de las faunas pleistocenas sudamericanas conocidas fuera de Argentina, parecen corresponder al Lujanense. Sin embargo es posible que fósiles recolectados en Anzaldo y Ayo Ayo (Bolivia) y en Cocha Verde (Sur de Colombia) pertenezcan al Pleistoceno temprano (Uquiense). Por otra parte, la fauna del Chichense (Ecuador) se sitúa probablemente en el Pleistocene medio (Ensenadense o Lujanense temprano). Por fin, datos paleomagnéticos y radioisotópicos (MacFadden *et al.*, 1983) establecen claramente la edad Ensenadense de la mayor parte de la fauna de Tarija (Bolivia).

En Sudamérica, el final del Pleistoceno y el comienzo del Holoceno coinciden con la extinción de casi todos los grandes mamíferos herbívoros y de sus grandes predatores especializados. Dataciones por el radiocarbono sugieren que extinciones de megafauna en gran escala tuvieron lugar entre 15000 y 8000 años antes del Presente.

INTRODUCTION

Early in the 17th century, reports of huge bones and of dome-like shells from South America, thought to be the remains of giant creatures, had been carried to the outside world by Spanish chroniclers and friars. In the course of time, scientists in Europe identified these curiosities as the teeth and bones of animals long extinct. Some of these ***huesos de gigantes*** or bones of giants found their way into museums and were eventually studied, described, and named.

In 1787 the skeleton of an immense ground sloth was found at Luján about 65 km west of Buenos Aires, Argentina, by the Dominican Manuel Torres and taken that same year to Spain by the Marqués de Loreto. It was mounted at the Gabinete Real by J.B. Bru. Cuvier (1796, 1804) described and named it *Megatherium americanum* and reported it to have come from "Paraguay", a term which then designated a vast country including the basin of the Río Paraguay, but also a large part of present day Argentina (Hoffstetter, 1959, 1978). This was the first South American fossil mammal to be scientifically studied.

Shortly thereafter Alexander von Humboldt collected mastodon teeth which Cuvier (1806) recognized as three distinct species. *Mastodonte à dents étroites*, a name also used for a Miocene species from Simorre, France was applied to specimens collected from Colombia. *Mastodonte des Cordillères* and *Mastodon humboldien* were based respectively on specimens found at the foot of the Imbabura volcano, Ecuador and from Concepción, Chile (Hoffstetter, 1952, p. 159, 174-180).

D'Orbigny (1842) reports in the narrative of his South American travels between 1826 and 1833, that in the banks along the Río Paraná, Argentina, he found fossil remains of a large quadruped, the size of an ox, another the size of a cat (apparently of the order Carnivora), and a third of a rodent the size of a rat. In the same publication Laurillard described vertebrates recovered from the *limon pampéen* (a term created by d'Orbigny) from Argentina and a mandible of *Mastodon andium* from Tarija, Bolivia collected by N. Matson. Glyptodont remains collected by Sellow in 1826 from along the Río Arapey, northwestern Uruguay, were described by Weiss (1830) and d'Alton (1834). The genus *Glyptodon* (order Edentata) was described by Owen (1838, 1839) based on specimens collected by Charles Darwin from along the Río Matanzas and Río Salado south of Buenos Aires, Argentina (Hoffstetter, 1955).

In 1830 a large and diverse late Pleistocene-Holocene vertebrate fauna from the now famous caves of the Lagoa Santa region in the Río das Velhas Valley of eastern Brazil was discovered and reviewed in various papers by Peter Wilhelm Lund and later by Herluf Winge of Denmark.

Beginning in 1839, de Blainville published his monumental "Ostéographie", in which he figured specimens of *Smilodon, Mastodon, Macrauchenia, Toxodon*, and edentates based on collections made by von Humboldt in Colombia and Ecuador, Dombey in Peru, Claussen and A. St. Hilaire in Brazil, Gay in Chile, Vilardebó in Uruguay, and Muñiz and Dupotet in Argentina. Subsequently, specimens collected by Castelnau in 1843-1846 from the Caverna de Sansón Machay in Peru and Weddell (1851) from Tarija in Bolivia were studied by Gervais (1855).

The first detailed description of the Argentine fauna was made by Owen (1840) and was based on specimens collected by Charles Darwin between 1832-1836 during his epic voyage on the H.M.S. Beagle. All of these specimens were collected between 31°S and 50°S on the eastern side of South America. The localities are divisible into three regions:

1/ provinces bordering the Río de La Plata (including Bajada de Santa Fe, Entre Ríos Province, Argentina; and Sarandí, a small stream entering the Río Negro about 190 km northwest of Montevideo, Uruguay);

2/ Bahía Blanca at 39°S (including Monte Hermoso and Punta Alta); and

3/ southern Patagonia (including Puerto San Julián, 49°S).

Some of the described taxa include *Macrauchenia patachonica* from Puerto San Julián, *Glossotherium robustum* and *Toxodon platensis* from Sarandí, and *Mylodon darwinii* and *Scelidotherium leptocephalum* from Punta Alta. These fossils, together with other observations gathered during his famous trip, first suggested to Charles Darwin the concept of organic evolution.

Commenting on the sample of fossil mammals made by Lund from Lagoa Santa, Brazil, Darwin (1891), noted: "In this collection there are extinct species of all the thirty-two genera, excepting four, of the terrestrial quadrupeds now inhabiting the provinces in which the caves occur; and the extinct species are much more numerous than those now living; ...This wonderful relationship in the same continent between the dead and the living, will, I do not doubt, hereafter throw more light on the appearance of organic beings on our earth, and their disappearance from it, than any other class of facts."

Since the time of Darwin much work has been accomplished on South American Pleistocene mammals. Of special significance are the studies by Ameghino (1880-1909) in Argentina, and Lund (1836-1846) in Brazil. The literature is now in need of synthesis. A number of important papers have appeared in recent years dealing with faunal and/or taxonomic reviews on a regional level. For Argentina these include Feruglio (1950), Bordas (1967), Frenguelli (1957), Pascual *et al.* (1965, 1966), and Xicoy (1965; a bibliographic summary). Hoffstetter (1971) and Porta (1959-1974) review Colombian faunas and localities, and Simpson & Paula Couto (1957), Paula Couto (1970b), and Bombin (1975) discuss those for Brazil. The major reviews of Ecuadorian faunas are by Hoffstetter (1952, 1970b), as also for Bolivia (see Hoffstetter, 1963a,b, 1968). Churcher (1959, 1962, 1965), Churcher *et al.* (1965), Lemon & Churcher (1961), and Hoffstetter (1970c) deal with Peruvian faunas; Casamiquela (1968a,b, 1969, 1969-1970, 1970, 1972), and Casamiquela & Sepúlveda (1974) cover those for Chile. Hoffstetter (1978) gives a preliminary report on Pleistocene mammals of Paraguay; Mones & Francis (1973) give a list of fossil mammals of Uruguay including those of Pleistocene Age. General summaries of South American Pleistocene faunas are found in Scott (1937, 1942), Paula Couto (1953, 1979), and Simpson (1980).

From these data has emerged biostratigraphic refinement of the Quaternary history of South American land mammals. We revise the principles and practices employed in the establishment and recognition of these South American late Pliocene-Pleistocene land mammal ages. The zoological character and history of these faunas is then discussed and as all are defined from Argentine faunas, these are discussed first and at length. Each of the three South American land mammal ages presently included within the late Pliocene-Pleistocene (from oldest to youngest, the Uquian, Ensenadan, and Lujanian) is reviewed with discussion of type locality, stratigraphy, type faunas, and faunal correlations. Non-Argentine South American late Pliocene-Pleistocene faunas are then discussed country by country in alphabetical order.

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SOUTH AMERICAN PLEISTOCENE LAND MAMMAL AGES

TIME, ROCK, AND FAUNAL UNITS

Stratigraphic nomenclature, especially that of Cenozoic mammal-bearing strata in Argentina, has, as elsewhere, been confused by a lack of clarity in distinguishing units and names applicable respectively to time, rocks, and faunas. Discussions of these problems along with attempts to clarify their usage are given by Doering (1882), Ameghino (1903, 1906, 1909), Simpson (1940, 1941, 1971, 1980), J.L. Kraglievich (1952a), González'Bonorino (1965), Pascual *et al.* (1965, 1966), Pascual & Fidalgo (1972), and Bombin (1975) (fig. 1).

DOERING,1882		AMEGHINO,1889		AMEGHINO,1903		AMEGHINO,1909	L. KRAGLIEVICH,1930–34		SIMPSON,1940	J.L. KRAGLIEVICH,1952	FRENGUELLI,1952	THIS STUDY
FMS.	PISOS	FMS.	PISOS	FMS.	ETAGES	ETAGES	FMS.	HORIZONTES (FAUNAS)	NON–MARINE STAGES	EDADES (=AGES)		
TEHUELCHE =GLACIAL QUERANDINA =DILUVIAL ARIANA =ALUVIAL	ARIANO	TEHUELCHE CUATERNARIA RECIENTE	ARIANO AIMARÁ	POST–PAMPEENNE	AIMARÉEN =RECIENTE	RÉCENT					AIMARENSE CORDOBENSE	RECENT
	PLATENSE QUERANDINO		PLATENSE QUERANDINO		PLATÉEN /QUERANDINÉEN	PLATÉEN /QUERANDINÉEN			POSTPAMPEAN /QUERANDINE	RECIENTE	PLATENSE QUERANDINENSE	
	TEHUELCHE		TEHUELCHE		(HIATUS)	(HIATUS)						
	PAMPEANO LACUSTRE	PAMPEANA	LUJANENSE	PAMPEENNE	LUJANÉEN	LUJANÉEN	PAMPEANA	BONAERENSE (INCL. LUJANENSE)	BONAEREAN	LOBERIANA	LUJANENSE	LUJANIAN
PAMPEANA	EOLITICO		BONAERENSE		BONAERÉEN /BELGRANÉEN	BONAERÉEN /BELGRANÉEN				LUJANIANA		
			BELGRANENSE					BELGRANENSE (INCL. TARIJENSE & BARCOENSE)	BELGRANAN	BONAERIANA	BONAERENSE	
	PAMPEANO INFERIOR		ENSENADENSE		ENSENADÉEN	ENSEN. CUSPIDAL /INTERENSENADÉEN	UQUIANA	ENSENADENSE (INCL. CHARRUENSE & PREENSENADENSE)	ENSENADAN /INTERENSENADAN	ENSENADIANA SANANDRESIANA	ENSENADENSE	ENSENADAN
						ENSEN. BASAL PRÉENSENADÉEN				VOROHUANA		
ARAUCANA	PUELCHE =SUBPAMPEANO	ARAUCANA	PEHUELCHE	ARAUCANIENNE	PUELCHÉEN /FAIRWATHERÉEN	PUELCHÉEN		UQUIENSE	? (UQUIAN) ?	UQUIANA		UQUIAN
						CHAPALMALÉEN	ARAUCO– ENTRERRIANA	CHAPADMALENSE (CLAVEROENSE?, IRENENSE?)	CHAPADMALALAN	CHAPADMALALIANA	CHAPADMALENSE	CHAPADMALALAN
											PUELCHENSE	
			HERMÓSICO		HERMOSÉEN /LAZIARÉEN	HERMOSÉEN		HERMOSENSE	MONTEHERMOSEAN	MONTEHERMOSIANA	MONTEHERMOS?	MONTEHERMOSAN
								ARAUCANENSE TUNUYANENSE	TUNUYANAN			
	ARAUCANO		ARAUCANO		ARAUCANÉEN /ROSAEN	ARAUCANÉEN		HUAYQUERENSE	HUAYQUERIAN	HUAYQUERIANA		HUAYQUERIAN

Fig. 1. — Historical development of time and faunal nomenclature for the late Miocene, Pliocene, and Pleistocene of Argentina. Correlation of time boundaries are only approximate. The heavy line indicates the Pliocene-Pleistocene boundary as recognized by each author.

In Argentina, Ameghino (*e.g.* 1906) called his major stratigraphic units *formaciones*, which he subdivided into *pisos*, using the term for units and with a different meaning than is customary in most recent usage. L. Kraglievich (1934), following Ameghino, also called them *formaciones* and specified their faunal content by the alternative name *ciclos faunísticos*. Castellanos (1923, 1928) accepted L. Kraglievich's stratigraphic terminology.

Despite the fact that formation (lithostratigraphic units) and stages (chronostratigraphic units) are best kept in separate classifications, it has been usual in South America to apply to a stage the same name as that of a formation. In fact, names of South American land mammal ages (see for example Pascual *et al.*, 1965, 1966), are based on chronostratigraphic units (*pisos*).

The first part of the corresponding stage and age names are identical and have Argentine toponymic roots followed by the conventional ending *-an* or *-ian* in English, *-ense* in Spanish (Frenguelli, 1975, p. 36n, and table on p. 63; and Pascual *et al.*, 1965, p. 168n4), and accompanied by the appropriate term *piso* or *edad*. The term *piso* is equivalent to stage as used by North American workers and *étage* as used in French in a chronostratigraphic sense; *edad* is equivalent to age, both in English and in French, and has a geochronologic usage. The suffix *-iano* has been used with *grupo*, usually within scope of series (*e.g.* Frenguelli, 1950, 1957), and *-ense* with *horizonte* or *piso* usually within scope of a formation (*e.g.* Frenguelli, 1950, 1957; Simpson, 1941, p. 5; 1971, p. 287).

For the Quaternary, as for the Tertiary, a large number of fossil vertebrate-bearing deposits are found in Argentina. In fact, all of the South American land mammal ages now recognized (except the Friasian) were defined originally on Argentine faunas. The Argentine faunal sequence developed by Ameghino (1889) was based on the evolutionary grade of its fossil mammals (fig. 1). The stratigraphy and biostratigraphy of Ameghino's sequence was worked out in more detail by Frenguelli (1921, 1928, 1950), Roth (1921), J.L. Kraglievich (1952a), González Bonorino (1965), and Pascual *et al.* (1966) just to mention the more important contributors. Also, paleontological studies of this part of the Argentinian Cenozoic sequence were given special attention in what can be called the post-Ameghinian period (1911-1935) by Rovereto, L. Kraglievich, Castellanos, and Rusconi. After this period numerous authors contributed to the enrichment of our knowledge of the fossil mammals of this age and place (Reig, 1981). This sequence served as the framework for the South American land mammal ages formally proposed by Pascual *et al.* (1965, 1966).

The chronology and usage of late Cenozoic South American land mammal ages (figs. 1, 2) follows Marshall, Butler, Drake & Curtis (1982) where Uquian, Ensenadan, and Lujanian land mammal faunas are included within the late Pliocene-Pleistocene.

FAUNAS

ZOOLOGICAL CHARACTER AND HISTORY

It is well established that South America was an island continent during most of the Tertiary Period (Simpson, 1950, 1969; Patterson & Pascual, 1972; Tedford, 1974; Reig, 1981). As a result, the South American land mammal fauna developed in a world unto itself and, until the appearance of the Panamanian land bridge about 3.0 Ma (millions of years ago) was dominated by autochthonous endemic groups. By late Miocene time a faunal balance had been achieved by the descendants of the autochthonous inhabitants (notoungulates, litopterns, condylarths, edentates, marsupials) and of later (late Eocene or early Oligocene) waif immigrants (caviomorph rodents, platyrrhine primates) (Patterson & Pascual, 1972). A prominent feature of this fauna was the combination of carnivorous and omnivorous marsupials with placental herbivorous ungulates, subungulates, and edentates (Simpson, 1940, p. 675; Reig, 1981).

The distribution of plants and animals in South America has been influenced by alternating climatic changes corresponding to glacial and interglacial episodes (Caldenius, 1932a,b; Polanski, 1962; Flint & Fidalgo, 1963, 1964, 1968, 1969; Fidalgo & Riggi, 1970; Mercer, 1976, 1977; Vuilleumier, 1971; Marshall, 1979; Fidalgo & Tonni, 1978; Tonni & Fidalgo, 1979; Pascual & Bondesio, 1981). Geomorphic observations in southern Venezuela, central Brazil, eastern Peru, and northern Uruguay indicate that during part of the Quaternary arid climatic conditions prevailed over large parts of the Brazilian subregion (Haffer, 1969; Anton & Goso, 1974). In Colombia interglacial temperatures were estimated to have been several degrees (°C) above the present yearly average (van der Hammen, 1974).

Vegetation fluctuations during Pleistocene glacial maxima, as documented by dendrochronology (LaMarche, 1978), pollen analysis and faunal studies (van der Hammen, 1965, 1966, 1972, 1973, 1974; van der Hammen & González, 1960; van der Hammen *et al.*, 1973; Haffer, 1974; Heusser, 1974; Müller, 1973; Vuilleumier, 1971, 1975; Vanzolini & Williams, 1970), suggest that the repeated extension of savanna grasslands led to increased opportunities for dispersal of plants and animals between these areas (Marshall, 1979; Webb, 1978). Raven & Axelrod (1975) suggest that the arid glacial periods in the tropics would have been suitable times for interchange of grazing mammals such as horses, camels, and glyptodonts between North and South America.

Much attention has been given to details of this late Tertiary faunal interchange between North and South America (Simpson, 1950, 1980; Hershkovitz, 1966, 1972; J. Savage, 1974; Rosen, 1975; Webb, 1976, 1978; Marshall & Hecht, 1978; Marshall *et al.*, 1979, 1982; Reig, 1981). Mammals of North America origin are known to first appear in strata of Huayquerian (late Miocene) age in Argentina. Procyonids of the *Cyonasua* group apparently arrived as waif immigrants before the Panamanian land bridge came into existence. Three genera of extinct South American procyonids are known — *Cyonasua*, a generalized form ranges from Huayquerian to Chapadmalalan (late Pliocene); *Chapadmalania*, a large bear-like form in the Montehermosan (early Pliocene) and Chapadmalalan; and *Brachynasua* in the Ensenadan (middle Pleistocene) (Patterson & Pascual, 1972, p. 281; Linares, 1978).

Cricetine rodents of the subfamily Sigmodontinae are first known in South America from one species each of *Auliscomys* and *Bolomys* (Reig, 1978) from strata of Montehermosan age at Monte Hermoso along the Atlantic coast of Buenos Aires Province, Argentina. According to Reig (1981), the ancestors of these animals probably arrived to South America by waif dispersal sometime during the late Miocene or earlier.

Establishment of the Panamanian land bridge sometime in the late Pliocene provided a direct land connection between the two Americas. Across this portal an extensive interchange of terrestrial faunas occurred. The beginning of this interchange in South America is marked by the appearance of a number of mammals, which evolved from North American emigrants, in the Chapadmalal Formation in the southeast corner of Buenos Aires Province, Argentina. These include a mustelid (*Conepatus*), a tayassuid (*Argyrohyus*), and four genera [*Akodon* (*Abrothrix*), *Dankomys, Graomys, Reithrodon*] of Sigmodontinae. The appearance of this contingent of northern animals favors the existence of the Panamanian land bridge by this time, though the sigmodontines may have evolved from an earlier stock (Reig, 1978, 1981).

A marked increase in North American mammals occurs between the Chapadmalalan and the Uquian (late Pliocene-early Pleistocene) as indicated by the first recorded appearance during Uquian time of 20 immigrant genera (fig. 3). These include members of the Canidae, Felidae, Gomphotheriidae, Equidae, Tapiridae, Camelidae, and Cervidae (Patterson & Pascual, 1972, p. 287). There are also additional cricetine rodents, including *Scapteromys, Cholomys,* and *Akodon* (subgenus *Akodon*). Patterson & Pascual (1972, p. 287) note that this marked increase of northern taxa... "may reflect the real situation with some degree of accuracy." Montehermosan [and Chapadmalalan] faunas are, they note,... "rich and varied"... including over 80 mammalian genera of native families. Uquian faunas from Buenos Aires Province are not well known, and are in particular need of taxonomic study. These faunas nevertheless... "provide a good idea of South American faunal composition south of the tropical zone around the"... time of the Pliocene-Pleistocene boundary.

About 25 immigrant mammal genera are first recorded in the Ensenadan and about 15 in the Lujanian (late Pleistocene) (fig. 3). Ten of the latter are, however,... "known only from [late Pleistocene-Holocene deposits in] the caves of Lagoa Santa, Brazil, and are today largely or wholly tropical." Patterson & Pascual (1972, p. 287) further note that the data suggest... "that many of the Recent tropical genera of northern ancestry may have been present in northern South America throughout much of Pleistocene time."

Of the most recent immigrant taxa from North America, the Soricidae, Heteromyidae, and neotomine (peromiscine) Cricetidae are restricted to northwestern South America. The Soricidae are represented by *Cryptotis*, which has been recorded as fossil only in the Curití fauna of Colombia (Porta, 1965). There is no fossil record of Heteromyidae in South America, solely represented in the living fauna by *Heteromys*. The same is true of neotomines, represented by *Aporodon, Reithrodontomys,* and *Tylomys.*

Rabbits are represented in South America by one living genus, *Sylvilagus*, which has a wide continental distribution; it is recorded as fossil in the caves of Lagoa Santa, Brazil (Paula Couto, 1970a). The jack-rabbit (*Lepus*) is not native to South America but was introduced by European settlers, and was questionably reported as fossil at Muaco, Venezuela (*fide*, Royo y Goméz, 1940; Bryan, 1973, p. 246). The Sciuridae are also considered as recent immigrants and are restricted to the tropical and subtropical zones; they have no known fossil record in South America but are represented in the living fauna by the world-wide genus *Sciurus*, and by the endemic genera *Sciurillus* and *Microsciurus*. The living cervid *Odocoileus* appears to be a post-Lujanian immigrant at least in the High Andes of Peru (at Uchcumachay), but is present in the Puninian (Andes of Ecuador) and Carolinian (La Carolina, Talara) fossil faunas, considered late Lujanian in age (see below).

Osborn (1929, p. 20) described a new subspecies of mammoth, "*Parelephas*" *columbi cayennensis*, based on a tooth plate fragment of a right M3/ collected in Cayenne, French Guiana. Patterson & Pascual (1972, p. 285n) note that as no other specimens have turned up elsewhere in South America "the record has generally been discredited." They cautioned, however, that Stirton & Gealey's (1949) record of mammoth (and bison) in the late Pleistocene of El Salvador... "raises the faint possibility that a species of mammoth actually did extend its range for a brief period along the northern fringe of the [South American] continent."

The *Bison* recorded from El Salvador further raises the possibility that bovids may yet turn up in the fossil record in northern South America. However, the report of a bovid, *Colombibos atactodontus*, from late Pleistocene deposits at Soatá (Boyacá), Colombia by Hernández Camacho & Porta (1960) is now rejected, for the "fossil species" was founded on the upper dentition of a domestic cow, *Bos*, in which the dP4/ was interpreted as a molariform P4/ (Hoffstetter, 1971, p. 54). Likewise, reports of Bovidae from beds of late Lujanian Age in Argentina by Gervais & Ameghino (1880), Ameghino (1889), and Frenguelli (1933b) are regarded as highly dubious.

Much of the work done on Pleistocene mammals of North and South America... "has been carried out with little or no attention"... paid to the relationships between taxa occurring on the other continent (Patterson & Pascual 1972, p. 289). "As examples of what may be expected when adequate intercontinental comparisons are made"..., Patterson & Pascual (1972, p. 289)... "cite [J.L.] Kraglievich's (1952b) reference of '*Canis*' *texanus* to *Protocyon*; Kurtén's (1967) conclusion that *Arctotherium* and *Paractotherium* constitute at most a subgenus of *Arctodus*; and Paula Couto's (1955) ranking of *Smilodon californicus* [= *S. floridanus*] as a subspecies of *S. populator*."

