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

by

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SUMMARY

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ABSTRACT

The principles and practices employed in establishment and recognition of South American land mammal ages are reviewed along with previous and present concepts of distinguishing time, rock, and faunal units. Previous chronological arrangements of South American Tertiary land mammal faunas are appraised on the basis of recent geological and paleontological data. Twelve South American Tertiary land mammal ages are here recognized [from oldest to youngest, Riochican (middle to late Paleocene); Casamayoran (early Eocene); Mustersan (middle Eocene); Divisaderan (late Eocene); Deseadan (early [to middle?] Oligocene); Colhuehuapian (late Oligocene); Santacrucian (early Miocene); Friasan (middle Miocene); Chasicoan (late Miocene); Huayquerian (latest Miocene); Montehermosan (early to middle Pliocene); and Chapadmalalan (late Pliocene)]. As all except the Friasian were originally defined on the basis of Argentine faunas, these are discussed first and at length, and each is reviewed with discussion of type locality, stratigraphy, type fauna, and faunal correlations. Non-Argentine faunas are then discussed country by country in alphabetical order.

A review is given of radioisotope dates obtained on volcanic rocks (*i.e.*, basalts, tuffs) associated with mammal-bearing beds in Argentina. Based on these age determinations and on correlation of the late Tertiary land mammals involved in the interchange between North and South America, a chronology of South American land mammal ages correlated with North American land mammal ages and European marine stages is proposed.

It is concluded that South America was an island continent through most of the Tertiary Period (*ca* 65 to about 3 Ma). As a result, the land mammal fauna of South America developed in isolation and was dominated by autochthonous endemic groups. Toward the end of the Tertiary (*i.e.*, middle Miocene) a unique faunal balance had been achieved by the descendants of the ancient inhabitants (notoungulates, litopterns, condylarths, astrapotheres, edentates, marsupials) and of later (late Eocene) waif immigrants (caviomorph rodents, platyrrhine primates). A prominent feature of this mammal fauna was the combination of carnivorous and omnivorous marsupials with native placental herbivorous ungulates, subungulates, and edentates.

Sometime during the late Miocene, a limited but important interchange of mammalian taxa between North and South America took place. Procyonids (raccoons and their allies), a group of North American origin, first appear in South America in strata of Huayquerian Age, while members of the extinct South American ground sloth families Megalonychidae and Mylodontidae first appear in North America in early Hemphillian time. These groups dispersed along island arcs before the appearance of the Panamanian land bridge in the Pliocene (*ca* 3.0 Ma). Cricetine rodents, a group of North American origin, are first known in South America in strata of Montehermosan Age. The known taxa are too advanced and diversified to be considered the first of this group to invade South America. It is believed by some workers that these rodents arrived before the Montehermosan, possibly in the late Miocene or earlier, by waif dispersal from North America.

The isolation of South America ended with the appearance of the Panamanian land bridge, which provided a direct, dry land connection between the two Americas. Across this portal an extensive interchange of terrestrial faunas occurred, and the fossil record documents an intermingling of these long-separated land mammals faunas.

The beginning of this interchange by land route in South America is marked by the appearance of mammals which evolved from North American emigrants in the Chapadmalal Formation of Argentina. These include a mustelid (*Conepatus*), a tayassuid (*Argyrohyus*), and four genera (*Akodon, Dankomys, Graomys, Reithrodon*) of cricetine rodents. The appearance of this contingent of northern animals favors the existence of the Panamanian land bridge by this time. Likewise, a large number of terrestrial vertebrates of South American origin appear in North America in beds of late Blancan Age date around 2.7 Ma. Among the mammals are *Neochoerus, Erethizon, Glyptotherium, Glossotherium, Kraglievichia*, and *Dasypus*.

RÉSUMÉ

Les principes et pratiques employés pour obtenir et reconnaître en Amérique du Sud les Ages basés sur les Mammifères terrestres (land mammal ages) sont révisés avec les concepts anciens et actuels qui distinguent les unités chrono-, litho- et bio-stratigraphiques. Les arrangements chronologiques qui ont été proposés pour les faunes mammaliennes du Tertiaire sud-américain sont évalués sur la base des données géologiques et paléontologiques actuelles. Dans ce cadre, douze unités (Ages) biostratigraphiques sont reconnues ; ce sont, de la plus ancienne à la plus jeune : Riochiquien (Paléocène moyen et supérieur), Casamayorien (Eocène inférieur), Mustersien (Eocène moyen), Divisadérien (Eocène supérieur), Déséadien [Oligocène inf. (et moyen?)], Colhuéhuapien (Oligocène supérieur), Santacrucien (Miocène inférieur), Friasien (Pliocène moyen), Chasiquien ou Chasicoien (base du Miocène supérieur), Huayquérien (sommet du Miocène sup.), Montehermoséen (Pliocène inf. et moyen), et Chapadmalalien (Pliocène supérieur). Etant donné que toutes ces unités sauf le Friasien ont été originellement définies sur la base de faunes d'Argentine, celles de ce pays sont d'abord étudiées en détail, et chacune est révisée avec discussion de la localité type, de la stratigraphie, de la faune type, et des corrélations fauniques. Ensuite, les autres faunes mammaliennes sud-américaines sont discutées pays par pays, dans l'ordre alphabétique.

Une revue est faite des datations radioisotopiques obtenues sur des roches volcaniques (basaltes, tufs) associées à des couches à Mammifères en Argentine. En se basant sur ces déterminations d'âges et sur une corrélation des Mammifères terrestres du Tertiaire supérieur impliqués dans le grand échange faunique entre l'Amérique du Nord et celle du Sud, une chronologie des « land mammal ages » sud-américains, en corrélation avec les « land mammal ages » nord-américains et les étages marins européens, est proposée.

Il est conclu que l'Amérique du Sud était un continent insulaire durant presque tout le Tertiaire (env. – 65 à – 3 M.A.). Il en résulte que la faune mammalienne terrestre de l'Amérique du Sud s'est développée en isolement et était dominée par des groupes autochtones endémiques. Au cours du Néogène (notamment au Miocène moyen) un équilibre faunique unique a été réalisé par les descendants des anciens habitants (Notongulés, Litopternes, Condylarthres, Astrapothères, Edentés, Marsupiaux) et d'immigrants plus tardifs (Rongeurs caviomorphes, Primates platyrrhiniens) arrivés par transport passif (radeaux naturels) vers la fin de l'Eocène. Un trait saillant de cette faune mammalienne était la combinaison de Marsupiaux carnivores et omnivores avec des Placentaires autochtones herbivores (Ongulés, Subongulés, Edentés).

A un certain moment durant le Miocène supérieur, un échange de Mammifères, limité mais important, a eu lieu entre l'Amérique du Nord et celle du Sud. Des Procyonidés (Ratons laveurs et leurs parents), de souche nord-américaine, apparaissent en Amérique du Sud dans des strates d'âge huayquérien ; tandis que des Megalonychidae et Mylodontidae (Gravigrades = Ground sloths, originaires d'Amérique du Sud) apparaissent en Amérique du Nord dès le Hemphillien inférieur. Ces groupes ont migré au long d'arcs insulaires, avant l'émersion de l'isthme de Panama, survenu au Pliocène (env. – 3 M.A.). Des Rongeurs cricétinés, originaires d'Amérique du Nord, sont attestés en Amérique du Sud à partir du Montehermoséen ; mais les taxons connus sont trop avancés et diversifiés pour être considérés comme les premiers représentants du groupe ayant envahi l'Amérique du Sud ; certains auteurs pensent que ces Rongeurs sont arrivés avant le Montehermoséen, possiblement au Miocène supérieur ou même plus tôt, par transport passif à partir de l'Amérique du Nord.

L'isolement de l'Amérique du Sud se termine avec l'émersion de l'isthme de Panama, qui a formé une connexion terrestre directe entre les deux Amériques. Grâce à cette voie, un échange intensif de faunes terrestres a eu lieu, et les fossiles illustrent un mélange de ces deux faunes de Mammifères terrestres, longtemps séparées.

Le début de cet échange par voie terrestre est marqué en Amérique du Sud par l'apparition, dans la Formation Chapadmalal d'Argentine, de Mammifères variés qui ont évolué à partir d'immigrants venus d'Amérique du Nord. Ils comprennent un Mustélidé (*Conepatus*), un Pécari (le Tayassuidé *Argyrohyus*) et quatre genres (*Akodon, Dankomys, Graomys* et *Reithrodon*) de Rongeurs Cricétinés. L'apparition de ce contingent d'animaux nordiques est en faveur de l'existence d'un isthme de Panama déjà émergé à ce moment. De même, un grand nombre de Vertébrés terrestres d'origine sud-américaine apparaissent en Amérique du Nord dans des couches du Blanquien (Blancan) supérieur, datées d'environ 2,7 M.A. ; parmi les Mammifères on peut citer *Neochoerus, Erethizon, Glyptotherium, Glossotherium, Kraglievichia* et *Dasypus.*

RESUMEN

Los principios y prácticas usadas para establacer y reconocer en Sudamérica las Edades basadas en mamiferos terrestres (land mammal ages) se revisan con los conceptos anteriores y actuales que distinguen unidades crono-, lito- y bio-estratigráficas. Las ordenaciones cronológicas propuestas para las faunas de mamíferos terrestres delTerciario sudamericano, se evalúan basándose en datos geológicos y paleontológicos actuales. En este marco, se reconocen doce unidades (edades) bio-estratigráficas ; éstas son, de la más antigua a la más joven : Riochiquense (Paleoceno medio y tardío) ; Casamayorense (Eoceno temprano) ; Mustersense (Eoceno medio) ; Divisaderense (Eoceno tardío) ; Deseadense [Oligoceno temprano (y medio?)] ; Colhuehuapense (Oligoceno tardío) ; Santacrucence (Mioceno temprano) ; Friasense (Mioceno medio) ; Chasiquense (Mioceno tardío) ; Huayqueriense (Mioceno cuspidal) ; Montehermosense (Plio. temprano y medio) ; y Chapadmalalense (Plio. tardío). Dado que todas, con excepción del Friasense, fueron originalmente definidas basándose en faunas de Argentina, las de este país se discuten en primer lugar y con más detalles, siendo cada una revisada con discusión de localidad tipo, estratigrafía, fauna tipo y correlaciones fáunicas. Luego, las otras faunas sudamericanas se discuten país por país en orden alfabético.

Se da una revisión de las dataciones radioisotópicas obtenidas en rocas volcánicas (basaltos, tobas) asociadas con capas mamalíferas en Argentina. Basándose en estas determinaciones de edades y en la correlación de los mamíferos terrestres del Terciaro superior implicados en el intercambio fáunico entre Norte- y Sud-América, se propone una cronología de las « land mammal ages » sudamericanas en correlación con las « land mammal ages » norte-americanas y con los pisos marinos europeos.

Se concluye que Sudamérica era un continente insular durante casi todo el Terciario (o sea aproximadamente de – 65 a – 3 M.A.). Resulta de eso que la fauna de mamíferos terrestres sudamericanos se desarrolló en aislamiento y fue dominada por grupos autóctonos endémicos. En el Terciario tardío (p.ej. en el Mioceno medio) un equilibrio fáunico único ha sido realizado por los descendientes de los antiguos habitantes (notoungulados, litopternos, condi-

lartros, astrapoterios, desdentados, marsupiales) y de inmigrantes más tardíos (roedores caviomorfos, primates platirrinos) llegados por balsas hacia fines del Eoceno. Un rasgo notable de esta fauna de mamíferos era la combinacion de marsupiales carnívoros y omnívoros con placentarios autóctonos herbívoros (ungulados, subungulados y desdentados).

En algún momento del Mioceno tardio, sucedió un limitado pero importante intercambio de mamíferos entre Norte- y Sudamérica. Prociónidos (ositos lavadores y sus parientes), procedentes de Norteamérica, aparecen por primera vez en Sudamérica en estratos del Huayqueriense ; mientras tanto Megalonychidae y Mylodontidae (Gravigrados o perezosos terrestres, oriundos de Sudamérica) aparecen en Norteamérica desde el Hemphillense temprano. Estos grupos migraron a lo largo de arcos insulares antes de la emersión del istmo de Panamá, que sucedió en el Plioceno (*ca* − 3 MA). Roedores cricetinos, originarios de Norteamérica, están presentes en Sudamérica desde el Montehermosense. Pero los taxa conocidos son demasiado avanzados y diversificadas para que se pueda considerarlos como los primeros miembros del grupo que invadieron Sudamérica. Algunos autores piensan que estos roedores llegaron antes del Montehermosense, posiblemente en el Mioceno tardío o más temprano, gracias a una migración por balsas a partir de Norteamérica.

El aislamiento de Sudamérica se terminó con la emersión del istmo de Panamá, el cual proporcionó una conexión terrestre directa entre ambas Américas. Gracias a esta vía, ocurrió un intercambio extensivo de faunas terrestres, y los fósiles ilustran una mezcla de estas dos faunas de mamíferos continentales, por largo tiempo separadas.

El comienzo de dicho intercambio por vía terrestre está marcado en Sudamérica por la aparición, en la Formación Chapadmalal de Argentina, de mamíferos variados que evolucionaron a partir de immigrantes llegados de Norteamérica. Incluyen un mustélido (*Conepatus*), un pécari (*Argyrohyus*) y cuatro géneros (*Akodon, Dankomys, Graomys, Reithrodon*) de roedores cricetinos. La aparición de este contingente de animales norteños habla en favor de la existencia del istmo de Panamá ya emergido en aquel momento. En la misma forma, un gran número de vertebrados terrestres originarios de Sudamérica, aparecen en capas norteamericanas del Blanquense (Blancan) tardío, datadas aproximadamente de 2,7 M.A. Entre los mamíferos se puede citar *Neochoerus, Erethizon, Glyptotherium, Glossotherium, Kraglievichia* y *Dasypus*.

INTRODUCTION

The land mammal-bearing Tertiary of South America was last reviewed, by Simpson, in 1940. This was a milestone study which brought order to and synthesized a vast amount of scattered data originally published in six languages. Since that time our knowledge of South American Tertiary rocks and faunas has been greatly increased. Some of these studies have been reviewed in a series of papers published in 1970 under the title of *Paleontología Sudamericana* in Actas del IV° Congreso Latinoamericano de Zoología, Volume II, and based on a symposium in Caracas, 10-16 November 1968. In addition, new stratigraphic concepts have been developed for recognition of time, rock, and faunal units.

The purpose of this paper is to review all pertinent geological and faunal studies on the land mammal-bearing Tertiary of South America and to provide a synthesis incorporating present stratigraphic concepts. Our chronology of the South American rocks and faunas with those in North America and Europe is tentative and may be subject to change. Much order and stability will only be attained with more detailed comparative faunal studies, more radioisotopic age determinations, and magnetostratigraphic studies of associated rocks.

At present there are no existing summaries of Tertiary rocks and biotas for all of the South America. It is not our purpose to attempt a full synthesis at this time. Fossil mammals, however, have proven so useful in establishing chronological sequences and stratigraphic relationships, either locally or on a continent-wide basis, that an interim review of this nature seems appropriate.

The first and as yet most detailed studies of Tertiary rocks and land mammal

Table 1. Historic development of time and faunal nomenclature for the Tertiary and early Quaternary of Argentina

F. Ameghino 1906	L. Kraglievich 1930c	Frenguelli 1930a	L. Kraglievich 1934	Castellanos 1937	Simpson 1940	Feruglio 1949	Pascual 1970	This Paper
Ensenadéen	Ensenadense		Ensenadense	Ensenadense	Ensenadan	Terrestrial beds	Ensenadense	Ensenadan
Puelchéen	Uquiense	Tehuelchiano	Uquiense	Uquiense	(Uquian)	of this period	Uquiense	Uquian
(not distinguished)	Chapadmalense		Chapadmalense	Chapadmalense	Chapadmalalan	not recognized	Montehermosense	Chapadmalalan
Hermoséen	Hermosense		Claveroense?	Montehermosense	Montehermosan	in Patagonia.		Montehermosan
			Irenense?					
			Hermosense					
Araucanéen	Araucanense	Puelchense	Tunuyanense	Araucanense	Tunuyanian			
			Huayqueriaense		Huayquerian			
			Araucanense					
Rionegréen	Rionegrense	Rionegrense	Rionegrense		(excluded as a stage)	Rionegrense	Huayqueriense	Huayquerian
Mesopotaméen	Mesopotamiense		Mesopotamiense	Mesopotamiense	Mesopotamian	(excluded as a stage)		
(not known)	Chasicoense	Araucanense	Chasicoense	Chasicoense	Chasicoan	Chasicoense	Chasiquense	Chasicoan
Paranéen	Paranense		Paranense	Paranense	(excluded as a stage)	(excluded as a stage)	(excluded as a stage)	(excluded as a stage)
(hiatus)	Mayoense		Mayoense	Mayoense	(Mayan)			
Friaséen	Friasense	Friasense	Friasense	Friasense	Friasian	Friasense	Friasense	Friasian
Magellanéen	Colloncurense		Colloncurense	Colloncurense	(Colloncuran)			
Santacruzéen	Santacrucense		Santacrucense	Santacrucense	Santacrucian			
Notohippidéen	Karaikense	Santacruzense	Karaikense	Karaikense	(Karaikenian)	Santacrucense	Santacrucense	Santacrucian
Astrapothericuléen				Pinturense	(excluded as a stage)			
Colpodonéen	Trelewense	Colhuehuapiense	Trelewense	Trelewense	Colhuehuapian	Colhuehuapiense	Colhuehuapiense	Colhuehuapian
Tequéen	(excluded as a stage)	(excluded as a stage)	(excluded as a stage)	Teckaense	(excluded as a stage)			
			Castillense?	Castillense?				
Pyrothéréen	Deseadense		Deseadense	Deseadense	Deseadan	Deseadense	Deseadense	Deseadan
							Divisaderense	Divisaderan
		Deseadense						
Astraponotéen	Mustersense		Mustersense	Mustersense	Mustersan	Mustersense	Mustersense	Mustersan
Notostylopéen	Casamayorense	Casamayorense	Casamayorense	Casamayorense	Casamayoran	Casamayorense	Casamayorense	Casamayoran
	Colhuehuapiense		Colhuehuapiense	Colhuehuapiense				
(not clearly recognized)	(not clearly recognized)	(not clearly recognized)		(not clearly recognized)	Riochican	Riochiquense	Riochiquense	Riochican

faunas were made in Argentina, especially in the southern region known as Patagonia[1]. All but one of the South American Tertiary land mammal ages presently recognized were based on Argentine faunas, and these serve as a standard for calibrating mammal evolution on a continent-wide basis.

That we have this record is very largely due to the work of two extraordinary men, the brothers Ameghino — Florentino working mainly in the lab, Carlos in the field. They recognized in one form or another, although for the most part under different names, nearly all of the land mammal ages as shown in table 1; the only ones unknown to them were the Riochican, Chasicoan, Divisaderan, and Uquian (Simpson, 1948, 1980). The magnitude of their achievement, as summarized largely by Florentino Ameghino (1906) can be appreciated by a look at the 'state of the art' around 1880 (table 2), about the time they began their work in earnest. No mammals were known from the continental 'Guaranitic', and the mammalian assemblage ascribed to the marine 'Patagonian' was such that no one could have made sense of it (the European genera were listed due to mistaken identifications by Bravard). Within about 25 years, the Ameghino's brought the succession nearly to its present state of knowledge (Bryan Patterson, personal communication).

Table 2. The South American Cenozoic *ca.* 1880

I. *Pampean "Fm."* = Ensenadan and Lujanian.

II. *Patagonian "Fm."* Included marine deposits at Paraná and in Patagonia, terrestrial deposits of Huayquerian and Santacrucian ages. Mammals: "*Palaeotherium*", "*Anoplotherium*", "*Megamys*", "*Anchitherium*", *Nesodon* (*s.l.*), *Homalodotherium*, *Astrapotherium*, cetaceans.

III. *Guaranitic "Fm."* Based primarily on rocks exposed in Corrientes, Argentina; used as a catch-all.

The principles and practices employed in establishment and recognition of South American land mammal ages are reviewed, along with previous and present concepts of distinguishing time, rock, and faunal units. As all but one of the South American Tertiary land mammal ages are defined on Argentine faunas, they are discussed first and at length. Each of these ages is reviewed with discussion of type locality, stratigraphy, type fauna, and faunal correlations. Non-Argentine faunas are then discussed country by country in alphabetical order. The zoological character and history of the South American Tertiary land mammal faunas are summarized. Lastly, a review is given of radioisotope dates obtained on volcanic rocks (*i.e.*, basalts, tuffs) associated with mammal-bearing strata in Argentina (and Bolivia). Based largely on these age determinations, a chronology of South American land mammals ages, North American land mammal ages, and European marine stages is proposed.

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[1] Patagonia is a geographical, not political, name generally applied to that part of Argentina which extends from south of the Rio Colorado to the Straits of Magellan, and from the Andes in the west to the Atlantic Ocean in the east.

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SOUTH AMERICAN TERTIARY LAND MAMMAL AGES

TIME, ROCK, AND FAUNAL UNITS

For many years stratigraphic nomenclature in Argentina has, as elsewhere, been confused by a lack of clarity in distinguishing units and names applicable to time, rocks, and faunas. Discussions of these problems along with attempts to clarify usage are given by Fossa-Mancini *et al.* (1938), Simpson (1940, 1941a, 1971), Pascual, Ortega Hinojosa, Gondar, & Tonni (1965, 1966), and Pascual & Fidalgo (1972).

F. Ameghino (*e.g.*, 1906), working in Argentina, called his major stratigraphic units *formaciones*, using the term for much larger units and with a different meaning than is now customary in most usage. L. Kraglievich (1934), following Ameghino (*e.g.*, 1906), also called them *formaciones* and specified their faunal content by the alternative name ***ciclos faunísticos***. By formation (*formación*) we mean a strictly lithostratigraphic unit defined as a distinct and mapable body of rock. Formations are given geographic names, without such endings as ***-an***, ***-ense***, or ***-iano*** (see below).

Stage and corresponding age names are identical and have Argentine geographic roots followed in English by the conventional ending ***-an*** or ***-ian***, in Spanish by the ending ***-ense*** and the appropriate term ***piso*** or ***edad***. The Spanish term equivalent to stage in Argentina is ***piso***, synonymous with the Portuguese ***andar***, now commonly adopted in Brazil; both are chronostratigraphic units. The Spanish word ***edad*** is equivalent to age and is a geochronologic unit. The suffix ***-iano*** was typically used with ***grupo*** (usually with scope of a series), and ***-ense*** with ***piso*** (usually with scope of a formation) (Simpson, 1941a, p. 5; 1971, p. 287).

By stage we mean all the rocks of a given age; it is a chronostratigraphic unit usually enclosing one or more formations, although one formation may well overlap more than one defined stage (Simpson, 1974, p. 4). By age we mean a strictly geochronologic unit, a segment of geological time. The meanings of these terms are thus in accord with the North American Code of Stratigraphic Nomenclature, despite the fact that most, if not all, the ages have not been defined in terms of stages (article 16a).

Formations (lithostratigraphic units) and stages (chronostratigraphic units) are placed in different stratigraphic classifications; however, it has been usual in Argentina to apply to a stage the same geographic name as that of an included formation.

Also, names of South American land mammal ages, as in Pascual, Ortega Hinojosa, Gondar & Tonni (1965, 1966) are based intentionally on lithostratigraphic units, even though it could be argued that some of the lithostratigraphic units in question never were defined as such, and that this is in opposition to the requirements of the Argentine Code of Stratigraphic Nomenclature (article 34, remark)[2].

For the Tertiary, as for the Quaternary, principal mammal-bearing deposits were long known only from Argentina. In fact, all but one (the Friasian) of the South American land mammal ages now recognized were defined originally on the basis of Argentine faunas. The Argentine faunal sequence proposed by Ameghino was based on the *evolutionary grade* of its fossil mammals. This sequence served as the framework for the South American land mammal ages formally recognized by Pascual, Ortega Hinojosa, Gondar & Tonni (1965, 1966). These land mammal ages have proven applicable throughout South America (Simpson, 1971, p. 283).

The chronology and usage of South American land mammal ages in this study (table 1) follow Patterson & Pascual (1972, p. 248, table 1). The only modification is the tentative recognition of a Chapadmalalan Age, upper part of Montehermosan of Pascual, Ortega Hinojosa, Gondar & Tonni (1965, 1966) and Pascual & Odreman Rivas (1971, 1973). One of us, R. P., is not in agreement with this procedure; R. H. has found it difficult, if not impossible to distinguish Chapadmalalan and Montehermosan Ages in the non-Argentine countries as well.

ARGENTINA

SALAMANCAN (EARLY PALEOCENE)

The marine Salamanca Formation of Chubut Province, eastcentral Patagonia (Lesta & Ferello, 1972), is an important datum plane, as it disconformably underlies the Río Chico Formation (Andreis, Mazzoni & Spalletti, 1975) in which the oldest known fossil mammals in the Argentine succession occur. The age of the Salamanca Formation has been disputed by early workers and was placed at various times in the Cenomanian, Maestrichtian, Danian, Paleocene and early Eocene. Stenzel (1945), based on a study of the oyster genus *Odontogryphaea*, suggested that it was Thanetian or Ypresian in age. Recent studies of foraminifera (Bertels, 1970, p. 495, 1975, 1979; Méndez, 1966) and the long-known absence of undoubtedly and fully Cretaceous guide fossils (*i.e.*, dinosaurs) (Feruglio, 1937) indicate the Salamanca Formation to be of early Paleocene (late Danian) Age. The Salamanca Formation is largely marine in origin, but with littoral facies containing crocodiles and turtles, while the overlying Río Chico Formation is entirely continental (Archangelsky, 1976, p. 43).

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[2] Florentino Ameghino's criteria for distinguishing stratigraphic units were clearly stated by him in 1906 (p. 201) : « Depuis quelques années j'emploie une désinence uniforme pour les noms des étages, et distincte de celle également uniforme des noms de formations. Dans mes travaux en langue française, je donne aux noms des formations les terminaisons ***ien*** et ***ienne***, selon que le mot est masculin ou féminin : patagonien, patagonienne, etc. Les noms des étages portent la terminaison ***éen*** : santacruzéen, superpatagonéen, colpodonéen, etc. Voilà aussi pourquoi j'écris ***formation pampienne*** et non ***pampéenne, étage santacruzéen*** et non ***santacruzien***, etc. ».