The end of the Pleistocene and the beginning of the Holocene in South America are marked by the extinction of nearly all large mammalian herbivores and their specialized large predators. Representatives of this extinct megafauna in South America include ground sloths, glyptodonts, proboscideans, horses, notoungulates, litopterns, sabre-tooth cats, and several genera of other families (fig. 3).

Radiocarbon age determinations (table 1) suggest that large-scale extinctions of megafauna occurred between 15,000 and 8,000 yrs. B.P. (years before present). The cause(s) of these late Quaternary extinctions has been the subject of growing literature in recent years. For different views on this topic consult Bombin (1980a, 1980b, 1980e), Borrero (1977), Guilday (1967), Hoffstetter (1954a), Martin (1967, 1973, 1975), Long & Martin (1974), Martin & Wright (1967), Patterson & Pascual (1972), Paula Couto (1968), and van Valen (1969).

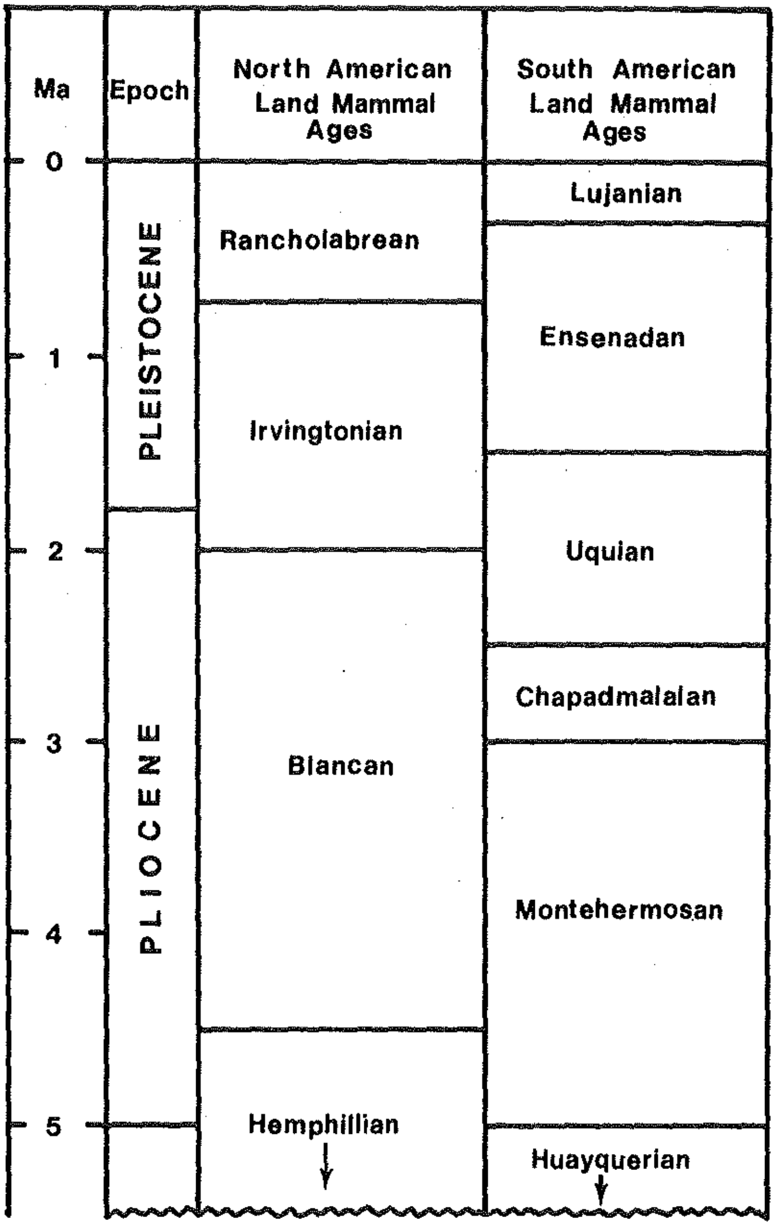

Fig. 2. — Tentative chronology of North and South American late Cenozoic land mammal ages (after Marshall, Butler, Drake, & Curtis, 1982).

PLIOCENE-PLEISTOCENE BOUNDARY

The disputed question of the continental Pliocene-Pleistocene boundary in South America is not yet subject to any general agreement, although the problem has been reviewed by Pascual & Fidalgo (1972) and Fidalgo, de Francesco & Pascual (1975). The appearance of a large number of Nearctic mammals in South America has been the paleontological criterion long used for marking this boundary. An extensive fauna of North American origin appears in the Uquian, leading most recent workers to place the boundary between rocks of Chapadmalalan and Uquian Age. This situation is complicated by the first appearance of immigrant taxa in strata of Huayquerian (late Miocene) Age (Marshall *et al.*, 1979) and of other groups in the Chapadmalal Formation which is regarded as Pliocene in age (Marshall *et al.*, 1979, 1982; Mones, 1979; Reig, 1978). Since the invasion by North American forms was evidently gradual, it is difficult using this line of reasoning to define any boundary with precision.

Radioisotope age determinations of rocks associated with Pleistocene mammal-bearing strata and calibration of land mammal ages in terms of a radioisotope time scale, as has been done for North America (Evernden *et al.*, 1964), are now available for two localities in South America. MacFadden *et al.* (1981, 1983) reports biostratigraphic studies in Bolivia which integrate Pleistocene vertebrate bearing sequences within a paleomagnetic and radioisotopic framework. Likewise, Marshall, Butler, Drake & Curtis (1982) calibrate beds and faunas of Uquian Age in Argentina using radioisotopic age determinations and paleomagnetostratigraphy. These data, along with knowledge of aspects of faunal evolution, suggest the following tentative time durations for the South American land mammal ages — Uquian (2.5 to 1.5 Ma), Ensenadan (1.5 to 0.3 Ma), and Lujanian (0.3 Ma to 10,000 yrs. B.P.). A tentative chronology of North and South American late Cenozoic land mammal ages is given in figure 2. The Pliocene-Pleistocene boundary would thus lie within the upper part of the Uquian.

ARGENTINA

The three South American late Pliocene-Pleistocene land mammal ages conventionally recognized (Uquian, Ensenadan, Lujanian) are all defined on Argentine beds and faunas. In Argentina, the terms Pleistocene, *pampean, pampeano*, or *pampiano* are often used interchangeably or nearly so. An understanding of the use and concept of the term *pampean* is thus of key importance to the study of these land mammal faunas.

PAMPEAN

Studies of late Cenozoic stratigraphy in South America have been intense in Argentina, particularly in the Pampean Region[1]. Pampean deposits, almost exclusively of Pleistocene Age[2], extend as a continouous mantle from the Pampas of southernmost Buenos Aires Province to the Chaco plains in the north (Teruggi, 1957) (fig.

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[1] *Pampa* is a Quechua Indian name which to some authors means plain and to others sea. The Pampean Region, an area of extensive flat grasslands, comprises the provinces of Buenos Aires and the southern half of Santa Fe, part of La Pampa, the eastern part of Córdoba, the western part of Entre Rios, and southernmost Corrientes in Argentina, as well as much of Uruguay and Rio Grande do Sul, Brazil (fig. 4). This is the area which first received the attention of geologists and paleontologists particularly because of the high frequency with which fossil mammals are encountered (Pascual & Fidalgo, 1972, p. 225).

[2] Many workers have included under the name Pampean, stratigraphic units which are unequivocally of Tertiary Age (*e.g.* beds of Montehermosan Age at Monte Hermoso).

4). These deposits consist of subaerial, fluvial, and lacustrine interbedded tuffites and clays. The average thickness of these deposits is 30 meters (Teruggi, 1957), and the maximum registered is over 200 meters (Pascual, personal note). Similar deposits occur in Bolivia, Ecuador, and Uruguay (Ahlfeld, 1956; Lewis *et al.*, 1956; Scott, 1942, p. 350).

The *argile pampéenne* or *pampéen* was originally named and described by d'Orbigny (1842, III-3 Géologie, p. 23-24) as follows :

> En partant de Montevideo — quelques lieues avant d'arriver à Canelones... les argiles... me firent reconnaître la présence de cette couche argileuse de couleur grise ou rougeâtre, remplie de concrétions calcaires, appartenant à la dernière époque de terrains tertiaires, qui forme tout le fond des Pampas proprement dites, et contient de beaux restes de megatherium et de tatous gigantesques... Cette *argile*, que je nomme *pampéenne*, non seulement occupe tout l'intervalle compris entre les plaines de Canelones et le ruisseau de Canelón grande, mais encore paraît s'étendre au loin vers le nord.

The above definition was originally applied by Darwin (1838, p. 542-544; 1840, p. 4) under the name of "reddish argillaceous earth" to deposits in Uruguay. D'Orbigny (1842, p. 72-74) later extended his concept to include beds in the pampean regions of Argentina and Uruguay (Canelones, Las Vacas, Valle del Río Negro) (Goñi & Hoffstetter, 1964, p. 109).

The *argile pampéenne* has received various names since its recognition [*e.g. Pampean mud* or *Pampean Formation* of Darwin (1846); *Formación Pampa* or *Terreno Pampa* of Bravard (1875); *loess pampeano* of Heusser & Claraz (1863); *Formación Pampeana* of Ameghino (1875, 1881, 1889, etc.), Roth (1921), and Stappenbeck (1926); *serie pampiana* or *Pampiano* of Frenguelli (1933a, 1950, 1957); *loess y limos pampeanos* of Frenguelli (1925); *Pampean Group* of Harrington (1956c, p. 153); *Pampeano Formation* of Padula & Mingramm (1963); *Formación Pampeana* of González Bonorino (1965); *Formación Pampiano* of Fidalgo, Colado, & de Francesco (1973), Fidalgo, de Francesco & Colado (1973)]. Most Argentine workers have adopted the term *Formación Pampeana* or simply *Pampeano* or *Pampiano*, which they have applied to all terrestrial and marine deposits of late Cenozoic, mostly Pleistocene, Age. In Uruguay the names *Formación Pampeana* or *loess Pampeano* have been restricted to terrestrial deposits (Goñi & Hoffstetter, 1964, p. 109). These names are now generally abandoned [for exception see González Bonorino, 1965; Fidalgo, Colado, & de Francesco, 1973] because until now no one has defined this extended and complex unit according to the existing stratigraphic code of nomenclature (Pascual *et al.*, 1965, p. 182; Pascual & Fidalgo, 1972, p. 214).

In both Uruguay and Argentina the *pampeano* corresponds to nearly all of the Pleistocene and the two terms are generally considered synonymous. Nevertheless, various authors (*e.g.* Frenguelli, 1957) include the latest part of the Tertiary within the *pampiano*. According to Goñi & Hoffstetter (1964, p. 110), in Uruguay there is no paleontological evidence to support this as all known fossils are clearly Pleistocene in age. But if we accept the *pampeano* as a lithostratigraphic unit in the southern Argentine Pampean region it is also interbedded with Tertiary units (Pascual & Fidalgo, 1972). For a characterization of these *loessoid sediments* (Pampean Formation) see Teruggi (1957), and Teruggi, Etchichuri & Remiro (1957).

Ameghino (1889), who considered the Pampeana Formation as Pliocene in age, divided it into four *pisos* or *horizons* based on faunal content (from oldest to youngest — ***Ensenadense, Belgranense, Bonaerense, Lujanense***). This sequence and these names have been generally accepted by subsequent authors, although the chronology of these *pisos* has been employed in various ways and is still the subject of debate (Rovereto, 1914a,b; L. Kraglievich, 1934; Frenguelli, 1957; Pascual & Fidalgo, 1972, p. 208).

Due to the alleged discovery of remains and artifacts of early man in Montehermosan (Ameghino, 1907; Lehmann-Nitsche, 1907) and Chapadmalalan (Ameghino, 1911; Frenguelli & Outes, 1924; Vignati, 1922, 1941) strata as well as in later strata (Ameghino, 1909)[3], the problem of correlation of those strata with the European standard geological time scale became highly controversial and colored by ideological prejudices. Ameghino, in accordance with his general tendency to make the Cenozoic strata of Argentina one epoch older than is now generally accepted, placed the deposits of Monte Hermoso and Chapadmalal (now considered Pliocene in age) in the Miocene, and the Ensenadan (now considered middle Pleistocene) in the Pliocene. Scholars became divided into two opposing fields with regard to the relative chronology of corresponding strata, and this division pervaded for years the work of stratigraphers and paleontologists. Ameghino's followers grouped to defend the Tertiary Age of the geological strata involved, whereas authors with opposing views tended to place them in the Pleistocene. Evidence for supposed hominoids was eventually discarded or thoroughly reinterpreted (see for instance, Bordas, 1942; J.L. Kraglievich, 1954), but even then the controversies about the Tertiary or Quaternary Age of the Monte Hermoso and Chapadmalal beds outlived in Argentina their origins, and in some contexts they resulted in a topic of acrimonious dispute which produced some oddly militant pieces of scientific literature (Reig, 1972).

Most controversies during the first four decades of this century on the relative chronology of the late Cenozoic sequence of Argentina, may now be considered as basically settled. This was certainly the result of a new outlook coming from a new generation, but, the important landmark in obtaining a consensus of opinion is Simpson's (1940) well-balanced and authoritative survey of the mammal-bearing Cenozoic of South America.

In the Pampean Region of Argentina are three classic areas where combined geological and paleontological studies of Pleistocene deposits and faunas have been made: 1/ the Atlantic cliffs between Mar del Plata and Miramar, Buenos Aires Province; 2/ Buenos Aires city and vicinity, including La Plata and Ensenada; and 3/ cliffs along the eastern bank of the Río Paraná, Entre Ríos Province (Pascual & Fidalgo, 1972, p. 227).

The first of these regions was studied originally by Ameghino (1908). Because of the homogeneous lithological characteristics of the sediments, usually called *loess*, there has been difficulty in recognizing different lithostratigraphic units. J.L. Kraglievich (1952a, 1959a), expanding upon the work of Risso Domínguez (1949), recognized, however, that the fossil mammals came from at least five distinct formations — from oldest to youngest, the Chapadmalal, Barranca de Los Lobos, Vorohué, Miramar, and Arroyo Seco Formations — corresponding to the ***Chapalmalense*** and ***Ense-***

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[3] A complete account of alleged early man in Argentina, can be found in Castellanos (1937).

nadense of Ameghino (1908), and the *Chapalmalense, Ensenadense,* and *Bonaerense* of Frenguelli (1957). These strata were distinguished by J.L. Kraglievich on differences in color, type of stratification, and on the occurrence of distinct and extensive erosional surfaces between them. These distinctions have been confirmed by the work of O.A. Reig and G. Scaglia. Not all of these lithostratigraphic units are clearly formations as this term is usually defined (*i.e.*, a *major* mappable lithologic unit), but they are clearly distinguishable members of a complex stratigraphic sequence, and it has proven useful to recognize this distinction with local names. Therefore, we recommend retention of Kraglievich's names for these rock units until a better characterization is available.

The sediments from these five formations were studied by Teruggi *et al.* (1957) who found a similar mineralogical composition consistent with the general composition of the so-called loess. Fundamentally this loess is the same in all post-Friasian strata recognized on the basis of fossil mammal faunas [*i.e.* Chasicoan, Huayquerian, Montehermosan, Chapadmalalan and Uquian (in part) of Tertiary Age, and Uquian (in part), Ensenadan, and Lujanian of Quaternary Age] collected from different areas in the Pampean Region (Pascual *et al.*, 1965).

Since about 1945 these strata have and are now being continuously prospected for fossil vertebrates, largely by staff and associates of the Museo de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" under the direction of Galileo Scaglia. These collections were made using a *tight* stratigraphic framework and with good biostratigraphic control. Most of this well documented collection has been prepared and is well curated, but has been only partially described. Some of the biostratigraphic information reported here for this sequence is based on unpublished data of Reig (1972).

The second region comprises the city of Buenos Aires and vicinity where various *pampean* units have been recognized largely on the basis of excavations and drillings (Frenguelli, 1957, fig. 2). Good exposures are few, although along the Río de La Plata occurs a *loess y limo* formation from which mammal remains have been known since last century and which Ameghino (1889) called *piso ensenadense* (see below), and also known as *toscas del Río de La Plata*. These deposits were carefully explored during the 1920's and 1930's by Carlos Rusconi and Federico Henning. Most of these classic exposures have now been covered and are no longer available for paleontological exploration.

The third region where *pampean* strata are exposed is along the right bank of the lower Río Paraná. The lower marine and fluviatile strata, originally studied by d'Orbigny (1842) and Darwin (1846, 1851), are succeeded by discontinuous sandy and silty beds, gradually passing upwards into more homogeneous and extensive argillaceous and loessic sediments (Aceñolaza, 1976). Unfortunately, no complete fossiliferous section exists along this part of the river, most of the fossils coming from different localities and lacking good stratigraphic control. The fossils, nevertheless, demonstrate the existence of different mammal-bearing horizons, representing Tertiary (Huayquerian-Montehermosan) through Quaternary (Ensenadan) Age sediments in the *pampean* sequence (Pascual & Fidalgo, 1972, p. 233; for stratigraphic profiles see Frenguelli, 1957, figs. 6,7; Aceñolaza, 1976, p. 96, 100).

Marine intercalations with *pampean* continental sediments are thin and locally developed only along the coast (Cortelezzi & Lerman, 1971). The oldest lies within the

Ensenada Formation (middle Pleistocene, see below); it varies from 1 to 3 meters in thickness and was named ***Interensenadense*** by Ameghino (1889). It is restricted to the coast between the cities of La Plata and Buenos Aires, and was discovered in excavations made during the construction of the La Plata harbor at Ensenada. During excavations of the Buenos Aires harbor this marine ingression was found about 7 meters below the level of the Río de La Plata (Ameghino, 1889). According to Frenguelli (see especially 1957) these sediments represent a local ingression of the Río de La Plata estuary. Along the coast, three marine transgressions of late Pleistocene-Holocene Age were recognized (from oldest to youngest the ***Belgranense***, ***Querandinense***, and ***Platense marino***). Recent stratigraphic studies along the lower Río Salado, Buenos Aires Province, by Fidalgo, Colado & de Francesco (1973) permitted them to recognize three different marine lithostratigraphic units — the Pascua, Destacamento Río Salado, and Las Escobas Formation — which respectively probably correspond to the ***Belgranense, Querandinense***, and ***Platense marino*** (Fidalgo & Tonni, 1978; Tonni & Fidalgo, 1979; and Fidalgo, de Francesco & Pascual, 1975 and references therein). The ***Belgranense*** corresponds to a higher sea level stand probably between 30,000 and 34,000 yrs. B.P. (Bombin, 1980c), and the ***Querandinense*** and ***Platense Marino*** to middle Holocene higher sea level stands (Bombin, 1980d).

Fig. 3. — South American Quaternary land mammal ages and known range distributions of mammalian genera. Modified and expanded after Pascual *et al.* (1966). For the sake of presentation we questionably(?) assigned the taxa from Tarija to the Ensenadan; according to MacFadden *et al.* (1983: published during the printing of the present paper), most of them are really Ensenadan in age; but it is possible that some are Lujanian. Those from Lagoa Santa have all been considered to range into the Lujanian, although some may be restricted to the Holocene in those deposits.

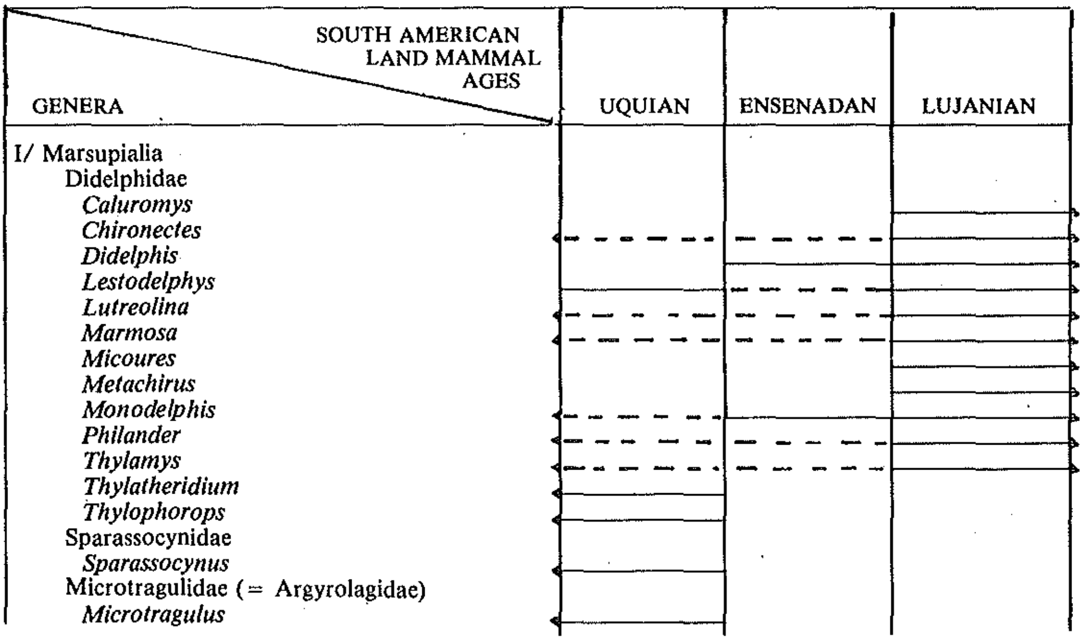


Fig. 3 (cont.)

GENERA	UQUIAN	ENSENADAN	LUJANIAN
II/ Insectivora			
Soricidae			
Cryptotis			—→
III/ Edentata			
Dasypodidae			
Cabassous			—→
Chaetophractus	←—	—	—→
Chlamyphorus			—→
Dasypus	- - - - -	—	—→
Euphractus		—	—→
Eutatus	—	—	—
Pampatherium (incl. *Holmesina* = *Hoffstetteria*)	—	—	—
Propraopus	←- - ? - -	—	—
Tolypeutes	?←- - - - -	—	—→
Zaedyus	←—	—	—→
Glyptodontidae			
Chlamydotherium (= *Boreostracon*) (1)		—	—
Daedicuroides		—	
Doedicurus	—	—	—
Glyptodon	—	—	—
Hoplophorus		- - - ? - -	—
Lomaphorus		—	—
Neothoracophorus		—	—
Neuryurus		—	
Panochthus	—	—	—
Paraglyptodon	←- - - ? - -		
Plaxhaplous		—	—
Prodaedicurus	—		
Sclerocalyptus	—	—	—
Megalonychidae			
Nothropus		- - - ? - -	—
Nothrotherium		—	—
"Ocnopus" (2)			—
Valgipes			—
Megatheriidae			
Eremotherium			—
Megatherium (= *Essonodontherium*)	—	—	—
Plesiomegatherium	←- - - ? - -		
Mylodontidae			
Glossotherium (= *Eumylodon*; incl. *Oreomylodon*)	—	—	—
Lestodon		—	—
Mylodon	- - - ? - -	—	—
Proscelidodon?, *Scelidotheridium*? or *Scelidotherium*?	- - - ? - -		
Scelidodon	—	—	—
Scelidotherium	—	—	—
IV/ Lagomorpha			
Leporidae			
Sylvilagus			—→

Fig. 3 (cont.)

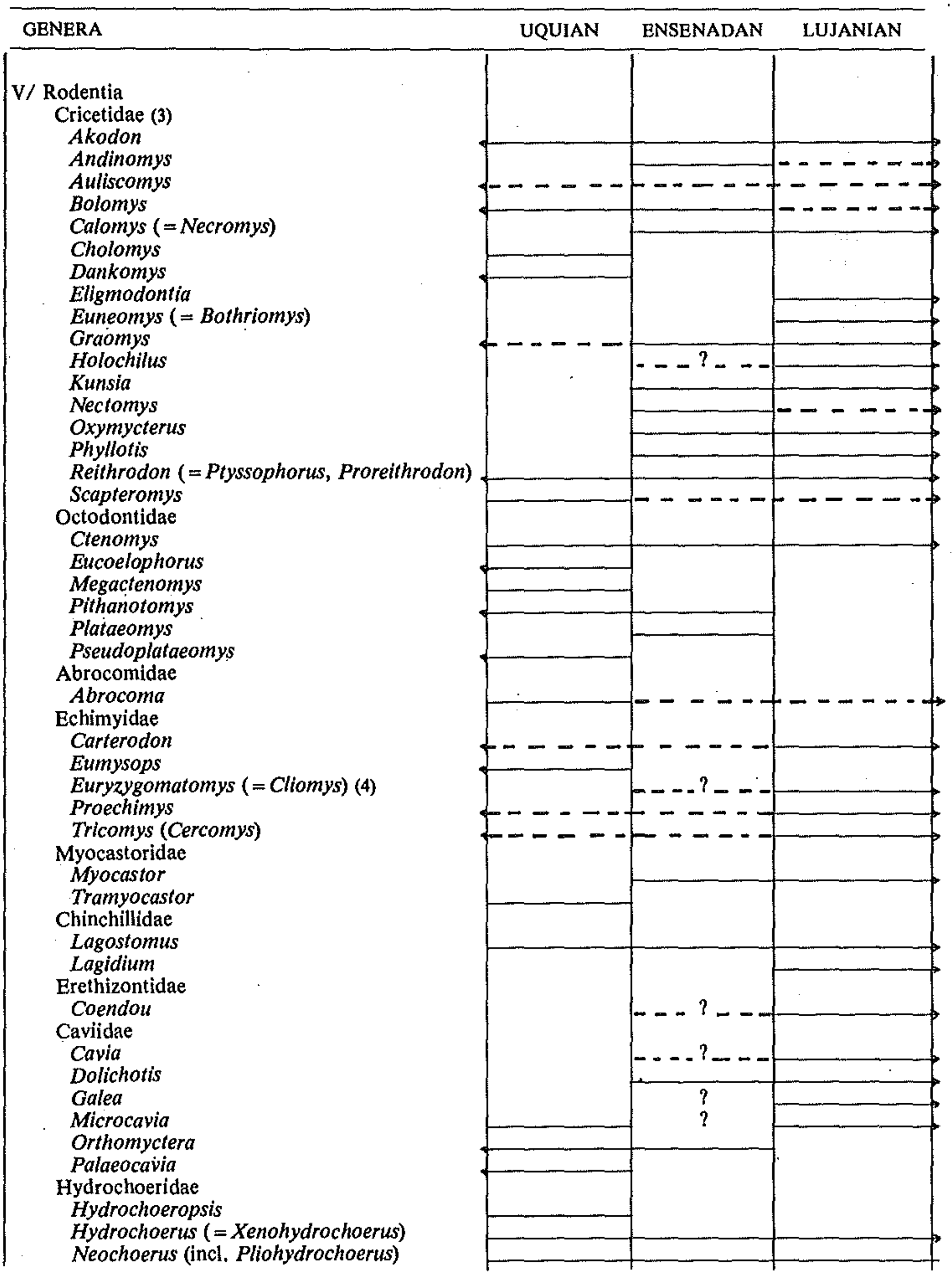

GENERA
UQUIAN
ENSENADAN
LUJANIAN
V/ Rodentia
Cricetidae (3)
Akodon
Andinomys
Auliscomys
Bolomys
Calomys (= Necromys)
Cholomys
Dankomys
Eligmodontia
Euneomys (= Bothriomys)
Graomys
Holochilus
Kunsia
Nectomys
Oxymycterus
Phyllotis
Reithrodon (= Ptyssophorus, Proreithrodon)
Scapteromys
Octodontidae
Ctenomys
Eucoelophorus
Megactenomys
Pithanotomys
Plataeomys
Pseudoplataeomys
Abrocomidae
Abrocoma
Echimyidae
Carterodon
Eumysops
Euryzygomatomys (= Cliomys) (4)
Proechimys
Tricomys (Cercomys)
Myocastoridae
Myocastor
Tramyocastor
Chinchillidae
Lagostomus
Lagidium
Erethizontidae
Coendou
Caviidae
Cavia
Dolichotis
Galea
Microcavia
Orthomyctera
Palaeocavia
Hydrochoeridae
Hydrochoeropsis
Hydrochoerus (= Xenohydrochoerus)
Neochoerus (incl. Pliohydrochoerus)
?
?
?
?
?
?
?

Fig. 3 (cont.)

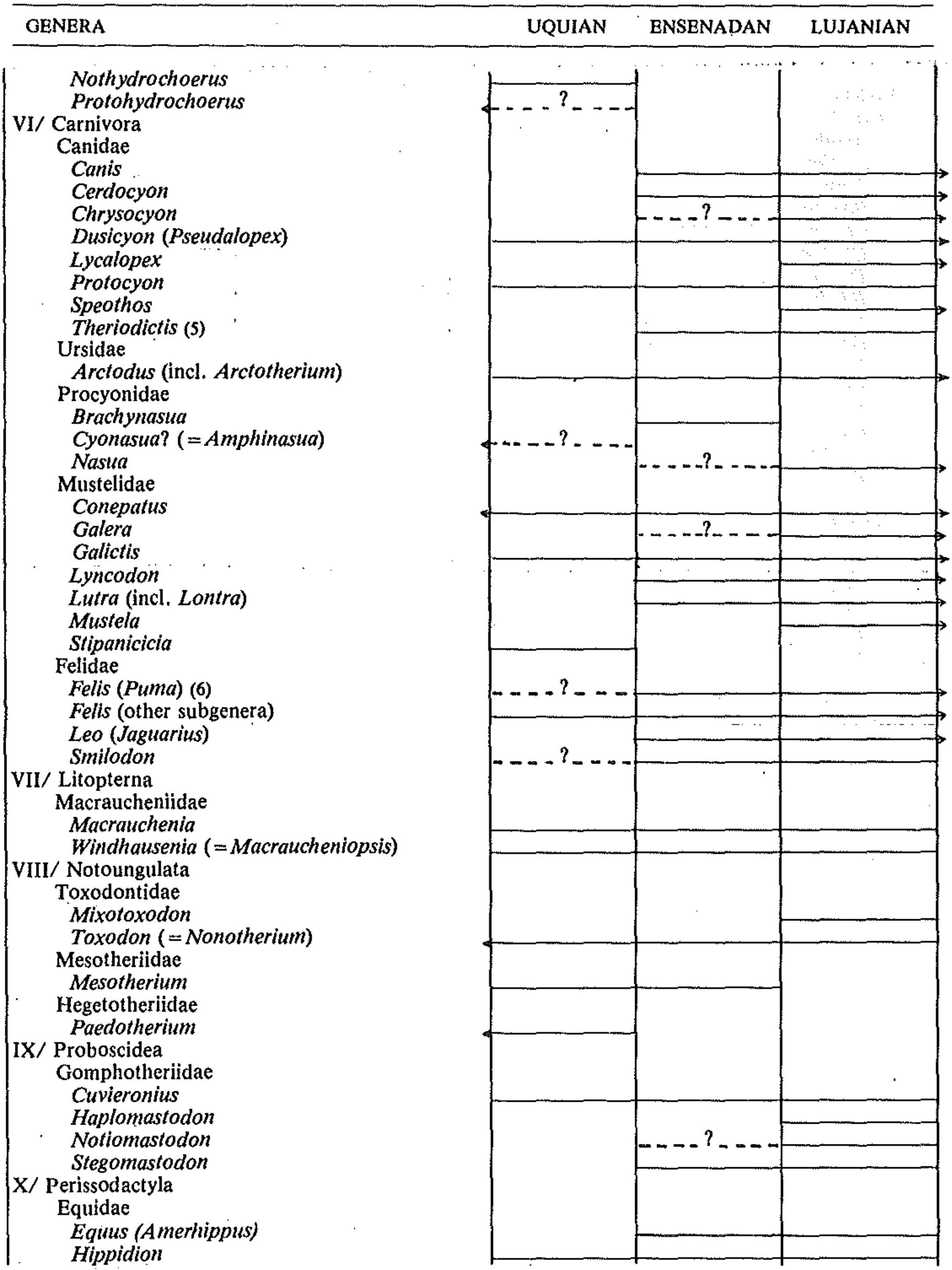
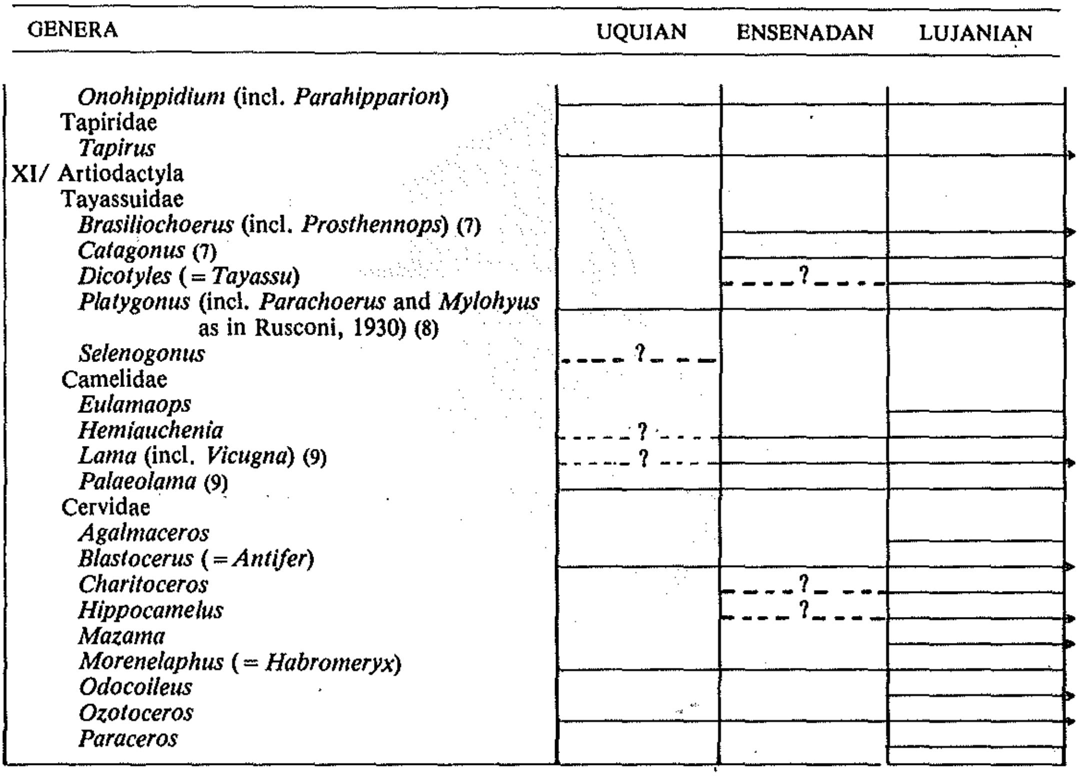

GENERA
UQUIAN
ENSENADAN
LUJANIAN
Nothydrochoerus
Protohydrochoerus
VI/ Carnivora
Canidae
Canis
Cerdocyon
Chrysocyon
Dusicyon (Pseudalopex)
Lycalopex
Protocyon
Speothos
Theriodictis (5)
Ursidae
Arctodus (incl. Arctotherium)
Procyonidae
Brachynasua
Cyonasua? (=Amphinasua)
Nasua
Mustelidae
Conepatus
Galera
Galictis
Lyncodon
Lutra (incl. Lontra)
Mustela
Stipanicicia
Felidae
Felis (Puma) (6)
Felis (other subgenera)
Leo (Jaguarius)
Smilodon
VII/ Litopterna
Macraucheniidae
Macrauchenia
Windhausenia (=Macraucheniopsis)
VIII/ Notoungulata
Toxodontidae
Mixotoxodon
Toxodon (=Nonotherium)
Mesotheriidae
Mesotherium
Hegetotheriidae
Paedotherium
IX/ Proboscidea
Gomphotheriidae
Cuvieronius
Haplomastodon
Notiomastodon
Stegomastodon
X/ Perissodactyla
Equidae
Equus (Amerhippus)
Hippidion
?

Fig. 3 (cont.)



1. Synonyms according to Paula Couto (1954, p. 4).
2. The genus *Ocnopus* needs to be revised and given a new name (see Hoffstetter, 1982, n. 10, p. 428).
3. Most of Pleistocene cricetid records are from Reig (1972).
4. The presence of *Euryzygomatomys* in the Lujanian is based on abundant remains in the Museum of Paris found in Tarija and Padcaya (Bolivia), studied by Reig (unpublished). But, according to MacFadden *et al.* (1983), the greater part of the Tarija (and Padcaya) fauna is Ensenadan in age.
5. *Theriodictis* has been considered as a separate genus or as a subgenus of *Canis*. *Theriodictis* appears to be phylogenetically closer to *Protocyon* than to *Canis* (Hoffstetter, personal note; Berta, 1981).
6. The Uquian occurrence is based on *Felis pumoides* Castellanos, 1958, from the *Brocherense*.
7. *Brasiliochoerus*, proposed by Rusconi (1930) as a subgenus of *Platygonus*, deserves full generic status. This is most surely the animal found alive in the Chacoan region by Wentzel (1977) and referred to *Catagonus*. The latter, as based on the type species, *C. metropolitanus* is a different animal. Specimens referred by Rusconi to *Prosthennops* may also belong to *Brasiliochoerus* (Reig, personal note).
8. The status of South American forms of the peccary genus *Platygonus* are unclear and the group is in need of revision. The presence of *Mylohyus* in the Uquian, reported by Rusconi (1930) is based on undiagnostic remains which can be tentatively referred to *Platygonus* with the above mentioned reservation (Reig, personal note).
9. *Astylolama*, *Protauchenia* and possibly *Hemiauchenia*, are most likely sub-genera of *Palaeolama*. Moreover, the Uquian occurrence of *Hemiauchenia* needs confirmation. *Lama* and *Vicugna* interbreed and should be placed in the same genus, *Lama* (Hoffstetter, personal note).

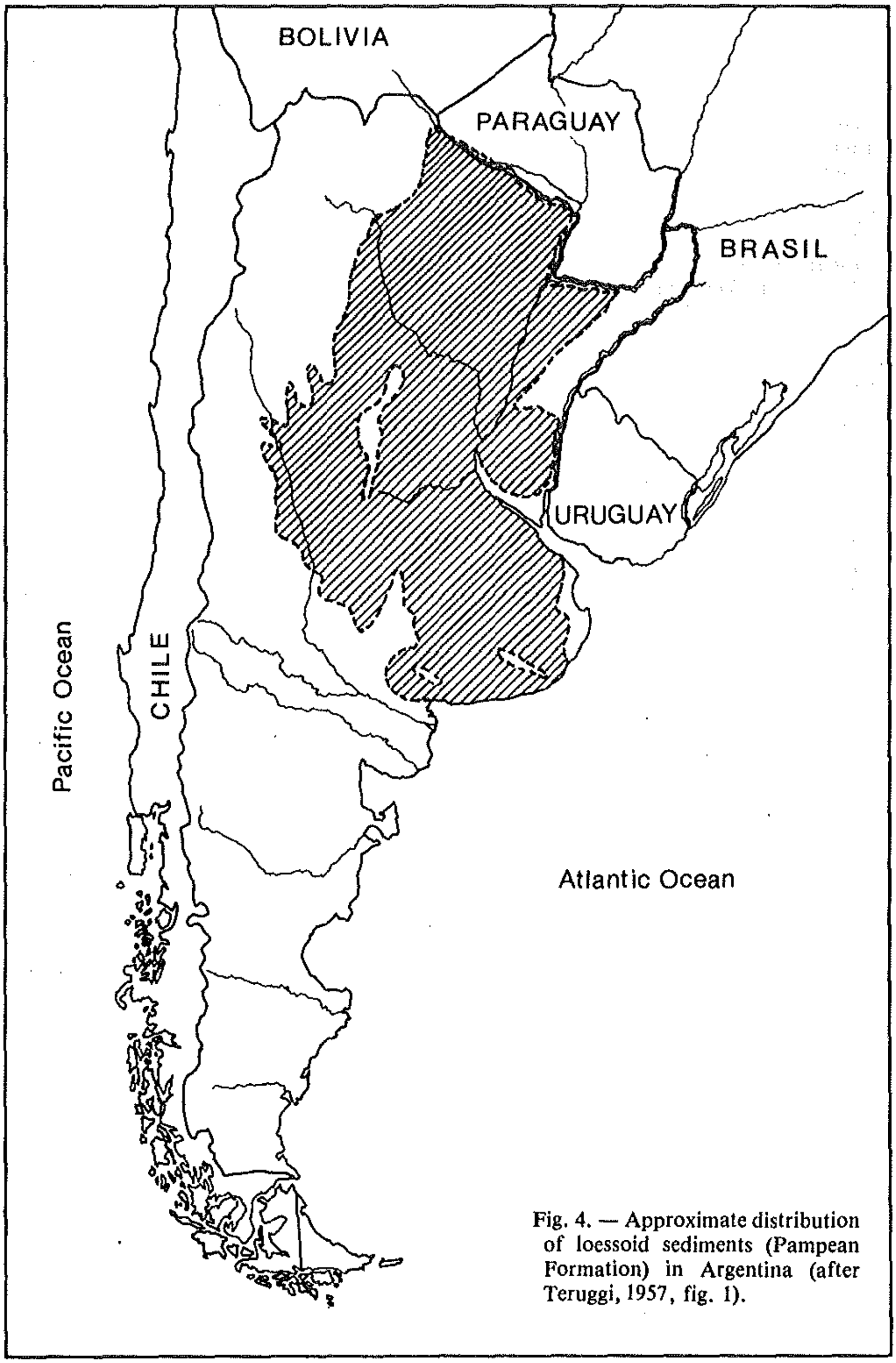


Fig. 4. — Approximate distribution of loessoid sediments (Pampean Formation) in Argentina (after Teruggi, 1957, fig. 1).

Uquian (Uquiense and Puelchense)

The mammal-bearing Uquía Formation in Jujuy Province (23°18'S, 65°21'W), northwestern Argentina (=Uquía, fig. 5), were discovered in 1912 by Enrique de Carles and later explored by Castellanos (1950). Small collections of mammals were made from these beds as summarized by L. Kraglievich (1930a, 1934),... "but their exact stratigraphic occurrence and associations are unknown" (Simpson, 1940, p. 696). From the time of discovery of this fauna, de Carles and Carlos Ameghino were of the opinion that it partially filled the paleontological hiatus between the Ensenadan and Chapadmalalan as established by F. Ameghino (L. Kraglievich, 1930a, p. 158). The Uquía fauna and Formation were formally recognized by L. Kraglievich (1930a) when he spoke of the *Fauna Uquiana* and *Formación Uqueana*, as transitional between Chapadmalalan and Ensenadan Age faunas.

Examination of the mammals from Uquía indicates that they came, more or less, from two different time intervals and horizons. The older of these "faunas", the *Uquiense*, is similar to the Chapadmalal fauna, and the other is related to the Ensenadan fauna according to L. Kraglievich (1930a, p. 158; 1934, p. 114). L. Kraglievich also noted that it is probable that there exists in the Uquía region various faunas transitional between the Chapadmalalan and Ensenadan, suggesting, in view of this, an intermediate age for the Uquía fauna (*sensu lato*). Simpson (1940, p. 696) cautioned, however, that since faunas of more than one age seem to be represented in the collection from Uquía, a fauna indicative of an intermediate age... "has not yet been determined on an objective basis." He further noted (p. 696) that:

> "of 15 genera recorded by [L.] Kraglievich [1934] (8 of them doubtfully), 5 are supposedly confined to this stage, 4 occur in both Ensenadan and Chapadmalalan (or earlier), 3 in the Ensenadan but not Chapadmalalan, and 3 in Chapadmalalan or earlier but not Ensenadan."

The fauna from Uquía was reanalyzed by Castellanos (1950) who agreed with previous workers that it represented a mixture of taxa... "araucanianos y pampeanos" ... (*i.e.* taxa of Pliocene and Pleistocene age respectively). He further noted (p. 52) that:

> "El material faunístico descripto no es suficiente, se requieren nuevos elementos más completos para las determinaciones exactas de los géneros."

To resolve this controversy it will be necessary to make more extensive collections of fossil mammals with good stratigraphic control. The Uquía Formation at its type locality, Esquina Blanca, was recently calibrated using paleomagnetostratigraphy and radioisotopic age determinations of mineral separates, and ranges in age from 2.5 to 1.5 Ma (Marshall, Butler, Drake, & Curtis, 1982). The fossil mammals thus far collected appear to come from the lower part of the formation from a level ranging from 2.5 to 2.4 Ma.

In the vicinity of Buenos Aires, beneath typical *pampean* deposits, occurs ..."a thick stratum of saturated, semiliquid sand"..., considered fluvial in origin (Simpson, 1940, p. 696). These subsurface sediments occur in the provinces known as *litoral fluvial argentino* (*i.e.* those provinces along the Río Paraná). This unit was improperly called

Arenas Puelches or *Puelchense* by various workers, and Doering (1882) utilized *Puelche* as equal to *Subpampeano* (see fig. 1). The long bibliographic history of the *Puelchense* has been summarized by Castellanos (1928) and Santa Cruz (1972). According to some authors an erosion surface separates the *Puelche* from the overlying *Ensenadense* (Simpson, 1940, p. 696-697; Pascual & Fidalgo, 1972, p. 229).

The *Puelche* from Buenos Aires Province is known only from excavations and drillings, and until the 1930's had no known fauna except for a few equivocal molluscs (Simpson, 1940, p. 697).

> "For many years most geologists have applied the name *Puelche* to almost any sands lying below the identified *pampean*. The *Puelche* of literature includes deposits of many different sorts and ages scattered from Bolivia to southern Patagonia and from the Andes to the Atlantic" (Simpson, 1940, p. 697).
> "Ameghino's lists of the '*Puelche* fauna', for instance, include animals from Tarija in Bolivia, from Córdoba, and from the Playa del Barco in southern Buenos Aires Province, probably of three or more different ages and none known really to be of the same age... as true *Puelche*" (Simpson, 1940, p. 697).