This lithostratigraphic unit is based on the designation ***Salamancanéen*** of H. von Ihering (1903, p. 195). Two members are now recognized (Andreis, Mazzoni & Spalletti, 1975). The lower or Bustamente Member is largely calcareous and was deposited in an open or neritic environment. It is exposed in Bahía Bustamente and in isolated areas in the vicinity of Tetas de Pinedo. The upper or Hansen Member is characterized in the coastal zone by epiclastic sediments, predominantly gray and in part yellow and/or green. This member was deposited in a transitional environment characterized by restricted circulation and includes the classic beds commonly attributed to the Salamanca Formation (*i.e.*, Banco Negro Inferior, Banco Verde) in the Golfo de San Jorge. The Banco Negro Inferior of Feruglio (1949) includes 10 cm of a fine white tuff and contains remains of turtles, crocodiles, and silicified wood. Based on the work of McCartney (1933), Simpson (1935b, p. 7) included the Banco Negro Inferior within the Salamanca Formation, although Feruglio (1949) later considered it as the base of the Río Chico Formation. Andreis, Mazzoni & Spalletti (1975, p. 91), based on the similar lithology between the Banco Negro and those beds below it and in the presence of a marked change in the sedimentation above the Banco Negro, included the Banco Negro Inferior in the Hansen Member of the Salamanca Formation. On the basis of this marked change in sedimentation those workers recognized an erosional unconformity, which is particularly evident in the area of Puerto Visser. The Banco Verde is composed largely of glauconitic sands (McCartney, 1933, p. 15; Simpson, 1935b, p. 7).

The sediments referred to the Salamanca Formation are testimony of the first Tertiary Atlantic marine ingression in this basin; the sea was shallow, regressing in at least two pulses (Archangelsky, 1976, p. 55). The Salamanca Formation accumulated in a shallow marine basin which, as evidenced by the abundance of glauconite and the presence of invertebrates and microplankton, was represented by a tectonically stable environment (Lesta & Ferello, 1972).

RIOCHICAN (MIDDLE AND LATE PALEOCENE)

The Río Chico Formation was formally recognized by Simpson (1933, p. 11) for those mammal-bearing beds which occur below the Casamayor Formation and above the Salamanca Formation. The name was given for the Río Chico del Chubut, in the valley of which these beds are well developed (fig. 1). The type locality is at Cañadón Hondo (fig. 1). The Riochican beds were informally referred to by earlier workers under a diversity of names, including ***dinosaur sandstones*** (Roth, 1908), ***upper dinosaur beds*** (Windhausen, 1924), ***Pehuenche*** (Feruglio, 1929), ***Sehuense*** or ***Sehuenense*** (Ameghino, 1898, p. 121) and ***Notostylopéen... partie basale*** (Ameghino, 1900-02). Simpson (1940, p. 655) noted that these beds were long thought to represent the terminal part of the late Cretaceous dinosaur bearing Chubut Group. It is now established that the Río Chico Formation is somewhat later in age than the Salamanca Formation, that it does not contain dinosaurs, and that it does contain early Tertiary mammals (Simpson, 1940, p. 655-7).

The Río Chico Formation is composed predominantly of sands and clays, some bentonitic (Simpson, 1935b, p. 7) and some of fluviatile origin (Andreis, Mazzoni &

Spalletti, 1975, p. 86). The largest section yet measured (131 meters) is at Pico Salamanca (Andreis, Mazzoni & Spalletti, 1975, p. 93, table 2), although Feruglio (1949) reported that it reaches a maximum known thickness of 250 meters in the subsurface of Cañadón Perdido.

Andreis, Mazzoni & Spalletti (1975) divided the Río Chico Formation into two members, the lower Las Violetas and the upper Visser; both represent fluvial meandering cycles. The Las Violetas Member is characterized by epi- and pyroclastic gray and yellowish sediments, and contains some paleosol levels. The Visser Member is identified by the epiclastic, arkosic (feldspathic) nature of its sandstones and conglomerates, by gray green interbedded bentonites, and by fossil vertebrates and tree trunks. The top of the Visser Member is difficult to define, given that this passage is at times transitional with the ***Tobas de Sarmiento*** (see below).

Fossil mammals, first reported from what is now called the Río Chico Formation by Feruglio (1931a), Piatnitzky (1931), and Bordas (1935a), were later described by Simpson (1935a, b, 1948, 1967b). They have been reported from six local faunas at four localities (fig. 1, table 3): Bajo de la Palangana (two levels), Cañadón Hondo,

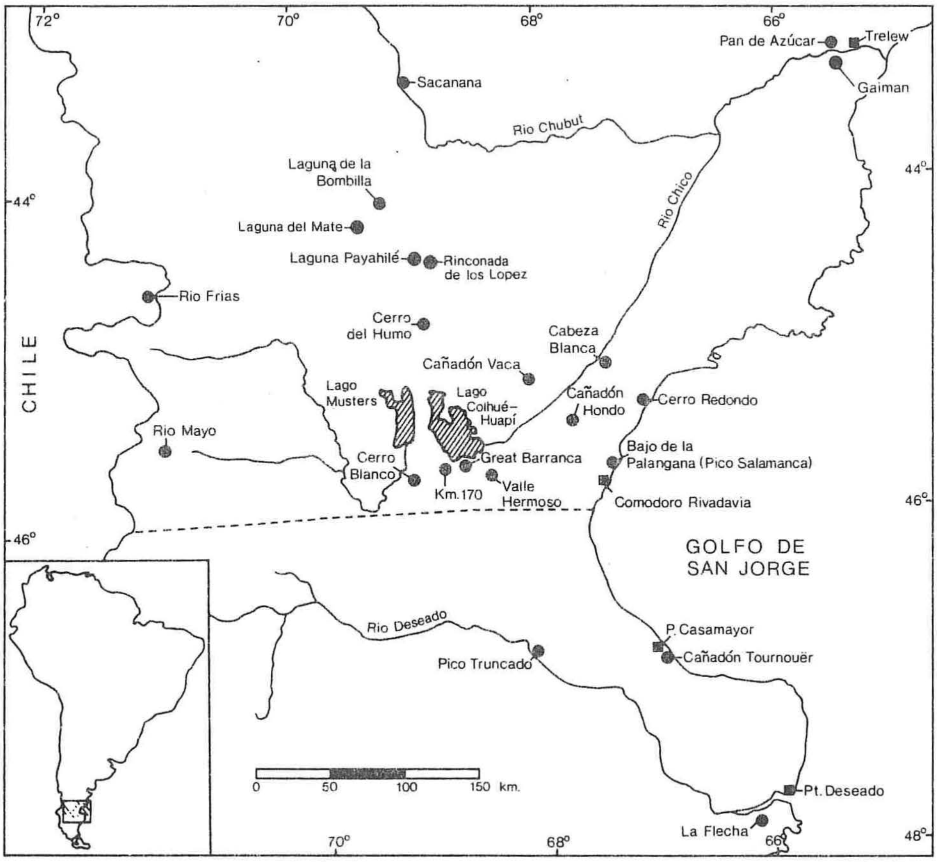

Fig. 1. — Map of central Patagonia, southern Argentina, showing principal mammal-bearing localities of Tertiary age.

Cerro Redondo (two levels), and Pan de Azúcar. Other localities are also known along the northcentral part of Chubut Province and at the Barranca south of Lago Colhué-Huapí (Pascual, unpublished).

Simpson (1935b) arranged these local faunas into «faunal zones» based on the relative stage of evolution of the taxa. These faunal zones include, from oldest to youngest: the *Carodnia* faunal zone (lower faunas from Bajo de la Palangana and Cerro Redondo), the *Kibenikhoria* faunal zone (fauna from Cañadón Hondo), and the *Ernestokokenia* faunal zone (fauna from upper level at Bajo de la Palangana). The upper local fauna from Cerro Redondo and that from Pan de Azúcar could not be confidently assigned to any of these zones. Based on this arrangement, Simpson (1948, p. 29) later noted that there is evidence that the Riochican (tentatively regarded by Simpson as late Paleocene) land mammal age includes two and probably three different "successive faunas so distinctive that separate designations and stage names will probably be necessary for them". He further suggested that in itself, this age suggests a lapse of time probably great enough to include both the middle and late Paleocene. "At present, however, few of these successive phases are known, and each is represented only by a scanty local fauna" (Simpson, 1948, p. 29). It is thus premature to attempt a definite stratigraphic or temporal subdivision. All fossils from these beds are therefore considered as representing a broad Riochican Age (Simpson, 1948, p. 30) which, based on paleomagnetic analysis of a stratigraphic section of Cerro Redondo, is shown to encompass middle and late Paleocene time (Marshall, Butler, Drake & Curtis, 1981).

All of the well-preserved, identifiable Riochican mammals are specifically distinct from Casamayoran (early Eocene) taxa. One of us (Pascual, unpublished) has found, however, that the upper Riochican fauna from Bajo de la Palangana contains species which have been considered to be typical of Casamayoran Age. There are many genera which occur in both faunas (see p. 65), indicating that there is little time between late Riochican (*i.e.*, uppermost fauna from Bajo de la Palangana) and early Casamayoran as now known (Simpson, 1967b, p. 250). Recently, Andreis (1977, p. 86) reported an angular unconformity between the Río Chico Formation (Visser Member) and the overlying Casamayoran Age strata (Cañadón Hondo Formation) exposed in Cañadón Hondo. Despite this, "even in the latest Riochican faunule, where most of the genera and perhaps some species are the same as in the immediately following Casamayor, neither *Notostylops* (a typical Casamayoran genus) nor a forerunner has yet been found" (Simpson, 1948, p. 171).

Pascual, Vucetich & Fernández (1978) have reported a probable Riochican fauna from red siltstones of the Mealla Formation, Santa Bárbara Subgroup (the Santa Bárbara Subgroup includes, from oldest to youngest, the Mealla, Maíz Gordo, and Lumbrera Formations) upper part of Salta Group, in Jujuy Province, northwestern Argentina. The locality is south of the railroad station of Tres Cruces (fig. 2), between 23° 0'-15'S and 66° 30'-45'W (for map of exact locality, see fig. 1, Fernández, Bondesio & Pascual, 1973). This locality occurs in the southern part of the Andean Basin (*sensu* Reyes, *in* Reyes & Salfity, 1973), a large sedimentary basin which includes rocks of Cretaceous and early Tertiary Age in the northwestern corner of Argentina, southwestern Bolivia and southern Peru (see fig. 1, Reyes & Salfity, 1973). The fauna includes a new henricosborniid genus with two species, *Simpsonotus praecursor* and *S. major* (Pascual, Vucetich & Fernández, 1978).

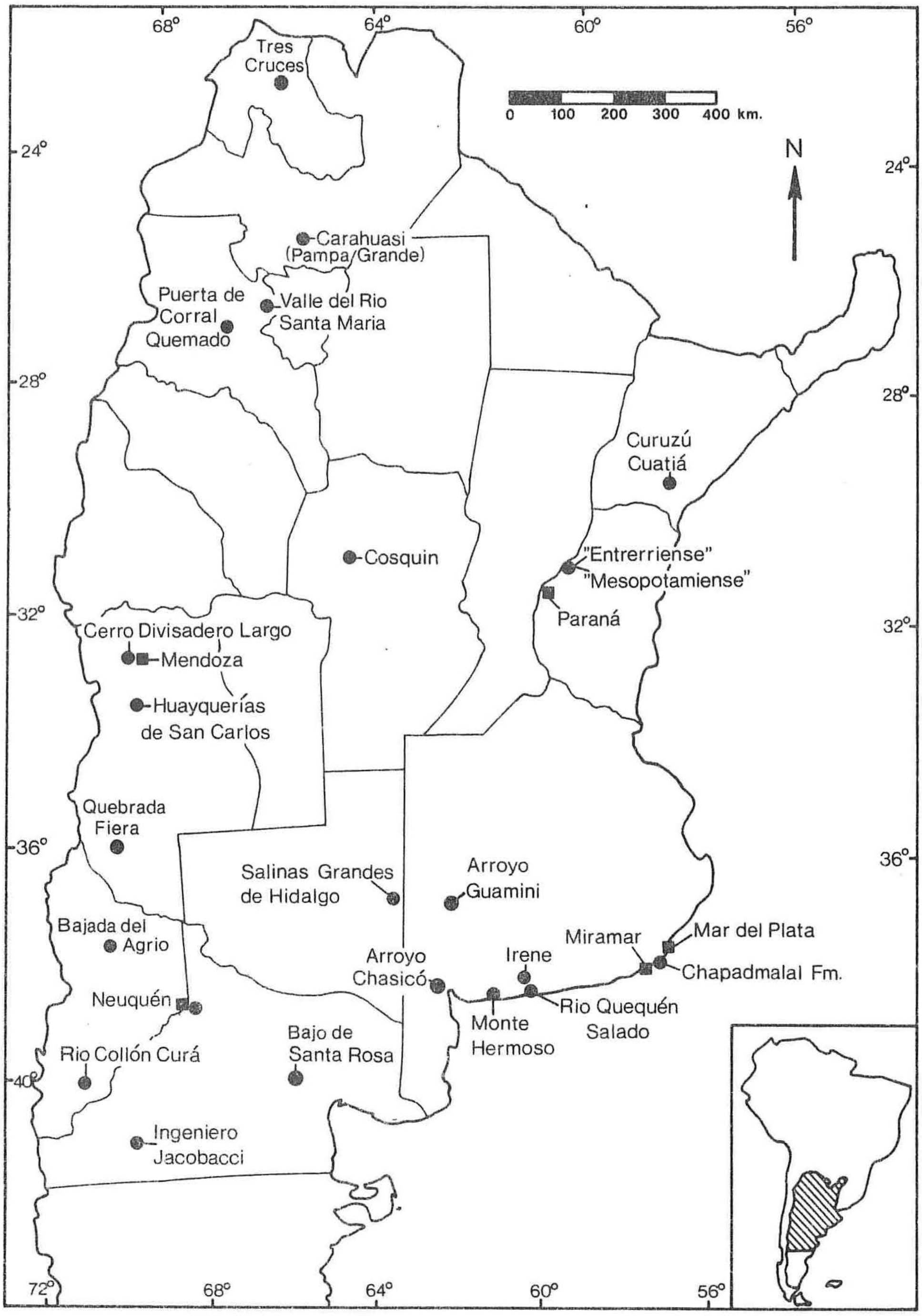

Fig. 2. — Map of central and northern Argentina showing principal mammal-bearing localities of Tertiary age.

Table 3. List of Riochican local faunas from Argentina

A. Chubut Province (Patagonia)

I. BAJO DE LA PALANGANA

1. Lowest mammals -- 19 to 20 meters above the "Banco Negro Superior", in fine red sandstone.

Order Xenungulata
  Family Carodniidae
    Carodnia feruglioi SIMPSON (1935), see Simpson (1935a)

2. Highest mammals -- 85 to 88 meters above the "Banco Negro Superior", and about 6 meters below the Casamayor tuffs, in coarse gray to pink sandstone.

Order Marsupialia
  Family Borhyaenidae
    ?*Nemolestes* sp. see Simpson (1948)

  Family Polydolopidae
    Polydolops winecage SIMPSON (1935), see Simpson (1935a)

Order Condylarthra
  Family Didolodontidae
    Ernestokokenia chaishoer SIMPSON (1935), see Simpson (1935a)
    Ernestokokenia ?*yirunhor* SIMPSON (1935), see Simpson (1948)

Order Notoungulata
  Family Henricosborniidae
    Henricosbornia ?*lophodonta* AMEGHINO (1901), see Simpson (1948)
    ?*Othnielmarshia* sp. see Simpson (1948)

  Family Isotemnidae
    Isotemnus sp. see Simpson (1935b)
    ?*Pleurostylodon* sp. see Cabrera (1935) and Simpson (1967b)

  Family Interatheriidae
    Notopithecus sp. see Cabrera (1935) and Simpson (1967b)

  Family Archaeohyracidae
    ?*Eohyrax* sp. see Cabrera (1935) and Simpson (1967b)

  Notoungulata, *incertae sedis*
    Brandmayria simpsoni CABRERA (1935)

Order Litopterna
  Family Macraucheniidae
    Victorlemoinea sp. see Simpson (1948)

  Family Proterotheriidae
    Ricardolydekkeria sp. see Simpson (1948)
    Josepholeidya sp. see Simpson (1948)

Order Trigonostylopoidea
  Family Trigonostylopidae
    Trigonostylops sp. see Simpson (1935b)

II. CAÑADÓN HONDO (*KIBENIKHORIA* FAUNA)

Order Marsupialia
  Family Borhyaenidae
    Patene sp. see Simpson (1948)
  Family Polydolopidae
    ?*Polydolops kamektsen* SIMPSON (1935), see Simpson (1935a)
  Incertae sedis
    Gashternia ctalehor SIMPSON (1935), see Simpson (1935a)

Order Condylarthra
  Family Didolodontidae
    Ernestokokenia yirunhor SIMPSON (1935), see Simpson (1935a)

Order Notoungulata
  Family Henricosborniidae
    Henricosbornia waitehor SIMPSON (1935), see Simpson (1935a)
    ?*Peripantostylops orehor* SIMPSON (1935), see Simpson (1935a)
  Family ?Notostylopidae
    Seudenius cteronc SIMPSON (1935), see Simpson (1935a)
  Family Isotemnidae
    ?*Isotemnus ctalego* SIMPSON (1935), see Simpson (1935a)
  Family Interatheriidae
    ?*Transpithecus* sp. see Simpson (1967b)
  Family Oldfieldthomasiidae
    Kibenikhoria get SIMPSON (1935), see Simpson (1935a)

Order ?Litopterna
  Gen. et sp. indet. see Simpson (1935b)

Order Trigonostylopoidea
  Family ?Trigonostylopidae
    Shecenia ctirneru SIMPSON (1935), see Simpson (1935a)

III. CERRO REDONDO

1. Lowest mammals -- 32 to 33.5 meters above top of "Banco Negro Inferior", and 37 meters above "Banco Verde". The fossils are from a clay and sandstone horizon, base of level "h", Figure 3, Simpson (1935b, p. 8).

Order Marsupialia
  Family ?Borhyaenidae
    Gen. et sp. indet. see Simpson (1935b)
  Family Polydolopidae
    Seumadia yapa SIMPSON (1935), see Simpson (1935a)

Order Litopterna
  Family Proterotheriidae
    Wainka tshotshe SIMPSON (1935), see Simpson (1935a)

2. Highest mammals -- 85 to 86 meters above lowest mammals (see above), and about 117 to 118 meters above top of the "Banco Negro Inferior". The fossils are found in lenses of hard cross-bedded gray sandstone, weathering reddish. Level "m", Figure 3, Simpson (1935b, p. 8).

Order Edentata
  Family Dasypodidae
    Gen. et sp. indet. see Simpson (1948, *nec* 1935b)

Order Notoungulata
  Family Isotemnidae
    Gen. et sp. indet. see Simpson (1935b)
  Family ?Interatheriidae
    Gen. et sp. indet. see Simpson (1935b)

IV. PAN DE AZÚCAR

Order Marsupialia
  Family Polydolopidae
    Polydolops rothi SIMPSON (1936)

Order Notoungulata
  Family Henricosborniidae
    Henricosbornia minuta (ROTH, 1903), see Simpson (1948)
  Family Isotemnidae
    Isotemnus haugi (ROTH, 1902), see Simpson (1967b)
  Family Interatheriidae
    Gen. et sp. indet. see Simpson (1935b)

B. Jujuy Province (Northwestern Argentina)

V. SSW OF TRES CRUCES

Order Notoungulata
  Family Henricosborniidae
    Simpsonotus praecursor PASCUAL, VUCETICH, and FERNÁNDEZ (1978)
    Simpsonotus major PASCUAL, VUCETICH, and FERNÁNDEZ (1978)

SARMIENTO GROUP (EOCENE AND OLIGOCENE)

The term *Tobas de Sarmiento* was proposed by Feruglio (1938) for those pyroclastic sediments which occur above the terrestrial Río Chico Formation and below the "Patagonian" marine stage (see below). "Despite the relatively uniform source materials and the tendency of many geologists to refer to [these pyroclastic sediments] as a unit, this series is really highly varied in lithology and... structure" (Simpson, 1940, p. 659). The Grupo Sarmiento is recognized by Spalletti & Mazzoni (1977, p. 279-82) as a peculiar and unique loessic deposit of Tertiary Age. This succession is comparatively thin, 150-190 meters in thickness according to Feruglio (1949). It was recognized as the Sarmiento Group (Andreis, Mazzoni & Spalletti, 1975) and includes mammal-bearing beds of Casamayoran, Mustersan, Deseadan, and Colhuehuapian Age (Simpson, 1948, p. 30; Bordas, 1943).

In these sediments Carlos Ameghino found an abundance of fossil mammals; his brother Florentino (*e.g.*, 1906) formally recognized them as representing four distinct faunas, which he named for a characteristic, but not the most abundant, mammalian genus. From oldest to youngest, these are the *Notostylops, Astraponotus, Pyrotherium*, and *Colpodon* faunas. "The rock units from which these [faunas] come were named for these genera [*e.g.*, *Notostylopense*], names also used for time units in correlation. These have since given way to geographic names developed by Gaudry (1906, following work by Tournouër, 1903), [L.] Kraglievich (1930c), Frenguelli (1930a), and [among others, Simpson (1933), and are]... usually given in Spanish with the suffix *-ense*" (Simpson, 1940, p. 659). Gaudry (1906), relying largely on the faunal studies of F. Ameghino and the field work of Tournouër (1903), united the *Colpodon* and *Pyrotherium* beds in an *Étage du Deseado* and called the *Notostylops* beds the *Étage du Casamayor*. He did not distinguish the *Astraponotus* beds. Loomis (1914) redefined this unit to include only the *Pyrotherium* beds; this has become universal usage. Frenguelli (1930a) applied to the *Colpodon* beds the name Colhué-Huapí (*Colhuehuapiense*) [Kraglievich (1930c) used the term *Colhuehuapiense* in a different sense], which had been suggested in this sense by Ameghino in 1898. L. Kraglievich (1930c) gave the name Musters (*Mustersense*) to the *Astraponotus* beds (Simpson, 1942); Simpson (1940, p. 659) proposed "to use the unmodified geographic name for rock units and suffix *-an* to form the names of standard time units. The sequence is, then, as follows :

Fauna (Ameghino)	Typical Rock Unit	Time Unit (Age)
Colpodon	Colhué-Huapí	Colhuehuapian
Pyrotherium	Deseado	Deseadan
Astraponotus	Musters	Mustersan
Notostylops	Casamayor	Casamayoran

The successive faunas of Ameghino correspond with sufficiently clear-cut temporal units approximately equivalent in status to North American or European Tertiary provincial ages and stages and [are] well definable as such" (Simpson, 1948, p. 29-30).

At the Great Barranca south of Lago Colhué-Huapí (fig. 1), "all four faunas occur superposed in a single sequence and the type descriptions of three of them [Casamayoran, Mustersan, Colhuehuapian] were based, for the most part, on material from this locality" (Simpson, 1940, p. 659). There, as elsewhere in Patagonia, these faunas have been clearly identified and the type faunas show that there is a marked hiatus in time between each. "Until now these local faunas have seldom been clearly distinguished as such and their sequence has not been established, almost all publications simply referring material in hand to the one of the four faunas that it most resembles, without further or precise details" (Simpson, 1940, p. 659).

Local faunas which occur within these hiatuses are now known from diverse localities in the provinces of Chubut and Río Negro. Data on one of these *transitional* faunas has been published (see Pascual, 1965a; Odreman Rivas, 1969), but many others are as yet unpublished.

Andreis *et al.* (1975) and Spalletti & Mazzoni (1977) studied the Sarmiento Group at various localities and at most were unable to recognize unconformities between the mammal-bearing units or distinct mapable units or formations. Because of this peculiarity, Spalletti & Mazzoni (1979) now recognize it as the Sarmiento Formation. They were, however, able to recognize sedimentary cycles which, on preliminary analysis, appear to correspond to the different land mammal ages. Three of these sedimentary units, for example, have been recognized by them at the Great Barranca south of Lago Colhué-Huapí.

CASAMAYORAN (EARLY EOCENE)

Fossils of Florentino Ameghino's *Notostylops* fauna were first found by his brother Carlos in 1895-1896 at the Great Barranca south of Lago Colhué-Huapí (fig. 1; Simpson, 1967a, p. 67). However, Tournouër (1903) found a few fossils referrable to this same fauna near Punta Casamayor, Santa Cruz Province, on the coast of the Gulf of San Jorge, roughly halfway from Comodoro Rivadavia to Cabo Blanco (fig. 1). The locality is southeast of Punta Casamayor along the coast between that point and Puerto Mazaredo, especially in a small *cañadón* that the Ameghino's named after Tournouër. Dealing with these fossils Gaudry (1906) applied the name *Étage du Casamayor* to the beds now known by that name, which in turn has given its name to the Casamayoran land mammal age (Pascual, Ortega Hinojosa, Gondar & Tonni, 1965; Simpson, 1967a, p. 68). This, the type Casamayor, is poorly fossiliferous; the largest known collections come from the Great Barranca south of Lago Colhué-Huapí.

Fossil localities yielding Casamayoran mammals have been reviewed by Simpson (1948, 1967a). In addition to the Great Barranca and Cañadón Tournouër (near Punta Casamayor), other important localities include kilometer 170 (of railroad from Comodoro Rivadavia to Colonia Sarmiento), Cerro Blanco, Valle Hermoso, Cerro del Humo, Cañadón Vaca, Cañadón Hondo, vicinity of Cabeza Blanca, Pico Salamanca, and probably Pico Truncado (fig. 1). Pascual (1965a, unpublished) recorded new Casamayoran localities from Laguna de la Bombilla and vicinity of Paso de Los Indios, and near Paso del Sapo, all in Chubut Province; another has been reported from the Lumbrera Formation (Salta Group, Santa Bárbara Subgroup) north of Pampa Grande, Salta Province (fig. 2), between the small village of Carahuasi and the Río Bordo along National Route 9 (25° 48'S, 65° 27'W) (for exact locality see fig. 1 in Carbajal *et al.*, 1977), northwest Argentina (see Pascual, 1980a; Carbajal, Pascual, Pinedo, Salfity & Vucetich, 1977; Pinedo & Carbajal, 1975). The mammals recorded thus far from the red siltstones of the Lumbrera Formation, and collected from just below the *Faja Verde*, include two didelphoid marsupials, *Prepidolops* and *Bonapartherium* (Pascual, 1980b, c; Pascual & Bond, 1981), a new species of ?*Albertogaudrya*, *A. carahuasensis*, family Astrapotheriidae (a trigonostylopoid after Simpson or an astrapothere after, among others, Pascual & Vucetich — *in* Carbajal *et al.*, 1977), and

Table 4. Generic list of Casamayoran mammals from Patagonia

- **Order Marsupialia**
  - Family Didelphidae
    - *Coona*
    - *Eomicrobiotherium*
  - Family Caroloameghiniidae
    - *Caroloameghinia*
  - Family Borhyaenidae
    - *Angelocabrerus*
    - *Argyrolestes*
    - *Arminiheringia*
    - *Nemolestes*
    - *Patene*
  - Family Polydolopidae
    - *Amphidolops*
    - *Eudolops*
    - *Polydolops*
- **Order Edentata**
  - Family Dasypodidae
    - *Astegotherium*
    - *Coelutaetus*
    - *Machlydotherium*
    - *Meteutatus*
    - Peltephilinae *indet.*
    - *Prostegotherium*
    - *"Pseudostegotherium"*
    - *Utaetus*
- **Order Condylarthra**
  - Family Didolodontidae
    - *Argyrolambda*
    - *Asmithwoodwardia*
    - *Didolodus*
    - *Enneoconus*
    - *Ernestokokenia*
    - *Oxybunotherium*
    - *Paulogervaisia*
    - *Proectocion*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Anisolambda*
    - *Guilielmofloweria*
    - *Josepholeidya*
    - *Ricardolydekkeria*
  - Family Macraucheniidae
    - *Ernestohaeckelia*
    - *Victorlemoinea*
- **Order Notoungulata**
  - Family Henricosborniidae
    - *Henricosbornia*
    - *Othnielmarshia*
    - *Peripantostylops*
  - Family Notostylopidae
    - *Edvardotrouessartia*
    - *Homalostylops*
    - *Notostylops*
  - Family Oldfieldthomasiidae
    - *Maxschlosseria*
    - *Oldfieldthomasia*
    - *Paginula*
    - *Ultrapithecus*
  - Family Archaeopithecidae
    - *Acropithecus*
    - *Archaeopithecus*
  - Family Interatheriidae
    - *Antepithecus*
    - *Notopithecus*
    - *Transpithecus*
  - Family Archaeohyracidae
    - *Eohyrax*
  - Family Isotemnidae
    - *Acoelohyrax*
    - *Anisotemnus*
    - *Isotemnus*
    - *Pleurostylodon*
    - *Thomashuxleya*
    - *Coelostylodon*
  - Family Sparnotheriodontidae
    - *Sparnotheriodon*
- **Order Astrapotheria**
  - Family Astrapotheriidae
    - *Albertogaudrya*
    - *Scaglia*
- **Order Trigonostylopoidea**
  - Family Trigonostylopidae
    - *Trigonostylops*
- **Order Pyrotheria**
  - Family Pyrotheriidae
    - *Carolozittelia*
- **Mammalia *inc. sed.***
  - *Florentinoameghinia*

several families of the order Notoungulata — including, among others, Notostylopidae (*Boreastylops* VUCETICH, 1980) and Isotemnidae (Pascual, unpublished). A skull of a notoungulate was collected from the upper part of the Lumbrera Formation at a locality about 30 kilometers north of the village of Carahuasi, Salta Province (Pascual, unpublished). Remains of the notoungulate family Isotemnidae have also been collected (Pascual, unpublished) from just below the ***Faja Verde*** of the Lumbrera Formation south of the railroad station of Tres Cruces, Jujuy Province (fig. 2).

The deposits of Casamayoran Age appear to be the thickest, in most sections, and the most widespread of the Sarmiento Group; they extend as " a thick mantle of successive ash falls over all of central Patagonia and probably far beyond. Locally they are fluviatile, lacustrine, and other diverse facies. The deposits seem to have rested on an almost flat lowland " (Simpson, 1940, p. 660). According to Ameghino (1900-1902), the ***étage Notostylopéen*** represents a long period of time, and the then known fauna appeared to represent gradual change between its different levels. For this reason he recognized three distinct mammal-bearing ***horizons*** — " une partie basale... une partie inférieure... une partie supérieure ". Discussions of Casamayoran Age strata and faunas are given by Pascual (1965a, p. 63) and Simpson (1967a, p. 69).

The notoungulate genus *Notostylops* is the primary mammal guide fossil for the Casamayoran, although it is not necessarily found in all local faunas of that age. Additional mammalian guide fossils of Casamayoran Age include *Coona, Eomicrobiotherium, Caroloameghinia, Angelocabrerus, Argyrolestes, Arminiheringia, Eudolops, Astegotherium, Coelutaetus, Argyrolambda, Didolodus, Enneoconus, Oxybunotherium, Paulogervaisia, Proectocion, Ernestohaeckelia, Guilielmofloweria, Edvardotrouessartia, Maxschlosseria, Oldfieldthomasia, Paginula, Ultrapithecus, Acropithecus, Archaeopithecus, Antepithecus, Anisotemnus, Thomashuxleya, Sparnotheriodon, Scaglia, Albertogaudrya, Carolozittelia,* and *Florentinoameghinia* (table 4).

MUSTERSAN (TENTATIVELY ASSIGNED TO THE MIDDLE EOCENE)

The *Astraponotus* fauna was first found and later recognized on the bases of specimens collected in 1895-96 by Carlos Ameghino from the Great Barranca south of Lago Colhué-Huapí (Simpson, 1967a, p. 64). This then may be regarded as the type locality of the Mustersan land mammal age and a majority of Ameghino specimens are from here. Classic Mustersan localities (see Simpson, 1948, p. 27; 1967a, p. 68) include the Great Barranca, Cerro Blanco, and Cerro del Humo (fig. 1). Two new and very rich localities have been found by Pascual and fellow workers in the Gran Hondonada near Laguna del Mate (fig. 1), Chubut Province (Odreman Rivas, 1969; Andreis, 1972).

" The beds of Mustersan age are the most restricted in known extent and usually appear as local channel deposits, frequently incised " into rocks of Casamayoran Age (Simpson, 1940, p. 660). During Mustersan time forces causing "uplift and erosion were evidently increasingly active, because the Musters was not deposited or was entirely removed in many localities and the Deseado often rests directly on the Casamayor " (Simpson, 1940, p. 660).

Mammalian guide fossils for Mustersan Age faunas include *Plesiofelis, Procladosictis, Pseudeutatus, Xesmodon, Heteroglyphis, Polyacrodon, Polymorphis, Otronia, Tsamnichoria, Guilielmoscottia, Bryanpattersonia, Pseudhyrax, Distylophorus, Periphragnis, Rhyphodon, Eomorphippus, Eohegetotherium, Eopachyrucos, Pseudopachyrucos, Astraponotus, Heterolophodon, 'Stenogenium'*, and *Trilobodon* (table 5).

Table 5. Generic list of Mustersan mammals from Patagonia

- **Order Marsupialia**
  - Family Borhyaenidae
    - *Plesiofelis*
    - *Procladosictis*
  - Family Polydolopidae
    - *Polydolops*
- **Order Edentata**
  - Family Dasypodidae
    - *Machlydotherium*
    - *Meteutatus*
    - Peltephilinae *indet.*
    - *Pseudeutatus*
  - Family Glyptodontidae
    - *Glyptatelus*
  - Family Palaeopeltidae*
    - *Palaeopeltis*
  - Family ?Megalonychidae
    - ?*Proplatyarthrus*
- **Order Condylarthra**
  - Family ?Didolodontidae
    - *Xesmodon*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Heteroglyphis*
    - *Polyacrodon*
    - *Polymorphis*
- **Order Notoungulata**
  - Family Notostylopidae
    - *Otronia*
  - Family Oldfieldthomasiidae
    - *Tsamnichoria*
  - Family Interatheriidae
    - *Guilielmoscottia*
    - ?*Notopithecus*
  - Family Archaeohyracidae
    - *Bryanpattersonia*
    - ?*Eohyrax*
    - *Pseudhyrax*
  - Family Isotemnidae
    - ?*Acoelohyrax*
    - *Distylophorus*
    - *Periphragnis*
    - *Rhyphodon*
  - Family Notohippidae
    - *Eomorphippus*
    - *Interhippus*
- **Suborder Hegetotheria** ***inc. sedis***
  - *Eohegetotherium*
  - *Eopachyrucos*
  - *Pseudopachyrucos*
- **Order Astrapotheria**
  - Family Astrapotheriidae
    - *Astraponotus*
- **Order Trigonostylopoidea**
  - Family Trigonostylopidae
    - *Trigonostylops*
- **Order Pyrotheria**
  - Family Pyrotheriidae
    - *Propyrotherium*
- **Mammalia** ***inc. sedis***
  - *Heterolophodon*
  - *"Stenogenium"*
  - *Trilobodon*

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*This family was founded on a parataxon.

DIVISADERAN (TENTATIVELY ASSIGNED TO THE LATE EOCENE)

The Divisaderan land mammal age was proposed by Pascual, Ortega Hinojosa, Gondar & Tonni (1965) for the fauna from the Divisadero Largo Formation at Cerro Divisadero Largo, about 8 kilometers west of the city of Mendoza in westcentral Argentina (fig. 2). The fossils (table 6) come from units F-I of the lower and middle parts of the Divisadero Largo Formation which are composed of chocolate, buff fine-grained sandstone (Simpson, Minoprio & Patterson, 1962). Two localities, Divisadero Largo and Papagallos, are known.

The age of the Divisadero Largo fauna is disputed. On the basis of a detailed review of the fauna, Simpson, Minoprio & Patterson (1962, p. 290) concluded that its age is approximately early Deseadan or latest pre-Deseadan (*i.e.* late Eocene).

"As regards the latter possibility, it has long been realized from the evolutionary change in groups present in both Mustersan and Deseadan that a considerable time must have intervened. No mammalian faunas of intermediate age have been definitely identified, and at least one stage is here missing in the standard continental provincial sequence based on fossil mammals. The Divisadero Largo fauna may well belong in that gap, although if so, it probably belongs toward or at the end of the gap and does not fill the latter or divide it evenly. This cannot be made the basis for supplying a previously missing age between Mustersan and Deseadan. In the first place, it is not certain that the Divisadero Largo does indeed belong there, and in the second place the known fauna is so scanty and what is known is so peculiar that it could not become a proper and useful standard for correlation" (Simpson *et al.*, 1962, p. 290).

Largely based on the fact that rodents are unknown in the Divisadero Largo fauna, and that their ecological niche was occupied by a specialized group of native marsupials (Groeberiidae), Pascual, Ortego Hinojosa, Gondar & Tonni (1965, 1966) suggested that the fauna probably falls within the final part of the hiatus recognized between the Mustersan and Deseadan. They thus regarded this fauna as late Eocene in age and recognized it as a distinct land mammal age, the Divisaderan.

The older age of the Divisaderan with respect to that of the Deseadan is indirectly ratified by the regional correlation of the ***Rodados Lustrosos*** from southern Mendoza Province with the ***Conglomerado Violáceo*** which disconformably overlies (Regairaz, 1969, p. 253) the Divisadero Largo Formation (Rolleri & Criado Roque, 1969, p. 41). From a level above the ***Rodados Lustrosos*** has recently been found mammals of typical Deseadan character (Gorroño, Pascual & Pombo, 1979).

Pascual & Odreman Rivas (1971, p. 386) suggested that ***Estratos de Cosquín*** in the zone of Santa María-Cosquín, Córdoba Province (see Linares *et al.*, 1961) and the ***Horizonte Castillense*** of L. Kraglievich (1930c) at Curuzú-Cuatiá, Corrientes Province (see Martínez, 1958) may be of Divisaderan Age. From the former is reported ?*Eohyrax rusticus* AMEGHINO, 1901 (order Notoungulata, family Archaeohyracidae) and from the latter *Ameghinotherium curuzucuatiense* PODESTÁ, 1899 (order Notoungulata, family 'Trachytheriidae' — famille non reconnue dans le reste du texte, rattachée aux Mylodontidae; Hoffstetter, personal note) (see Pascual, 1970, p. 1017). Based on new collections of fossil mammals the latter local fauna is now regarded as Deseadan in age (Pascual, unpublished). Non-marine rocks corresponding in time to the Divisaderan have either not yet been found or are not recognized in Patagonia.

Table 6. List of fossil mammal species from the Divisadero Largo Formation

- **Order Marsupialia**
  - Family Groeberiidae
    - *Groeberia minoprioi* PATTERSON, 1952
    - *Groeberia pattersoni* SIMPSON, 1970
- **Order Litopterna**
  - Family Adianthidae
    - *Adiantoides leali* SIMPSON and MINOPRIO, 1949
  - Family Proterotheriidae ?
    - *Phoradiadius divortiensis* SIMPSON, MINOPRIO and PATTERSON, 1962
- **Order Notoungulata**
  - Family Oldfieldthomasiidae?
    - *Brachystephanus postremus* SIMPSON, MINOPRIO and PATTERSON, 1962
    - *Xenostephanus chiottii* SIMPSON, MINOPRIO and PATTERSON, 1962
    - *Allalmeia atalaensis* RUSCONI, 1946
  - Family Mesotheriidae
    - *Trachytherus*? *mendocensis* SIMPSON and MINOPRIO, 1949
  - Family Hegetotheriidae
    - *Ethegotherium carettei* (MINOPRIO, 1947)
- **Order and Family uncertain**
  - *Acamana ambiguus* SIMPSON, MINOPRIO and PATTERSON, 1962

DESEADAN [EARLY (AND MIDDLE?) OLIGOCENE]

During Carlos Ameghino's seventh expedition to Patagonia, 1893-1894, he collected a Deseadan fauna from a locality or area known as La Flecha in northeastern Santa Cruz Province, a little distance to the south of the mouth of the Río Deseado (fig. 1). The material collected during the expedition formed the basis of Florentino Ameghino's first paper on the Deseadan (*Pyrotherium*) fauna (Ameghino, 1895, p. 603-606; Wood & Patterson, 1959, p. 283n). Several years later the French collector André Tournouër (1903) made a collection of Deseadan fossils from this same locality (and elsewhere) and sent them to the Museum National d'Histoire Naturelle, Paris. Part of these collections were studied by Gaudry, who on the basis of the one from La Flecha, proposed (1906) the name ***Étage du Deseado*** to replace Ameghino's faunal name "couches à *Pyrotherium*". La Flecha then is the type locality of the Deseadan (Wood & Patterson, 1959, p. 283n; Patterson & Marshall, 1978). However, the first Deseadan mammal to the named, *Pyrotherium romeroi*, was by Ameghino (1888b) and was based on specimens from Neuquén Province, northwestern Patagonia. According to Uliana (cited in Pascual *et al.*, 1978) these specimens probably came from strata mapped as the Collón Curá Formation near the headwaters of the Río Neuquén, north of the Bajada del Agrio (fig. 2). The exact locality has not yet been relocated and mammal faunas of this age are unknown in Neuquén Province. This is even more unfortunate since *Pyrotherium*, the best known Deseadan guide fossil, was made the namesake of Ameghino's "couches à *Pyrotherium*" and hence of the Deseadan land mammal age.

Principal Deseadan fossil localities in Argentina are reviewed by Patterson & Marshall (1978). These include La Flecha[3], Cabeza Blanca (Loomis Locality), Pico Truncado, Great Barranca, Neuquén (Pascual, Bondesio, Scillato Yané, Vucetich & Gasparini, 1978), Rinconada de los López (Scarritt Pocket), Paso de los Indios (Laguna de la Bombilla and El Pajarito, see Scillato Yané, 1977c), Laguna Payahilé, probably Curuzú Cuatiá, and Ingeniero Jacobacci (figs. 1, 2). A new locality has recently been reported from the Agua de La Piedra Formation at Quebrada Fiera in the southwestern part of Mendoza Province (Gorroño, Pascual & Pombo, 1979) (fig. 2). For other possible, but at present dubious, localities for Deseadan mammals see Chaffee (1952, p. 554-555).

Mammalian guide fossils for Argentine Deseadan faunas include *Notogale, Pharsophorus, Proborhyaena, Pseudhalmarhiphus, Clypeotherium* (see Scillato Yané, 1977c), ?*Chubutherium, Octodontotherium, Orophodon, Platypittamys, Deseadomys, Xylechimys, Cephalomys, Litodontomys, Asteromys, Chubutomys, Protosteiromys, Protheosodon, Deuterotherium, Eoproterotherium, Proadiantus, Coniopternium* (= *Notodiaphorus*), *Pternoconius* (see Cifelli & Soria, 1983), *Pleurocoelodon, Trimerostephanus, Asmodeus, Ancylocoelus, Henricofilholia, Leontinia, Scarrittia, Morphippus, Nesohippus, Rhynchippus, Archaeophylus, Phanophilus, Plagiarthrus,* ?*Progaleophithecus, Trachytherus, Archaeohyrax, Prohegetotherium, Propachyrucos, Prosotherium*, and *Pyrotherium* (table 7).

COLHUEHUAPIAN (LATE OLIGOCENE)

"The first unequivocal, well marked tectonic phase in the meseta region [of central Chubut Province] with local folding and extensive faulting, is post-Deseadan[4]." There are no localities where this phase "can surely be dated with respect to Colhuehuapian time, but it is [clearly] pre-Patagonian [early Miocene — see below]. This tectonic phase appears to mark the beginning of the definitive uplift and structural formation of the southern Andes, which has continued rhythmically and periodically ever since with occasional climaxes in the later Tertiary" [see below] (Simpson, 1940, p. 660-661). The diastrophic phase apparently occupied the greater part of the middle Oligocene and, according to differences between the Deseadan and Colhuehuapian mammals, appears to have been of lesser duration than the hiatus recorded between the Mustersan and Deseadan (Pascual & Odreman Rivas, 1971, 1973).

Central Patagonia "was widely and deeply eroded after the more important tectonic movements and sank, relative to sea-level. Colhuehuapian deposits were formed locally in depressions on the sinking land and in places can be seen passing without

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[3] Chaffee (1952, p. 554-555, fig. 9) shows a locality which he calls La Flecha (his loc. 11) south and east of Pico Truncado, and north and west of Puerto Deseado. The true La Flecha locality is the same as his loc. 10 — 'Rio Deseado'. Chaffee's loc. 11 could represent the Cerro Alto locality of E. S. Riggs (unpublished field notes in Department of Geology, Field Museum of Natural History, Chicago), but this is not certain.

[4] It is important to note that in the Andean, as opposed to the Meseta Region, the most marked tectonic phase, with folding and extensive faulting occurred during the late Eocene. This was one of the most important orogenic phases during the Cenozoic, and has been recognized as the ***Incaic Phase*** all along the Andean Cordillera. Along most of the Patagonian part of the Cordillera, as well as that of the southern part of Mendoza Province, the so-called ***Serie Andesítica*** (which includes at least two different volcanic cycles) is associated with this diastrophic phase (see Gorroño, Pascual & Pombo, 1979).

Table 7. Generic list of Deseadan mammals from Argentina

- **Order Marsupialia**
  - Family Borhyaenidae
    - *Notogale*
    - *Pharsophorus*
    - *Proborhyaena*
  - Family Caenolestidae
    - *Palaeothentes*
    - *Parabderites*
    - *Pseudhalmarhiphus*
- **Order Edentata**
  - Family Dasypodidae
    - *Meteutatus*
    - *Stenotatus*
    - *Peltecoelus*
    - *Peltephilus*
  - Family Glyptodontidae
    - *Clypeotherium*
    - *Glyptatelus*
    - Palaeohoplophorinae gen. et sp. indet.
  - Family Palaeopeltidae*
    - *Palaeopeltis*
  - ?Family Mylodontidae (or Orophodontidae?)
    - ?*Chubutherium*
    - *Octodontotherium*
    - *Orophodon*
  - Family Megalonychidae
    - *"Hapalops"*
- **Order Rodentia**
  - Family Octodontidae
    - *Platypittamys*
  - Family Echimyidae
    - *Deseadomys*
    - *Xylechimys*
  - Family Chinchillidae
    - *Scotamys*
  - Family Dasyproctidae
    - *Cephalomys*
    - *Litodontomys*
  - Family Eocardiidae
    - *Asteromys*
    - *Chubutomys*
  - Family Erethizontidae
    - *Protosteiromys*
- **Order Condylarthra** or **Litopterna** idae
  - *Protheosodon*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Deuterotherium*
    - *Eoproterotherium*
  - Family Macraucheniidae**
    - *Coniopternium* (= *Notodiaphorus*)
    - *Pternoconius*
  - Family Adianthidae
    - *Proadiantus*
- **Order Notoungulata**
  - Family Isotemnidae
    - *Pleurocoelodon*
    - *Trimerostephanus*
  - Family Homalodontheriidae
    - *Asmodeus*
  - Family Leontiniidae
    - *Ancylocoelus*
    - *Henricofilholia*
    - *Leontinia*
    - *Scarrittia*
  - Family Notohippidae
    - *Argyrohippus*
    - *Interhippus*
    - *Morphippus*
    - *Nesohippus*
    - *Rhynchippus*
  - Family Toxodontidae
    - *Proadinotherium*
  - Family Interatheriidae
    - *Archaeophylus*
    - *Cochilius*
    - *Phanophilus*
    - *Plagiarthrus*
    - ?*Progaleopithecus*
  - Family Mesotheriidae
    - *Trachytherus*
  - Family Archaeohyracidae
    - *Archaeohyrax*
  - Family Hegetotheriidae
    - *Prohegetotherium*
    - *Propachyrucos*
    - *Prosotherium*
- **Order Astrapotheria**
  - Family Astrapotheriidae
    - *Parastrapotherium*
- **Order Pyrotheria**
  - Family Pyrotheriidae
    - *Pyrotherium*

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*This family was founded on a parataxon.

**See Cifelli & Soria 1983.

noteworthy unconformity into the overlying marine beds of the Patagonian group" (Simpson, 1940, p. 661). However, Simpson (1935c) earlier demonstrated the existence of an erosional unconformity or a parallel disconformity between Colhuehuapian beds (his level e, section 1) and 'Patagonian' beds in the barranca south of Gaiman along the Río Chubut (also see Marshall & Pascual, 1977, p. 97-98).

The mammals upon which the Colhuehuapian Age is recognized (table 8) were collected from strata along the lower course of the Río Chubut just south of Trelew

Table 8. Generic list of Colhuehuapian mammals from Patagonia

- **Order Marsupialia**
  - Family Didelphidae
    - *Pachybiotherium*
  - Family Microbiotheriidae
    - *Microbiotherium*
  - Family Borhyaenidae
    - *Acrocyon*
    - *Arctodictis*
    - *Borhyaena*
    - *Cladosictis*
    - *Pseudothylacynus*
    - *Sipalocyon*
  - Family Caenolestidae
    - *Abderites*
    - *Palaeothentes*
    - *Parabderites*
    - *Pichipilus*
    - *Pitheculites*
- **Order Primates**
  - Family Cebidae
    - *Dolichocebus*
    - *Tremacebus*
- **Order Edentata**
  - Family Dasypodidae
    - *Parapeltecoelus*
    - *Peltecoelus*
    - *Peltephilus*
    - *Proeutatus*
    - *Prozaedius*
    - *Pseudostegotherium*
    - *Stegotheriopsis*
    - *Stegotherium*
    - *Stenotatus*
  - Family Glyptodontidae
    - *Propalaehoplophorus*
  - Family Megalonychidae
    - *Hapaloides*
    - *Holomegalonyx*
    - *Proschismotherium*
- **Order Rodentia**
  - Family Octodontidae
    - *Acaremys*
  - Family Echimyidae
    - *Paradelphomys*
    - *Protacaremys*
    - *Protadelphomys*
    - *Prospaniomys*
  - Family Neoepiblemidae
    - *Perimys*
    - ?*Scotamys*
  - Family Dasyproctidae
    - *Gen. et sp. indet.*
  - Family Eocardiidae
    - *Luantus*
  - Family Erethizontidae
    - *Eosteiromys*
    - *Hypsosteiromys*
    - *Steiromys*
- **Order Litopterna***
  - Family Proterotheriidae
    - *Prolicaphrium*
    - *Prothoatherium*
  - Family Macraucheniidae
    - *Cramauchenia*
    - *Theosodon*
  - Family Adianthidae
    - *Proheptaconus*
- **Order Notoungulata**
  - Family Homalodotheriidae
    - ?*Homalodotherium*
  - Family Leontiniidae
    - *Colpodon*
  - Family Notohippidae
    - *Argyrohippus*
    - *Perhippidium*
    - *Stilhippus*
  - Family Toxodontidae
    - *Proadinotherium*
  - Family Interatheriidae
    - *Cochilius*
    - *Paracochilius*
    - *Protypotherium*
  - Family Hegetotheriidae
    - *Hegetotherium*
    - *Pachyrukhos*
- **Order Astrapotheria**
  - Family Astrapotheriidae
    - *Astrapothericulus*
    - *Astrapotherium*
    - *Parastrapotherium*

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*Taxonomy follows Soria (1981).

and at localities just north and south of Lago Colhué-Huapí, Chubut Province (fig. 1). The latter, the Great Barranca, is the principal known locality for mammals of this age (Ameghino, 1902, p. 71-140; 1900-1902, p. 25-39; 1906, fig. 54; Simpson, 1932c). A Colhuehuapian fauna is also known in Chubut Province from Sacanana (Rusconi, 1933; Hershkovitz, 1974) (fig. 1), and a few rich new localities have been found near the western end of Cañadón Grande, especially near the pueblo of La Curandera, and between La Herrería and El Pajarito (Scillato Yané, 1977c, p. 250).