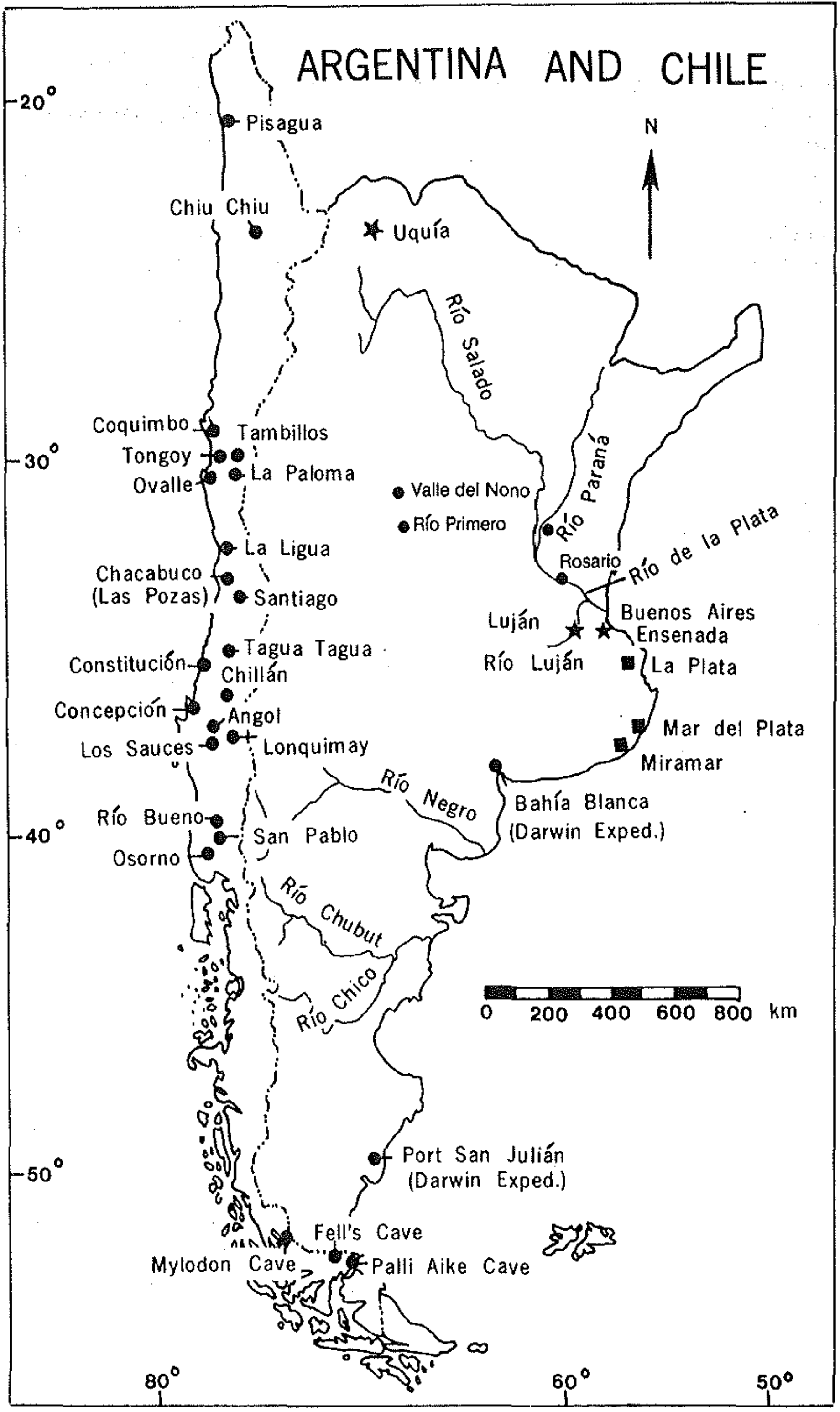
Rovereto (1914b, p. 86) proposed the term *Tarijense*, which he defined on the basis of the Tarija fauna of Bolivia, to replace the *Puelchense* as applied to the Quaternary of Argentina.

In the 1930's a fauna was recovered from the *Puelche* near the city of Buenos Aires (Rusconi, 1937, 1948, 1949). The fauna contains fossils derived from older rocks, but also includes remains of a fairly rich mammalian fauna of post-Chapadmalalan aspect (Pascual *et al.*, 1965, p. 180). This fauna is, in fact, suggestive... "of a rather ancient *pampean* fauna"... and ..."could well be considered as basal Ensenadan"..., or older, but still included in the *pampean* (Simpson, 1940, p. 697). Rusconi (1948, 1949) correlated this *Puelche* with the Uquía fauna of Jujuy, even though the supposed in situ taxa appear to be younger than part of the fauna known from Uquía (Simpson, 1940, p. 697). In addition, the mammal remains from the *Puelche* are, in most cases, fragmentary and their determination is, according to Pascual *et al.* (1965, p. 180), more doubtful than believed by Rusconi.

Pascual *et al.* (1965, p. 180) note that many mammals currently restricted to the Ensenadan are already represented in the *Puelchense*, such that — not withstanding the distinct stratigraphic position and lithologic character — the *Puelche* and Ensenada Formation can be assigned to the same age. Tentatively, however, these workers accept an Uquian Age largely on the basis of the existence in Uquía of certain taxa of post-Chapadmalalan but pre-Ensenadan character. They further refer the *Puelche* to an Uquian Age, realizing that better knowledge of its mammalian fauna may demonstrate closer affinity with faunas of Ensenadan Age. Santa Cruz (1972) recognized the so-called *Puelche* as a well defined lithostratigraphic unit under the name of *Formación Puelche*. These fluvial beds were deposited by the pre- Río Paraná (Pascual & Bondesio, 1961, p. 95) during its displacement to the south-southwest (Sala & Auge, 1970; Pascual & Odreman Rivas, 1971).

→

Fig. 5. — Map of Argentina and Chile showing principal mammal-bearing localities of Pleistocene Age. Type localities of Land Mammal Ages are marked with a star (Uquía, Ensenada, Río Luján). Solid squares = towns and cities.


ARGENTINA AND CHILE
N
20°
30°
40°
50°
80°
60°
50°
Pisagua
Chiu Chiu
Uquía
Río Salado
Coquimbo
Tambillos
Tongoy
La Paloma
Ovalle
Valle del Nono
Río Primero
Río Paraná
Río de la Plata
La Ligua
Rosario
Chacabuco
(Las Pozas)
Santiago
Luján
Buenos Aires
Ensenada
Tagua Tagua
Constitución
Chillán
Río Luján
La Plata
Concepción
Angol
Mar del Plata
Los Sauces
Lonquimay
Miramar
Río Negro
Bahía Blanca
(Darwin Exped.)
Río Bueno
San Pablo
Osorno
Río Chubut
Río Chico
0 200 400 600 800 km
Port San Julián
(Darwin Exped.)
Fell's Cave
Mylodon Cave
Palli Aike Cave

Sediments underlying Ensenadan beds in the mountain valleys of Nono and Los Reartes, Córdoba Province (fig. 5), provided two faunules described by Castellanos (1941, 1951, 1958 and elsewhere), assigned to the ***horizonte Brocherense***, which he correlated with the ***piso Uquiense*** in Jujuy. These faunules include *Paedotherium, Orthomyctera, Microcavia, Ctenomys (Paractenomys), Felis (Puma), Doellotatus, Plaina* (= *Pampatherium*?), *Isolinia* (a sclerocalyptine), *Nopachtus, Propanochthus*, and the toxodont *Nonotherium*. This "fauna" is now believed to represent a mixture of Montehermosan and Ensenadan taxa.

Ameghino (1909) reported *Paedotherium bonaerense* from a level underlying the classical Ensenadan in the base of the Pampean sequence at Buenos Aires harbour. The ***Preensenadan*** level may represent an Uquian equivalent. Uquian age beds also occur in Chaco Province in northern Argentina as indicated by the occurrence of a species of *Hydrochoeropsis* from a depth of 8 meters near La Sábana (J.L. Kraglievich & Reig, 1945).

Perhaps the best representation of an Uquian Age fauna occurs in formations superjacent to the Chapadmalal Formation along the coast between Mar del Plata and Miramar, Buenos Aires Province, Argentina (fig. 5). J.L. Kraglievich (1952a) named these the Barranca de Los Lobos, Vorohué, and San Andrés Formations. The fossil mammals from these beds have served to "fill", in part, the paleontological hiatus between Chapadmalalan and Ensenadan faunas (Pascual *et al.*, 1965, p. 180; 1966), and our concept of an Uquian fauna is essentially based on the fossils from these beds (Pascual, 1970, p. 1061).

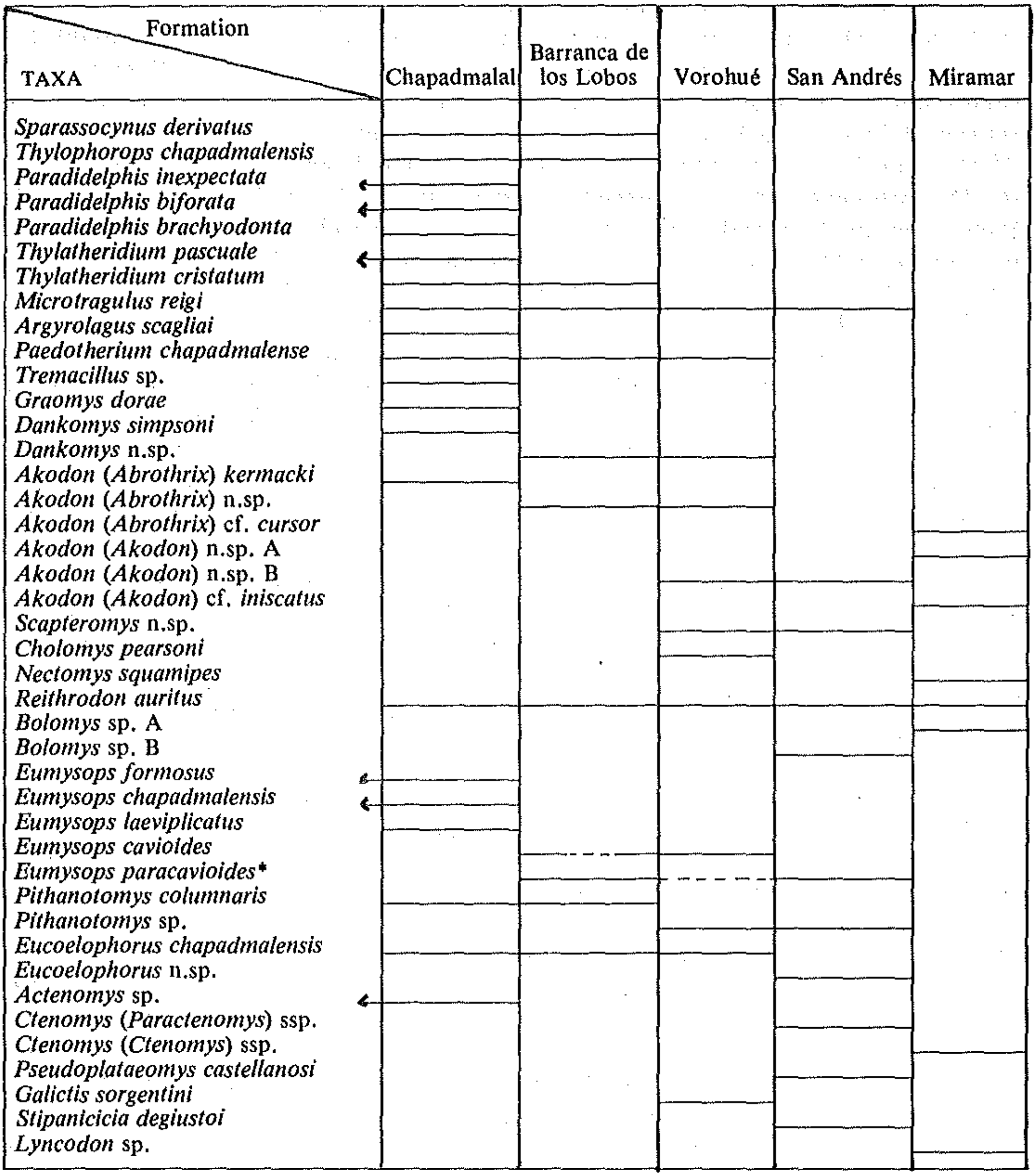
J.L. Kraglievich (1952a, table opposite p. 30) subdivided this sequence as follows:

rock unit "formations"	land mammal ages	sub-epochs
Santa Isabel/Cobo	Lujanian	Neopleistocene
Arroyo Seco	Bonaerian	
Miramar	Ensenadan	Mesopleistocene
San Andrés	Sanandresian	Eopleistocene
Vorohué	Vorohuean	
Barranca de Los Lobos	Uquian	
Chapadmalal	Chapadmalalan	Neopliocene

Pascual *et al.* (1965) did not recognize the validity of Kraglievich's ages Vorohuean and Sanandresian. They noted (1965, p. 179) that...

> "No one has yet clearly demonstrated that the Vorohuean is distinct from the Uquian. Therefore, we accept the Uquian Age as the intermediate one between the Montehermosan [*sensu lato*] and the Ensenadan, and disregard the others [*i.e.* Vorohuean and Sanandresian] which have been proposed" (translated from Spanish).

Fig. 6. — Known biochrons for various species of small mammals from the Mar del Plata-Miramar sequence (compiled by O.A.R.).



*For the biochron of *Eumysops* species, see J.L. Kraglievich (1965).

Because of the independence of rock and time units, J.L. Kraglievich's (1959a, p. 6) later inclusion of the San Andrés Formation as a member of the Vorohué Formation did not necessarily imply abandonment of his concept of a Sanandresian Age. However, this was the view which was later taken by Pascual *et al.* (1965, p. 179, n° 15).

Reig (personal comment) strongly feels that there is sufficient evidence for retention of Kraglievich's chronological subdivisions for what we here recognize as Uquian. The evidence for this comes from the studies of J.L. Kraglievich (1965), Reig (1956, 1957, 1980), Marshall & Reig (in preparation), and is corroborated by unpublished studies of the small mammals by Reig (1972) as summarized in figure 6. Reig proposed subdivision of the Uquian Age into three subages — from oldest to youngest, the Barrancalobian, to include the faunas from the Barranca Lobos, *Puelche* and Uquía "formations"; the Vorohuean, to include the faunas from the Vorohué Formation, the *Preensenadense*, and the *Ensenadense Basal*; and the Sanandresian, to include the fauna from the San Andrés Formation of J.L. Kraglievich (1952a). This approach of recognizing subages for Quaternary land mammal ages in South America is also being done in similar age beds in North America (Schultz *et al.*, 1978).

Guide fossils (*sensu* American Commission of Stratigraphic Nomenclature, 1961, article 21e) useful in recognizing Uquian Age faunas include *Cholomys, Hydrochoeropsis, Ctenomys (Paractenomys)*, and *Stipanicicia*. This time interval in Argentina is further delineated by the first record in South America of *Glyptodon, Scelidodon, Hydrochoerus, Ctenomys,* Canidae, Felidae, Ursidae, Gomphotheriidae, Equidae, Tapiridae, Camelidae, Cervidae; and the last record of *Thylophorops, Thylatheridium, Dankomys, Eumysops, Eucoelophorus, Pithanotomys*, Hegetotheriidae, Sparassocynidae, and Microtragulidae (fig. 3). Referable mammal-bearing strata in Argentina include the *Uquiense*, Barranca de los Lobos Formation, Vorohué Formation, San Andrés Formation, Puelche Formation, Ensenada Formation (*Preensenadense* and *Ensenadense Basal*), and possibly the lower part of the Malacara Formation.

Ensenadan (Ensenadense or Pampeano inferior)

The Ensenadan land mammal age derives its name from the close proximity of a locality studied by Ameghino to the city of Ensenada (34°51'S, 57°55'W) near la Plata, Buenos Aires Province (fig. 5). The Ensenada Formation was exposed in excavations made during construction of the La Plata harbor at Ensenada. The strata were encountered at a depth of seven to eight meters below the water level of the Río de La Plata (Ameghino, 1889; L. Kraglievich, 1934, p. 21).

Ameghino (1889) called these beds *piso Ensenadense*, although he earlier (1880) referred to them as *Pampeano inferior* following Doering (1882). The type locality is, according to Ameghino (1908), in the city of Buenos Aires and is based on the *Pampeano inferior* which is exposed on the banks of the Río de La Plata. In the type area the Ensenada Formation is variable in thickness, in some places exceeding 40 meters (Pascual & Fidalgo, 1972, p. 229). In the city of Buenos Aires the Ensenada Formation outcrops four to seven meters above the water level of the Río de La Plata, and it descends below this level for some 30 meters. In general, these beds increase in thickness toward the south (Ameghino, 1889).

As summarized by Frenguelli (1957, fig. 2), the Ensenada Formation has been divided into three units: the *Ensenadense inferior (Preensenadense)*, the *Ensenadense medio (Ensenadense basal)*, and the *Ensenadense superior (Ensenadense cuspidal = Ensenadense típico)*. A thin marine bed, the *Interensenadense (Intercalación estuariana con*

moluscos), lies between the ***basal*** and ***cuspidal*** units. The Ensenada Formation (***Pampeano inferior***) is distinguished from overlying units by the presence of numerous siliceous concretions (Ameghino, 1889).

Ameghino (1909) reported the occurrence of *Paedotherium bonaerense* in the ***Ensenadense basal*** on the basis of a specimen recovered during excavation of the Buenos Aires harbor. This find supports our belief that the ***Ensenadense basal*** and the underlying ***preensenadense*** may be of Uquian Age, while the ***Ensenadanse cuspidal*** should be considered the ***Ensenadense tipico*** (*s.s.*) (L. Kraglievich, 1934, p. 23).

Only in a few places is the upper part of the Ensenada Formation exposed, particularly in the city of Buenos Aires along the Río de La Plata, and in the base of the cliffs along the lower Río Paraná. Exposures of the Ensenada Formation also occur in the basal part of the cliffs in San Nicolás, Rosario, and along the Río Primero in Córdoba (capa M of Doering, 1882) (Frenguelli, 1957).

In Argentina, Ensenadan Age guide fossils include *Daedicuroides, Neuryurus, Theriodictis*, and *Brachynasua*. The first record of *Euphractus* (see Scillato Yané, 1980), *Lomaphorus, Neothoracophorus, Plaxhaplous, Lyncodon, Lutra, Dicotyles*, and *Vicugna*, and the last record of *Orthomyctera, Mesotherium*, and *Brachynasua* define this time interval (see Rusconi, 1936, 1938) (fig. 3). Referable mammal-bearing beds in Argentina include the Ensenada and Miramar Formations, Buenos Aires Province (Pascual *et al.*, 1965, p. 190); capa M of Doering (1882), Córdoba Province; and the lower member of the Yupoí Formation, Corrientes Province (Alvarez, 1974)[4].

Lujanian (Lujanense or Pampeano lacustre)

The Lujanian Age, following Pascual *et al.* (1965), includes two basic types of lithologic units. The ***Lujanense*** *s.s.* of Ameghino (1889), which includes beds of Lujanian Age in Argentina, consists typically of fluvio-lacustrine deposits occupying stream beds, channels, and shallow basins, often incised into beds of early Lujanian (*i.e.* ***Bonaerian***) and Ensenadan Age. The most characteristic facies of the Luján Formation, for example those in the bed of the Río Luján from which this unit derives its name (located 34°17'S, 58°54'W, about 65 km west of the city of Buenos Aires, fig. 5), consists mostly of gray-green sandy silts, clays, and reworked loess. Beds of the Luján Formation vary in thickness from a few centimeters to five or six meters depending upon the mode of deposition (*e.g.* pools, lakes or stream channels; Frenguelli, 1957, p. 45-47). The ***Bonaerense*** of Ameghino (1889), which is included in the uppermost part of Frenguelli's (1957, p. 63) ***Pampiano***, consists of reddish beds of eolian origin (Groeber, 1952, p. 86). As yet, no clear distinction has been made between faunas occurring in the fluvio-lacustrine (*i.e.* lower part of the Luján Forma-

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[4] Alvarez (1974, p. 309) reported the occurrence of "unos pocos restos de dientes, pertenecientes a las subfamilias Proterotheriinae (Orden Litopterna)... y Haplodontheriinae (Orden Notoungulata)" found in association with typical Pleistocene mammals. She figured (Pl. 1, fig. 6) a nearly complete left mandibular ramus of a proterotheriid and suggested (p. 309) that this association was due to redeposition of this specimen from older beds because members of this group had not previously been reported from the Quaternary. However, due to the completeness of this specimen we question this interpretation and suggest two alternatives. 1) These specimens are last occurrences and represent temporal extensions of these groups into the Quaternary in Corrientes, or 2) these specimens were collected from the underlying Ituzaingo Formation which is usually assigned to the Pliocene (Herbst, 1969, 1971).

tion) and eolian (*i.e.* Buenos Aires Formation) beds of Lujanian Age (Pascual *et al.*, 1965). In some regions (*e.g.* the lower course of the Río Salado, Buenos Aires Province) this formation has been divided into two members, the lower Guerrero Member containing extinct megafauna is clearly of Lujanian Age, and the upper Río Salado Member containing only living taxa is of Holocene Age (Fidalgo, de Francesco & Colado, 1973; Fidalgo & Tonni, 1978; Tonni & Fidalgo, 1979). Bombin (personal note) is of the opinion that the eolic and fluvio-lacustrine units are members of the same Luján Formation deposited as different facies which interfinger at the footslope-toeslope level (Bombin, 1975, 1980d).

Lujanian faunas are recognized by an aggregate of taxa largely distinct from those of the Ensenadan, and with the appearance of many new forms which persist to the present as conspicuous representatives of the Neotropical Region (fig. 3). It is also characterized by the last record of a large number of taxa found in the Uquian and Ensenadan (Pascual *et al.*, 1965, p. 181).

In Argentina, guide fossils for Lujanian Age faunas include *Equus, Eulamaops, Macrauchenia,* and *Notiomastodon.* This interval is marked by the first known record of *Chlamyphorus, Holochilus,* and *Cavia*; and the last record of Megatherioidea, Glyptodontoidea, *Arctodus, Smilodon*, Litopterna, Notoungulata, Proboscidea, Equidae, and *Morenelaphus* (fig. 3). Referable mammal-bearing strata in Argentina include the Buenos Aires Formation, Luján Formation (lower part = Guerrero Member - *sensu* Fidalgo, de Francesco & Colado, 1973; Tonni & Fidalgo, 1979), Arroyo Seco Formation, Santa Isabel Formation, Venado Formation (lower member), Del Aguila Formation, Junin Formation, Tandileufú Formation, Pascua Formation, Member Guerrero (Luján Formation from the lower Río Salado region), and continental *Belgranense*, beds F to L of Doering's sequence at Río Primero Valley, Córdoba Province; and *Reartense, Pucarense, Quillincense*, and *Bonaerense* of Córdoba Province as described by Castellanos (1942) (Pascual *et al.*, 1965, 1966; de Salvo, Ceci & Dillon, 1969; Fidalgo, de Francesco & Pascual, 1975); and upper member of Yupoí Formation, Corrientes Province (Alvarez, 1974).

POST-PAMPEAN (HOLOCENE)

The *Post-Pampeano* of Ameghino (1889) includes all beds deposited after Lujanian time. Included are the *Platense, Aimarense, Cordobense, Querandino*, and *Ariano* of early workers (see J.L. Kraglievich, 1952; Groeber, 1952; Frenguelli, 1957; Tonni & Fidalgo, 1979; Fidalgo & Tonni, 1978). The term *Post-Pampeano*, which has fallen into disuse, and Holocene are generally regarded as synonymous (Bordas, 1957, p. 78) (fig. 1), in spite of the fact that Frenguelli (1957) included within it the unquestionable Pleistocene Lujanian (*Lujanense*). It has been demonstrated (Tonni & Fidalgo, 1979) that the Luján Formation is composed of two members (see above).

BOLIVIA

Bolivia is second only to Argentina in its wealth of known Pleistocene Age deposits and vertebrate faunas, reviews of which are given by Hoffstetter (1963a,b, 1968). Of these, the faunas from Tarija and Ñuapua are the richest and best known (fig. 7).