The Colhuehuapian mammals (table 8), as reported and/or described by Ameghino (1902), Simpson (1935c, p. 9-12) and Bordas (1939), represent a stage of evolution earlier, but similar to those in post-'Patagonian' (or probably contemporaneous) beds (*i.e.* in the ***Astrapothericuléen, Notohippidéen*** and ***Santacruzéen*** of Ameghino, 1906; see Marshall & Pascual, 1977). The mammal faunas from the ***Trelewense*** (conventionally late Colhuehuapian) near Gaiman, Chubut Province, along the Río Chubut (fig. 1), and the *Notohippidense* (early Santacrucian) at Karaiken near Lago Argentino, Santa Cruz Province (fig. 3) have yet to be adequately compared; the possibility exists that they may prove to be contemporaneous (in part) or nearly so (Marshall & Pascual, 1977). For these reasons Pascual, Ortega Hinojosa, Gondar & Tonni (1965, p. 177) have questioned the validity for recognizing a Colhuehuapian Age distinct from that of the Santacrucian.

Mammalian guide fossils for Colhuehuapian faunas include *Pachybiotherium, Pseudothylacynus, Pitheculites, Dolichocebus, Tremacebus, Parapeltecoelus, Stegotheriopsis, Hapaloides, Proschismotherium, Holomegalonyx* (see Scillato Yané, 1977d), *Paradelphomys, Protacaremys, Protadelphomys, Prospaniomys, Eosteiromys, Hypsosteiromys, Prolicaphrium, Prothoatherium, Cramauchenia, Proheptaconus, Colpodon, Perhippidium, Stilhippus, Paracochilius*, and *Astrapothericulus.*

PATAGONIAN MARINE STAGE

The marine deposits comprising the ***Patagonian Stage*** (*sensu* Simpson, 1940) [which includes the ***Formation Patagonienne*** and the ***Étage superpatagonéen*** of the ***Formation Santacruzienne*** of Ameghino (1900-1902)], once believed to be latest Oligocene or earliest Miocene in age, are now thought to represent three or more distinct formations ranging in age from Eocene to early Miocene (W. Zinsmeister, personal communication). Three formations (or more?) have been characterized by Camacho (1974) and assigned ages mainly on the basis of their molluscan faunas — the Monte León Formation (late Oligocene), the "Estratos con *Monophoraster* y *Venericor*" [which includes two or more unnamed formations] (late Eocene), and the San Julián Formation [early (and middle?) Eocene] (Zinsmeister, 1981). Bertels (1970, p. 495; 1975) studied the planktonic foraminifera from the former two and assigned them to the following European marine stages — Monte León Formation (upper Rupelian and Chattian) and San Julián Formation (upper Priabonian and lower Rupelian), which respectively, represent middle to late Oligocene, and late Eocene to early Oligocene. No planktonic foraminifera have yet been collected from Camacho's "Estratos con *Monophoraster* y *Venericor*".

The Monte León Formation conformably underlies the Santa Cruz Formation along the Atlantic coast between Monte León and the mouth of the Río Gallegos (Camacho, 1974). To the north of this region, between Camarones and Trelew, especially in the lower valley of the Río Chubut, marine sediments occur with cetaceans and penguins similar to those of the Monte León Formation and with which they correlate in time (Camacho, 1974). The latter represent the marine beds which overlie the Colhué-Huapí Formation. The Colhué-Huapí strata underlie "the base of the Patagonian, but with no marked hiatus so that it is possible that the earliest Patagonian beds do in part overlap the latest Colhuehuapian in time, although this is not established as a fact" (Simpson, 1940, p. 663).

It must be emphasized that there is no continuous section in which the Colhué-Huapí, Monte León and Santa Cruz Formations occur together. The Colhué-Huapí beds occur below the Monte León marine equivalent in the lower course of the Río Chubut, while the Santa Cruz Formation overlies the Monte León Formation only along the coastal region of southern Santa Cruz Province (Marshall & Pascual, 1977). Furthermore, "the Colhuehuapian and Santacrucian mammals are recognizably different, but the average difference is so slight that they suggest closely successive stages of the same general fauna despite the [apparent] intercalation of the marine beds between them" (Simpson, 1940, p. 665).

SANTACRUCIAN (EARLY MIOCENE)

The Santa Cruz Formation is one of "the most widespread and most richly fossiliferous of all the non-marine Tertiary formations of Argentina, [and for that matter for all of South America]. It appears at scattered localities throughout southern Patagonia from near the northern end of the Gulf of San Jorge to northern Tierra del Fuego and from the Atlantic to the Andes [fig. 3]. The best exposures and richest fossil beds are in Santa Cruz [Province] along the coast from Monte León [the nominal type locality of the Santacrucian] to Puerto Gallegos and inland" along the valley of the Ríos Chico, Shehuén (= Chalía), Santa Cruz, Coyle, and Gallegos (Simpson, 1940, p. 664-665). Maps showing the distribution of the Santa Cruz beds are given by F. Ameghino (1906, fig. 57) and Feruglio (1938, fig. 6), and known fossil localities are reviewed by Marshall (1976, figs. 1-3). Localities yielding Santacrucian mammals in the region of the Golfo de San Jorge, are reviewed by Feruglio (1949, p. 182-183), although we strongly feel that these faunas are from the uppermost part of the ***Tobas de Sarmiento*** and are thus of Colhuehuapian Age.

The Santa Cruz Formation "was widely spread over an emergent lowland. It contains enormous quantities of volcanic ash,... much gravel and other detrital material derived from the rising Andes to the west" (Simpson, 1940, p. 665). The earlier Santa Cruz Formation is over 800 meters thick in the west and thins to about 200 meters along the Atlantic coast in the southern part of Santa Cruz Province (Russo & Flores, 1972, p. 723).

Charles Darwin was the first scientist to observe the terrestrial deposits of what is now recognized as the Santa Cruz Formation in the valley of the Río Santa Cruz (see Darwin, 1846). F. Ameghino (1889) first applied the name ***Formación Santacruceña*** to a sedimentary sequence consisting of two parts. The lower marine beds or ***Piso Subpatagónico*** was later considered equivalent to the ***superpatagoniense*** of the ***Formación Patagoniana*** but is now regarded as the Monte León Formation. The upper terrestrial beds or ***Piso Santacrucence*** has come to represent that is here called the Santa Cruz Formation (Russo & Flores, 1972, p. 723).

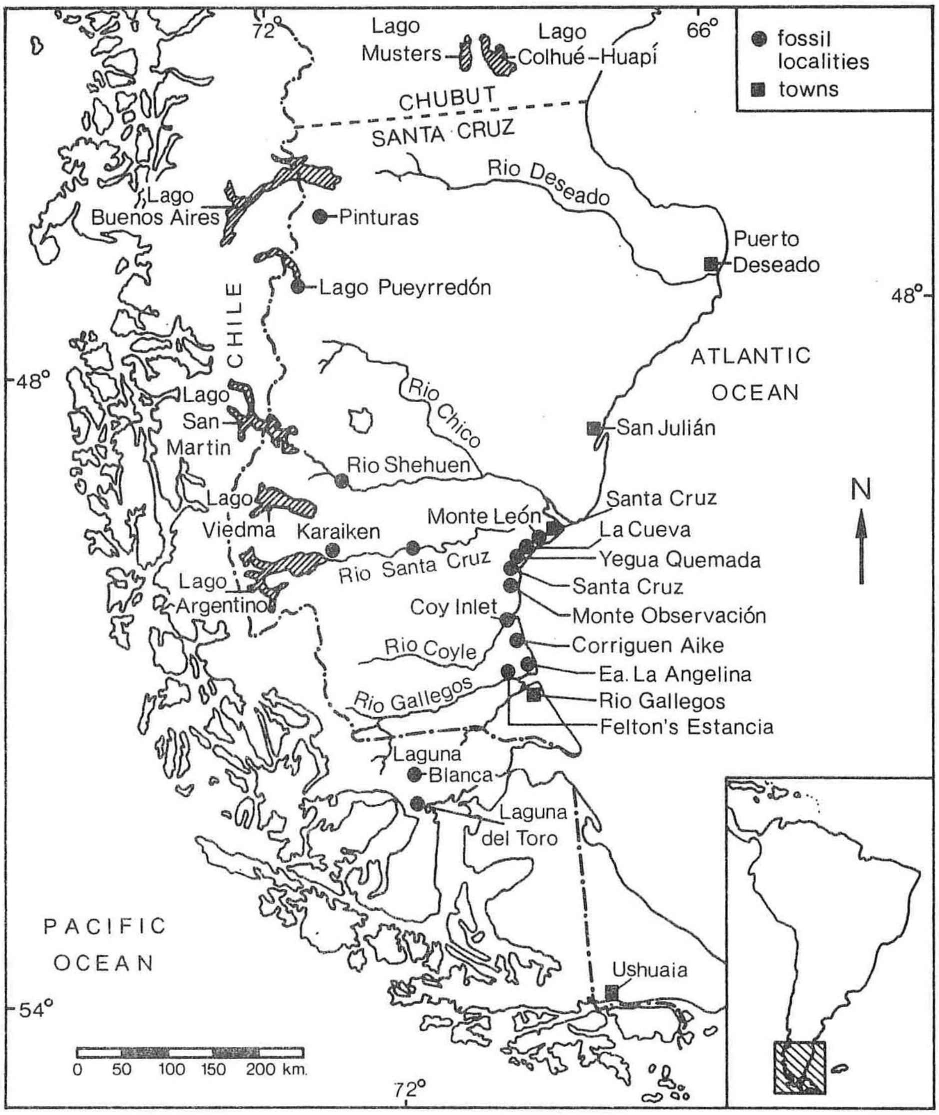

Fig. 3. — Map of southern South America showing principal mammal-bearing localities of early Miocene (Santacrucian) age.

Table 9. Generic list of Santacrucian mammals from Argentina

- **Order Marsupialia**
  - Family Microbiotheriidae
    - *Microbiotherium*
  - Family Borhyaenidae
    - *Acrocyon*
    - *Arctodictis*
    - *Borhyaena*
    - *Cladosictis*
    - *Lycopsis*
    - *Perathereutes*
    - *Prothylacynus*
    - *Sipalocyon*
  - Family Caenolestidae
    - *Abderites*
    - *Palaeothentes*
    - *Parabderites*
    - *Phonocdromus*
    - *Pichipilus*
    - *Stilotherium*
- **Marsupialia?**
  - Family Necrolestidae
    - *Necrolestes*
- **Order Primates**
  - Family Cebidae
    - *Homunculus*
- **Order Edentata**
  - Family Dasypodidae
    - *Anantiosodon*
    - *Paraeutatus*
    - *Peltecoelus*
    - *Peltephilus*
    - *Proeutatus*
    - *Prozaedius*
    - *Stegotherium*
    - *Stenotatus*
    - *Vetelia*
  - Family Glyptodontidae
    - *Asterostemma*
    - *Cochlops*
    - *Eucinepeltus*
    - *Metopotoxus*
    - *Propalaehoplophorus*
  - Family Megalonychidae
    - *Analcimorphus*
    - *Eucholoeops*
    - *Hapalops*
    - *Hyperleptus*
    - *Megalonychotherium*
    - *Pelecyodon*
    - *Pseudhapalops*
    - *Schismotherium*
    - *Xyophorus*
  - Family Megatheriidae
    - *Planops*
    - *Prepotherium*
  - Family Mylodontidae
    - *Analcitherium*
    - *Nematherium*
  - Family Entelopidae
    - *Entelops*
  - Family Myrmecophagidae
    - *Protamandua*
- **Order Rodentia**
  - Family Octodontidae
    - *Acaremys*
    - *Sciamys*
  - Family Echimyidae
    - *Adelphomys*
    - *Stichomys*
    - *Spaniomys*
  - Family Chinchillidae
    - *Pliolagostomus*
    - *Prolagostomus*
  - Family Neoepiblemidae
    - *Perimys*
    - *Scotaeumys*
  - Family Dasyproctidae
    - *Neoreomys*
    - *Olenopsis*
    - *Scleromys*
  - Family Eocardiidae
    - *Eocardia*
    - *Luantus*
    - *Phanomys*
    - *Schistomys*
  - Family Erethizontidae
    - *Steiromys*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Diadiaphorus*
    - *Licaphrium*
    - *Licaphrops*
    - *Proterotherium*
    - *Thoatherium*
  - Family Macraucheniidae
    - *Theosodon*
  - Family Adianthidae
    - *Adianthus*
- **Order Notoungulata**
  - Family Homalodotheriidae
    - *Homalodotherium*
  - Family Notohippidae
    - *Notohippus*
  - Family Toxodontidae
    - *Adinotherium*
    - *Hyperoxotodon*
    - *Nesodon*
  - Family Interatheriidae
    - *Epipatriarchus*
    - *Interatherium*
    - *Protypotherium*
  - Family Hegetotheriidae
    - *Hegetotherium*
    - *Pachyrukhos*
- **Order Astrapotheria**
  - Family Astrapotheriidae
    - *Astrapotherium*

"Local facies [of the Santa Cruz Formation] are sometimes distinguishable but no real faunal sequence has been demonstrated. The fauna evidently was remarkably uniform, although doubtless evolutionary advance will be more clearly demonstrable by the application of more refined field and laboratory methods. The only probable distinction yet made between Santa Cruz faunules, as noted by Scott (1932), is that certain beds at a high elevation in the foothills near Lake Pueyrredón yielded a fauna with several distinctive species, possibly later than the typical [coastal] Santa Cruz" (Simpson, 1940, p. 665). This distinction has led to the suggestion that Santa Cruz and Collón Curá faunas may, in part, overlap in time (see Bondesio, Rabassa, Pascual, Vucetich & Scillato Yané, 1978). Furthermore, the small and fragmentary faunas from Pinturas, on the eastern edge of the Meseta del Lago Buenos Aires [the ***couches à Astrapothericulus*** or ***étage Astrapothericuléen*** of F. Ameghino (1900-1902, p. 73-75; 1906, p. 226, fig. 54) (=***Pinturense*** of Castellanos, 1937)] and from Karaiken (fig. 3) on the eastern edge of Lago Argentino [the ***étage Notohippidéen*** of F. Ameghino (1900-1902, p. 179-180, 220-224; 1906, p. 228, fig. 57)] are now regarded as representing early Santacrucian local faunas (Wood & Patterson, 1959, p. 366-367; Marshall, 1976, p. 1140; Marshall & Pascual, 1977, p. 97). The ***Karaikense*** of L. Kraglievich (1930c, p. 160) was proposed to include the ***Notohippidense*** and ***Astrapothericulense*** of F. Ameghino.

Mammalian guide fossils for Argentine Santacrucian faunas include *Perathereutes, Prothylacynus, Phonocdromus, Stilotherium, Necrolestes, Homunculus, Paraeutatus, Asterostemma, Cochlops, Metopotoxus, Analcimorphus, Hyperleptus, Megalonychotherium, Pelecyodon, Schismotherium, Planops, Analcitherium, Nematherium, Entelops, Protamandua, Sciamys, Adelphomys, Spaniomys, Scotaeumys, Phanomys, Schistomys, Licaphrium, Proterotherium, Notohippus*, and *Interatherium* (table 9).

FRIASIAN (MIDDLE MIOCENE)

Only a few small local mammal faunas are known in the time interval between Santacrucian and Chasicoan. Included herein are the mammals discussed by Roth (1908, 1920, 1925), Ameghino (1904, 1906), Rovereto (1914), and L. Kraglievich (1930c) "obtained from scattered localities along and east of the Andine front in central Patagonia,... particularly on the rivers Frías, Fénix, Senguerr, Guenguel, Huemules, and Mayo, and near the lakes Blanca and Buenos Aires" (Simpson, 1940, p. 666; also see Bondesio *et al.*, 1980b) (fig. 2). "Virtually no stratigraphic data have been published, or [were there any] apparently preserved with the collections, and the little that is known includes the statement (Roth, 1920, 1925) that the fossils from the most important locality, Río Frías, were found at several different levels and are not all of the same age" (Simpson, 1940, p. 666; also see Hoffstetter, Fuenzalida & Cecioni, 1957, p. 133; Bondesio *et al.*, 1980b). The type Friasian fauna is from the Alto Río Frías (= Río Cisnes), Chile (Hoffstetter, Fuenzalida & Cecioni, 1957, p. 133; for location see Feruglio, 1950, fig. 266).

Three local faunas have been described from the Friasian — the Río Collón Curá, the Río Frías, and the Río Mayo. "Roth (1898, 1908, 1920), who found the beds and fauna, and Ameghino (1906) agreed that they were of Santacrucian Age. Later students, Groeber (1929), L. Kraglievich (1930c) believed them to be somewhat younger"

Table 10. Generic list of Friasian mammals from Argentina and Chile

Order Marsupialia
- Family Borhyaenidae
  - *Borhyaena*?
- Family Caenolestidae
  - *Abderites*?

Order Edentata
- Family Dasypodidae
  - *Epipeltephilus*
  - *Proeutatus*
  - *Prozaedyus*
  - *Stenotatus*
  - *Vetelia*
- Family Glyptodontidae
  - *Eucinepeltus*
  - ?*Palaehoplophorus*
  - *Propalaehoplophorus*
- Family Megalonychidae
  - *Eucholoeops*
  - *Diellipsodon*
  - *Hapalops*?
  - *Pseudhapalops*
- Family Megatheriidae
  - *Eomegatherium*
  - *Megathericulus*
  - *Promegatherium*
  - ?*Prepotherium*
- Family Mylodontidae
  - *Glossotheriopsis*
  - *Neonematherium*

Order Rodentia
- Family Octodontidae
  - *Massoiamys*
- Family Echimyidae
  - ?*Stichomys*
- Family Chinchillidae
  - *Prolagostomus*
- Family Dinomyidae
  - *Eusigmomys*
  - *Simplimus*
- Family Eocardiidae
  - *Eocardia*
  - *Megastus*
- Family Caviidae
  - ?*Cardiomys*
- Family Dasyproctidae
  - *Alloiomys*
  - *Neoreomys*
- Family Erethizontidae
  - *Disteiromys*

Order Litopterna
- Family Proterotheriidae
  - *Diadiaphorus*
- Family Macraucheniidae
  - *Phoenixauchenia*
  - *Theosodon*

Order Notoungulata
- Family Homalodotheriidae
  - *Homalodotherium*
- Family Toxodontidae
  - *Adinotherium*
  - ?*Hyperoxotodon*
  - *Nesodon*
  - *Nesodonopsis*
  - *Palyeidodon*
  - *Prototrigodon*
  - *Stereotoxodon*
- Family Interatheriidae
  - *Caenophilus*
  - *Epipatriarchus*
  - *Interatherium*
  - *Protypotherium*
- Family Mesotheriidae
  - *Eutypotherium*
  - *Typothericulus*
- Family Hegetotheriidae
  - *Hegetotherium*
  - *Pachyrukhos*

Order Astrapotheria
- Family Astrapotheriidae
  - *Astrapotherium*

(Simpson, 1940, p. 666). A separate name was assigned to each (*e.g.* Colloncurense, Friasense and Mayoense), although this arrangement has not been followed by subsequent workers (*e.g.* Simpson, 1940; Pascual & Odreman Rivas, 1973). These local faunas are currently regarded as Friasian in age with the Collón Curá local fauna representing the earlier part of that age, and the Río Mayo local fauna the later (Pascual & Odreman Rivas, 1973; Bondesio *et al.*, 1980b). It is unfortunate that the Friasian is so poorly defined, because the best known northern fauna, the La Venta of Colombia (fig. 6), appears to correlate with some part of it (Stirton, 1953; Patterson & Pascual, 1972; Hoffstetter & Rage, 1977).

It now appears probable that the Colhuehuapian (including *Trelewense*), Santacrucian (including *Karaikense, Pinturense, Notohippidense*, and *Astrapothericulense*) and Friasan (including *Colloncurense* and *Mayoense*) are based upon a successive and relatively continuous evolutionary sequence without such hiatuses as those recognized between the early Tertiary land mammal ages (Marshall & Pascual, 1977; Pascual & Odreman Rivas, 1973).

Mammalian guide fossils for Friasian faunas in Argentina and Chile include *Glossotheriopsis, Epipeltephilus, Megathericulus, Diellipsodon, Neonematherium, Eusigmomys, Simplimus, Massoiamys, Alloiomys, Megastus, Disteiromys, Phoenixauchenia, Palyeidodon, Nesodonopsis, Prototrigodon, Stereotoxodon, Caenophilus, Eutypotherium*, and *Typothericulus* (table 10).

CHASICOAN (LATE MIOCENE)

A Chasicoan Age was first recognized by L. Kraglievich (1930c) [his *Chasicoense* (*sic*)] and was based on the fauna from the Arroyo Chasicó Formation, Department of Villarino, southwest corner of Buenos Aires Province (fig. 2) (Pascual, 1965b, p. 104, fig. 1). These sediments are composed primarily of yellowish silty clays, fine sands, and calcareous concretions (*i.e.*, *tosca*; Pascual, 1965b, p. 102-104) which represent the oldest sediments known as *loess y limos* in the pampean region. Studies of the geology and fauna have been made by Pascual (1961, 1965b, 1967), Pascual *et al.* (1966, p. 13-14), Cabrera & L. Kraglievich (1931), L. Kraglievich (1934), Fidalgo, Laza, Porro & Tonni (1979), Bondesio, Laza, Scillato Yané, Tonni & Vucetich (1980a), and Scillato Yané (1977a, b, d, 1978).

Fidalgo *et al.* (1979) and Bondesio *et al.* (1980a) recognize two members of the Arroyo Chasicó Formation. Most of the fossil vertebrates considered as typical Chasicoan taxa have been collected from the lower Vivero Member. Nevertheless, various taxa cited as characteristic of the Chasicoan almost certainly have come from the upper Las Barrancas Member. These workers have demonstrated that the Las Barrancas Member does not include *pan-santacrucian* taxa, and may very probably be referable to the Huayquerian land mammal age (see below).

The following list of mammal guide fossils for each member of the Arroyo Chasicó Formation was compiled by Dr. Tonni (personal communication): Vivero Member — *Pseudolycopsis cabrerai, Plesiomegatherium halmyronomum, Octomylodon robertoscagliai, Chasicomys octodontiformis, Chasichimys bonaerensis, Cullinia levis, Chasicotherium rothi, Paratrigodon eugui, Protypotherium distinctum*, and *Protypothe-*

Table 11. Generic list of Chasicoan mammals from Argentina

- **Order Marsupialia**
  - Family Borhyaenidae
    - *Chasicostylus*
    - *Pseudolycopsis*
  - Family Caenolestidae
    - *Pliolestes*
- **Order Edentata**
  - Family Dasypodidae
    - *Chasicotatus*
    - *Kraglievichia*
    - Peltephilinae *indet.*
    - *Proeuphractus*
    - *Vetelia*
  - Family Glyptodontidae
    - Palaehoplophorini
    - ?*Palaehoplophorus*
    - Plohophorini *indet.*
    - Sclerocalyptini *indet.*
  - Family Megatheriidae
    - *Plesiomegatherium*
  - Family Megalonychidae
    - *Protomegalonyx*
    - *Xyophorus*
  - Family Mylodontidae
    - *Octomylodon*
- **Order Rodentia**
  - Family Octodontidae
    - *Chasicomys*
  - Family Echimyidae
    - *Cercomys*
    - *Chasichimys*
    - *Pattersomys*
  - Family Chinchillidae
    - *Lagostomopsis*
  - Family Dinomyidae
    - *Carlesia*
    - *Diaphoromys*
    - *Gyriabrus*
    - *Potamarchus*
    - *Tetrastylus*
  - Family Caviidae
    - *Allocavia*
    - *Cardiomys*
    - *Orthomyctera*
    - *Procardiomys*
  - Family Hydrochoeridae
    - ?*Cardiatherium*
    - *Procardiatherium*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Gen. et sp. indet.*
  - Family Macraucheniidae
    - *Cullinia*
    - *Theosodon*
- **Order Notoungulata**
  - Family Homalodotheriidae
    - *Chasicotherium*
  - Family Toxodontidae
    - *Hemixotodon*
    - *Ocnerotherium*
    - *Paratrigodon*
    - *Pisanodon*
  - Family Interatheriidae
    - *Protypotherium*
  - Family Mesotheriidae
    - *Typotheriopsis*
  - Family Hegetotheriidae
    - *Hemihegetotherium*
    - *Paedotherium*
    - *Pseudohegetotherium*

rium minutum; Las Barrancas Member — *Chasicotatus ameghinoi, Pisanodon nazari, Procardiatherium* sp., and *Pseudohegetotherium torresi* (table 11).

It is very probable that other genera (*e.g. Pattersomys, Allocavia, Hemixotodon, Ocnerotherium*) will eventually prove to be guide fossils for the Vivero Member, although the types of these taxas were collected without stratigraphic record of occurrence. Referable mammal-bearing beds of Chasicoan Age in Argentina include the

Arroyo Chasicó Formation, Los Llanos Formation (*partim*), Buenos Aires Province; Chiquimil Formation (*partim*) at Puerta de Corral Quemado and in the Valle del Santa María, Catamarca Province; Agua de los Berros Formation (*partim*), Huachipampa Formation (*partim*), San Juan Province (Pascual, 1965b, p. 105-106; Pascual *et al.*, 1966, p. 14); and Las Mulitas Formation, San Luis Province (Pascual, 1954; Flores, 1979).

HUAYQUERIAN (LATE MIOCENE)

Simpson (1940), using L. Kraglievich's (1934) term *Huayqueriaense*, proposed Huayquerian as a time and time-rock (age and stage) designation, deriving the name from the Huayquerías region in the Department of San Carlos, Mendoza Province (fig. 2). Fossil vertebrates were first collected from this region by de Carles (1911) and later studied by Rovereto (1914). The name Huayquerian was applied to beds and faunas formerly included within the *Araucanense* of Doering (1882). "Doering (1882) only applied the name *Araucano* [to strata in the Famatina region, La Rioja Province, western Argentina] on the primary basis of Tertiary beds in southern Argentina, primarily in Río Negro, Patagonia, but with extension to rocks of supposedly similar age elsewhere in Argentina. In times when lithostratigraphic, chronostratigraphic, and geochronologic classifications were not distinguished, Doering's *Araucano* was applied also to rocks and faunas including those in Catamarca [see Marshall & Patterson, 1981], believed to be synchronous" (Simpson, 1974, p. 4). However, Doering's original *Araucano* is derived from the name of an Indian tribe from southern Argentina and Chile (*i.e.*, *araucanos* or *mapuches* from the Arauco region of Chile) and is thus not acceptable as a time or rock unit name in current geological nomenclature (Simpson, 1974, p. 4). Huayquerian (= Araucanian) faunas were reviewed by Rovereto (1914).

The geology in the region studied by de Carles (1911) has been investigated by Groeber (1929) and by Frenguelli (1930b), and mapped by Groeber (1939). An erosional unconformity has been reported by Dessanti (1946) between this, and the overlying Tunuyán Formation, regarded as Montehermosan in age (Pascual & Odreman Rivas, 1973, p. 312).

Mammalian guide fossils for Huayquerian Age faunas in Argentina include *Borhyaenidium, Elassotherium, Paleuphractus, Hoplophractus, Aspidocalyptus, Coscinocercus, Neosteiromys, Epecuenia*, and *Macrauchenidia* (table 12).

Referable mammal-bearing beds in Argentina (fig. 2) include the Huayquerías Formation, Mendoza Province; Río Jachal and Mogna Formations, San Juan Province (Pascual *et al.*, 1966, p. 16); Epecuén Formation from Lago Epecuén and vicinity and the Arroyo Guaminí, Buenos Aires Province; cliffs of Salinas Grandes de Hidalgo, La Pampa Province (see Pascual & Bocchino, 1963, p. 100; Zetti, 1967, 1972); *Araucanense* (*sensu stricto* = Andalhualá Formation in the Valle del Río Santa María), Catamarca Province (Riggs & Patterson, 1939; Marshall & Patterson, 1981); India Muerta Formation, Tucumán Province (Bossi, 1969, p. 50); *Mesopotamiense* (*partim*) north of Paraná, Entre Ríos Province (Reig, 1957, p. 224; Bianchini & Bianchini, 1971, p. 3; Pascual & Odreman Rivas, 1973); El Palo Formation on border of Río Negro and

Table 12. Generic list of Huayquerian mammals from Argentina

- **Order Marsupialia**
  - Family Didelphidae
    - *Hyperdidelphis*
    - *Lutreolina*
    - *Thylatheridium*
  - Family Sparassocynidae
    - *Gen. et sp. indet.*
  - Family Borhyaenidae
    - *Borhyaenidium*
    - *Notictis*
    - *Stylocynus*
  - Family Thylacosmilidae
    - ?*Achlysictis*
    - *Thylacosmilus*
  - Family Argyrolagidae
    - *Microtragulus*
- **Order Edentata**
  - Family Dasypodidae
    - *Chorobates*
    - *Doellotatus*
    - *Kraglievichia*
    - *Paleuphractus*
    - *Paraeuphractus*
    - *Vassallia*
  - Family Glyptodontidae
    - *Aspidocalyptus*
    - *Coscinocercus*
    - *Cranithlastus*
    - ?*Eleutherocercus*
    - *Eoscleroclyptus*
    - *Eosclerocalyptus*
    - *Glyptodontidium*
    - *Hoplophractus*
    - *Peiranoa*
    - *Phlyctaenopyga*
    - *Stromaphorus*
    - ?*Urotherium*
  - Family Megalonychidae
    - *Pronothrotherium*
  - Family Megatheriidae
    - *Plesiomegatherium*
    - *Pyramiodontherium*
  - Family Mylodontidae
    - *Elassotherium*
    - *Sphenotherus*
  - Family Myrmecophagidae
    - *Neotamandua*
    - *Palaeomyrmidon*
- **Order Rodentia**
  - Family Octodontidae
    - ?*Neophanomys*
    - *Phtoramys*
    - *Pseudoplateomys*
  - Family Abrocomidae
    - *Protabrocoma*
  - Family Echimyidae
    - *Carterodon*
    - *Proechimys*
    - *Trichomys*
  - Family Chinchillidae
    - *Lagostomopsis*
  - Family Dinomyidae
    - *Diaphoromys*
    - ?*Potamarchus*
    - *Telicomys*
    - *Tetrastylopsis*
    - *Tetrastylus*
  - Family Caviidae
    - *Cardiomys*
    - ?*Caviodon*
    - *Orthomyctera*
    - *Palaeocavia*
  - Family Hydrochoeridae
    - ?*Cardiatherium*
    - *Kiyutherium*
    - ?*Procardiatherium*
  - Family Erethizontidae
    - *Neosteiromys*
- **Order Carnivora**
  - Family Procyonidae
    - *Cyonasua*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Brachytherium*
    - ?*Diadiaphorous*
    - *Eoauchenia*
    - *Epecuenia*
  - Family Macraucheniidae
    - *Macrauchenidia*
    - *Promacrauchenia*
- **Order Notoungulata**
  - Family Toxodontidae
    - *Pisanodon*
    - *Xotodon*
  - Family Mesotheriidae
    - *Pseudotypotherium*
    - ?*Typotheriopsis*
  - Family Hegetotheriidae
    - *Hemihegetotherium*
    - *Paedotherium*
    - *Raulringueletia*
    - *Tremacyllus*

Neuquén Provinces, northwestern Patagonia (Uliana, 1978, p. 72; Pascual *et al.*, 1978, p. 183); ***Rionegrense (partim)***, Río Negro Province (Scillato Yané, Uliana & Pascual, 1976; Pascual, Pisano & Ortega, 1965); the ***Cantera Santa Isabel***, San Luis Province (*sensu* Pascual & Bondesio, 1981, based on reinterpretation of Bordas, 1934); ***Brocherense (= Claveroense)***, Córdoba Province (Castellanos, 1942, 1944); and Piquete Formation (Jujuy Subgroup), Jujuy Province (Arias, Alonso & Malanca, 1978).

MONTEHERMOSAN (EARLY AND MIDDLE PLIOCENE)

The Monte Hermoso Formation[5], type of the Montehermosan land mammal age, is exposed along cliffs of the Atlantic coast of Buenos Aires Province, between Monte Hermoso and Punta Alta (fig. 2). This classic locality was visited by Charles Darwin during his voyage on the H.M.S. Beagle. The fauna was described and/or discussed by Ameghino (1887a, b, c, 1888a, 1889, 1904, 1907, 1908, 1910, among others), Rovereto (1914), and L. Kraglievich (1934). Many more specific papers on the fauna have been published by later authors, among which include Bordas (1935b), Parodi & Kraglievich (1948), Pascual & Bondesio (1961), Patterson & J. L. Kraglievich (1960), Reig (1950, 1978), Reig & Simpson (1972), and Tonni (1974). The geology has been described by Bravard (1857), Willis (1912), Kantor (1922), Vignati (1925), Frenguelli (1928), J.L. Kraglievich (1946), Leanza (1949), Bonaparte (1960), and Fidalgo, de Francesco & Pascual (1975).

At Monte Hermoso, Bonaparte (1960) recognized five different lithostratigraphic units, separated by erosional unconformities, and retained the name ***Piso Hermosense*** or ***Hermosense típico*** only for the lower one which was composed of six silty beds (***bancos***). ***Miembro de Limolitas Claras*** of Bonaparte was called ***Chapadmalense*** by Vignati (1925). Bonaparte's ***Miembro de Limolitas Estratificadas*** and ***Miembro de Limolitas Claras*** could be, as has been postulated by many authors, intermediate in time between the typical Montehermosan and Chapadmalalan Ages. Some mammals coming from those levels (*e.g. Chapalmatherium, Actenomys, Isomyopotamus*) favor such a correlation (see Parodi & Kraglievich, 1948; Reig, 1950).

L. Kraglievich (1934) tentatively recognized a ***Horizonte Irenense***, based on a fauna from the banks of the Río Quequén Salado, between the Atlantic coast and the pueblo of Irene, Buenos Aires Province (fig. 2). Reig (1955) distinguished this unit as the Irene Formation. Simpson (1940, p. 670), Pascual *et al.* (1966), and Pascual & Herrera (1973, p. 38), as most Argentine vertebrate paleontologists, have regarded the Irene Formation as of Montehermosan Age, and probably intermediate in time between the ***Hermosense típico*** and the Chapadmalalan (*s.s.*) (see Fidalgo *et al.*, 1975, p. 125-126).

Mammalian guide fossils for Montehermosan Age faunas include *Notocynus, Parahyaenodon, Nopachtus, Neocavia, Anchimysops, Neoanchimys, Xenodontomys, Diplasiotherium, Alitoxodon,* and *Trigodon* (table 13).

Referable mammal-bearing strata in Argentina (fig. 2) include the Monte Hermoso Formation, ***Irenense*** (L. Kraglievich, 1934) or Irene Formation (Reig, 1955), probably Saldungaray and La Toma formations, Buenos Aires Province (Furque, 1967); Corral Quemado Formation, Catamarca Province (Riggs & Patterson, 1939; Marshall & Pat-

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[5] A Monte Hermoso Formation has not yet been defined in accordance with the present Code of Stratigraphic Nomenclature. Nevertheless, most current Argentine geologists and paleontologists recognize it as a valid lithostratigraphic unit. For sake of convenience we also do so here. As the type locality is Monte Hermoso (*nec* Hermoso), the name of the derived age should be Montehermosan, in Spanish ***Edad Montehermosense*** (Pascual *et al.*, 1965) ***nec Edad Montehermosiana*** as was used by J. L. Kraglievich (see 1952, plate between p. 30-31; J. L. Kraglievich & Olazábal, 1959, plate on p. 45). Because of these reasons J. L. Kraglievich used ***Formación Monte Hermoso*** instead of the prior though complex name ***Hermósico*** (Ameghino, 1889), ***Hermoséen*** (Ameghino, 1906), or ***Hermosense*** (L. Kraglievich, 1930c).

Table 13. Generic list of Montehermosan mammals from Argentina

- **Order Marsupialia**
  - Family Didelphidae
    - *Chironectes*
    - *Hyperdidelphis*
    - *Lutreolina*
    - *Marmosa*
    - *Philander*
    - *Thylatheridium*
    - *Zygolestes*
  - Family Sparassocynidae
    - *Sparassocynus*
  - Family Borhyaenidae
    - *Borhyaenidium*
    - *Notocynus*
    - *Parahyaenodon*
  - Family Thylacosmilidae
    - *Achlysictis*
    - *Thylacosmilus*
  - Family Argyrolagidae
    - *Argyrolagus*
    - *Microtragulus*
- **Order Edentata**
  - Family Dasypodidae
    - ?*Chaetophractus*
    - *Chorobates*
    - *Doellotatus*
    - *Kraglievichia*
    - *Macroeuphractus*
    - *Plaina*
    - *Ringueletia*
    - ?*Tolypeutes*
  - Family Glyptodontidae
    - *Eleutherocercus*
    - *Nopachtus*
    - *Palaeodaedicurus*
    - *Plohophorus*
    - ?*Trachycalyptus*
    - *Urotherium*
  - Family Megalonychidae
    - *Pronothrotherium*
  - Family Megatheriidae
    - ?*Plesiomegatherium*
  - Family Mylodontidae
    - *Proscelidodon*
  - Family Myrmecophagidae
    - *Myrmecophaga*
- **Order Rodentia**
  - Family Cricetidae
    - *Auliscomys*
    - *Bolomys*
  - Family Octodontidae
    - *Actenomys*
    - *Eucoelophorus*
    - *Phtoramys*
    - *Pithanotomys*
    - *Pseudoplataeomys*
    - *Xenodontomys*
  - Family Abrocomidae
    - *Protabrocoma*
  - Family Echimyidae
    - *Eumysops*
    - *Trichomys*
  - Family Myocastoridae
    - *Isomyopotamus*
  - Family Dinomyidae
    - *Telicomys*
  - Family Chinchillidae
    - *Lagostomopsis*
  - Family Caviidae
    - *Cardiomys*
    - ?*Caviodon*
    - *Neocavia*
    - *Orthomyctera*
    - *Palaeocavia*
  - Family Hydrochoeridae
    - *Anchimysops*
    - *Chapalmatherium*
    - *Neoanchimys*
    - *Protohydrochoerus*
- **Order Carnivora**
  - Family Procyonidae
    - *Chapalmalania*
    - *Cyonasua*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Brachytherium*
    - *Diplasiotherium*
    - *Eoauchenia*
  - Family Macraucheniidae
    - *Promacrauchenia*
- **Order Notoungulata**
  - Family Toxodontidae
    - *Alitoxodon*
    - ?*Palaeotoxodon*
    - *Trigodon*
    - *Xotodon*
  - Family Mesotheriidae
    - *Pseudotypotherium*
  - Family Hegetotheriidae
    - *Paedotherium*
    - *Tremacyllus*

terson, 1981); Tunuyán Formation, Mendoza Province (de Carles, 1911; Dessanti, 1946[6]; J.L. Kraglievich & Olazábal, 1959; Rovereto, 1914, p. 214-224; L. Kraglievich, 1934, p. 117); ***Rionegrense*** *(partim)* or Río Negro Formation from its type locality (Pascual, Pisano & Ortega, 1965, p. 21-25; Andreis, 1965) and ***Mesopotamiense*** *(partim)* along the east bank of lower Río Paraná near the city of Paraná, Entre Ríos Province (Bianchini & Bianchini, 1971, p. 3; Pascual & Odreman Rivas, 1971, p. 404; Bondesio, 1975; Scillato Yané, 1975).

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[6] According to Dessanti (1946) there exists an erosional disconformity between the Tunuyán Formation and the underlying Las Huayquerías Formation in Mendoza Province. This hiatus may be temporarily equivalent to that reported by Stahlecker *in* Riggs Patterson (1939) between the ***Araucanense*** and Corral Quemado beds in Catamarca Province.

CHAPADMALALAN (LATE PLIOCENE)

The "*Chapalmalense*" was first recognized by F. Ameghino (1908, p. 367). Good exposures of the Chapadmalal Formation, type of the Chapadmalalan land mammal age, occur along the Atlantic coast between Mar del Plata and Miramar, Buenos Aires Province (fig. 2). The fauna (table 14) was discussed and described by L. Kraglievich (1934), Reig (1958a, b), Simpson (1972), Rovereto (1914), Risso Domínguez (1949), and Pascual *et al.* (1966); the geology is described by Frenguelli (1928), and J. L. Kraglievich (1952). The latter distinguished 15 beds (bancos) or levels (niveles), numbered from oldest to youngest I-XV.

For many years it was customary to recognize a Chapadmalalan Age district from that of the Montehermosan, the latter being defined largely on the fauna from Monte Hermoso. Strata with diagnostic Montehermosan and Chapadmalalan "mammals are not well known in a continuous section, but the faunas demonstrate beyond any doubt that the Monte Hermoso beds are older than those of Chapadmalal" (Simpson, 1940, p. 670). Recently, Pascual *et al.* (1966), and Pascual & Odreman Rivas (1971, 1973) restudied the faunas of the Chapadmalal and Monte Hermoso formations. They found them to differ less than had usually been believed (*e.g.* L. Kraglievich, 1934) and proposed that the Chapadmalal fauna and formation be included within the Montehermosan Age. Simpson (1972, p. 4) recommended retention of the designation Chapadmalalan, "not in confirmed opposition to Pascual... [and his fellow workers]... but simply because no one has yet re-analyzed and replaced the meticulous but outdated work of L. Kraglievich (1934) on which the supposed distinction mainly rests".

We tentatively recognize a distinct Chapadmalalan Age, as to do so permits a more precise understanding of late Tertiary faunal changes. This age is here distinguished by the first known record in South America of new mammalian families[7] of North America origin (Mustelidae, Tayassuidae: see below). It is further defined by the autochthonous guide fossils *Thylophorops, Scelidotheridium, Glossotheridium, Plohophoroides, Paraglyptodon*, and *Dolicavia* (table 14).

Referable mammal-bearing strata in Argentina (fig. 2) include the Chapadmalal Formation (Pascual *et al.*, 1966, p. 19) and possibly Bonaparte's (1960) *Miembro de Limolitas Claras* at Monte Hermoso.

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[7] Note that the cited genera belong to North American families, but the genera are properly South American. It is also important to note that Rusconi (1933) attributed the name *Palaeolama weddeli parodii* to an astragalus of a camelid from the *Chapadmalense* (*sic*) and recorded this same subspecies from the *Puelchense de Villa Bellaster.*

Table 14. Generic list of Chapadmalalan mammals from Argentina

- **Order Marsupialia**
  - Family Didelphidae
    - *Hyperdidelphis*
    - *Lutreolina*
    - *Marmosa*
    - *Thylatheridium*
    - *Thylophorops*
  - Family Sparassocynidae
    - *Sparassocynus*
  - Family Thylacosmilidae
    - *Hyaenodonops*
    - *Notosmilus*
  - Family Argyrolagidae
    - *Argyrolagus*
    - *Microtragulus*
- **Order Edentata**
  - Family Dasypodidae
    - *Chaetophractus*
    - *Chorobates*
    - *Doellotatus*
    - *Kraglievichia*
    - *Macroeuphractus*
    - *Plaina*
    - ?*Propraopus*
    - *Ringueletia*
    - ?*Tolypeutes*
    - *Zaedyus*
  - Family Glyptodontidae
    - *Palaeodaedicurus*?
    - *Paraglyptodon*
    - *Plohophoroides*
    - *Trachycalyptus*
    - *Urotherium*
  - Family Megalonychidae
    - *Diheterocnus*
  - Family Mylodontidae
    - *Glossotheridium*
    - *Scelidotheridium*
- **Order Rodentia**
  - Family Cricetidae
    - *Akodon*
    - *Dankomys*
    - *Graomys*
    - *Reithrodon*
  - Family Octodontidae
    - *Actenomys*
    - *Eucoelophorus*
    - ?*Megactenomys*
    - *Pithanotomys*
    - *Pseudoplataeomys*
  - Family Abrocomidae
    - *Protabrocoma*
  - Family Echimyidae
    - *Eumysops*
    - *Trichomys*
  - Family Myocastoridae
    - *Isomyopotamus*
  - Family Chinchillidae
    - *Lagostomopsis*
  - Family Dinomyidae
    - *Telicomys*
  - Family Caviidae
    - *Cardiomys*
    - *Caviodon*
    - *Caviops*
    - *Dolicavia*
    - *Orthomyctera*
    - *Palaeocavia*
    - ?*Pascualia*
    - ?*Propediolagus*
  - Family Hydrochoeridae
    - *Chapalmatherium*
    - *Protohydrochoerus*
- **Order Carnivora**
  - Family Procyonidae
    - *Chapalmalania*
    - *Cyonasua*
  - Family Mustelidae
    - *Conepatus*
- **Order Litopterna**
  - Family Proterotheriidae
    - *Brachytherium*
  - Family Macraucheniidae
    - *Promacrauchenia*
- **Order Notoungulata**
  - Family Toxodontidae
    - *Toxodon*
    - *Xotodon*
  - Family Mesotheriidae
    - *Pseudotypotherium*
  - Family Hegetotheriidae
    - *Paedotherium*
    - *Tremacyllus*
- **Order Artiodactyla**
  - Family Tayassuidae
    - *Argyrohyus*

BOLIVIA

A brief review of Bolivian Cenozoic vertebrate faunas and localities is given by Ortega (1970). Since the publication of that paper a large number of new localities and faunas have been discovered, and some described by R. Hoffstetter, C. Martinez, J. Muñoz-Reyes, J. Ponce, P. Tomasi, and C. Villarroel (fig. 4).

Ortega (unpublished report in GEOBOL, La Paz, 1968) recorded remains of mammals, including a fragment of a jaw of *Notopithecus*, from the ***areniscas rojas del Anticlinal de San Andrés*** to the west of San Andrés de Machaca, probably from the upper part of the Puca Group of Russo & Rodrigo (1965). This group is equivalent, at least in part, to the Salta Group of Argentina. If the determination of this fossil is correct this is the first evidence of an Eocene mammal fauna in Bolivia. This report is reasonable as a radioisotope date of 38 Ma (millions of years ago) has been reported from the upper part of the *areniscas de San Andrés* (Evernden, Kriz & Cherroni, 1966). Unfortunately, this fossil was not described or figured, and it cannot be located in the GEOBOL collections. Moreover, it is curious that Ortega did not make mention of this fauna in his 1970 review.

Large and diverse faunas of Deseadan Age have been collected from beds in the Salla-Luribay Basin and near Lacayani (Hoffstetter, 1968a, 1976a) (fig. 4). The main fossil bearing unit is the *Strates ou Couches de Salla* of Hoffstetter (1976a, p. 4) or *Estratos Salla* of Evernden, Kriz & Cherroni (1966) which consist mainly of consolidated red to pink clays alternating with green or yellow-gray marly clays or gypsiferous marls (for stratigraphic section see Hoffstetter, 1976a, fig. 3; Villarroel & Marshall, 1982). The localities and faunas have been described by Hoffstetter (1968a, 1969, 1976a), Hoffstetter & Lavocat (1970), Hoffstetter, Martinez, Mattauer & Tomasi (1971b), Hartenberger (1975), Lavocat (1976), Patterson & Marshall (1978), Patterson & Wood (1982), Villarroel & Marshall (1982), Hoffstetter & Petter (1983), Soria & Hoffstetter (1983) and Petter & Hoffstetter (1983). This faunal association comprises 8 orders and at least 22 families; its age is clearly established by the presence of Deseadan guide fossils, among others *Pyrotherium, Trachytherus, Rhynchippus, Plagiarthrus, Proadiantus, Cephalomys, Peltephilus, Glyptatelus, Notogale*, etc. This fauna includes the latest record of the marsupial family Polydolopidae (Patterson & Marshall, 1978), and the first record of South American primates (*Branisella boliviana* — Hoffstetter, 1969). A Deseadan fossil (*Rhynchippus* sp.) from the Petaca Formation, Quebrada Saguayo, in the subandine zone of eastern Bolivia was described and illustrated by Villarroel, *in* Sanjinés & Jiménez (1976) (fig. 4; see Hoffstetter, 1977a, p. 1519).

A fauna of possible Friasian (middle Miocene) Age is recorded from the middle part of the Totora Formation at Choquecota (fig. 4) on the Altiplano (see Hoffstetter, Martinez & Tomasi, 1972). It is characterized by the small mesotheriid *Microtypotherium choquecotense* (Villarroel, 1974b) which is also found farther to the south in the lower part of the Cerdas beds (improperly called "Formación Quehua superior" on the geologic map hoja 6331 (Quechisla), half way between Cerdas and Atocha (see Hoffstetter, 1977a; Villarroel, 1978). At 3 kilometers southeast of Cerdas another mesotheriid, *Plesiotypotherium minus*, was collected from the upper part of these same beds. This species appears to be more progressive than *M. choquecotense*, suggesting a possible Chasicoan Age. In southernmost Bolivia, Hoffstetter (1977a) also recorded a Friasian fauna at Quebrada Honda, about 65 kilometers southwest of Tarija, in which five orders and 11 families [Dasypodidae, Glyptodontidae, Megalonychidae ('Megatheriidae' *sensu* Romer; the ground sloth from Quebrada Honda resembles *Hapalops* and *Pelecyodon*, classically considered as Megalonychidae, but included by Romer, 1966, in the Megatheriidae *sensu lato* — Hoffstetter, personal note), Protero-

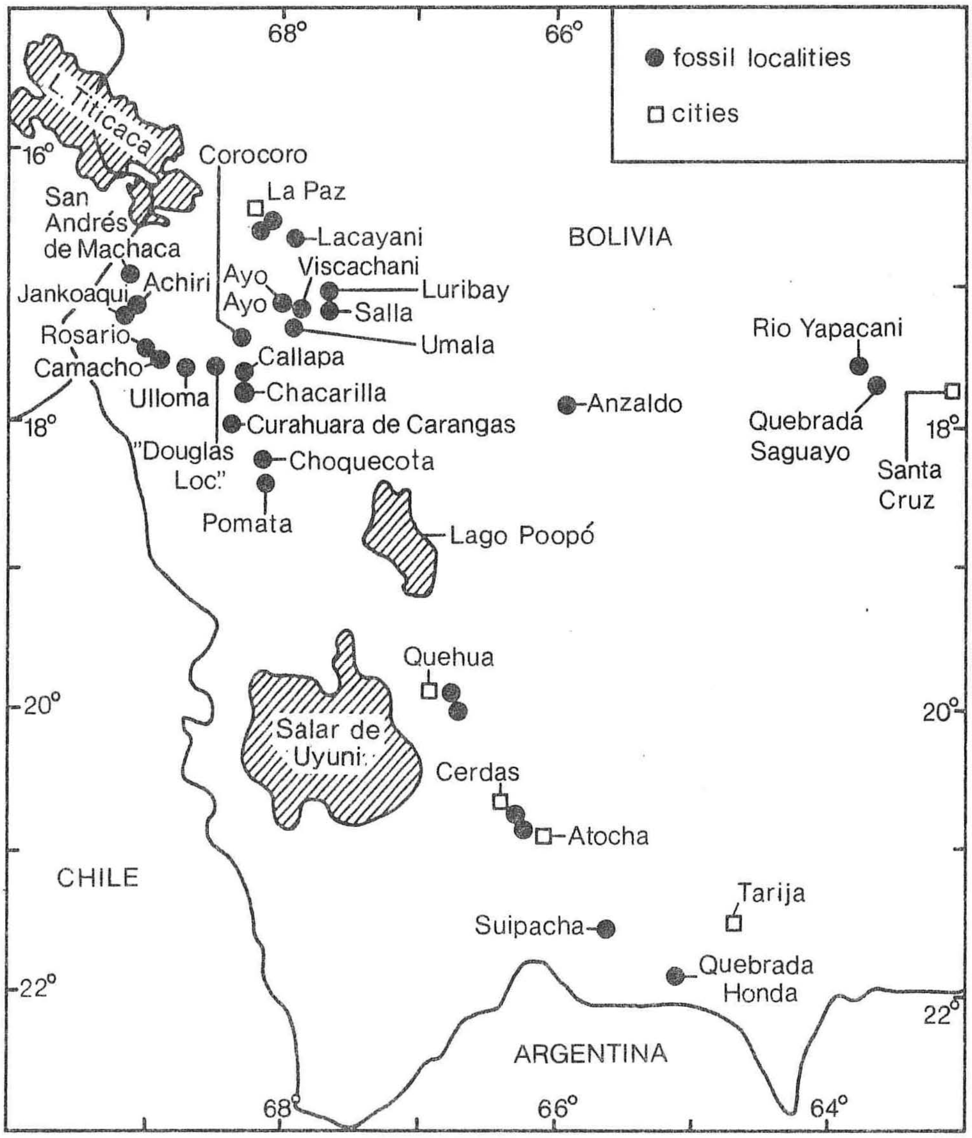

Fig. 4. — Map of southwest Bolivia showing principal mammal-bearing localities of Tertiary age (modified after Hoffstetter, 1977a, p. 1519).

theriidae, Macraucheniidae, Mesotheriidae, Hegetotheriidae, Astrapotheriidae, Chinchillidae, Octodontidae and Echimyidae] are represented.