I. TARIJA

The classic fauna of Tarija, located in the southern part of the Bolivian Andes at an elevation of 1950 meters (fig. 7) has been the subject of numerous studies as reviewed by Hoffstetter (Lex. Strat, in preparation). The fossiliferous deposits of Tarija were first cited by Diego Avalo de Figueroa (*fide* d'Orbigny, 1842, III-4, Paléont., p. 145). Joseph de Jussieu, in a letter to his brother in 1761 (*fide* Cuvier, 1823, p. 266-267) noted the presence of fossil bones and teeth at Tarija. Laurillard (in d'Orbigny, 1842, III-4, Paléont., p. 145, pl. X-XI) described mastodonts from these deposits. In 1846 Weddell, as a member of the F. de Castelnau expedition visited Tarija and collected fossils (Weddell, 1851, p. 196-207) which he send to Paris. These specimens were subsequently studied by P. Gervais (1855), and H. Gervais & F. Ameghino (1880) (Hoffstetter, 1970d). Collections made by de Carles (1888) for the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires were studied by F. Ameghino (1902). In 1902 E. Nordenskiöld sent a collection to Upsala, Sweden which resulted in publications by Nordenskiöld (1903) and Sefve (1912, 1915a).

In 1903, Créqui-Montfort and Sénéchal de la Grange of Paris, purchased a large number of fossil mammals from the Echazú family of Tarija which they gave to the Museum National d'Histoire Naturelle, Paris, France. This collection served as the basis for the monographic work of Boule & Thevenin (1920). The stratigraphy was described by de Mortillet (1922), a member of the 1902 party.

Various taxonomic groups have been described by L. Kraglievich (1928, 1930b; Canidae, Hydrochoeridae), Cabrera (1929, 1931; mastodonts, Camelidae), López Aranguren (1930, Camelidae), and the stratigraphy has been reviewed by Oppenheim (1943). Known collections of this fauna have come from various stratigraphic levels in the basins of Tarija, Concepción (=Uriondo), and Padcaya (Hoffstetter, 1963a,b). The distribution of fossil vertebrates, based on the above collections, was considered by Hoffstetter (1963a,b) to represent a single faunal assemblage which he designated, following a term proposed by Rovereto (1914b, p. 86), *Tarijense*. Hoffstetter now believes that this interpretation may be oversimplified and that further stratigraphic work and refinement of correlations among these basins is needed to establish the relative ages of the diverse fossiliferous levels. The predominant lithologies within the Tarija Basin are silty clays, sands, conglomerates, and volcanic ash. It appears as though these fluviatile deposits accumulated in an accreting stream and floodplain system (MacFadden & Wolff, 1981).

The Tarija "fauna" includes 62 species, representing 55 genera, and 28 families. Representative genera include *Lutreolina, Nothropus, Megatherium, Glossotherium, Lestodon, Scelidodon, Chaetophractus, Euphractus, Propraopus, Pampatherium,*

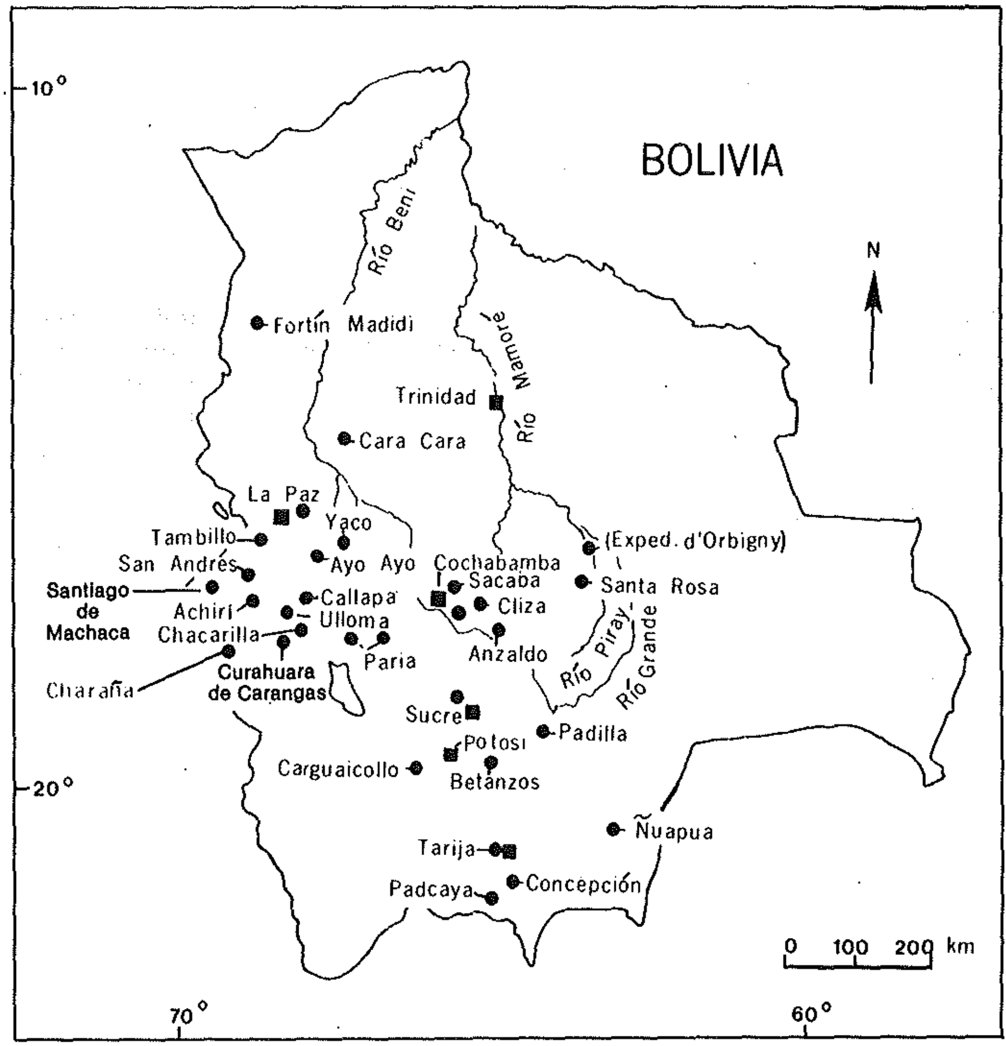

Fig. 7. — Map of Bolivia showing principal mammal-bearing localities of Pleistocene Age. Slightly modified after Hoffstetter (1968, p. 824, fig. 1). Solid squares = towns and cities.

Glyptodon, Chlamydotherium, Neothoracophorus, Hoplophorus, Panochthus, Coendou, Cavia, Galea, Neochoerus (Pliohydrochoerus), cf. *Hydrochoerus, Myocastor, Ctenomys, Euryzygomatomys* (Reig, unpublished), *Kunsia, Oxymycterus, Nectomys, Phyllotis, Andinomys, Calomys, Canis, Theriodictis, Chrysocyon, Dusicyon (Pseudalopex), Arctodus (= Arctotherium), Nasua* (of questionable age), *Conepatus*, cf. *Galera, Smilodon, Leo (Jaguarius), Felis (Puma), Felis (Herpaillurus), Macrauchenia, Toxodon, Cuvieronius*, cf. *Notiomastodon?*, cf. *Stegomastodon?, Equus, Amerhippus, Hippidion, Onohippidium* (includes *Parahipparion*), *Tapirus, Platygonus, Palaeolama, Lama, Vicugna, Hippocamelus*, and *Charitoceros* (Hoffstetter, 1963a, 1968, p. 829n1; Reig, 1972; Frailey, Campbell & Wolff, 1980; MacFadden & Wolff, 1981). With the exception of mammals, the Tarija fauna is depauperate in other vertebrates, although fish, frog and reptile remains are recorded in the various collections (Hoffstetter, 1963a, p. 201-202); C. Villarroel (unpublished) has recorded remains of birds from Padcaya; and Vergnaud-Grazzini (1968) studied the frogs from Tarija.

Following Ameghino, Boule & Thevenin (1920) placed Tarija (as well as all of the Pampean) in the Pliocene. Rovereto (1914b) considered the Tarija fauna to be of a separate land mammal age, the ***Tarijense***, which should correspond to the ***Puelchense*** in the stratigraphic sequence of Argentina. This proposal, however, is inadmissible since the ***Tarijense*** is clearly younger than the ***Puelchense***. In accordance with the work of L. Kraglievich (1930a) the ***Tarijense*** seems to be younger than the Ensenadan but older than the Lujanian *s.s.*, and would correspond to the ***Bonaerense*** of Ameghino (1889). L. Kraglievich (1934) later stressed the post-Ensenadan character of the Tarija fauna. Patterson, as quoted by Simpson (1940, p. 691) considered the Tarija fauna to be middle Pleistocene in age on the basis of the magnificent, mostly undescribed collection in the Field Museum of Natural History, Chicago made by E.S. Riggs (Marshall, 1978). Patterson & Pascual (1972, p. 249) considered this fauna to be Lujanian in age. Most recently Webb (1974, p. 176) proposed an Ensenadan Age for the Tarija fauna on the basis of stage of evolution of *Palaeolama* and *Lama* species. However, there are several species of *Palaeolama* from this fauna (Hoffstetter, unpublished material in the MNHN, Paris), some of which are poorly known.

Recently, MacFadden *et al.* (1983) calibrated the Tarija Formation using radioisotopic age determinations and magnetostratigraphy. They demonstrate that this unit corresponds to the late Matuyama period (reversed polarity, with the short normal Jaramillo event) and the early normal Brunhes period. This formation spans a time interval from about 1.0 to 0.7 Ma, or perhaps younger. Consequently these workers assign the Tarija fauna to the Ensenadan land mammal age. But it is possible that some fossils from this locality are younger.

II. ÑUAPUA

Ñuapua is located in southeastern Bolivia, between the villages of Carandaití and Capirendi (fig. 7), department of Chuquisaca. Bonarelli (1921, p. 80) mentioned this locality, under the erroneous name Ñap-ña, and reported the remains of proboscideans and other mammals. Hoffstetter and Branisa, from 1962 to 1965, made two expeditions to Ñuapua studying the stratigraphy, sedimentology, and vertebrate paleontology (Hoffstetter, 1968). In 1978 an American team revisited the locality (report by R.G. Wolff, F.M. Wahl & K.E. Campbell; and publication by MacFadden & Wolff, 1981).

The Ñuapua Formation, composed of 9 meters of sediments including volcanic ash (MacFadden & Wolff, 1981), rests unconformably on non-fossiliferous gray and red clays of the Tertiary Chaco Series. On the basis of color and fossil content Hoffstetter (1968) divided the Ñuapua Formation into three members. MacFadden & Wolff (1981) also recognize three stratigraphic units within this formation though these workers bring new data for their age interpretation.

The lower member, Ñuapua 1, is composed of two to three meters of pink to reddish consoldated cinerite. This is the level from which the remains of Pleistocene mammals are believed to have been recovered by early workers. Hoffstetter (1968) reported the following mammalian genera from Ñuapua 1 — *Panochthus, Sclerocalyptus, Glyptodon, Chlamydotherium, Pampatherium,* cf. *Nothrotherium, Megatherium, Mylodon, Hydrochoerus, Protocyon, Arctodus, Leo (Jaguarius), Smilodon, Macrauchenia, Toxodon, Stegomastodon, Equus (Amerhippus), Hippidion, Palaeolama,* and Cervidae.

Early workers suggested similarities between the Ñuapua 1 and the Tarija faunas. Hoffstetter (1968), however, noted significant differences between the two. Among the glyptodonts, *Panochthus* is rare at Tarija, but relatively abundant in Ñuapua 1. *Hoplophorus* and *Neothoracophorus,* known from Tarija, are absent from Ñuapua 1. *Theriodictis* and *Canis* (formerly *Aenocyon*) are present at Tarija, while canids are represented at Ñuapua 1 by *Protocyon.* The notoungulate, *Toxodon,* rare at Tarija is a frequent element in Ñuapua 1. The only mastodon known from Ñuapua 1 is *Stegomastodon* which is rare at Tarija. Hoffstetter (1968) suggested these faunal differences are due to a difference of environments — Tarija being an "andean" fauna and Ñuapua 1 being a lowland "plains" fauna.

A second member of the Ñuapua Formation, Ñuapua 2, contains fossil vertebrates recovered from a gray reworked tuff, ranging in thickness from 1.5 to 2.0 meters (MacFadden & Wolff, 1981). The fauna from this stratigraphic unit was discovered by Branisa in 1955 who suggested that it accumulated under a humid, lacustrine environment. Hoffstetter (1968) recorded amphibians (Vergnaud-Grazzini, 1968), reptiles, birds, and a diverse mammal fauna. The latter includes *Eumops* (Linares, unpublished), *Calomys, Graomys, Holochilus* (see Reig, 1972), *Euphractus, Chaetophractus, Tolypeutes, Dasypus, Propraopus, Scelidodon, Galea, Lagostomus, Myocastor, Hydrochoerus, Ctenomys, Dusicyon (Pseudalopex), Toxodon, Paleolama, Morenelaphus* and a Holocene human skull dated at 7200 ± 400 yrs B.P. (on bone apatite: Wolff, Wahl & Campbell's report); mammalian bones yielded 6600±370 B.P. (MacFadden & Wolff, 1981). The Ñuapua 2 fauna differs significantly from the Ñuapua 1 fauna. The Ñuapua 2 fauna is characterized by small vertebrates [*e.g.* amphibians, birds (including forms with aquatic habits: Anseridae, Podicipidae, Plataleidae, Rallidae, Jacanidae), and rodents (*Myocastor, Holochilus*)] indicative of a humid environment. Hoffstetter (1968) suggested that these faunal differences may be due to the disappearance of certain large mammals from Ñuapua 1, and the appearance of a contemporaneous fauna of smaller sized animals in Ñuapua 2. Alternatively, the faunal differences may simply be due to changing environmental conditions or to those of preservation and/or insufficient sampling. The Ñuapua 2 fauna is, in fact, interpreted to have accumulated during a period of locally stagnant water conditions which would have altered the biocoenose. The Ñuapua 1 fauna has been considered Ensenadan in age, based on the presence of *Toxodon ensenadensis* (R. Pascual, personal note), but the exact stratigraphic range of this species is unknown outside of Argentina. The Ñuapua 2 fauna, which comes from a different unit and is younger in age, could correspond to the Lujanian or even to the early Holocene.

Fossil vertebrates have not yet been recorded from the third member of the Ñuapua

Formation, Ñuapua 3, which MacFadden & Wolff (1981) regard as Quaternary alluvium. An ulna referred to *Toxodon* was recovered by Hoffstetter (1968, p. 834) at the basal contact of Ñuapua 3 with the underlying Ñuapua 2, but not within the tuff of the Ñuapua 3 level.

The paleomagnetic data (MacFadden & Wolff, 1981) indicate that the Ñuapua Formation is entirely located in the normal Brunhes period, which begins at 0.73 Ma. Consequently Ñuapua 1 is probably Lujanian in age; but it can also include a part of late Ensenadan, if the Ensenadan-Lujanian boundary is conventionally located at 0.3 Ma (see above). According to the same authors, Ñuapua 2 is Holocene in age; it must be noted that the human skeleton dated 7200 yrs B.P. proceeds from Ñuapua 2 and not from Ñuapua 1 where it is erroneously placed in the table 3 of MacFadden & Wolff 1981 (rectification according to Wolff, Wahl & Campbell's report, confirmed by MacFadden's letter to Hoffstetter).

III. DEPOSITS OF THE ALTIPLANO

A number of mammal bearing deposits of Pleistocene Age are known from the Bolivian Altiplano, at an elevation of 4,000-3,650 m. between Lake Titicaca on the north and Salar de Uyuni on the south (fig. 7). However, these deposits have been little explored and their faunas are incompletely known.

The oldest known of these is at Ulloma, on the south side of the Río Desaguadero. Pleistocene fossils have been collected from the Ulloma Formation which unconformably overlies the folded beds of the late Miocene Totora Formation. Fossils from the Ulloma Formation described by Philippi (1893), Pompekj (1902), and Sefve (1912, 1914, 1915a,b) include *Megatherium, Scelidodon, Glyptodon, Macrauchenia, Cuvieronius*, and *Onohippidium* (includes *Parahipparion*). According to Servant & Fontes (1978), the Ulloma Formation represents deposits of Lake Ballivián, an ancient extension of Lake Titicaca, and occur at an elevation of 3,880 meters. These well stratified deposits are composed of fine grained sands rich in calcareous nodules with some argillaceous layers. The Ulloma Formation is bounded below by a tuff and above by a diatomite; the latter is overlain by a pebbly sand.

Many early workers placed the Ulloma Formation in the early Pleistocene. The extension of Lake Ballivián (Ulloma Formation) corresponds approximately to the phase of retreat of the third glaciation (*i.e.* Sorata) of Servant. If we accept that the four glaciations recognized by Servant (*i.e.* Calvario, Kaluyo, Sorata, Choqueyapu) correspond to those of Groeber which were adopted by J.L. Kraglievich (1952a) (*i.e.* Vallimanca, Colorado, Diamante, Atuel), then the Ulloma Formation is contemporaneous with the Diamante glaciation and was deposited just prior to the Lujanian (*s.s.*). On the geomorphological evidence it seems that the Ulloma Formation was deposited sometime after the Ensenadan (*s.s.*) but before the Lujanian (*s.s.*), that is the Bonaerian of Ameghino.

Another Altiplano deposit is Ayo Ayo, located north of Ulloma (fig. 7). Pleistocene fossils were recovered from a sandy horizon which occurs above an undated tuff, which in turn conformably overlies strata which yield a Pliocene fauna. Based on its stratigraphic position these beds have been assigned to the early Pleistocene; but

Lavenu (1978) observed a paleosol at the top of the Pliocene unit, suggesting that the cinerite and overlying beds are of Pleistocene Age. The known fauna includes *Macrauchenia, Scelidodon,* and a cervid (Hoffstetter *et al.*, 1971; Hoffstetter, unpublished). The successive Pliocene and Pleistocene faunas contrast with one another, and even their homologous taxa (*e.g.* macrauchenids, mylodontids) do not favor evolution *in situ.* Apparently, the Pliocene fauna left no direct descendents in this area and was replaced in the Pleistocene by an allochthonous fauna.

At Charaña (western Altiplano near the Chilean border) M. Blanco discovered in 1979 remains of mammals in the Charaña Formation whose stratigraphic position, above the Pérez ignimbrites, indicates an age younger than 2.5 Ma. The fossils, identified by Hoffstetter (unpublished), include *Plaxhaplous* (recorded for the first time in Bolivia), *Glossotherium, Macrauchenia,* and a cervid.

IV. BEDS OF THE CORDILLERA ORIENTAL

The most interesting of the Pleistocene localities in this area is that of Anzaldo, located 55 kilometers southeast of Cochabamba (fig. 7), where M. Montaño (unpublished thesis, Department of Geology, Univ. Nat. Autónoma San Andrés, La Paz, 1968) described a fossiliferous section which he assigned to the Pleistocene. A subsequent visit to the locality by Hoffstetter, Montaño, and Ortega revealed that within the Quebrada Tijascka, three kilometers west of Anzaldo, a small macrauchenid, cf. *Promacrauchenia,* of Pliocene aspect was collected from a low stratigraphic level in a two meter siltstone unit. From a pebbly unit above the latter, Montaño recovered a complete caudal tube (1.3 meters in length) of the glyptodont *Prodaedicurus* cf. *P. devicenzii* Castellanos (identified by Hoffstetter). This species was erected by Castellanos (1940) on specimens from Uruguay collected from beds (the *Castellanosense*) located stratigraphically between those of Montehermosan and Ensenadan Age. Mones (1979, p. 16-17) discusses the status of the *piso castellanosense* of Uruguay and concludes that it is of Montehermosan Age. Above the bed with *Prodaedicurus,* which appears to correspond to the Uquian, have been collected specimens of *Megatherium, Glyptodon,* and a camelid, which are clearly Pleistocene in age.

V. AMAZONIAN REGION

From Fortín Madidi and Cara Cara in the Río Beni Basin have been found remains of Toxodontidae (fig. 7). Further to the southeast d'Orbigny recovered bones of large mammals (which were unfortunately lost during the same expedition) in the bed of the lower course of the Río Piray. Within the same river valley, but further south near Santa Cruz (fig. 7), mastodont teeth were recovered in 1960 (Hoffstetter, 1968).

BRAZIL

The most famous localities yielding Quaternary Age fossils in Brazil are the calcareous caves in Minas Gerais State, known through the studies of the Danish naturalist Peter W. Lund from 1836 to 1845, and Herluf Winge — who described the collection sent by Lund to the Universitets Zoologiske Museum, Copenhagen, Denmark — from 1884 to 1915 (Lund, 1950). However, Quaternary fossil mammals have been found in every state of Brazil (see for example Bombin, 1975, 1976; Oliveira, 1956; Simpson & Paula Couto, 1957, 1981; Paula Couto, 1953, 1956, 1970a,b; Cunha, 1959, 1966; Price & Campos, 1970; Hoffstetter, 1954b; Orsted, 1956; Winge, 1893).

For purposes of the following discussion, the Pleistocene vertebrate bearing deposits of Brazil (fig. 8) are grouped into four areas (fig. 9). Area 1 corresponds to the southern half of the state of Río Grande do Sul, and is a natural continuation of the Argentinian and Uruguaian Pampas. Area 2 corresponds largely to the Brazilian Plateaus (*Planalto Central e Meridional*), is covered by forests and savannas (*cerrado*), and includes the northern part of Río Grande do Sul, the states of Santa Catarina, Paraná, São Paulo, Rio de Janeiro, Espirito Santo, Minas Gerais, and parts of Bahia, Goiás, and Mato Grosso. Area 3 corresponds to the Brazilian northeast (Nordeste), is covered by forests and xerophytic vegetation (*caatinga*), and includes the states of Alagoas, Ceará, Paraíba, Pernambuco, Piauí, Río Grande do Norte, Sergipe, and parts of Bahia, Goiás, and Maranhão. Area 4 comprises the Amazon Basin, is dominated by tropical forest and includes the states and territories of Acre, Amapá, Amazonas, Pará, Rondônia, Roraima, and parts of Goiás, Maranhão, and Mato Grosso.

With the exception of the Touro Passo local fauna (Bombin, 1976), the stratigraphic positions of the fossils in question are poorly known. The above mentioned collections from Minas Gerais, for example, are a mixture of late Pleistocene and Holocene specimens without stratigraphic control. As a generalization it is possible to say that the fossils from area 1 were found in fluvial and lacustrine deposits; in area 2 they come from fluvial, lacustrine, and particularly, from cave deposits (*e.g.* Lagoa Santa region; Minas Gerais; and Iporanga region, São Paulo); in area 3 they are generally found in lacustrine and waterhole (*cacimbas*) deposits; and in area 4 they are from lacustrine, and particularly fluvial sediments.

It is important to consider the different depositional histories of the localities when comparing their composite faunas, given the obvious taphonomic contrasts to be expected. Another important factor which needs to be considered is the amount of research which has been accomplished at each locality. The apparent higher diversity of the fauna in area 2, is explained by a combination of three factors: 1) it represents mainly cave deposits, 2) was intensively collected (principally by Lund over a 10 years period), and 3) includes Holocene fauna. If the marsupials, bats, rodents, and other animals likely to be overrepresented in cave deposits are subtracted from the 109 genera present in area 2, the result is a fauna composed of 30-40 genera which compares better to the other South American assemblages (the list of genera for the Lujanian in Argentina, for example, comprises 59 genera). On the other hand, if only the megafauna is counted, the area 2 set has 31 genera, which compares well with the 39 of the Lujanian in Argentina, and the 26 of area 1.

Fig. 8. — Occurrence of Pleistocene mammals in Brazil grouped in areas, see fig. 9 (based on Bombin, 1975, 1976; Cunha, 1959, 1966; Paula Couto, 1953, 1956, 1970a,b, 1975; Pinto & Closs, 1967; Rolim, 1974; Simpson & Paula Couto, 1957; and unpublished studies of Bombin).

x = present; - = not present; ? = questionable occurrence.
+ = extinct; 1 = could be Holocene; 2 = older than late Pleistocene.

Area Taxa	1	2	3	4
Marsupialia	-	x	-	-
Didelphidae	-	x	-	-
Didelphis	-	x	-	-
Marmosa	-	x^1	-	-
Philander	-	x^1	-	-
Metachirus	-	x^1	-	-
Lutreolina	-	x^1	-	-
Monodelphis	-	x^1	-	-
Caluromys	-	x^1	-	-
Chironectes	-	x^1	-	-
Chiroptera	-	x	-	-
Emballonuridae	-	x	-	-
Peropterix	-	x^1	-	-
Phyllostomatidae	-	x	-	-
Micronycteris	-	x^1	-	-
Tonatia	-	x^1	-	-
Chrotopterus	-	x^1	-	-
Phyllostomus	-	x^1	-	-
Anthorhina	-	x^1	-	-
Glossophaga	-	x^1	-	-
Lonchoglossa	-	x^1	-	-
Hemiderma	-	x^1	-	-
Artibeus	-	x^1	-	-
Chiroderma	-	x^1	-	-
Vampyrops	-	x^1	-	-
Sturnira	-	x^1	-	-
Desmodontidae	-	x	-	-
Desmodus	-	x^1	-	-
Natalidae	-	x	-	-
Natalus	-	x^1	-	-
Vespertilionidae	-	x	-	-
Myotis	-	x^1	-	-
Eptesicus	-	x^1	-	-
Lasiurus	-	x^1	-	-
Molossidae	-	x	-	-
Molossus	-	x^1	-	-
Tadarida	-	x^2	-	-
Primates	x	x	x	?
Callitrichidae	-	x	-	-
Callithrix	-	x^1	-	-
Cebidae	-	x	-	-
Cebus	-	x^1	-	-
Callicebus	-	x^1	-	-
Alouatta	-	x^1	-	-
Brachyteles	-	x^1	-	-
Hominidae	x	x	x	?
Homo	x	x	x	?

Fig. 8 (cont.)

Area Taxa	1	2	3	4
Edentata	x	x	x	x
Megalonychidae	x	x	x	x
+ *Nothrotherium*	-	x	x	-
+ *«Ocnopus»*	-	x	-	-
+ *Valgipes*	-	x	-	-
Megatheriidae	x	x	x	x
+*Megatherium*	x	-	-	-
+*Eremotherium*	-	x	x	x
Mylodontidae	x	x	x	x
+*Scelidotherium*	x	-	-	-
+*Scelidodon*	-	x	x	-
+*Glossotherium*	x	x	x	?
+*Lestodon*	x	x	-	x
Dasypodidae	x	x	x	x
Euphractus	-	x	-	-
Cabassous	-	x	-	-
+*Propraopus*	x	x	-	-
Dasypus	-	x	-	-
+*Pampatherium*	x	x	x	x
Glyptodontidae	x	x	x	x
+*Hoplophorus*	-	x	?	-
+*Panochthus*	x	-	x	-
+*Parapanochthus*	-	-	x	-
+*Doedicurus*	x	x	-	-
+*Glyptodon*	x	x	x	?
Myrmecophagidae	-	x	-	-
Myrmecophaga	-	x[1]	-	-
Tamandua	-	x[1]	-	-
Lagomorpha	-	x	-	-
Leporidae	-	x	-	-
Sylvilagus	-	x[1]	-	-
Rodentia	x	x	?	x
Sciuridae	-	x	-	-
Sciurus	-	x[1]	-	-
Cricetidae	-	x	-	-
Hesperomys	-	x[1]	-	-
Akodon	-	x[1]	-	-
Zygodontomys	-	x[1]	-	-
Blarinomys	-	x[1]	-	-
Oxymycterus	-	x[1]	-	-
Kunsia	-	x[1]	-	-
Oryzomys	-	x[1]	-	-
Rhipidomys	-	x[1]	-	-
Nectomys	-	x[1]	-	-
Calomys	-	x[1]	-	-
Scapteromys	-	x[1]	-	-
Erethizontidae	-	x	-	-
Coendou	-	x	-	-
Caviidae	-	x	-	-
Galea	-	x[1]	-	-
Cavia	-	x	-	-

Fig. 8 (cont.)

Area Taxa	1	2	3	4
Hydrochoeridae	x	x	-	-
Hydrochoerus	x	x	-	-
+*Neochoerus*	-	x	-	-
Dinomyidae	-	x	-	x
+*Tetrastylus*	-	x	-	-
+*Phoberomys*	-	-	-	x[2]
Dasyproctidae	-	x	-	-
Dasyprocta	-	x[1]	-	-
Cuniculus	-	x[1]	-	-
Myocastoridae	x	x	-	-
Myocastor	x	x	-	-
Octodontidae	-	x	-	-
+*Dicolpomys*	-	x	-	-
Echimyidae	-	x	-	-
Kannabateomys	-	x[1]	-	-
Isothrix	-	x[1]	-	-
Echimys (incl. *Phyllomys*)	-	x[1]	-	-
Cercomys	-	x[1]	-	-
Proechimys	-	x[1]	-	-
Cliomys	-	x[1]	-	-
Euryzygomatomys	-	x[1]	-	-
Carterodon	-	x[1]	-	-
Odontoceti	-	-	-	x
Platanistidae	-	-	-	x
+*Plicodontinia*	-	-	-	x[2]
Carnivora	x	x	x	?
Canidae	-	x	-	-
Dusicyon (*Pseudalopex*)	-	x[1]	-	-
Chrysocyon	-	x[1]	-	-
Speothos	-	x[1]	-	-
+*Protocyon*	-	x	-	-
Ursidae	-	x	?	-
+*Arctodus*	-	x	-	-
Procyonidae	-	x	-	-
Nasua	-	x[1]	-	-
Procyon	-	x[1]	-	-
Mustelidae	-	x	-	-
Galera	-	x[1]	-	-
Grison	-	x[1]	-	-
Lutra	-	x[1]	-	-
Pteronura	-	x[1]	-	-
Conepatus	-	x[1]	-	-
Felidae	x	x	x	?
Felis (*Puma*)	?	x	-	-
Felis (*Noctifelis*)	-	x[1]	-	-
Felis (*Leopardus*)	-	x[1]	-	-
Leo (*Jaguarius*)	-	x	-	-
+*Smilodon*	x	x	x	-
Litopterna	x	x	x	-
Macraucheniidae	x	x	x	-
+*Macrauchenia*	x	x	x	-

Fig. 8 (cont.)

Area Taxa	1	2	3	4
Notoungulata	x	x	x	x
Toxodontidae	x	x	x	x
+ *Toxodon*	x	x	x	x
+ *Trigodonops*	-	-	?	x^2
+ *Abothrodon*	-	-	-	x^2
Proboscidea	x	x	x	x
Gomphotheriidae	x	x	x	x
+ *Stegomastodon*	x	-	-	-
+ *Haplomastodon*	x	x	x	x
Sirenia	-	-	-	x
Trichechidae	-	-	-	x
Trichechus	-	-	-	x
Perissodactyla	x	x	x	x
Equidae	x	x	x	?
+ *Equus*	x	x	x	-
+ *Hippidion*	x	x	x	-
Tapiridae	x	x	x	x
Tapirus	x	x	x	x
Artiodactyla	x	x	x	x
Tayassuidae	x	x	x	-
Dicotyles	x	x	x	-
+ *Platygonus*	-	x	-	-
Camelidae	x	x	x	-
+ *Palaeolama*	x	x	x	-
Lama	x	-	x	-
Cervidae	x	x	x	x
Ozotoceros	x	x	-	-
Blastocerus	x	x	-	-
+ *Morenelaphus*	x	-	-	-
Mazama	x	x	-	-

The paucity of taxa collected from area 4 is readily explained by the lack of systematic field work and study of existing museum collections. The same can be said with reference to area 3.

The similarity between the fauna in area 1 and the faunas of Lujanian Age in Argentina and Uruguay was clearly established by Bombin (1975). It is possible to compare the faunal similarity of each one of the four areas in relation to the Lujanian fauna of Argentina, and among themselves, using Fager's Index of Similarity:

$$\text{F.I.S.} = \frac{\text{number of genera in common for two sets}}{\sqrt{\text{product of total genera in each set}}}$$

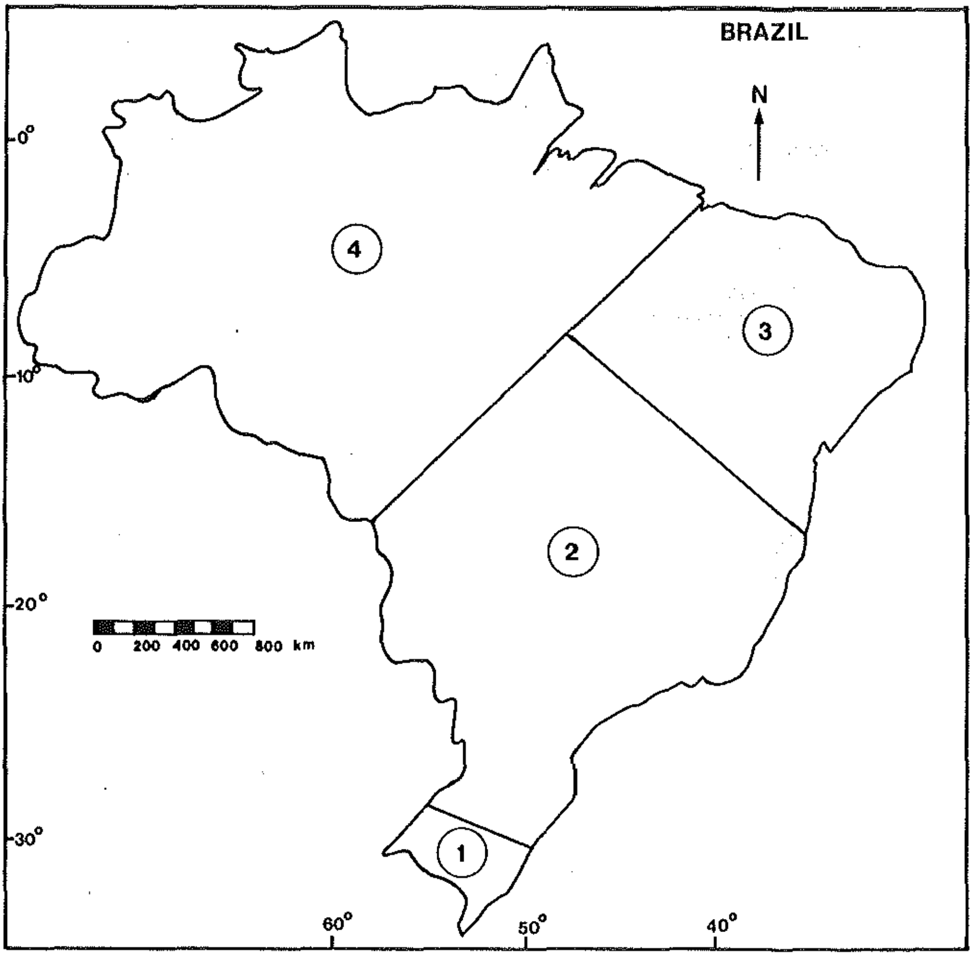

Fig. 9. — Map of Brazil showing the four areas for which composite faunas were listed in fig. 8, and discussed in the text. Area 1 - Southern Grasslands; area 2 - Brazilian Plateaus; area 3 - Northeastern Brazil; and area 4 - Amazonian Basin.

Subtracting the bats from the total number of genera to minimize the biasing factor of having cave faunas in area 2, the following matrix of F.I.S. values is obtained:

	Lujanian	Area 1	Area 2	Area 3
Area 1	55			
Area 2	43	43		
Area 3	36	66	39	
Area 4	16	39	26	47

Additionally, it is possible that many of the genera included in area 2 (fig. 8) are Holocene. To avoid this noise, a matrix of similarity can be generated using only the megafauna:

	Lujanian	Area 1	Area 2	Area 3
Area 1	69			
Area 2	66	67		
Area 3	48	68	66	
Area 4	20	40	44	47

These comparisons suggest a gradient of decreasing similarity from the Lujanian through areas 1, 2, 3, and 4, respectively. This clinal situation is compatible with a correspondent ecological gradient from temperate to tropical, a fact supported also by the generic differences, where *Eremotherium, Haplomastodon,* and *Tapirus* characterize faunas with tropical affinities.

From what is known, the genera common to all four areas and the Lujanian of Argentina are *Homo, Pampatherium, Toxodon,* and possibly *Glossotherium* and *Glyptodon.* This low degree of generic similarity reinforces the arguments against homogeneous paleozoogeographic conditions over the entire area in question. However, at the family level, Megalonychidae, Megatheriidae, Dasypodidae, Glyptodontidae, Toxodontidae, Gomphotheriidae, Tayassuidae, Cervidae, and possibly Hominidae, Felidae, and Equidae, are common to the Lujanian of Argentina and the four Brazilian areas (35 % of the families, if the bats and the aquatic families are subtracted).

With the exception of *Tadarida* (found in the Tremembé bituminous shales in São Paulo), and *Phoberomys, Plicodontinia, Trigodonops,* and *Abothrodon* (found in the fluvial sediments of the Amazon Basin), all the faunas listed here are considered as late Pleistocene-Holocene in age by Bombin. The most useful geochronological markers for the late Pleistocene seem to be *Eremotherium, Lestodon, Haplomastodon,* and *Equus.* The radiocarbon dates associated with extinct genera are listed in table 1.

A fact of geochronological importance in South America, when using land mammals as time indicators, is the differential survival of certain genera in different areas. *Scelidodon, Tetrastylus,* and *Palaeolama*(?) apparently long gone from temperate Argentina, were living up to the beginning of the Holocene in tropical areas of Brazil, and other sub-tropical and tropical areas of South America. *Phoberomys* may have survived at least to the early Pleistocene in Amazonia. Therefore, the sole presence of a given genus in a sedimentary unit does not necessarily indicate chronologic contemporaneity.

The late Pleistocene faunas of Brazil has a megafaunal component dominated by mammals better adapted to open or semi-open vegetation systems, although certain genera (*e.g. Tapirus*) indicate the presence of forested areas, even if exclusively in the form of lowland or riparian vegetation. Therefore, a mosaic of grasslands, including savannas, and xerophytic vegetation, intermingled with forests adjacent to water sources is the best scenario to place the faunas in consideration. The presence of Megalonychidae, *Eremotherium, Glossotherium*(?), *Lestodon, Pampatherium,* Glyptodontidae, *Toxodon, Haplomastodon,* Equidae(?), and Cervidae in deposits of the Amazonian area is an indication favoring the existence of more extensive areas of open vegetation in the region, and therefore drier conditions and/or more concentrated distribution of rain, during the late Pleistocene, which effects could have been enhanced by fire (Bombin, 1980f). The forest would then have been contracted to refugia (*e.g.* Absy & van der Hammen, 1976; Haffer, 1969; Meggers, 1977; Prance, 1973; Vanzolini & Williams, 1970; Vuilleumier, 1971).

Of the 116 land mammal genera in the Brazilian late Pleistocene, 30 became extinct (26 %), and of the 39 genera of megafauna, 29 became extinct (74 %), at the beginning of the Holocene.

CHILE

Pleistocene mammals reported from Chile include *Ctenomys, Dusicyon (Pseudalopex), Arctodus, Leo (Jaguarius), Macrauchenia, Mylodon, Scelidodon, Glossotherium, Megatherium* (*"Pseudomegatherium"*), *Onohippidium* (includes *Parahipparion*), *Hippidion, Equus, ?Palaeolama, Lama, Blastocerus* (=*Antifer*), *Hippocamelus,* and *Cuvieronius* (Hoffstetter & Paskoff, 1966; Oliver Schneider, 1926, 1935; Fuenzalida Villegas, 1936; Casamiquela, 1968-1972; Casamiquela & Sepúlveda, 1974). Hoffstetter & Paskoff (1966) also describe a tooth fragment of *Hippidion* from the upper terrace of the Río Grande near Ovalle, and *Macrauchenia* remains from a sand-silt unit near Tongoy and Tambillos (fig. 5). Both localities are reported to be of Pleistocene Age. Casamiquela (1969) refers to either early Pleistocene or late Pliocene, a macrauchenid cuneiform and "*Equus*?" teeth collected from the Río Salado at its confluence with the Loa. Additional taxonomic lists of Pleistocene faunas and localities from Chile are provided by Casamiquela (1968a,b, 1969, 1969-70, 1970, 1972), Casamiquela & Sepúlveda (1974), and Casamiquela *et al.* (1967).

Several mammalian genera, in some cases reportedly associated with early man, are known from faunas found in caves in southern Chile (fig. 5). Mylodon Cave (=Gruta del Milodon, Eberhart Cave, or Ultima Esperanza Cave), located 30 km north-northwest of Puerto Natales (51°36'S, 72°36'W), yielded remains of *Mylodon* and *Onohippidium* (*Parahipparion*) (Emperaire & Laming, 1954; Woodward, 1900). Sloth dung, hide, hair, and bone from this cave has yielded ^{14}C dates ranging from 10,200 ± 200 (SA-49) to 13,560 ± 190 (A-1390) yrs B.P. (Long & Martin, 1974, p. 639; Burleigh, Hewson & Meeks, 1977, p. 143; Libby, 1952, p. 94). An extinct fauna, including *Mylodon* and *Onohippidium*, is recorded from Fell's Cave in the Río Chico valley (Bird, 1938, 1970; Bird & Bird, 1937; Emperaire *et al.*, 1963). Several ^{14}C dates on charcoal from fire pits in Fell's Cave range from 10,720 ± 30 (W-915) to 11,000 ± 170 (I-3988) yrs B.P. (table 1). Palli Aike Cave, located near Fell's Cave contains the same fauna as both Fell's Cave and Mylodon Cave (Bird, 1938, 1970). Additional mammalian taxa reported from caves of southern Chile include *Dusicyon* (*Pseudalopex*), *Leo* (*Jaguarius*), and *Lama*.

Recovered from an early man site in central Chile, Laguna de Tagua Tagua (fig. 5), situated in the valley of the Río Cachapoal, were remains of *Equus, Cuvieronius,* and *Blastocerus* (= *Antifer*) (Montané, 1968a,b; Mostny, 1968). A ^{14}C date of 11,380 ± 320 (GX-1205) yrs B.P. was obtained on a sample of charcoal from Tagua Tagua (table 1). Other mammal taxa reported from central Chile include *Megatherium, Scelidodon, Glossotherium,* Rodentia indeterminate, Canidae indeterminate, *Cuvieronius, Macrauchenia, Hippidion, Onohippidium* (*Parahipparion*), *Equus* (*Amerhippus*), *Hippocamelus, Blastocerus* (= *Antifer*), ?*Palaeolama*, and *Lama.*

From the provinces of Antofagasta and Tarapaca, that is in the Norte Grande, have been recorded *Megatherium,* Nothrotheriinae indeterminate, *Scelidodon, Ctenomys, Dusicyon, Equus,* and *Lama.*

COLOMBIA

Numerous Pleistocene vertebrate localities are known from Colombia (fig. 10). Unfortunately, most of these discoveries are poorly documented and lack stratigraphic control. Much of our present knowledge of Colombian Pleistocene faunas was founded on a series of papers by Porta (1959, 1960, 1961a,b,c, 1962, 1965, 1968), and Porta *et al.* (1974) dealing primarily with the Toxodontidae, Equidae, and Megatheriidae. All pertinent literature on Colombian Pleistocene faunas and localities has been reviewed by Hoffstetter (1970a, 1971).

The principal Pleistocene vertebrate localities occur in the "Cordillera Oriental", particularly in lacustrine deposits (the Sabana Formation) in the Sabana de Bogotá (Porta, 1960), and at more northern localities (El Cocuy, Málaga). The "Cordillera Central", as represented by the southern localities of Pasto and Túqueres, has proven less fossiliferous. In the lowland regions additional localities are known (*e.g.* Cúcuta and Garzón). On the whole, little attention has thus far been given to the stratigraphic study of these fossiliferous localities and at none has the fauna been extensively inventoried.

Several Colombian Pleistocene localities have been worked more extensively than others. Porta (1965) reported a fissure fill at Curití (1500 meters) which has yielded *Cryptotis, Hydrochoerus, Haplomastodon, Tapirus, Dicotyles* (= *Tayassu*), and *Mazama.* Stirton (1953), Porta (1961b), and van der Hammen (1965) report on the Las Cátedras fauna located in the Mondoñedo and Balsillas hills approximately 20 km northwest of Bogotá. Pleistocene vertebrates collected from these fluvial and lacustrine sediments include *Glossotherium, Haplomastodon,* and *Equus* (*Amerhippus*). The fauna from Las Cátedras is identical to that of the Sabana de Bogotá (Porta *et al.*, 1974).

Hoffstetter (1971) distinguished two faunal assemblages defined in terms of Altiplano and lowland habitats among Colombian Pleistocene vertebrate localities. The altiplano habitat and corresponding high altitude fauna is best represented by deposits situated above 2000 meters (*e.g.* Sabana de Bogotá). Dominant faunal elements include *Haplomastodon, Equus* (*Amerhippus*), and *Glossotherium.* In many respects this fauna is similar to the Puninian fauna of Ecuador, although differences between

Fig. 10. — Map of Colombia and Venezuela showing principal mammal-bearing localities of Pleistocene Age. Slightly modified after Hoffstetter (1971, p. 61, fig. 2).

the two exist (*e.g.* the Colombian fauna contains fewer equids and camelids). Faunal representatives of the lowland habitat include *Eremotherium* known from Cúcuta (300-350 meters), Villavieja (400-450 meters), El Boquerón (ca. 1000 meters), and Fusagasugá (in the terrace of ca. 1000 meters; de Porta, personal communication), *Mixotoxodon*, and *Haplomastodon*. Comparable fauna characterized by the association of *Eremotherium-Haplomastodon* are found in northern Venezuela (Barquisimeto-San Miguel, Muaco, Lago de Valencia), Panamá (Pesé y Ocú), coastal Ecuador (Carolinense fauna), and northern Peru (Talara). Hoffstetter (1952, 1968, 1971) also attempted to demonstrate similarities among the Pleistocene *andean* faunas of Colombia, Bolivia, and Ecuador in contrast to the lowland *pampean* faunas of Argentina.

Most known Colombian Pleistocene vertebrate faunas are assignable to a Lujanian Age (Porta, 1965; Hoffstetter, 1971). According to Porta *et al.* (1974) the Sabana de Bogotá fauna ranges from 10,800 to 21,900 years ago (at most 42,800 yrs B.P.). Other faunas now classified as Pliocene-Pleistocene may prove referable to the early Pleistocene. In Cocha Verde (Nariño), Royo y Gómez collected a partial dentary which Stirton (1946) described as *Selenogonus narinoensis* (Tayassuidae). Stirton (1953) suggested that this deposit may be of late Pliocene or early Pleistocene (*i.e.* Uquian) Age. Other questionable early Pleistocene faunas include Ortega (Tolima) and Santa Rosa de Viterbo (Boyacá), although no fossils have as yet been listed, described, or figured (figs. 10, 13). Bombin (1981) reports on *Glyptodon*, and Bombin & Huertas (1981) describe mastodonts assignable to *Cuvieronius, Haplomastodon, Stegomastodon*, and *Notiomastodon* from several late Pleistocene localities in Colombia.