A large number of faunas of Chasicoan and/or Huayquerian Age are known from Bolivia. The richest of these are from southwest of La Paz at Achiri and vicinity (Jankoaqui, Rosario, General Camacho, etc.; fig. 4), and from the upper member (Mauri 6) of the Mauri Formation. The Mauri 6 was deformed and eroded at the end of the Miocene. There are no Pliocene sediments in the region, but the horizontal Pérez Ignimbrite which disconformably overlies these Miocene beds has been radioisotopically dated at 2.5 Ma (Evernden, Kriz & Cherroni, 1966, 1977). A stratigraphic section spanning the time interval of about 8.0 to 6.0 Ma at the Achiri locality is given by Villarroel (1974a). The Achiri fauna comes from the upper part of the Mauri 6, above the level dated at 8.0 Ma by Evernden, Kriz & Cherroni (1966, 1977). Somewhat older beds including large amounts of volcanic ash, occur further to the west, especially at Jankoaqui. Evernden, Kriz & Cherroni (1966, 1977) have dated ash beds from Mauri 6 and have obtained ages ranging from 5.9 to 10.5 Ma. The 10.5 Ma date comes from Cerro Hakakota, 13 kilometers southeast of Santiago de Machaca, which is probably the same as Cerro Jancocota from which Berry (1922) described a fossil flora.

The known vertebrate fauna from the Mauri 6 is dominated by the mesotheriids *Plesiotypotherium achirense* and *P. majus*, which apparently come from two different stratigraphic levels (Villarroel, 1974a), and some Toxodontidae and a variety of edentates (Glyptodontidae, Dasypodidae, Megatheriidae, Mylodontidae,...).

Fossils have been collected further toward the east from the upper part of the Totora Formation, which is equivalent to Mauri 6, to the west of Callapa, to the north of Ulloma, and to the north of Chacarilla and at or near Curahuara de Carangas (fig. 4). The Totora Formation is deformed as is the Mauri 6, and is unconformably overlain by either the Pérez Ignimbrite or by the Pleistocene Ulloma Formation. Two ash beds from the upper part of the Totora Formation, the toba Callapa and the toba Ulloma, have given radioisotope dates of ca. 7.25 and 9.1 Ma, respectively (Evernden, Kriz & Cherroni, 1966, 1977). Fossils have been found above the former, and are thus from a level approximately equivalent to Achiri.

Two localities to the east-southeast of Quehua in the southern part of the Altiplano have yielded (Hoffstetter & Villarroel, unpublished) *Plesiotypotherium* cf. *P. majus* (from the highest level) and *P. achirense* (from 40 meters stratigraphically lower), and establish the equivalence of the Quehua Formation (*sensu stricto*) with the sequence at Achiri. These beds also occur below a regional unconformity (Martinez, personal communication). *Plesiotypotherium* is a good guide fossil for the late Miocene of the Bolivian Altiplano. The euphractine armadillo *Dasypodon*, described by Castellanos (1925) from an elevation of 3200 meters at Suipacha, south of Tupiza, Department of Potosí, is also regarded as late Miocene in age (Hoffstetter, 1977a) (fig. 4).

The end of the Miocene on the Bolivian Altiplano is marked by a major tectonic phase, the Quechua phase of Steinmann, and beds of this age are disconformably overlain by Pliocene (Montehermosan and Chapadmalalan) deposits to the south and southeast of La Paz. Likewise, the Pliocene strata are separated from those of the Pleistocene by one or several undated ash beds. One of the most important of the fossiliferous Pliocene deposits is the Umala Formation which has a sample of its basal ash unit (*Toba 76*) from Umala dated at 5.5 Ma[8] (Evernden, Kriz & Cherroni, 1966, 1977) and which disconformably overlies the Totora Formation. Diverse mammalian faunas have been collected from the Umala Formation at Ayo Ayo, Vizcachani, and Umala (fig. 4) and include representatives of the families Microtragulidae, Dasypodidae, Megatheriidae, Mylodontidae, Hydrochoeridae, Ctenomyidae, Macraucheniidae, and Toxodontidae (Hoffstetter, Martinez, Munoz-Reyes & Tomasi, 1971; Hoffstetter & Villarroel, 1974; Villarroel, 1975). The occurrence of *Chapalmatherium* nov. sp. at Ayo Ayo (Hoffstetter *in* Hoffstetter, Martinez, Muñoz-Reyes & Tomasi 1971) is confirmed by Villarroel's unpublished new findings.

A similar fauna has been found from a stratigraphic position situated above an ash bed which Martinez (personal communication) believes is the *Toba 76*, to the north of Pomata in strata improperly designated as the 'Formación Mauri' (Geologic Map, hoja 6039, Choquecota), and to the south and southeast of La Paz under the Chijini tuff (3.27 Ma; after Clapperton, 1979) in the La Paz Formation, a time equivalent of the Umala Formation. This Pliocene fauna differs markedly from that of the late Miocene (*i.e.* Achiri and equivalents) in that the Mesotheriinae, so abundant up to that time, disappear and are unknown in the Bolivian Pliocene and Pleistocene. On the Altiplano the large Pliocene herbivores are Macraucheniidae (cf. *Promacrauchenia*), Xotodontinae (*Posnanskytherium*), and edentates (Megatheriidae, Mylodontinae, Pampatheriinae).

The toxodont *Posnanskytherium desaguaderoi* LIENDO (1943) which Bordas synonymized with *Toxodon*, is indeed a valid genus and species of Xotodontinae and is of Pliocene (Montehermosan) Age (see Hoffstetter, Martinez, Muñoz-Reyes & Tomasi, 1971; Villarroel, 1977).

At Anzaldo, on the east slope of the Cordillera (fig. 4), Montaño (Geology thesis, University of La Paz, 1968) described a fossiliferous section which he assigned a Pleistocene Age. Hoffstetter, Montaño and Ortega later visited this locality and found (unpublished) that the lower level of the Quebrada Tijascka, which consists of 2 meters of siltstone, is referable to the Pliocene as is indicated by the presence of cf. *Promacrauchenia.* Above this unit begins the Pleistocene as marked by a gravel layer which yielded a complete caudal tube of *Prodaedicurus* cf. *P. devincenzii* CASTELLANOS, which is new for Bolivia. Above this unit are sands, siltstones, and gravels which have yielded *Megatherium* and *Glyptodon.*

Finally, from the Petaca (*sic*) Formation on the Río Yacapani in the subandian zone, was found half of a jaw of *Vassallia minuta* (Pampatheriinae) described by Villarroel (*in* Sanjines & Jiménez, 1976). A Pliocene Age for these beds is suggested.

Douglas (1914, p. 24) reported that "a few miles below the Mauri [River] bridge were obtained specimens of a silicified tree-trunk and a fragment of the symphysis of a mandible of *Nesodon* [a Santacrucian... genus from Patagonia]." This fossil came from volcanic beds of the Desaguadero Formation at an elevation of 13,000 feet ('Douglas Loc.', fig. 4). This specimen was submitted to and identified by C. W. Andrews of the British Museum (Natural History), although the specimen is no longer

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[8] A second date, 6,4 Ma in the Pomata area attributed to *Toba 76* by Hoffstetter, Martinez & Tomasi (1972) after data from Evernden *et al.* (1966, 1977) probably represents a tuff unit distinct from that of the *Toba 76* (see p. 78).

in those collections. Because of this the exact identity of this specimen and age of these beds is uncertain.

Huxley (1860) described and illustrated *Macrauchenia boliviensis* from the locality of Corocoro, a copper mine between Ayo Ayo and Achiri. This specimen is indeed a macrauchenid, but it is not referable to the Pleistocene genus *Macrauchenia*. It is a Neogene (Miocene?) form, smaller than *Theosodon* (see Hoffstetter & Paskoff, 1966, p. 483).

Simpson (1940, p. 705) noted that the toxodont ('haplothere') *Pachynodon validus* BURMEISTER, is similar to the Mesopotamian genus *Haplodontherium* AMEGHINO, from Argentina and is thus probably of late Tertiary Age. *Pachynodon validus* was probably found in Bolivia, but the accompanying data are vague. "As far as I know, the only available information as to provenience is that the specimen was sent to Vaca Guzmán (then Bolivian Minister in Buenos Aires) from Santa Cruz de la Sierra, Santa Cruz, Bolivia. The implication is that the specimen was found at that place, but this is not definitely established" (Simpson, 1940, p. 705).

BRAZIL

A review of Cenozoic vertebrate localities and faunas of Brazil is presented by Paula Couto (1970c). The oldest known fossil mammals in Brazil are from the limestone quarry at São José de Itaboraí, about 14 miles northeast of Niteroi, and on approximately the same latitude as the city of Rio del Janeiro (fig. 5). This is the largest, in both numbers of specimens and taxa (table 15), known Riochican fauna and the only fauna of that age known outside of Argentina.

Table 15. List of Riochican mammals from the fissure fills
at São José de Itaboraí, Brazil

Order Marsupialia
  Family Didelphidae
    Bobbschaefferia fluminensis (PAULA COUTO, 1952c) see Paula Couto, 1970b
    Derorhynchus singularis PAULA COUTO, 1952c
    Didelphopsis cabrerai PAULA COUTO, 1952c
    Eobrasilia coutoi SIMPSON, 1947a
    Gaylordia macrocynodonta PAULA COUTO, 1952c
    Gaylordia mendesi PAULA COUTO, 1970b
    Guggenheimia brasiliensis PAULA COUTO, 1952c
    Marmosopsis juradoi PAULA COUTO, 1962
    Minusculodelphis minimus PAULA COUTO, 1962
    Mirandatherium alipioi (PAULA COUTO, 1952c) see Paula Couto, 1952e
    Monodelphopsis travassosi PAULA COUTO, 1952c
    Protodidelphis vanzolinii PAULA COUTO, 1952c
    Sternbergia itaboraiensis PAULA COUTO, 1970b
    Xenodelphis doelloi PAULA COUTO, 1962
  Family Caroloameghiniidae
    Procaroloameghinia pricei MARSHALL, 1982b

Family Borhyaenidae
  cf. *Nemolestes* sp. (see Marshall, 1978)
  Patene simpsoni PAULA COUTO, 1952a (includes *Ischyrodidelphis castellanosi* PAULA COUTO, 1952c)

Family Polydolopidae
  Epidolops ameghinoi PAULA COUTO, 1952a (includes *Epidolops gracilis* PAULA COUTO, 1952a)

Order Edentata
Family Dasypodidae
  Prostegotherium aff. *P. astrifer* (see Scillato Yané, 1976b)

Order Condylarthra
Family Didolodontidae
  Ernestokokenia protocenica PAULA COUTO, 1952b
  Ernestokokenia parayirunhor PAULA COUTO, 1952b
  Lamegoia conodonta PAULA COUTO, 1952b
  Asmithwoodwardia scotti PAULA COUTO, 1952b

Order Notoungulata
Family Oldfieldthomasiidae
  Colbertia magellanica (PRICE and PAULA COUTO, 1950) see Paula Couto, 1952d
  Itaboraitherium atavum (PAULA COUTO, 1954a) see Paula Couto, 1970a

Family Henricosborniidae
  Othnielmarshia pristina (PAULA COUTO, 1978d) see Paula Couto, 1979a

?Notoungulata, *incertae sedis*
  Palaeocladosictis mosesi PAULA COUTO, 1961 (see Marshall, 1978)

Order Litopterna
Family Macraucheniidae
  Victorlemoinea prototypica PAULA COUTO, 1952b

Family Proterotheriidae
  Anisolambda prodromus PAULA COUTO, 1952b

Order Trigonostylopoidea
Family Trigonostylopidae
  Tetragonostylops apthomasi (PRICE and PAULA COUTO, 1950) see Paula Couto, 1963

Order Xenungulata
Family Carodniidae
  Carodnia vieirai PAULA COUTO, 1952b

The fossils come from a marl which fills channels and underground caves in a limestone quarry, produced in the limestone by pluvian and underground water (Rodrigues Francisco & de Souza Cunha, 1978). The age of this limestone, the Itaboraí Formation, and of its invertebrate fauna as described by Maury (1935) and Parodiz (1969), is possibly early Paleocene, or in part, late Cretaceous (Ferreira & Santos Coelho, 1971, p. 471). Rodrigues Francisco & de Souza Cunha (1978) have suggested that the vertebrate bearing fillings in the Itaboraí Formation may be early (but not earliest) Paleocene in age.

The fossil mammals from Itaboraí have been described in a series of papers by Paula Couto (1948, 1949, 1950, 1952a-e, 1954a,b, 1958, 1961, 1962, 1963, 1970a,b, 1978b-d, 1979a), Price & Paula Couto (1946, 1950), and Simpson (1947a). Paula Couto (1952b, p.

360) has noted that as the mammals from Itaboraí are more primitive than the corresponding groups in the Casamayor faunas of Patagonia, and as one of the genera, *Carodnia*, is known elsewhere only in the Río Chico beds of Patagonia, it seems that the Río Chico and Itaboraí faunas must be considered nearly synchronous in age.

A Deseadan fauna has recently been found in the Tremembé Formation in the Taubate Basin, state of São Paulo (fig. 5). These beds had long been regarded as Pliocene or Pleistocene in age on the basis of fossil remains, mainly fishes, consistent with but not diagnostic of such an age. The known fauna includes a notoungulate of the family Leontiniidae (cf. *Leontinia gaudryi*, see Paula Couto & Mezzalira, 1971), a pampatheriine armadillo (Patterson, in press), and a bat (*Tadarida faustoi*, see Paula Couto, 1956, 1979b).

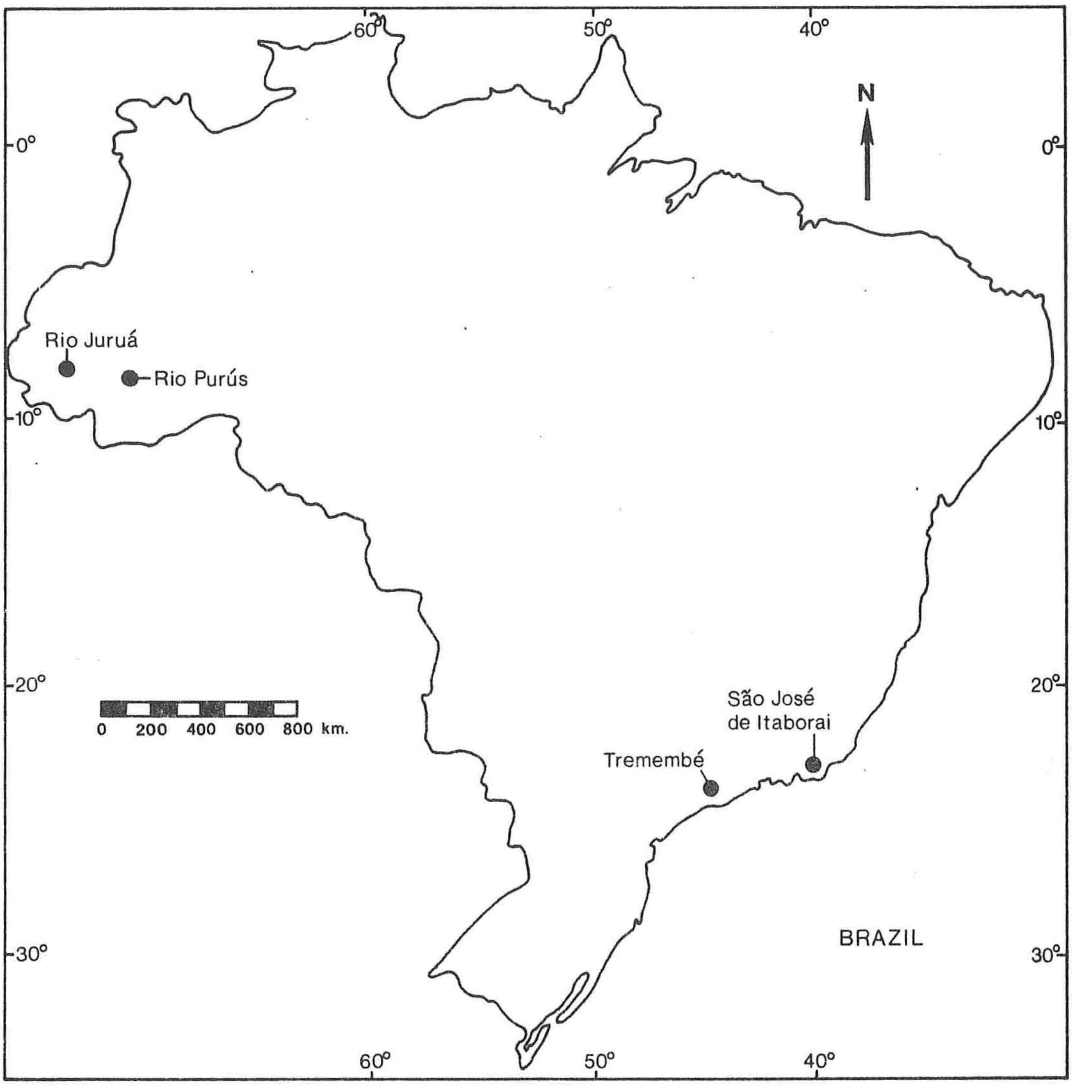

Fig. 5. — Map of Brazil showing principal mammal-bearing localities of Tertiary age.

Deposits in western Brazil near the Peruvian border have yielded the astrapothere *Synastrapotherium*, thought to be Oligocene in age by its describer (Paula Couto, 1976).

The first record of Tertiary mammals in Brazil "were perhaps those found by José Bach some time before 1911 at the first rapids of the Yuruá River*... [fig. 5]. The specimens... seem to have been lost..., but von Ihering had a photograph which he showed to [F.] Ameghino and later sent to Schlosser... (1925)... [who]... identified the mammals as including a toxodont, otherwise undetermined,... and [a]... heptaxodontid rodent. That there is a Tertiary mammal deposit in this region was to some extent confirmed by the description of a new genus, *Trigodonops*, by [L.] Kraglievich (1931), a toxodont of Pliocene aspect, based on *Toxodon lopesi* Roxo [1921] of unknown geologic origin and uncertain geographic position but probably from the Alto Yuruá" (Simpson, 1940, p. 702). Also reported from these beds are the toxodonts *Abothrodon pricei* PAULA COUTO (1944, p. 1), a form of uncertain affinity (see Paula Couto, 1956, p. 41); an astrapothere (Paula Couto, 1970c, p. 917; 1976); and a dinomyid rodent, *Phoberomys burmeisteri* (Paula Couto, 1978a, p. 6). Additional late Tertiary and Quaternary fossil localities in the Río Juruá* region are listed by Paula Couto (1978a, p. 4-5).

Another late Tertiary (Pliocene?) fauna is reported from the Paraná Formation, a level at or near the base of Singewald's (1937) *Brown Beds* series in the upper Río Purús region, Amazonas Province, western Brazil (Paula Couto, 1956) (fig. 5). The fauna includes a small mylodontoid? ground-sloth (Paula Couto, 1956, p. 18; Simpson, 1940, p. 702); a rodent, *Phoberomys bordasi* Patterson (1942, p. 1); and a crocodile, *Brachygnathosuchus braziliensis*. The fossiliferous beds of the upper Ríos Purús and Juruá regions, discussed by Paula Couto (1956), are tentatively regarded as late Miocene (Huayquerian) in age, although the presence of *Astrapotherium* suggests that at least some of these beds are somewhat older.

CHILE

Tertiary land mammals are known from the Palomares or Santa Cruz Formation in the Department of Magallanes, southern Chile. Hemmer (1935) reported a specimen of *Astrapotherium magnum* from Los Cruceros on the southern margin of the Laguna del Toro, and Simpson (1941b) reported *Nematherium birdi* from the east side of Laguna Blanca (fig. 3). Both specimens are Santacrucian in age.

The type Friasian fauna occurs at the Alto Río Frías (= Río Cisnes), approximately 71°7'-20'W, 44°34'37'S (fig. 1). This fauna was discovered in 1897 or 1898 by Roth (see Roth, 1908; Ameghino, 1906). A review of the history of this fauna is given by Hoffstetter (*in* Hoffstetter, Fuenzalida & Cecioni, 1957, p. 133), and is discussed in more detail on p. 31-33.

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*The Río Juruá (Brazil) is named Río Yuruá in its upper part, in Peru.

COLOMBIA

The majority of continental Tertiary sediments of Colombia are situated in the Magdalena Valley (fig. 6), an ancient trough separating the east and central cordilleras (see Bondesio & Pascual, 1977, fig. 1). Fewer and less fossiliferous deposits occur in the Valle del Cauca, between the central and western cordilleras, and in the Maracaibo depression, between the Sierras de Perijá and Mérida. These latter depressions were frequently inundated by marine transgressions during the Tertiary. Reviews of Tertiary mammal-bearing faunas of Colombia are given by Hoffstetter (1970a, 1971), Stirton (1953), and Porta (1961).

A vertebrate fauna, considered to be of possible late Eocene Age by Stirton (1953), is recorded from the Mugrosa Formation in the La Circa-Las Infantas oil fields in Santander. Stirton (1953, p. 609, fig. 4) figured and described an incomplete lower molar of what he considered an astrapothere of the subfamily Albertogaudryinae, from the Tama fauna (fig. 6). Based on palynological data, Van der Hammen (1957) assigned the Mugrosa Formation to the early or middle Oligocene.

From the middle or lower part of the Gualanday Formation, about 3 kilometers east-northeast of Gualanday, Department of Tolima (fig. 6), Hoffstetter (1970d) described a new pyrothere, *Colombitherium tolimense*, of the family Colombitheriidae. This specimen is thought to be of late Eocene or perhaps early Oligocene Age.

Stirton (1946b; 1953, p. 609) described a possible early Oligocene fauna from the Tuné Formation, just northeast of Chaparral, Department of Tolima. Among the mammals are included megalonychid ground sloths, a proterotheriid litoptern or didolodontid condylarth? (*Protheosodon*), a toxodontid notoungulate (*Proadinotherium*), an astrapothere, and a sirenian? (*Lophiodolodus*).

The Peneyita fauna is represented by a single specimen of a rodent, *Eosteiromys* (family Erethizontidae), collected from a calcareous marly claystone at the confluence of the Ríos Peneyita and Caquetá (Stirton, 1953, p. 610, fig. 7). This is the only known fossil mammal locality east of the Andes in Colombia (fig. 6) and is believed to be of early Oligocene Age.

The only late Oligocene (Colhuehuapian) mammal-bearing fauna in Colombia (the Coyaima fauna) is from a gray ferruginous sandstone unit of the Honda Group, near the village of Coyaima adjacent to the Castilla-Ataco carretera, Department of Tolima (Stirton, 1953, p. 611, fig. 8). Among the known mammals are included edentates (Megalonychidae and Dasypodidae — including a large pampathere), rodents (cf. *Scleromys*), Litopterna, Notoungulata (Toxodontidae, Leontiniidae, Interatheriidae-*Cochilius*), and Astrapotheria.

By far, the best known and most taxonomically diverse mammal-bearing fauna of middle Tertiary Age in Colombia, or for that matter in all of northern South America, is the middle Miocene (Friasian) La Venta fauna (including the Carmen de Apicalá fauna of Stirton, 1953, p. 616). The La Venta fossils are found in a large section of sandstones, conglomerates, and claystones of the Honda Group, north and northeast of Villavieja (Stirton, 1953, p. 613, fig. 9; Fields, 1959; Bondesio & Pascual, 1977; Hoffstetter & Rage, 1977) (fig. 6). Faunal lists (table 16) are given by Hoffstetter (1970a, p. 934; 1971, p. 40), Hirschfeld & Marshall (1976), and Hoffstetter & Rage (1977).

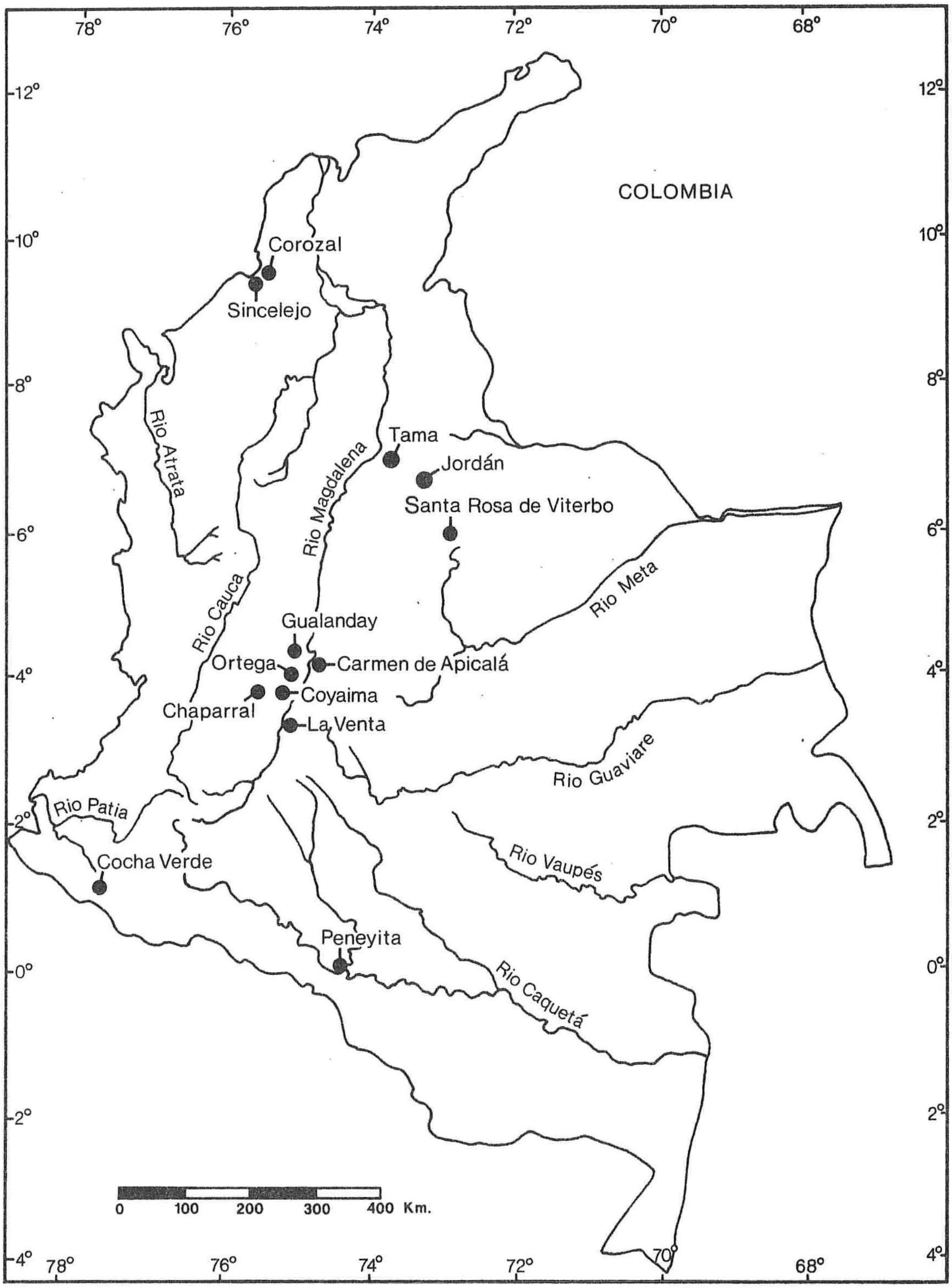

Fig. 6. — Map of Colombia showing principal mammal-bearing localities of Tertiary age.