Correal Urrego (1980) records an archeological locality (Tobito 1) of the Sabana de Bogotá, where artefacts are associated with remains of mammals (*Haplomastodon, Cuvieronius, Amerhippus* and *Odocoileus*) dated 11740 ± 110 yrs B.P. (^{14}C method).

ECUADOR

In 1553, Pedro Cieça de León recorded the "bones of giants" which he believed human from the Santa Elena Peninsula. These as well as other bones from near Riobamba, were also noted by Father Juan de Velasco in 1789. In 1802 von Humboldt collected the tooth of a mastodont (type of *Mastodonte des Cordillères* Cuvier, 1806) at the foot of the Imbabura volcano, about 75 km northeast of Quito. Fossils collected in 1859 by M. Wagner from near Chimborazo were reported by A. Wagner (1860). Orton (1870) first reported fossils from the now famous deposits of Punín which included mastodon, horse, deer, and llama. From this same locality, Wolf collected several fossils in 1870-71 which he named (Wolf, 1875) but did not describe. Reiss and Stübel collected a large number of fossils from the sierra and coastal regions. These were described by Branco (1883) and are the first systematic record of the Punín fauna which included *Equus andium, Protauchenia reissi, Cervus* sp., *Mastodon andium*, and *Smilodon populator.*

From Punín, H. Meyer in 1903 collected various fossils described by Etzold (*in* Meyer, 1907), among which are a mylodontid and a carnivore; the latter, tentatively referred to the Melinae (Mustelidae) by Etzold, could be *Dusicyon culpaeus* (Hoffstetter, 1952, p. 14).

Several American Museum of Natural History expeditions conducted from 1920-1930 resulted in new additions to the Pleistocene fauna of Ecuador. Anthony, in 1923, explored Chalán quebrada near Punín and listed the remains of *Equus andium*, "*Dibelodon*" *andium, Protauchenia*, and *Smilodon.* In 1929-1930 a party led by Frick and Falkenbach collected vertebrates in the andean region. Frick (1937) described the cervids recovered from this expedition.

From 1927 to 1941, F. Spillmann collected Pleistocene mammals from the sierra region and the Santa Elena peninsula and published on these between 1931 to 1948. He distinguished five faunas — one from the coast and four from the sierra (corre-

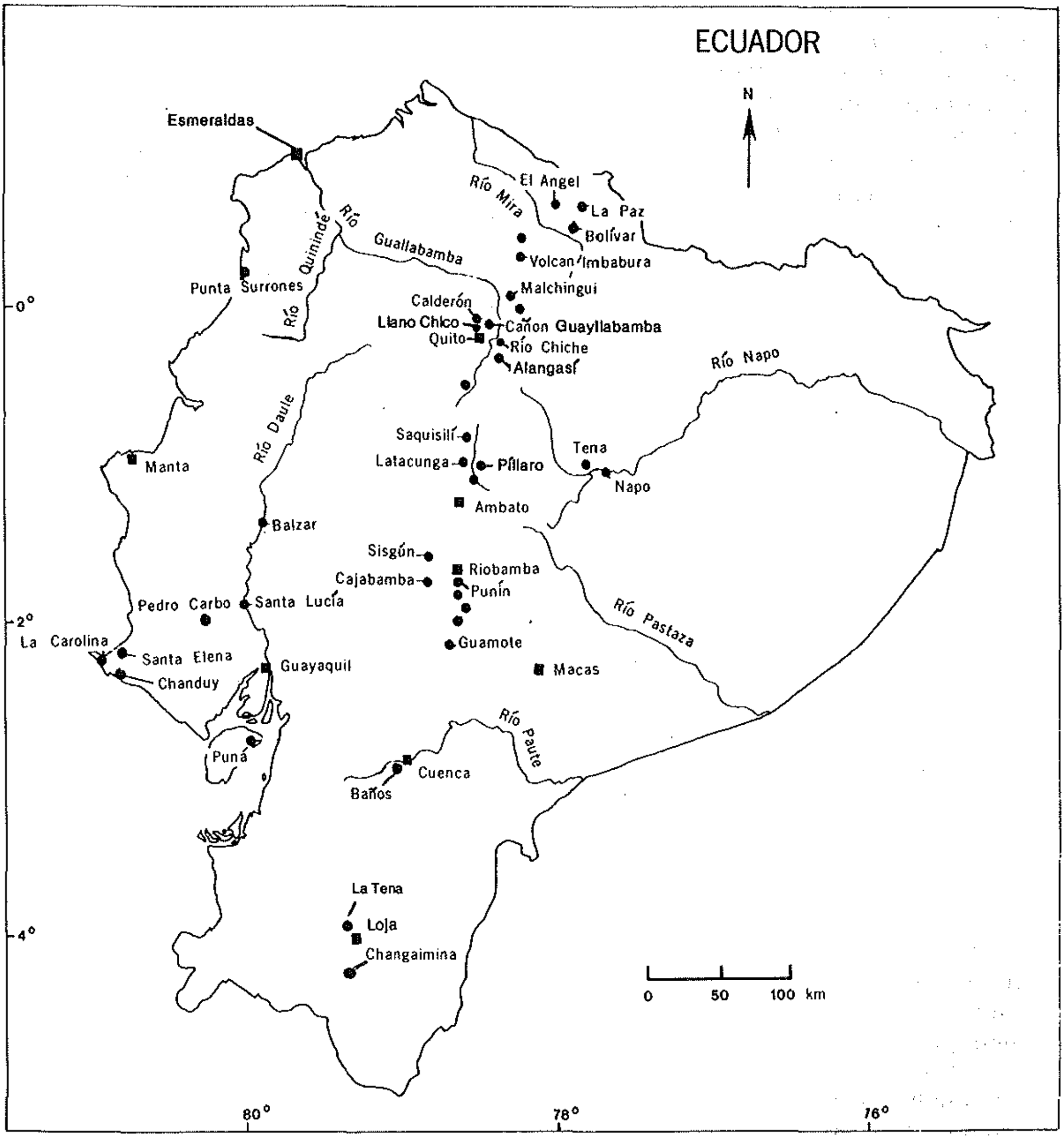

Fig. 11. — Map of Ecuador showing principal mammal-bearing localities of Pleistocene Age. Slightly modified after Hoffstetter (1952, fig. 1). Solid squares = towns and cities.

sponding, according to Spillmann, respectively to the 1st glaciation, the interglacial, the 2nd glaciation and the post-glacial) which he "characterized" using species of equids and mastodonts.

Sauer (1950) studied the Quaternary of Ecuador and recognized four glacial and three interglacial events. This chronology formed the framework for many later studies which attempted to correlate Pleistocene Ecuadorian faunas with European and North American glacial events.

Hoffstetter began his study of Ecuadorian vertebrate paleontology in 1946 and has provided (Hoffstetter, 1952, 1970b; Bristow & Hoffstetter, 1977) the most comprehensive review of Pleistocene faunas of that country to date.

Pleistocene vertebrate bearing deposits of Ecuador are divisible into three geographic regions: I) Andean, II) Coastal, and III) Oriental (or Amazon Basin) (fig. 11).

I. ANDEAN REGION

In the northern part of Ecuador (1°N to 2°S latitude), the Andes form two ranges separated by an interandean corridor. It is here where Sauer (1950) observed his glacial-interglacial sequence. The primary mammal-bearing units are found in loessoid sediments of the 3rd interglacial of Sauer known locally as *cangahua*. These fossiliferous beds are primarily of eolian-lacustrine origin and occur at elevations ranging from 2,300 – 3,100 meters.

Branco (1883) described the faunal assemblage typified at Punín, south of Riobamba, and designated by Hoffstetter (1952) as the Puninien (= *Puninense* or Puninian) fauna. Characteristic Puninien taxa include Megatheriidae, *Glossotherium* (*Oreomylodon*), *Propraopus, Dusicyon* (*Pseudalopex*), *Felis* (*Puma*), *Leo* (*Jaguarius*), *Smilodon, Haplomastodon, Equus* (*Amerhippus*), *Palaeolama* (*Protauchenia*), *Odocoileus, Mazama*, and *Agalmaceros*. Hoffstetter explained the absence of certain common genera of the South American Pleistocene (*e.g. Toxodon, Macrauchenia, Hippidion, Onohippidium*, and glyptodonts) from the Puninien fauna as due to differences in ecologic conditions. The presence of *Odocoileus virginianus peruvianus* and *Dusicyon culpaeus*, now restricted to regions above elevations of 2,000 meters, support the interpretation of an endemic high altitude fauna.

A second faunal assemblage collected from the region surrounding the Río Chiche (or Chichi) near Quito in sediments corresponding to the 2nd interglacial of Sauer (1950) was designated Chichéen (= *Chichense* or Chichean) by Hoffstetter (1952) to distinguish it from the *Puninense*. The *Chichense* fauna, which is incompletely known, includes *Equus* (*Amerhippus*) *martinei* and *Palaeolama crassa* which are not directly ancestral to *E.* (*A.*) *andium* and *P. reissi* respectively from Puninien. This suggests the possibility that the earlier *Chichense* fauna was replaced after the 3rd glaciation by southern immigrants. From beds yielding the type Chichéen fauna, Spillmann recorded the presence of a mastodon, a megatheriid, and a mylodontine, but these specimens have since disappeared and were never described or figured. A large incomplete femur of a ground sloth (?) from the same collection apparently represents a new, unnamed genus. Rare remains of *Cuvieronius* and *Dusicyon* specimens have been reported from

Cañón del Río Guayllabamba, at the base of the Quebrada Colorado at Punín, and a large *Dusicyon* was recovered from Llano Chico near Quito from stratigraphic horizons of possible Chichean Age.

At Guamote (50 km south of Riobamba) an incomplete mandible of *Protocyon* (*s.l.*, includes *Theriodictis* — Berta, unpublished) along with *Glossotherium* and a camelid were found by Hoffstetter and Torres in late Pleistocene deposits. At Baños de Cuenca numerous remains of *Cuvieronius hyodon* have been found, and further to the south in Loja Province are recorded remains of *Haplomastodon*.

Determinations of the precise ages of these faunas pose numerous problems. The Chichéen and Puninien correspond respectively to levels which Sauer designated as 2nd and 3rd interglacials. Hoffstetter remarks, however, that: 1) certain workers recognize only two glaciations in Ecuador; 2) Bristow (in Bristow & Hoffstetter, 1977) places the 2nd and 3rd interglacial of Sauer into a single interval and believes that the *cangahua* deposits were not necessarily accumulated during an interglacial; and 3) the Puninien fauna is very similar to that of the Sabana de Bogotá in Colombia which Porta places between 10,800 and 21,900 yrs B.P. (at most 42,800) in age. However, the ^{14}C date of $>$48,000 yrs B.P. reported by Bristow (in Bristow & Hoffstetter, 1977) on wood collected above deposits of the 2nd interglacial of Sauer and below deposits of the *cangahua* (Chichense? and Puninense) proves only that the underlying beds and possibly the lower part of the *cangahua* are beyond the limits of ^{14}C dating.

II. COASTAL REGION

The richest deposits by far in the coastal region are those of La Carolina, on the north side of the Santa Elena Peninsula near the town of La Libertad (fig. 11). These strata consist of fluvial sediments impregnated with asphalt and deposited in an estuarine environment. Hoffstetter (1952) proposed the name Carolinien (= *Carolinense* or Carolinian) for this rich faunal assemblage which includes indeterminate Didelphidae, indeterminate Megalonychidae, *Glossotherium, Scelidodon, Eremotherium*, an unnamed megatheriid genus ("*E*". *elenense*), *Pampatherium* (*Holmesina* = *Hoffstetteria*), *Neochoerus, Proechimys, Dusicyon* (*Pseudalopex*), *Protocyon, Felis* (*Puma*), *Smilodon, Haplomastodon, Equus* (*Amerhippus*), *Palaeolama* (*Astylolama*), *Odocoileus*, and a variety of plant and insect remains as well as some reptiles and numerous birds. This is a tropical fauna characterized by *Eremotherium*, and is very similar to low altitude faunas of Peru (Talara), Colombia, and Venezuela. The Carolinien fauna also shows affinities with eastern Brazilian faunas in its tropical aspect, but differs from the temperate and cool-temperate Argentine faunas (Hoffstetter, 1970b). From its stratigraphic position the Carolinien fauna is apparently late Pleistocene in age (fig. 13).

Carolinien faunal elements have been recovered from other localities on the Santa Elena Peninsula (*i.e.* Engabao de Chanduy), on Puná Island, and in the basin of the Río Daule (fig. 11). Much further north, near Punta Surrones, the remains of *Eremotherium, Haplomastodon*, and cervids have been recovered from the base of a coastal cliff. The latter is also apparently a Carolinien fauna, but by its stratigraphic position, seems to be slightly older than the type fauna from La Carolina (Hoffstetter, *in* Bristow & Hoffstetter, 1977, p. 77).

III. AMAZONIAN REGION

Several Pleistocene vertebrate fossils have been recovered from alluvial deposits of Río Napo (fig. 11). Spillmann (1949, p. 38) noted the presence of *Glyptodon, Mylodon, Cuvieronius, Dicotyles,* hystricomorph rodents, and Toxodontia(?). None of the specimens on which these identifications were based were described or figured. Hoffstetter (1952) reported a caudal vertebra of a megatheriid (cf. *Eremotherium*) and a milk tooth of a mastodont (cf. *Haplomastodon*) from near Tena.

PARAGUAY

Historically, Paraguay referred to a large area bounded by Brazil, Peru, Chile, and the Atlantic Ocean, with Asunción and Buenos Aires as principal cities (Charlevoix, 1796, t. 5, p. 7-8; Hoffstetter, 1978) and in this context Cuvier (1796) reported the type of *Megatherium americanum* from Paraguay. This specimen was, however, collected from what is now known as Luján, Argentina (fig. 5). According to Garriga (1796) a skeleton referred to the species was sent from "Paraguay" to Madrid (Hoffstetter, 1959, p. 543). Unfortunately, this specimen has since disappeared making it impossible to confirm its identity and its precise geographic origin.

Deposits of Pleistocene age cover the Chaco Plains and extensive areas of Paraguay, especially in the southern region between the Río Tebicuary and Paraná and the district between Concepción, Coruguatu, and Asunción. The sediments are fine grained silty sands and clays of eolian, fluvial, and lacustrine origins. Few fossil vertebrates have been recovered from these deposits. Near Asunción, a few glyptodontid and gravigrade remains have been reported (Harrington, 1956a, p. 110).

During September, 1976, Hoffstetter examined collections housed at the Facultad de Veterinaria and Museo del Jardín Botánico in Asunción. Fossil vertebrates in these collections are reported to have been collected from two localities: 1) Riacho Negro, north of Asunción (25°S); and 2) General Bruguer, 180 km west-northwest of Asunción on the Río Pilcomayo (24°20'S). Unfortunately, many of the specimens are unlabeled making locality assignment difficult, if not impossible.

Hoffstetter (1978) identified from these collections representatives of 14 genera belonging to 9 families and 5 orders. He referred material to the following taxa arranged by family — Glyptodontidae, *Glyptodon* cf. *G. clavipes, Panochthus tuberculatus, Sclerocalyptus* cf. *S. ornatus*; Dasypodidae, *Pampatherium* (= *Chlamytherium*) *humboldti* or *C. typus*; Megatheriidae, *Megatherium americanum*; Mylodontidae, *Scelidotherium s.l* (includes *Scelidodon*), *Glossotherium* cf. *G. robustum, Lestodon* cf. *L. armatus, ?Mylodon*; Toxodontidae, *Toxodon* (size of *T. platensis*); Macraucheniidae, *Macrauchenia* cf. *M. patachonica*; Gomphotheriidae, *Stegomastodon*; Camelidae, *Palaeolama s.l.* (includes *Hemiauchenia*); and Cervidae, *Morenelaphus brachyceros, Blastocerus dichotomus.*

With the exception of *Blastocerus*, all of the above named genera are extinct. The first six families (Glyptodontidae, Megatheriidae, Dasypodidae, Mylodontidae, Toxodontidae, Macraucheniidae) are autochthonous and the latter two families (Camelidae, Cervidae) are immigrants of North American origin. This fauna is similar to that of the *Pampean* faunas of Argentina and Uruguay showing closest affinities with the Ñuapua 1 fauna of the Bolivian Chaco.

The presence of *Megatherium, Sclerocalyptus, Morenelaphus*, and *Stegomastodon* suggest a southern character of the fauna, since these animals were apparently restricted to that portion of South America during the Pleistocene. Several taxa, *Stegomastodon, Panochthus,* and *Sclerocalyptus* suggest a lowland habitat since they are rarely found at high elevation. The absence of equids and the rarity of camelids and macraucheniids might indicate a more closely vegetated environment. It is unfortunately impossible to know whether the *Palaeolama* from Paraguay (known only from a lower jaw fragment) is related to *P. major* (Brazil and Bolivian Chaco) or to *Hemiauchenia paradoxa* (Argentina); the latter species is characterized by elongated metapodials, which indicate an adaptation to an open environment (Webb, 1974). However, the occurrences of *Blastocerus* (the marsh deer) and the absence of *Ozotoceros* (the pampas deer) are not in accordance with a Pampas-like environment in Paraguay at that time.

The apparent lack of micromammals from these localities is almost certainly the result of sampling bias. Reexamination of these localities using screen-washing techniques will undoubtedly increase the number and diversity of taxa known at present.

PERU

Between 1806 and 1914 a large number of papers were written by Cuvier, Gervais, Raimondi, Nordenskiöld, Sefve, Lisson, Eaton, and others on Peruvian Pleistocene faunas (see Hoffstetter, 1970c, p. 976 for a list of early references). More recent studies of Pleistocene mammals in Peru include those of Kalafatovich (1955) and Ramírez Pareja (1958) for the Cuzco region; Churcher (1959, 1962), Lemon & Churcher (1961) and Churcher *et al.* (1965) on the Talara-La Brea fauna along the coast; and Willard (1961, 1962, 1966) on the eastern region. The only attempted synthesis of these faunas is presented by Hoffstetter (1970c). Ongoing studies are those of Hoffstetter (unpublished) on faunas collected by Chauchat and Hoffstetter from along the coastal zone (Cupisnique desert), and by Hoffstetter within the Sierra (Junin and Cajamarca), and in the basin of the Río Ucayali (fig. 12).

I. COASTAL REGION

The Talara fauna along the northwest coast of Peru is one of the best known of South American Pleistocene vertebrate faunas (Lemon & Churcher, 1961; Churcher, 1959, 1962, 1965; Churcher *et al.*, 1965; Hoffstetter, 1970c). The main bone bearing deposits occur in tar seeps in the La Brea-Parinas oil fields, the largest being in the region about 14 km southeast of Talara (fig. 12). Plant and animal remains occur in irregularly alternating lenses of medium to coarse, poorly sorted, angular gravels, and

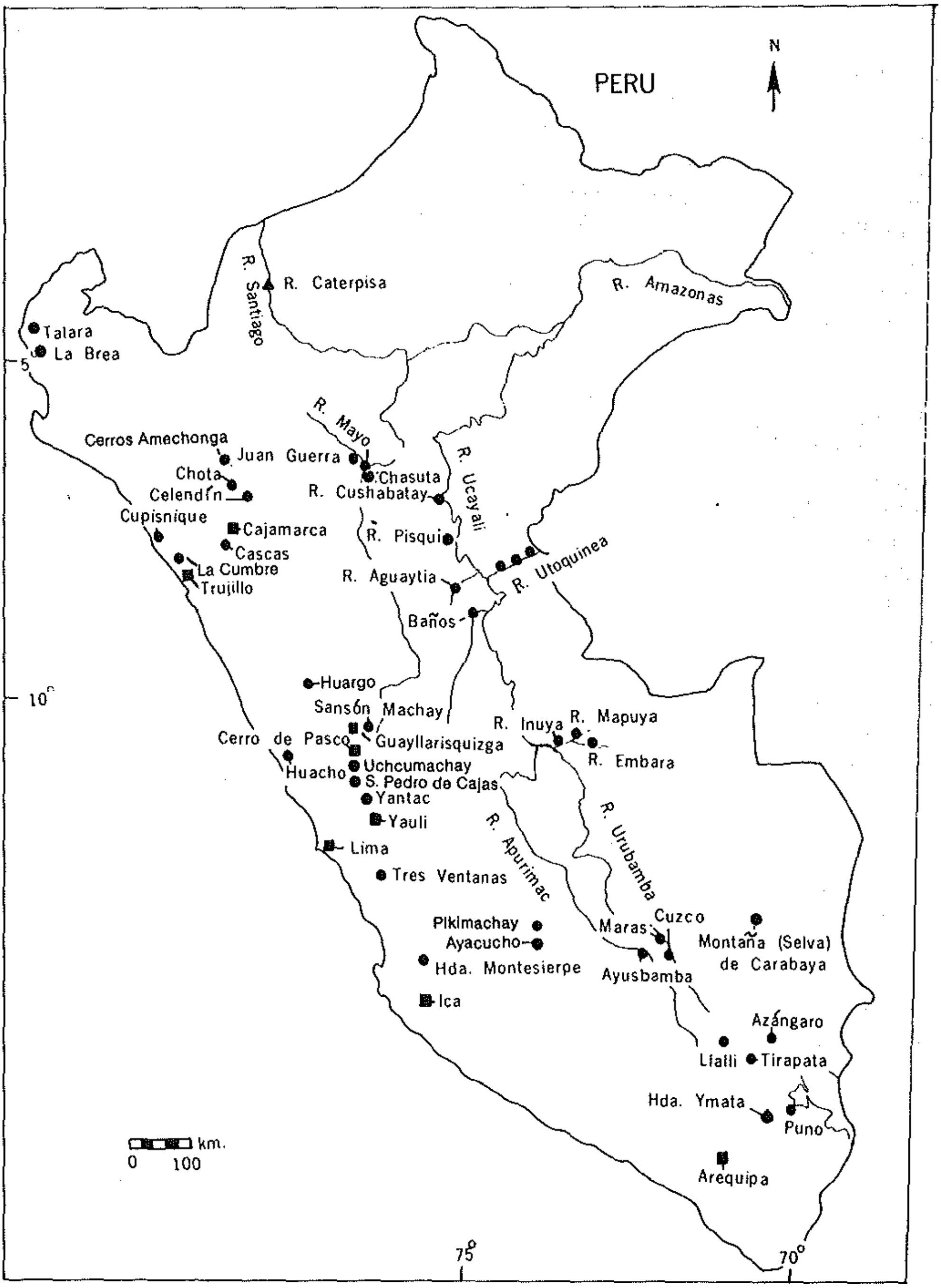

Fig. 12. — Map of Peru showing principal mammal-bearing localities of Pliocene-Pleistocene and Pleistocene Age. Slightly modified after Hoffstetter (1970c, fig. 1). Solid squares = towns and cities.

cross-bedded sands. Numerous representatives of the classes Amphibia, Aves (see Campbell, 1979), Reptilia, and Mammalia have been reported. Mammalian genera listed by Lemon & Churcher (1961) and Hoffstetter (1970c, p. 979) include *?Marmosa, Glossotherium, Scelidotherium s.l.* (includes *Scelidodon*), *Eremotherium, Pampatherium, ?Neochoerus, ?Phyllotis, ?Sigmodon, Canis, Dusicyon* (*Pseudalopex*), *Leo* (*Jaguarius*), *Smilodon, Conepatus, Haplomastodon, Equus* (*Amerhippus*), *?Tapirus, Palaeolama* (*Astylolama*), *Odocoileus*, and *Mazama*.