From Jordán (= Sube) along the Río Chicamocha near Los Santos, Department of Santander, has been collected an incomplete mandible of a scelidothere of Miocene aspect. This specimen, collected by ***R. Padre*** Rothereau, is now in the Museo del Instituto La Salle in Bogotá (Hoffstetter, unpublished).

Stirton (1946a) described a dinomyid rodent, ?*Gyriabrus royoi*, collected from a light greenish-gray, fine-grained sandstone unit of the Savana Formation (Porta, 1961). The specimen came from near kilometer 35 carretera de Toluviejo, north of Sincelejo, Department of Bolívar. This, the Sierra Peñata fauna, is regarded as late Miocene in age (Porta, 1961; Hoffstetter, 1971, p. 42).

In the region of Sincelejo the Savana Formation is covered unconformably by the *Areniscas de Sincelejo* which extends from Corozal to about El Carmen. Porta (1961) assigned these sands to the Pliocene, and from them recorded a toxodont which presents characters of both the Toxodontinae and Haplodontheriinae.

Stirton (1946a) described a tayassuid artiodactyl, *Selenogonus narinoensis*, collected from a dark-green, fine-grained sandstone near Cocha Verde, on the Túquerres-Tangua carretera, Department of Nariño (fig. 6). This, the Cocha Verde fauna of Stirton (1953, p. 620), is assigned a late Pliocene or early Pleistocene Age. Faunas recorded but not described by Botero Arango (1936) from Ortega[9], Department of Tolima, and by Royo y Gómez (1942, 1945) in Santa Rosa de Viterbo[10], Department of Boyacá, may be of similar age, but that needs confirmation (Hoffstetter, 1971, p. 43).

Table 16. List of Friasian mammals from the La Venta fauna of Colombia (modified from Hirschfeld and Marshall, 1976 - see that work for literature references of original authorship)

- **Order Marsupialia**
  - Family Didelphidae
    - *Marmosa laventica* MARSHALL, 1976
    - *Marmosa sp.*
    - *Hondadelphys fieldsi* MARSHALL, 1976
  - Family Borhyaenidae
    - *Lycopsis longirostrus* MARSHALL, 1977
    - borhyaenid, *gen. et sp. indet.*
- **Order Chiroptera**
  - Family Phyllostomatidae
    - *Notonycteris magdalenensis* SAVAGE, 1951
- **Order Primates**
  - Family Cebidae (incl. Atelidae)
    - *Cebupithecia sarmientoi* STIRTON and SAVAGE, 1951
    - *Stirtonia tatacoensis* (STIRTON, 1951)
    - *Neosaimiri fieldsi* STIRTON, 1951

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[9] "***Ortega.*** El doctor Gerardo Botero (1936 y 1937, p. 45) señala la existencia de fósiles del Terciario superior en este municipio pero no indica la localídad exacta ni de qué vertebrados se trata" (Royo y Gómez, 1945, p. 499).

[10] "***Santa Rosa de Viterbo.*** Hacienda Gratamira, de los señores Jiménez Suárez, a unos dos kilómetros al S. de la población. En el llamado yacimiento de fosfatos, fragmento del cuerpo de una vértebra, una cabeza incompleta de fémur y otra de metapodio de mamíferos pequeños. Terciario superior a Pleistoceno inferior. Col. R. Sarmiento, Serv. Geol. Nal. (Royo y Gómez, 1942a, p. 49)" (Royo y Gómez, 1945, p. 499).

Order Edentata
  Family Megalonychidae
    cf. *Hapalops* sp.
  Family Megatheriidae
    Subfamily Megatheriinae *gen. et sp. indet.*
  Family Mylodontidae
    Subfamily ?Mylodontinae
      Pseudoprepotherium sp.
    Subfamily Scelidotheriinae
      cf. *Neonematherium* sp.
  Family Myrmecophagidae
    Neotamandua borealis HIRSCHFELD, 1976
  Family Dasypodidae
    Subfamily Pampatheriinae
      Kraglievichia sp. (see Robertson, 1976)
  Family Glyptodontidae
    Subfamily Propalaehoplophorinae
      Asterostemma depressa AMEGHINO
      Asterostemma venezolensis SIMPSON, 1947
      Propalaehoplophorus sp.

Order Rodentia
  Family Erethizontidae
    cf. *Eosteiromys* sp.
  Family Caviidae
    Subfamily Dolichotinae
      Prodolichotis pridiana FIELDS, 1957
  Family Dasyproctidae
    Neoreomys huilensis FIELDS, 1957
    Scleromys schuermanni STEHLIN, 1940
    Scleromys colombianus FIELDS, 1957
    Olenopsis aequatorialis (ANTHONY, 1922)
  Family Echimyidae

Order Condylarthra
  Family Didolodontidae
    Megadolodus molariformis McKENNA, 1956

Order Litopterna
  Family Macraucheniidae
  Family Proterotheriidae

Order Notoungulata
  Family Leontiniidae
  Family Toxodontidae
  Family Interatheriidae
    Miocochilius anomopodus STIRTON, 1953
  Family Hegetotheriidae
  Family Isotemnidae?

Order Astrapotheria
  Family Astrapotheriidae
    Xenastrapotherium kraglievichi CABRERA, 1929
    Astrapotherium sp.

Order Sirenia
  Family Manatidae
    Ribodon magdalenensis (REINHART, 1951)

ECUADOR

Hoffstetter (1970b) reviewed occurrences of fossil vertebrates in Ecuador. A dinomyid rodent was described as *Drytomomys aequatorialis* ANTHONY (1922), from a cave near Nabón, Azuay Province (fig. 7). Anthony believed this specimen to be Pleistocene in age. However, according to Fields (1957), *Drytomomys* is a junior synonym for *Olenopsis*, and the same species, *O. aequatorialis*, is common in the La Venta fauna of Colombia. Thus, the rodent from Nabón is now regarded as Friasian in age (Hoffstetter, 1970b, p. 956; Bristow & Hoffstetter, 1977, p. 210, Nabón Formation).

Repetto (1977) recently recorded discovery of a mammalian tooth from the lower part of the Biblián Formation about 8 kilometers west of Azogues (fig. 7). According to G. G. Simpson (*in* Repetto, 1977) the tooth is of a toxodontid, similar to *Protoxodon rothi* KRAGLIEVICH, but distinct. This specimen suggests a tentative Santacrucian or Friasian Age for this level of the Biblián Formation (Hoffstetter *in* Bristow & Hoffstetter, 1977, p. 57).

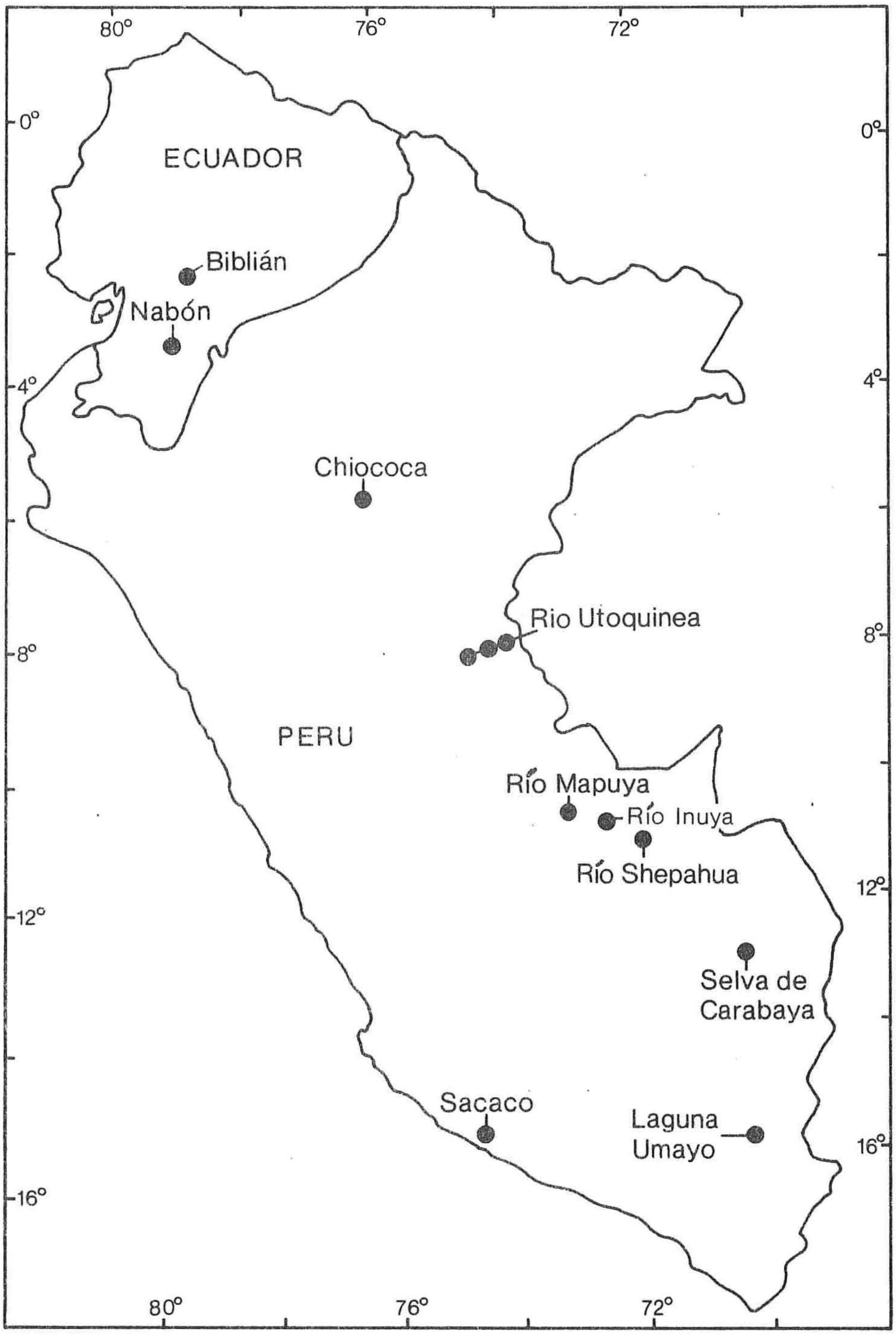

Fig. 7. — Map of Ecuador and Peru showing principal mammal-bearing localities of Late Cretaceous (Laguna Umayo) and Tertiary age (all others).

PERU

A review of Peruvian late Cretaceous and Cenozoic continental vertebrate localities and faunas is given by Hoffstetter (1970c). The oldest known fossil mammals in Peru are represented by the Laguna Umayo local fauna from the Vilquechico Formation on the Andean Altiplano near Lago Titicaca, southern Peru (fig. 7). These include a primitive condylarth (but see p. 61 for discussion of alternative affinities) *Perutherium altiplanense* THALER, 1967 (*in* Grambast *et al.*, 1967), various marsupials, notably a didelphid, *Peradectes austrinum* (Sigé, 1971; see Crochet, 1977, 1978, 1979a, b) and a single specimen questionably attributed by Sigé (1972) to the family Pediomyidae. The same rocks, mapped as late Cretaceous by Portugal (1974), have also yielded dinosaur eggs (Sigé, 1968). A late Cretaceous age for this earliest known South American mammal fauna is thus suggested and is confirmed by charophytes (*Porochara* and *Amblyochara*; see Grambast *et al.*, 1967).

A pyrothere, *Griphodon peruvianus* ANTHONY, 1924, has been described from a "15' embankment of gravelly red clay" near the farm house called Chiococa, "upstream from Chipeza,... situated approximately 1 km west of the junction of the Quebrada Chipaote with the Río Huallaga, about midway on the stretch of the river between the Pongo de Vaguero to the west and the Pongo de Aguirre to the east (map in Rosenzweig, 1953),... Departmento de San Martín, Provincia de San Martin" (Patterson, 1977, p. 421; also see Patterson, 1942) (fig. 7). Hoffstetter (1970c, p. 973) noted that in its stage of evolution *Griphodon* is intermediate between *Carlozittelia* from the Casamayor and *Pyrotherium* from the Deseado. He thus suggested that its age was Mustersan. On the stratigraphic data, Patterson (1977, p.422) estimated its age as approximately middle Eocene.

Buffetaut & Hoffstetter (1977, p. 1663) record a vertebrate fauna of possible Friasian Age containing mammals from the Ipururo Formation in the upper Ucayali Basin, eastern Peru (fig. 7). The mammals, as yet undescribed, include gravigrade edentates and astrapotheres.

Willard (1966, p. 73-74) listed a large number of mammal-bearing localities and faunas which apparently range from Miocene to Pleistocene in age. According to Hoffstetter (1970c, p. 974), beds from the Río Mapuya (as well as those of the Ríos Inuya and Shepahua) contain an astrapothere (cited and figured as '*Astracotherium*' *sic* by Willard) which is probably of Miocene Age. These beds, or those of the Ríos Purús and Yuruá of Brazil, are probably referable to the Ipururo Formation. [Faunas of possible Pliocene-Pleistocene Age occur at the Río Utoquinea at its confluence with the Río Ucayali, and in the Selva de Carabaya.]

Spillmann (1949, p. 25) described a toxodont, *Neotrigodon utoquineae*, from the late Miocene or early Pliocene ***Brown beds*** of Singewald (1937) along the Río Utoquinea, a tributary of the Río Ucayali, near the Brazilian border. Paula Couto (1956, p. 104) suggested that *Neotrigodon* may be a junior synonym of *Abothrodon* Paula Couto (1944) from deposits of similar age in southwestern Brazil (see p. 48). Unfortunately *Abothrodon* is known only from its lower dentition and *Neotrigodon* only from its upper, thus deterring direct comparison of these taxa.

Hoffstetter (1968b) reported on a primarily marine vertebrate fauna from the Pisco Formation at Sacaco in southern Peru (fig. 7). This fauna has yielded numerous remains of an edentate which shares features with both *Planops* and *Pseudoprepotherium*. The local fauna, being studied by C. de Muizon (*e.g.*, 1981), also includes marine molluscs, fish, crocodiles, birds, pinnipeds (five Monachinae, one Arctocephalinae), and cetaceans (two Balenopteridae, one Cetotheridae, one Platanistidae, one Phocaenidae, two Delphinidae and one Ziphiidae). The Pisco Formation was long considered as Miocene in age on the basis of the marine mollusc fauna. However, a late Miocene or Pliocene Age is suggested by the vertebrate faunas, the diatoms, radioisotopic age determinations, and local neotectonics. The fossiliferous localities (El Jaguay, Aguada de Lomas, South Sacaco, Sacaco) correspond to various ages from ca. 6.0 to ca. 3.0 Ma (de Muizon & Bellon, 1980).

URUGUAY

Reviews of mammal-bearing Tertiary strata and faunas in Uruguay are given by Simpson (1940, p. 699), Hoffstetter (*in* Goñi & Hoffstetter, 1964), Mones & Francis (1973), Francis (1975) and Mones (1979). These workers show that in Uruguay, principally in the southwest, there are mammal-bearing equivalents of several of the Argentine faunas of middle and late Tertiary Age. The known collections are scanty, "and the stratigraphic sequence and nomenclature are not yet well worked out" (Simpson, 1940, p. 699).

The oldest known Uruguayan mammals are from the Fray Bentos Formation (= Santa Lucía beds or *Santaluciense* of L. Kraglievich, 1932), Santa Lucía, Department of Montevideo (fig. 8). These beds consist of silty sands, with intercalations of loess and volcanic ash, and frequent calcareous concretions. *Propachyrucos schiaffinoi* KRAGLIEVICH, 1932 is from the locality of Cañadón de las Mulas. Mones & Ubilla (1978) recently reported the borhyaenid marsupial *Proborhyaena* cf. *P. gigantea* from the Fray Bentos Formation at Paso del Cuello, Department of Canelones, suggesting a Deseadan Age for these beds (typical *Santaluciense*) in this area.

From the Fray Bentos Formation (= *Palmirense* of L. Kraglievich, 1932) on the banks of the Río Uruguay near Nueva Palmira, was collected a calcaneum which L. Kraglievich (1932) named *Pseudohegetotherium palmirense*. From the cliffs of the Río Uruguay near Fray Bentos, Department of Río Negro, L. Kraglievich reported *Protypotherium* sp. From Punta Gorda, Department of Colonia, came a caviomorph rodent which L. Kraglievich named *Palmiramys waltheri*, and a hoplophorine glyptodont which Castellanos (1948) referred to *Berthawyleria* sp. From the Barranca de Los Loros has been reported a glyptodont, *Urotherium interundatum* (Castellanos, 1948, p. 21) and species of the dasypodids *Dasypodon* and *Doellotatus* (Castellanos, 1948, p. 21; Goñi & Hoffstetter, 1964, p. 158). These taxa are comparable with those in faunas of Chasicoan Age in Argentina, confirming such correlations as advanced by L. Kraglievich (1932), and Francis (1975, p. 556).

An astrapothere, *Uruguaytherium beaulieui* L. KRAGLIEVICH (1928), was collected from the arroyo Juanín tributary of the arroyo Román, Department of Río Negro

(Mones & Francis, 1973, p. 73). The age of this specimen is not surely known and it has been assigned to both the Oligocene and Miocene (Goñi & Hoffstetter, 1964). Simpson (1940, p. 699) notes that "it is an astrapothere of advanced type, different from and possibly more specialized than those of Argentina, where astrapotheres are last known in the Friasian".

L. Kraglievich (1930a) described a scrap of bone from the arroyo Perico Flaco, Department of Soriano, as *Proterotherium berroi.* This specimen may have come from the Fray Bentos Formation (Goñi & Hoffstetter, 1964, p. 158). *Proterotherium* is a typical Santacrucian genus.

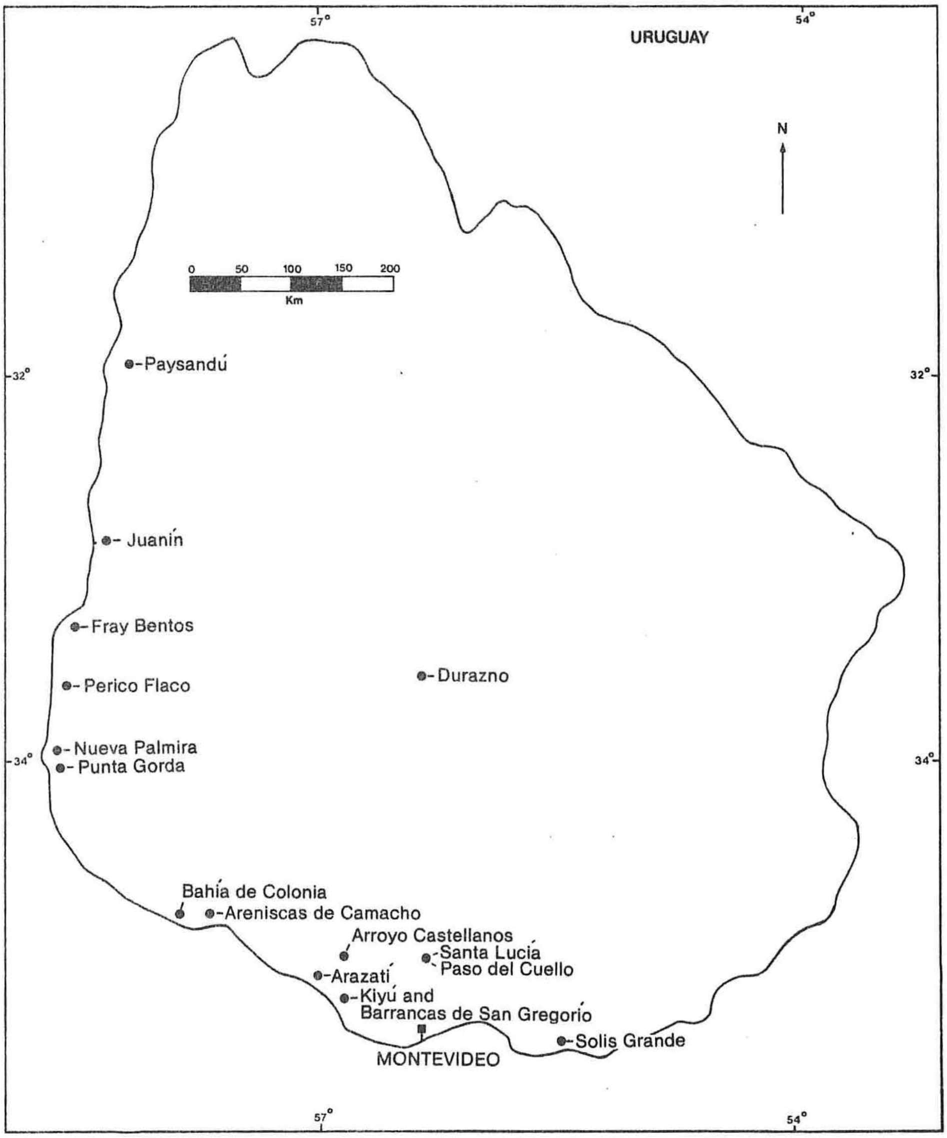

Fig. 8. — Map of Uruguay showing principal mammal-bearing localities of Tertiary age.

L. Kraglievich (1926) described a megalonychid ground sloth, *Megalonychops fontanai*, from the *Areniscas de Camacho*, Department of Colonia. *Megalonychops* is a *Mesopotamian* genus from Argentina and is thus probably Huayquerian in age (Pascual & Odreman Rivas, 1973).

A fauna of *Mesopotamian* character has been collected from the Barrancas de San Gregorio, along the coast of the Río de La Plata, west of Montevideo, in the Department of San José (fig. 8). Some of these fossils were collected in situ and others as float from the base of the cliff. The fauna includes *Berroia gregoriense, Palaeotoxodon paranensis, Xotodon smaltatus, Toxodontotherium listai, Scalabrinitherium ferreriai, ?Oxyodontherium zeballosi, Promegatherium* (*= Eomegatherium*) *nanum uruguayense, Pliomorphus* aff. *robustus, P.* (*Menilaus*) *berroi, Scelidodon corderoi, Stromaphoropsis scavinoi, S. benvenutii, S. rebuffoi, Berthawyleria uncinata, B. gracilis, Teisseiria compressa, T. berroi, Palaeodaedicurus catalanoi, P. antiquus, Castellanosia establei, C. excavata, Prodaedicurus wyleri*, an *Cardiomys* sp. (Goñi & Hoffstetter, 1964, p. 158).

A fauna of Montehermosan Age has been collected from the Kiyú Formation along the coast of San José, between the Arroyo San Gregorio and the "Club Náutico y de Pesca" of Playa Kiyú. The described taxa include a rodent of the subfamily Cardiatheriinae, family Hydrochoeridae, *Kiyutherium orientalis* (Francis & Mones, 1965b); the glyptodont *Pseudoplohophorus francisi* (Mones, 1970); and various species of the glyptodont genus *Stromaphoropsis* established by Castellanos and Kraglievich (Mones & Francis, 1973, p. 50).

Another fauna of Montehermosan or Chapadmalalan Age has been collected from the lower part of the San José Formation in the basal part of the cliffs of San Gregorio, Department of San José. The described taxa include *Cardiatherium talicei* (Francis & Mones, 1965a), of the rodent subfamily Cardiatheriinae; probably *Artigasia magna* of the family Dinomyidae (Mones & Francis, 1973, p. 65; Francis, 1975, p. 558); and the proterotheriid *Licaphrium* cf. *L. floweri* from the upper part of the section.

Another fauna also considered as *Mesopotamian* in age but which may be somewhat younger, has been collected from the Bahía de Colonia. The fauna includes *Scelidodon* cf. *S. corderoi, Lestodon (Prolestodon) atavus, Teisseiria coloniensis, Eleutherocercus vilardeboi, Palaeodaedicurus pasottii*, and *Gyriabrus teisserei* Goñi & Hoffstetter, 1964, p. 158).

Other *Mesopotamian* mammals have been reported from isolated finds, including *Pseudoplohophorus orientalis* (AMEGHINO, 1889) from the Department of Paysandú, western Uruguay; and *Trabalia guimaraense* (L. KRAGLIEVICH, 1932) from the Department of Durazno, central Uruguay (Goñi & Hoffstetter, 1964, p. 158).

In beds in the Department of Colonia which are correlated with the *Entrerriense* (= Montehermosan) of Argentina, L. Kraglievich (1930b) reported a dinomyid rodent, *Gyriabrus teisseirei.* He later (1932) suggested that it was from the *Mesopotamian* (= Huayquerian; Simpson, 1940, p. 701).

Also from beds of possible Pliocene Age have been found a fragment of the glyptodont *Plohophorus figuratus* AMEGHINO, 1887 encountered in the *arenales de Arazatí* along the southern coast; and the type of *Eleutherocercus antiquus* KOKEN, 1888 which is without locality data.