Taphonomic observations reveal a high percentage of broken bones, probably due to trampling by larger animals. Many bones show the effects of weathering prior to deposition. The presence of tooth marks on some bones has been attributed to rodent and carnivore gnawing. These *breas* or tar-pits are interpreted to have acted as animal traps, and are similar to the La Brea tar pits in Los Angeles, California. The trapped animals would have attracted predators and scavengers both while struggling to escape and after death.

A Lujanian Age for the Talara fauna has been proposed (Lemon & Churcher, 1961). Comparison of the Talara fauna with the contemporaneous Carolinian fauna of Ecuador reveals 10 genera common to both; one difference being the absence of megalonychid ground sloths from Talara, which are present but scarce in the Carolinian from Ecuador. Lemon & Churcher (1961) further suggest contemporaneous ecological replacement between these faunas, with *Protocyon* from Ecuador being replaced at Talara by *Canis* (formerly *Aenocyon*). Several ^{14}C dates on Talara wood range from 13616±600 to 14418±500 yrs B.P. (Bryan 1973, p. 244): see Table 1.

From the Cupisnique desert (7°30'S), northwest of Trujillo, the remains of fossil mammals were first recovered by Ubberlohde-Doering (1939). In 1976 Chauchat and Hoffstetter on the one hand, and Engel on the other, recovered the following taxa — cf. *Eremotherium*, cf. *Nothropus, Scelidodon, Pampatherium, Equus* (*Amerhippus*), *Palaeolama*, and *Neochoerus* (Hoffstetter, unpublished). This fauna is very similar to that of Talara and La Carolina in Ecuador. A nearly complete skeleton of *Scelidodon* yielded a ^{14}C age of 8,910±200 yrs B.P. (GIF-4116). This faunal assemblage is in part contemporaneous with the early man Paiján culture of the same region. At La Cumbre, near Trujillo, apatite of mastodont bones has been dated by ^{14}C at 12,360±700 yrs B.P. (GX-2494) and 10,535±280 yrs B.P. (GX-2019) (Ossa & Moseley, in Ossa, 1973).

Further to the south and along the coast, the remains of *Haplomastodon* have been recovered from Huacho (11°S) and from Cerro Montesierpe (14°S) northwest of Ica (fig. 12).

II. ANDEAN REGION

Fossil faunas of Pleistocene Age are rare in the northern part of the Peruvian Andes. Several localities in the region of Cajamarca and Celendín (fig. 12), at an altitude of about 2,500 meters, have yielded remains of *Haplomastodon* and Megatheriidae. Recently the French speleologist Sanmartino *et al.* (1979-published in 1981) explored caves at altitudes varying from 3,350 to 3,550 meters, in the karstic mountains of the same region (100 km north of Cajamarca, and 20 km southwest of Celendín); he observed abundant mammal bones in these caves; incomplete records and photos establish the presence of *Leo* (*Jaguarius*) *onca andinus, Odocoileus* sp., a mylodontid, and a small horse, possibly *Onohippidium* (see Hoffstetter, in press).

Further to the south (ca. 10°S to 15°S) occur a large number of caves at altitudes ranging from 3,500 to more than 4,000 meters. The more important ones are, from north to south, Huargo, south of La Uniόn (Cardich, 1978; Pascual & Odreman Rivas, 1973); Sanson-Machay, 2 km east of Guayllarisquizga (caves rediscovered and relocated by Hoffstetter and Ojeda in 1975 — these were originally discovered by the Castelnau expedition and described by P. Gervais in 1855); Uchcumachay (= Ushcumachay), between La Oroya and Junín (Wheeler Pires-Ferreira, Pires-Ferreira, Kaulicke, 1976); Tres Ventanas, east-southeast of Lima at elevation of 4,000 meters (fauna collected by F. Engel and taxonomic identifications made by Hoffstetter, 1970c); Pikimachay, near Ayacucho (MacNeish, 1971); and Casa del Diablo, near Tirapata (Nordenskiöld, 1908) (fig. 12). For the most part stratigraphic studies are not yet available for these cave deposits and it is not possible in all cases to distinguish successive faunas. Taxa recorded from the caves include Megatheriidae, Scelidotheriinae (*Scelidodon* or ?*Scelidotherium*), *Onohippidium* (*Parahipparion*, includes *Hyperhippidium*), *Lama, Vicugna, Agalmaceros* (at Uchcumachay), *Charitoceros* (at La Casa del Diablo), a peccary, *Lagidium*, and diverse carnivores (Canidae, Felidae, and Mustelidae) (Hoffstetter, 1970c, p. 977-978; unpublished). Some of these caves also contain evidence of human occupation.

Remains of *Onohippidium* [erroneously identified as *Equus* (*Amerhippus*)], *Lama*, and *Scelidotherium* (*s.l.* includes *Scelidodon*) recovered from bed 8 of Huargo Cave have given a ^{14}C age of 13,460 ± 700 yrs B.P. (Cardich, 1973; Pascual & Odreman Rivas, 1973b). According to Cardich, there is evidence from this same bed of sporadic human occupation.

At the Ayacucho Valley site which includes Pikimachay (Flea Cave) (fig. 12), MacNeish (1971) and MacNeish *et al.* (1970a,b) report an association of early man with *Palaeolama*, horse, and megatheriid ground sloths. Following MacNeish *et al.* (1975) the Pleistocene fauna of the Pikimachay cave includes (identification by Bryan Patterson) *Scelidotherium s.l.* (includes *Scelidodon*), *Megatherium, Equus,* Cervidae, *Lama,* Felidae, *Dusicyon* (*Pseudalopex*), *Conepatus, Lagidium, Phyllotis*; note that the occurrence of *Palaeolama* is not confirmed, and that various generic names are used in a broad sense. A ^{14}C date (USLA-1464) of 14,150 ± 180 yrs B.P. for the Ayacucho complex is reported (fig. 12, table 1). Remains of the extinct Pleistocene deer (*Agalmaceros* cf. *A. blicki*) and horse [*Parahipparion* (*Hyperhippidium*) *peruanum*] have been recovered from level 7 in Uchcumachay (= Tilarnoic) Cave in the Puna of Junín at an elevation of 4,050 meters. A tentative date of 12,000 to 9,000 yrs B.P. has been proposed for level 7 at Uchcumachay (Wheeler Pires Ferreira *et al.*, 1976, p. 484).

At Tres Ventanas a human occupation level dated around 10,000 yrs B.P. rests on sediment containing remains of a small megatheriid and a scelidothere which have yielded a ^{14}C age older than 40,000 yrs B.P.

Pleistocene deposits have also been found in the Peruvian Andes outside of the caves. These include San Pedro de Cajas, Yantac, Ayusbamba, Cuzco and vicinity, Azangaro, Llalli, and the vicinity around Puna (fig. 12). The faunas include *Megatherium*, megatherid genus indeterminate, Mylodontidae, *Glyptodon, Cuvieronius,* *Equus* (*Amerhippus*) (rare), *Agalmaceros* (species unnamed, collected at San Pedro de Cajas by C. Yurivilca and identified by Hoffstetter), and *Charitoceros* near Cuzco. Although incompletely known, these Andean faunas record maximal altitudinal limits reached by the various genera during the late Pleistocene (Hoffstetter, 1982).

III. AMAZON REGION

Little is known of Pleistocene faunas in the Amazonian region of eastern Peru. From Juan Guerra, near the confluence of the Río Mayo and Río Huallaga, have been reported remains of mastodont by Raimondi. In the Ucayali Basin, strata along the Río Inuya, Río Mapuya, Río Utoquinea, Río Pisqui, and Río Bellavista, have yielded remains of mastodont, toxodont, tapir, and peccary (Willard, 1961; Hoffstetter, 1970c, p. 979); and *Eremotherium, Toxodon*, and *Haplomastodon* are known from beds along the Ríos Inuya and Mapuya (Hoffstetter, unpublished). Spillmann (1949, p. 27-29) described a new species of *Protohydrochoerus* from the Río Tahuamanu which, according to Mones (unpublished), is a member of the family Dinomyidae.

URUGUAY

Continental deposits, several meters thick, of Pleistocene Age occur over large areas of Uruguay. These deposits are generally poorly stratified, subaerial, fluvio-lacustrine sediments consisting mainly of sandy-silts, clays, loess, volcanic ash, and conglomerates. The deposits range in color from reddish-brown to yellowish-brown, and contain remains of *Dasypus, Propraopus, Eutatus, Pampatherium, Hoplophorus, Sclerocalyptus, Neothoracophorus, Lomaphorus, Panochthus, Doedicurus, Glyptodon, Chlamydotherium, Nothrotherium, Scelidodon, Scelidotherium, Glossotherium, Mylodon, Lestodon, Megatherium, ?Eremotherium, Myocastor, Microcavia, Dolichotis, Hydrochoerus, Neochoerus, Lagostomus, Ctenomys, Holochilus, Toxodon, Macrauchenia, Felis (Puma), Leo (Jaguarius), Smilodon, Arctodus, Stegomastodon, ?Cuvieronius, ?Haplomastodon, Onohippidium, Hippidion, Equus (Amerhippus), Tapirus, Platygonus, Dicotyles, Lama, Palaeolama, Ozotoceros, Hippocamelus, Morenelaphus, Blastocerus* (includes *Antifer* and *Paraceros*), *Mazama* (Lambert, 1941, p. 78; Hoffstetter, unpublished; Mones, unpublished). Three genera of Lujanian Age of doubtful value were described by Roselli (1976) (Megatheriidae, *Perezfontanatherium*; Mylodontidae, *Lestodontidion*; and Glyptodontidae, *Heteroglyptodon*).

A taxonomic list of fossil vertebrates and localities from Uruguay, including Pleistocene mammals, is provided by Mones (1972, 1976), Mones & Castiglioni (1979), Mones & Francis (1973), and Francis (1975).

It is important to note that most of the Pleistocene fossil mammals are found in the southwestern and western departments (Canelones, Montevideo, San José, Colonia, Soriano, Río Negro, Salto, and Artigas). This is probably due to major collecting activities in these areas, and to better exposures of sediments which are younger than in the eastern region of Uruguay (see Mones, 1979; Mones & Figueiras, manuscript).

Early studies on Pleistocene deposits and/or fossils from Uruguay have been provided, among others, by Larrañaga (*in* Cuvier, 1823, p. 191), Weiss (1830), D'Alton (1834), Vilardebó & Berro (1838), Darwin (1838, 1840, 1846), Owen (1840), and d'Orbigny (1842). More recently, Anton (1975), Anton & Goso (1974), Bombin (1975, 1976), and Bossi *et al.* (1975), have tried to update knowledge of Pleistocene faunas, especially those of northern Uruguay. According to these workers, several Pleistocene formations can be recognized, but are poorly defined and not all the sediments bear mammalian remains or other fossils; therefore dating is only tentative.

The best defined formations are the Libertad Formation (=Arazatí or Pampeana Formation), and the Sopas Formation, of Pleistocene Age. The first, probably of Ensenadan Age, has yielded most of the mentioned genera; the latter of Lujanian Age, has been correlated with the Touro Passo Formation of Río Grande do Sul, Brazil, for which a ^{14}C date of 11,040 ± 190 yrs B.P. is reported by Bombin (1975, p. 81). The fauna of the Libertad Formation seems to be older than that of the Sopas Formation.

An Uquian Age fauna is probably represented in the uppermost part of the San José Formation. These strata have yielded fish, amphibian, bird, and mammal remains, none of which have yet been studied (Mones, 1979, p. 14-15).

VENEZUELA

Pleistocene Age faunas are principally known from the states of Lara and Falcón in Venezuela (fig. 10). The best known locality in Falcón is Muaco where vertebrates have been recovered from muds two to three meters thick suggesting bog entrapment as a mode of accumulation. The Muaco fauna has been reported by Royo y Gómez (1940) and includes Reptilia (Chelonia, ?Crocodilia, Serpentes), Aves, and Mammalia — including *Didelphis, Propraopus, Pampatherium, Glyptodon, Megatherium*[5], *Eremotherium, Mylodon*[5], *Glossotherium, Lepus*[5], *Neochoerus, Canis* (formerly *Aenocyon*), *Felis, Arctodus, Lynx*[5], *Mustela, Conepatus, Leo* (*Jaguarius*), *Windhausenia* (=*Macraucheniopsis*)[5], *Toxodon, Stegomastodon, Equus* (*Amerhippus*), *Palaeolama*, and *Odocoileus*. The fauna has been interpreted as Lujanian in age. Several ^{14}C dates on the Muaco fauna range from 14,300 ± 500 (M-1068) to 16,375 ± 400 (0-999) yrs B.P. (Rouse & Cruxent, 1963, p. 537) (table 1).

Cucuruchú, situated near Coro in the state of Falcón (fig. 10), has yielded a small Pleistocene fauna including *Eremotherium* and *Haplomastodon*. The megafauna, believed to be associated with early man, was collected from a clay pebble bone bed described by Cruxent (1970)[6].

Bryan *et al.* (1978) report an association of man with extinct megafauna at the site

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[5] It is necessary to confirm some taxonomic determinations given by Royo y Gómez (without figures or descriptions), notably those of *Lynx* and *Lepus* (genera whose occurrence in South America has never been demonstrated), and those of *Mylodon, Megatherium*, and *Windhausenia* (genera which are certainly known only from the southern part of South America) (Hoffstetter, personal note).

[6] The ages assigned to the Curucuchú fauna suggest a local survival of Pleistocene giant mammals to 3,350 yrs B.P., but the dates, obtained from carbonates, cannot be accepted as certain (Hoffstetter, personal note).

of Taima-Taima about three km north of Muaco. Artifacts of the El Jobo complex were recovered in direct association with the apparently butchered remains of a juvenile *Haplomastodon.* Radiocarbon dates of associated wood twigs (table 1) indicate a minimum age of 13,000 yrs B.P. for the mastodont kill, a date significantly older than that of the Clovis complex in North America. Other localities in Falcón state are Sacuragua, in Paraguaná, where Karsten (1886) cited the finding of a megathere; and Quebrada Ocando, near Guayabacoa, where Schaub (1950) reported "*Megatherium*" *rusconii.*

Pleistocene vertebrates have been recovered from the state of Lara at two quarries near San Miguel, approximately 35 km southwest of Barquisimeto (fig. 10). The principal fossil bearing quarry, Zanjón del Murcielago, has yielded *Mixotoxodon, Eremotherium,* Glyptodontidae, and Equidae (Van Frank, 1957). Another locality close to Barquisimeto is Quebrada del Totumo, and recent findings of mastodonts have been made to Aguada Grande, north of Lara (Linares, unpublished).

A fauna collected by F. Takacs from deposits near Lago Valencia, state of Carabobo, was identified by Hoffstetter and includes *Haplomastodon, Eremotherium, Glyptodon, Macrauchenia, Toxodon,* and *Pampatherium.* Bones from a skeleton of *Eremotherium* gave an age of ca. 9,000 yrs B.P. (H. Peñalver & F. Takacs, personal communication to Hoffstetter).

In eastern Venezuela, Karsten (1886) cited the finding of a megathere at the base of Cerro Turiniquire in Sucre. Near Cumana, in Caigüire, also in Sucre State, mastodonts and *Eremotherium* have been recently recovered (Linares, unpublished). But the richest deposit in eastern Venezuela is Cueva del Guácharo near Caripe, Monagas State. In these roughly late Pleistocene cave deposits about 25 species of bats have been recovered (Linares, 1966), among which is a giant new species of *Desmodus* (Ray & Linares, in preparation). Together with the bat remains excellent remains of *Arctodus, Proechimys,* and *Steatornis* (the oil-bird) have been found.

A recently found cave deposit has been excavated in Cerro Viruela, Sierra de Perijá, Zulia State. The fossils recovered include *Tapirus,* a megathere, *Mazama,* cf. *Blastoceros,* and *Lasiurus* (Linares, unpublished).

Other poorly known Quaternary mammal-bearing localities include Carora, Acarigua, Valera, San Juan de los Morros, Barbacoas, and Cumanacoa (south of Cumaná).

EPOCH	COUNTRIES SOUTH AMERICAN Land Mammal Ages	BOLIVIA	BRAZIL	CHILE	COLOMBIA	ECUADOR	PERU	VENEZUELA	URUGUAY
PLEISTOCENE	LUJANIAN	Ñuapua 2 Ñuapua 1* Ulloma	Areas 1, 2, 3 and 4 (fig. 8)	Mylodon, Fell's, and Palli Aike Caves; Tagua Tagua	Curití, Cátedras, and Sabana de Bogotá	Puninien Carolinien Chichéen	Cupisnique, Huargo, Uchcumachay Ayacucho, Talara	Cucuruchú, Lago de Valencia, Muaco, Taima-Taima	Sopas
	ENSENADAN	Tarija							Libertad
	UQUIAN	Ayo Ayo? Anzaldo?		Río Salado?	Cocha Verde?	Santa Rosa de Viterbo? Ortega?			?San José

*According to MacFadden & Wolff (1981), the age of Ñuapua 1 is younger than 0,73 Ma; Ñuapua 2 is Holocene.

Fig. 13. — Tentative age correlations of principal non-Argentine South American Pleistocene land mammal faunas.

Table 1

South American radiocarbon dates associated with extinct megafauna.

Locality	Laboratory Number	^{14}C (yrs B.P.)	Associated Fauna	Comments (material dated)	Source
Argentina					
1. Gruta del Indio	A-1351	10,740 ± 150	ground sloth	sloth dung	Long & Martin (1974:639)
	A-1371	11,350 ± 180		sloth dung	
	GRW-5558	10,950 ± 60		sloth dung	
	A-1370	24,730 ± 860		sloth dung	Martin (personal communication)
	A-1636	10,200 ± 300		sloth dung	
	Gr. N. 5394	8,045 ± 55	*Mylodon*	skin	Lagiglia (1968:161)
	Gr. N. 5558	9.040 ± 600	*Mylodon*	sloth dung	González & Lagiglia (1973:298)
2. Los Toldos	I.B.U.B. Arsenal, Wien	12,600 ± 600	*Onohippidium* *Lama*	charcoal	Cardich (1977)
Brazil					
3. Arroio Touro Passo (RS)	I-9628	11,010 ± 190	*Homo, Scelidotherium, Glossotherium, Propraopus, Pampatherium, Panochthus, Glyptodon, Hydrochoerus, Toxodon, Stegomastodon, Equus, Tapirus, Dicotyles, Palaeolama, Lama, Blastocerus, Ozotoceros, Mazama, Morenelaphus*	charcoal	Bombin (1976:81)
4. Arroio dos Fósseis (RS)	SI-800	12,770 ± 220	*Glossotherium*	bone	Simões (1972)
5. Lapa Vermelha IV (MG)	Gif-3208	9,580 ± 200	*Homo, Glossotherium*	charcoal	Laming-Emperaire *et al.* (1974:75, 145)
Chile					
6. Fell's Cave	I-3988	11,000 ± 170	*Onohippidium, Mylodon, Homo*	charcoal from fire pit dated, charcoal	Martin (1967:108)
	W-915	10,720 ± 30			Bird (1970)
	I-5146	10,080 ± 160			Saxon (1976:67)

Table 1 (cont.)

Locality	Laboratory Number	^{14}C (yrs B.P.)	Associated Fauna	Comments (material dated)	Source
7. Mylodon Cave (= Gruta del Milodon, Eberhart Cave, Ultima Esperanza Cave)	A-1390	13,560 ± 190	*Onohippidium,* *Mylodon* (= *Grypotherium*)	sloth dung	Long & Martin (1974:639)
	R-4299	13,500 ± 410		hair and skin	
	A-1391	10,400 ± 330		hide	
	SA-49	10,200 ± 400		dung	
	C-484	10,832 ± 400		sloth dung	Libby (1952:94)
	W-2998	13,040 ± 300		sloth hide	Martin (personal communication)
	BM-728	12,984 ± 76	"*Grypotherium listai*"	collagen from femur of sloth	Burleigh, Hewson and Meeks (1977:143)
	BM-1201A	5,366 ± 55	?*Mylodon***		Saxon (1976:67)
	BM-1201B	3,445 ± 58	?*Mylodon***	sloth remains	Borrero (1977:83-84)
	BM-1204A	3,734 ± 52			Borrero (1977:83-84)
	BM-1204B	3,693 ± 60			Borrero (1977:83-84)
	NZ-1680	13,500 ± 470	*Mylodon*	sloth remains	Saxon (1976:67)
8. Palli Aike Cave	C-485	8,639*	*Onohippidium* *Mylodon, Homo*	burnt bone	Libby (1952)
9. Tagua Tagua	GX-1205	11,380 ± 320	*Cuvieronius, Homo, Equus, Antifer*	charcoal	Montané (1968b)
Peru					
10. Talara	SM-852	13,616 ± 600	Talara local fauna	wood	Bryan (1973:244)
	SM-854	13,790 ± 535			
	SM-853-2	14,150 ± 564			
	SM-853-1	14,418 ± 500			
11. Cupisnique	GIF-4116	8,910 ± 200	Carolinian type fauna	collagen from *Scelidodon* ribs	
12. LaCumbre	GX-2019	10,535 ± 280	mastodon	apatite from fragment of long bone	Ossa & Moseley (1971:13, 15)
	GX-2494	12,360 ± 700	mastodon *Homo*	apatite from fragment of long bone	
13. Huargo Cave, bed 8	Lab. BVA Wien	13,460 ± 700	*Onohippidium*, *Homo*(?) *Lama*, scelidothere	animal bones	Cardich (1973)
14. Pikimachay Cave (= Flea Cave)	UCLA-1464	14,150 ± 180	Megatheriidae, ?*Palaeolama,* horse, *Homo*	sloth humerus	
		19,620 ± 3000		sloth vertebra	
		14,170 ± 180		sloth scapula	MacNeish *et al.* (1970a)
		16,050 ± 1200			

Table 1 (cont.)

Locality	Laboratory Number	^{14}C (yrs B.P.)	Associated Fauna	Comments (material dated)	Source
Uruguay					
15. Arapey		12,000	Lujanian fauna?	charcoal	Guidon (1979:401)
Venezuela					
16. Muaco	0-999	16,375 ± 400	*Eremotherium*, "*Stegomastodon*", *Toxodon* etc.	burnt bone (association with man needs verification)	Rouse & Cruxent (1963:537) Bryan (1973:244)
	M-1068	14,300 ± 500			
	IVIC-488	9,030 ± 240			
17. Cucuruchú	IVIC-514-B	3,350 ± 160***	*Eremotherium*, *Haplomastodon*, *Glyptodon*, etc.	associations with man need verification (carbonate dates)	Bryan (1973:244)
	IVIC-512-B	3,980 ± 70***			
	IVIC-511-B	5,860 ± 80***			
18. Taima-Taima	SI-3316	12,980 ± 85	*Haplomastodon*, *Glyptodon*, horse, sloth, felid, bear, *Homo*	small wood twig fragments collected in association with possibly butchered mastodon	Bryan *et al.* (1978:1277)
	Birm-802	13,000 ± 200			
	USGS-247	13,880 ± 120			
	UCLA-2133	14,200 ± 300			
	USGS-247a	13,830 ± 120			Robinson, 1979 (unpublished)
	USGS-247b	13,650 ± 140			

*This date is questionable and is based on solid carbon. The archaeological materials indicate same age as Fell's Cave.

**Probably from disturbed horizons. The floor of this cave has suffered much disturbance by *Mylodon* hide hunters over the past 100 years (M.B.).

***These dates were taken from carbonate and are certainly contaminated.

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