Of special interest is the type of *Prodaedicurus devincenzii* CASTELLANOS, 1927 which came from the Arroyo Castellanos, along the Río San José, Department of San José. For these beds Castellanos proposed the ***Castellanosense*** Age which he considered as post-Montehermosan and pre-Ensenadan, and later as post-Chapadmalalan and pre-Uquian (Hoffstetter *in* Goñi & Hoffstetter, 1964, p. 159).

The glyptodonts *Zaphilus larranagai* AMEGHINO, 1889 and *Z. lydekkeri* (AMEGHINO, 1889) where assigned to the ***Pampeano*** (= Pleistocene) by Ameghino, but were considered somewhat older by L. Kraglievich (1932).

Lastly, from the foot of the cliff on the left side of the mouth of the Solis Grande, Department of Maldonado, Rusconi (1933) described *Lagostomopsis aznarezi* which he assigned to a new age, the ***Maldonadense***, and which he considered as 'medial Pliocene' (note — Rusconi used 'Pliocene' *sensu lato*).

This long list of taxa is somewhat deceptive and requires much revision, as practically all of the fragments of glyptodonts have received specific names. Nevertheless, these records do demonstrate that Uruguay is exceedingly rich in Neogene terrestrial vertebrate faunas.

VENEZUELA

The oldest known Venezuelan mammal is *Proticia venezuelensis*, a colombitheriid pyrothere from the upper part of the Trujillo Formation near the head of the Quebrada Agua Viva, Sierra de Baragua, District of Torres, State of Lara (fig. 9). The fossil is probably of early Eocene Age (Patterson, 1977).

A review of possible late Tertiary Venezuelan mammals is given by Simpson (1940, p. 703). A toxodont, *Gyrinodon quassus* HOPWOOD (1928), of Montehermosan character, is reported from the El Mene oil field in western Falcón; Schaub (1935) reports a toxodont, ?*Nesodon* sp., from near San Pedro in central Falcón; Collins (1934) reports a sloth, *Prepotherium venezuelanum* [this species was later made the type of *Pseudoprepotherium* by Hoffstetter, 1961], from the Río Tucupido in the western Portuguesa; Stehlin (1928) and L. Kraglievich (1928) report an astrapothere, *Xenastrapotherium christi* from the llanos just north of Zaraza, northeastern Guárico; and Simpson (1947b) reports a glyptodont (subfamily Propalaehoplophorinae) *Asterostemma venezolensis* from the Santa Ines Formation, considered approximately middle Miocene, on the banks of the Río Guere, near the village of San Francisco, northwestern Anzoategui, eastern Venezuela. Simpson (1940, p. 703) further reports that "fragmentary remains, insufficient for useful identification, have also been found... in the same beds as *Xenastrapotherium* elsewhere in the Guárico llanos and in the late Pliocene or early Pleistocene beds at Valera, central Trujillo, in the Andes" (fig. 9).

Recently, a small but significant vertebrate fauna of Huayquerian Age has been described from the upper member of the Urumaco Formation in the northwestern part of the state of Falcón, near the El Mamón oil field, just north of the town of Urumaco. The mammals include caviomorph rodents of the families Dinomyidae, Hydrochoeridae, and Neoepiblemidae (Pascual & Diaz de Gamero, 1969, p. 370; Mones, 1981), and a toxodont. A large number of turtles (Wood, 1976a, b; Wood & Patterson, 1973; Wood & Diaz de Gamero, 1971), and a gavial (Sill, 1970) are also known.

From the Springvale beds on the neighboring Island of Trinidad (fig. 9), Schaub (1935) "described a femur of a gigantic rodent, not exactly determinable but evidently allied to the giant hystricomorphs of the late Tertiary of Argentina" (Simpson, 1940, p. 703).

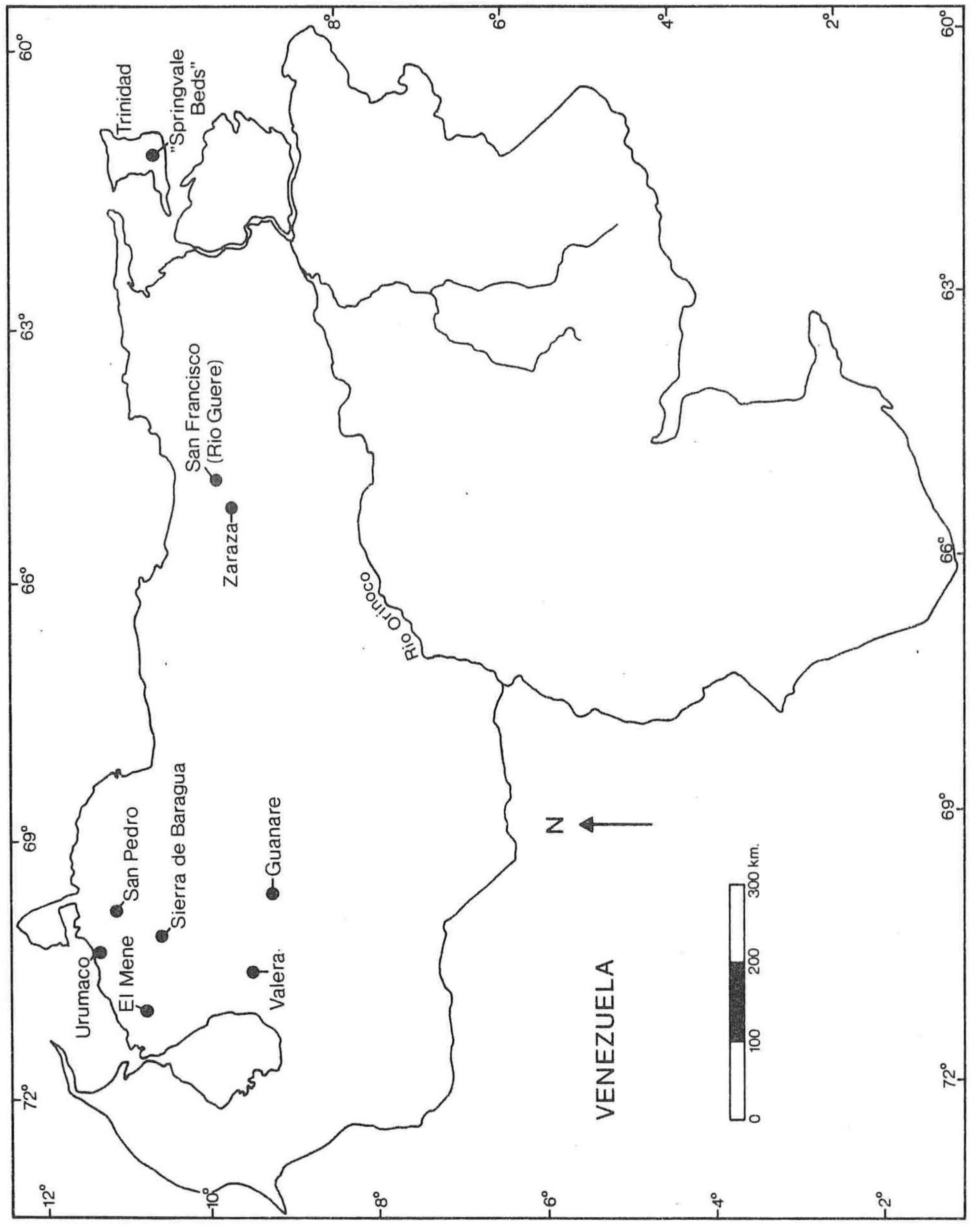

Fig. 9. — Map of Venezuela showing principal mammal-bearing localities of Tertiary age.

Table 17. Chronostratigraphic distribution of non-Argentine mammal-bearing Tertiary beds, faunas, and/or localities

	South American Land Mammal Age	BOLIVIA	BRAZIL	COLOMBIA	ECUADOR	PERU	URUGUAY	VENEZUELA
PLIOCENE	Chapadmalalan	Anzaldo, Pomata, Umala Fm. (Ayo Ayo, Vizcachani, Umala) La Paz Fm. (near La Paz), Yapacani		↑ Cocha Verde? Ortega? Santa Rosa de Viterbo? "Areniscas de Sincelejo"		Río Utoquinea?, Selva de Carabaya? ? ? ? ? ? ? ?	San José Fm.	
	Montehermosan					Pisco Fm. Río Utoquinea	Kiyú Fm.	El Mene
MIOCENE	Huayquerian	Suipacha Mauri 6 Fm. (Achiri, Rosario, Camacho) Totora Fm. (Callapa, Chacarrilla) Quehua Fm. (Quehua)	Río Juruá Río Purús ↓	[Savana Fm.]		Ipururo Fm. (Ríos Inuya, Mapuya, Shepahua) ↓	Camacho Fm. at Calera Camacho	Urumaco Fm.
	Chasicoan		↓ ?			↓ ?	Fray Bentos Fm. ("Palmirense")	
	Friasian	Between Cerdas and Atocha, Choquecota, Quebrada Honda	↓	La Venta fauna Carmen de Apicala	Nabón	↓	Arroyo Juanin	San Francisco (Santa Ines Fm.)
	Santacrucian	Río Mauri?			Biblián		Arroyo Perico Flaco	
OLIGOCENE	Colhuehuapian			Coyaima fauna				
	Deseadan	Salla-Luribay Basin, Lacayani, Quebrada Saguayo	Tremembé Fm.	Peneyita fauna Tuné Fm. Mugrosa Fm.			Fray Bentos Fm. ("Santaluciense")	
EOCENE	Divisaderan			Gualanday Fm.		Chiococa		
	Mustersan							
	Casamayoran							Trujillo Fm.
PALEOCENE	Riochican		São José de Itaboraí					

LAND MAMMAL FAUNAS

CHARACTER AND HISTORY

Through most of the Tertiary Period (65 to about 3 Ma) South America was an island continent. As a result of this the land mammal fauna developed in isolation and was dominated by autochthonous endemic groups. Isolation ended about 3 Ma when the Panamanian land bridge came into existence and united the two Americas. Thereafter the fossil record documents an intermingling of the long-separated American land mammal faunas (Patterson & Pascual, 1972).

The fossil mammals from the late Cretaceous (Sigé, 1971, 1972; Crochet, 1978, 1979b, 1980) Laguna Umayo local fauna of Peru, the oldest known land mammal fauna[11] in South America, represent the two major elements characteristic of the Tertiary fauna of that continent (table 18) — metatherian Didelphoidea and eutherian Condylarthra. The possible condylarth *Perutherium*, the only eutherian so far described, appears to be a member of the early Tertiary family Didolodontidae and according to Tedford (1974) is morphologically similar to the Riochican and Casamayoran genus *Ernestokokenia*. However, Van Valen (1978, p. 67) placed *Perutherium* in a new subfamily, Perutheriinae, family Periptychidae, order Condylarthra; and the possibility exists that *Perutherium* represents a bunodont marsupial, as suggested by Hoffstetter (1970c, p. 972). According to Crochet (1978, 1979b, 1980) the Didelphoidea from Laguna Umayo are the more ancient representatives of the genus *Peradectes* and the tribe Didelphini. Their descendants migrated to North America in the Paleocene and then to Europe in the early Eocene. The questionable pediomyid marsupial represents a group otherwise confined to the North American late Cretaceous.

The Riochican mammals are characterized by a marked grade of autochthonism as emphasized by the first and last record of the order Xenungulata (table 18). With the exception of the Astrapotheria and Pyrotheria, there are found in the Riochican representatives of all other known orders of native mammals.

The Riochican faunas from Patagonia, Argentina and Itaboraí, Brazil differ with regard to the groups found in them, and these differences may be attributable to biogeographical and/or ecological factors. At Itaboraí, didelphoid marsupials are extremely varied and abundant, notoungulates are known only from a few taxa, while the Xenungulata are relatively more abundant (table 15). In all known Tertiary faunas of Patagonia, didelphoids are extremely rare, the notoungulates constitute the most

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[11] Remains of reptiles? or mammals? have been recorded from a stratigraphic unit of indeterminate age from near the railroad station El Quemado near the pueblo San Pedro de Jujuy, Jujuy Province, Argentina (Feruglio, 1927, 1931b; Simpson, 1932a, p. 8). These specimens, collected by Feruglio, included an incomplete mandibular ramus, a fragment of another mandible, and a small scapula. He regarded these as a Mesozoic mammal and the beds as Jurassic or early Cretaceous in age. The fossils were neither described in detail nor illustrated, and were later lost. From this same unit, but from a somewhat higher level, von Huene (1931, p. 183, 184) described a small mandible which he named «*Carlesia*» *incognita* (=*Dicarlesia incognita* VON HUENE, 1932, p. 192 *nec Carlesia* KRAGLIEVICH, 1926b, a genus of fossil Rodentia). According to Simpson (1932a, p. 9), von Huene believed that this specimen had the general aspect of a Mesozoic mammal, although Simpson believed that it was referable to a reptile, possible to a Lacertilia. We feel, however, that this specimen is probably a bony fish. Casamiquela (1961) described footprints, which he named *Ameghinichnus patagonicus* from the upper Jurassic of Patagonia, Argentina and interpreted them as mammalian.

abundant mammals (in both numbers of species and individuals), while the Xenungulata are relatively rare (Pascual & Odreman Rivas, 1971, p. 377).

Paula Couto (1970a, p. 78) commented that the abundance of didelphoids at Itaboraí suggests the presence or predominance of tropical forests, and the known ungulates may have been forest dwellers as is the modern tapir. In contrast, the predominance of ungulates and scarcity of didelphoids in Patagonia suggests the presence of a savanna-woodland habitat, perhaps somewhat denser than the *llanos* or *sabanas* (South American savannas) of today.

Pascual & Odreman Rivas (1971, p. 377) noted that during Riochican time central Patagonia was relatively flat and was certainly lower than it is now. As evidenced by the presence of fossil palms and crocodiles, the climate was subtropical to warm temperate. The abundance of medium to large browsing herbivores, and the frequent presence of fossil tree trunks are consistent with a savanna-woodland habitat. The Andes mountains, if present, did not yet act as an effective barrier against moisture laden winds from the Pacific.

Several Riochican taxa show close structural affinity to similar aged taxa from North America and/or Asia. Paula Couto (1952b, p. 387) and Simpson (1967b, p. 240) have noted the morphological similarity between the South American *Carodnia* (order Xenungulata) and the North American *Uintatherium* (order Dinocerata). Both authors believe these taxa to have evolved independently from primitive condylarth ancestors.

Paula Couto (1952b, p. 366) pointed out similarities between the South American Riochican and Casamayoran condylarth *Asmithwoodwardia* and members of the North American Paleocene-Eocene condylarth family Hyopsodontidae. He noted that in size *A. scotti* is close to *Hyopsodus lepidus* from the lower Eocene Bridger beds and accordingly he placed *Asmithwoodwardia* in the subfamily Hyopsodontinae. Paula Couto no longer (*e.g.* 1978c) maintains this view, and now places *Asmithwoodwardia* in the endemic South American condylarth family Didolodontidae.

Notoungulates are abundant in Riochican and later faunas in South America. One genus, *Arctostylops* (family Arctostylopidae), is known from the late Paleocene-early Eocene (Clarkforkian) of North America and two others, *Palaeostylops* and *Sinostylops*, are known from the early Eocene (or possibly late Paleocene) Gashato and Naran Bulak faunas, both of central Asia. It has been suggested (*e.g.* Gingerich & Rose, 1977, p. 42) that notoungulates originated in Central or South America, migrated into North America during the early part of the Clarkforkian [or even before, since the laurasiatic forms constitute a separate family and since the Mongolian representatives are perhaps late Paleocene in age], and subsequently reached central Asia across a Bering land bridge. This is one of many alternative models to explain the biogeographic history of notoungulates and is clearly speculative (Simpson, 1978, p. 325).

A notable change occurs in some aspects of the fauna and flora from the Riochican to the Casamayoran. Fossil tree trunks are common in the Rio Chico Formation but are rare in the Casamayor beds in the same region. The ungulates of the Rio Chico Formation have primarily brachyodont dentitions, while hypsodont forms (*e.g.* Archaeohyracidae) occur in Casamayoran faunas (Pascual & Odreman Rivas, 1973, p. 321).

Table 18. South American Tertiary Land Mammal Ages and known range distributions of mammalian families

	Late Cretaceous	Riochican	Casamayoran	Mustersan	Divisaderan	Deseadan	Colhuehuapian	Santacrucian	Friasian	Chasicoan	Huayquerian	Montehermosan	Chapadmalalan
Marsupialia													
Argyrolagidae											—	—	—→
Bonapartheriidae			—										
Borhyaenidae		—	—	—	- -	—	—	—	—	—	—	—	
Caenolestidae			—	- -	- -	—	—	—	- -	—	- -	—	- -→
Caroloameghiniidae		—	—										
Didelphidae	—	—	- -	- -	- -	- -	- -	- -	—	—	—	—	—→
Groeberiidae					—								
Microbiotheriidae							—	—	- -	- -	- -	- -	- -→
Pediomyidae	—?—												
Polydolopidae		—	—	—	- -	—							
Prepidolopidae			—										
Sparassocynidae											—	—	—
Thylacosmilidae											—	—	—
Marsupialia?													
Necrolestidae								—					
Primates													
Cebidae (incl. Atelidae)						—	—	- -	—	- -	- -	- -	- -→
Edentata													
Dasypodidae		—	—	—	- -	—	—	—	—	—	—	—	—→
Entelopidae								—					
Glyptodontidae				—	- -	—	—	—	—	—	—	—	—→
Megalonychidae				—?—	- -	—	—	—	—	—	—	—	—→
Megatheriidae								—	—	—	—	—	- -→
Mylodontidae						—	- -	—	—	—	—	—	—→
Myrmecophagiidae								—	—	- -	—	—	- -→
Palaeopeltidae*				—	- -	—							
Condylarthra													
Didolodontidae	—	—	—	—?—	- -	—	- -	- -	—				
Litopterna													
Adianthidae					—	—	—	—					
Macraucheniidae		—	—	- -	- -	—	—	—	—	—	—	—	—→
Proterotheriidae		—	—	—	—?—	—	—	—	—	—	—	—	—

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*This name is actually based on a parataxon.

Table 18. (cont.)

	Late Cretaceous	Riochican	Casamayoran	Mustersan	Divisaderan	Deseadan	Colhuehuapian	Santacrucian	Friasian	Chasicoan	Huayquerian	Montehermosan	Chapadmalalan
Notoungulata													
Archaeohyracidae			—	—	?	?							
Archaeopithecidae			—										
Hegetotheriidae					—	—	—	—	—	—	—	—	—→
Henricosborniidae		—	—										
Homalodotheriidae						—	—	—	—	—			
Interatheriidae		—	—	—	- -	- -	—	—	—	—			
Isotemnidae		—	—	—	- -	—	- -	- -	—				
Leontiniidae						—	—	- -	—				
Mesotheriidae					—	—	- -	- -	—	—	—	—	—→
Notohippidae			—	—	- -	—	—						
Notostylopidae		?	—	—									
Oldfieldthomasiidae		—	—	—	—								
Sparnotheriodontidae			—										
Toxodontidae						—	—	—	—	—	—	—	—→
Astrapotheria													
Astrapotheriidae			—	—	- -	—	—	—	—				
Trigonostylopidia													
Trigonostylopidae		?	—	—									
Pyrotheria													
Colombitheriidae			—	- -	—	?							
Pyrotheriidae			—	—	- -	—							
Xenungulata													
Carodniidae		—											
Rodentia													
Abrocomidae											—	—	—→
Caviidae									—	—	—	—	—→
Chinchillidae						—	—	—	—	—	—	—	—→
Dasyproctidae						—	—	—	—	—	—	—	—→
Dinomyidae						—	—	—	—	—	—	—	—→
Echimyidae						—	—	—	—	—	—	—	—→
Eocardiidae						—	—	—	—				
Erethizontidae						—	—	—	—	- -	—	- -	- -→
Hydrochoeridae										—	—	—	—→
Myocastoridae												—	—→
Neoepiblemidae							—	—	- -	- -	—		
Octodontidae						—	—	—	—	—	—	—	—→
Cricetidae												—	—→
Carnivora													
Mustelidae													—→
Procyonidae											—	—	—→
Artiodactyla													
Tayassuidae													—→

There is, however, no significant gap or recognized hiatus between latest Riochican and earliest Casamayoran time (Simpson, 1948, 1978, p. 320). The composition of the Casamayoran mammal fauna is thus basically similar to that of the Riochican, and the following genera are recorded in both: *Nemolestes*?, *Patene, Polydolops, Prostegotherium, Ernestokokenia, Asmithwoodwardia, Henricosbornia, Homalostylops, Othnielmarshia, Peripantostylops, Isotemnus, Transpithecus, Notopithecus, Eohyrax, Victorlemoinea, Anisolambda, Josepholeidya, Ricardolydekkeria*, and *Trigonostylops*. Casamayoran faunas of Patagonia are characterized by the first record of Pyrotheria and Astrapotheria (Pascual & Odreman Rivas, 1971, p. 380) (table 18).

A marked hiatus, as indicated by differences between the characteristic mammalian faunas, occurs between known Casamayoran and known Mustersan deposits in Patagonia (Pascual & Odreman Rivas, 1973). Only six genera, at most, are known from both (*Polydolops, Trigonostylops*; and tentatively *Meteutatus, Notopithecus, Eohyrax*, and *Acoelohyrax*). One reason for the small number of genera shared by these faunas is the fact that Mustersan faunas are poorly represented. Known Mustersan faunas are more similar to Casamayoran than to Deseadan faunas, and are characterized by the first record of Glyptodontidae, Megalonychidae, Notohippidae, and primitive Hegetotheria; by the diversification and predominance of the Archaeohyracidae and Isotemnidae; by a marked scarcity of marsupials and condylarths; by an absence of Macraucheniidae (certainly a defect of preservation as this group is known from earlier and later faunas); and by the last record of the Notostylopidae, Notopithecinae, and Trigonostylopoidea (Pascual & Odreman Rivas, 1971, p. 382) (table 18).

A marked difference exists in Patagonia between the mammals which characterize Mustersan and those which characterize Deseadan faunas, indicating a major hiatus between these two ages. Only four genera, at most, are known from both (*Meteutatus, Interhippus*; and tentatively *Glyptatelus*, and *Palaeopeltis*). Part of this hiatus is apparently represented in eastern Patagonia by the "Estratos con *Monophoraster y Venericor*" marine beds of Camacho (1974), and by the vertebrate fauna from the Divisadero Largo Formation in westcentral Argentina (Simpson, Minoprio & Patterson, 1962).

"The most striking peculiarity of... [the Divisadero Largo]... fauna is its taxonomic distinctness... Certainly all of the species, probably all of the genera, perhaps about a third of the families, and possibly even an order (for *Acamana*) are, on present knowledge, unique to the fauna" (Simpson, Minoprio & Patterson, 1962, p. 290). Rodents are unknown in the Divisadero Largo fauna, while their role is apparently occupied, at least in part, by the rodent-like marsupial, *Groeberia*, known only from this fauna.

"*Pyrotherium* has long been considered a guide fossil for what is now called the Deseadan stage, and related genera are known from the earlier Casamayoran and Mustersan. The absence of pyrotheres from the Divisadero Largo fauna cannot, however, be considered particularly significant [even if that fauna is regarded as early Deseadan in age as suggested by Simpson, Minoprio & Patterson (1962)]. Fairly well known local faunas certainly of Deseadan age but without *Pyrotherium* have already been reported (*e.g.*, Chaffee, 1952). Leontiniids are in fact more constantly present in Deseadan faunas [from Argentina] and are more useful as guide fossils for that stage. [Leontiniidae are curiously rare, but *Pyrotherium* is present, in the Salla fauna of

Bolivia.] Their absence in the Divisadero Largo, if not accidental, may again be ascribed to the manifest ecological peculiarity of this fauna. Deseadan pyrotheres are larger than any mammals yet known from the Divisadero Largo, and Deseadan leontiniids are also larger than any of the latter with the possible exception of *Acamana*" (Simpson, Minoprio & Patterson, 1962, p. 291).

There was in the Deseadan a culmination of the adaptive radiation of primitive groups and the initiation of groups which came to be dominant in the late Tertiary. The Deseadan is characterized by the last record of the Proborhyaeninae, Polydolopoidea (in Bolivia), Condylarthra (in Bolivia - *Salladolodus*: see Soria & Hoffstetter, 1983), Archaeohyracidae, Pyrotheria, and Isotemniidae (in Patagonia) [but Didolodontidae and Isotemnidae are known as late as the Friasan (middle Miocene) in Colombia]; by the first record of Homalodotheriidae, Toxodontidae, and Mylodontidae; and by the first and last record of large mylodontoids (*e.g. Octodontotherium, Orophodon*) (Pascual & Odreman Rivas, 1971, p. 385). A feature of Deseadan faunas is the extraordinarily large size of many mammalian taxa (*e.g. Proborhyaena, Paraborhyaena, Pyrotherium, Clypeotherium, Leontinia, Scarrittia*).

Most importantly, primates (Hoffstetter, 1969) and caviomorph rodents (Wood & Patterson, 1959; Hoffstetter & Lavocat, 1970; Patterson & Wood, 1982) are first recorded in South America in the Deseadan (table 18). The geographic origin of these groups is debated, and they are believed by some workers to have come from North America (*e.g.* Wood & Patterson, 1959; Wood, 1972; Patterson & Wood, 1982) and by others to have come from Africa (*e.g.* Lavocat, 1971; Hoffstetter & Lavocat, 1970; Hoffstetter, 1972a, b, 1976b, 1977b, 1980b, c; Ciochon & Chiarelli *eds.*, 1980). Because of their taxonomic diversity in the Deseadan fauna these rodents are believed to have arrived in South America sometime during the late Eocene (or earlier).

There also occur in the known Deseadan large carnivorous marsupials (*i.e. Proborhyaena, Paraborhyaena*); the development of large dasypodids and glyptodontids; the first record of specialized Litopterna (*e.g.* Adianthidae) and the differentiation of the Proterotheriidae and Macraucheniidae; the differentiation of large Toxodonta (*e.g.* Leontiniidae); the climax in variety of modern lineages of Typotheria (*e.g.* Interatheriidae); and the adaptive radiation of the Hegetotheriidae (Pascual & Odreman Rivas, 1971, p. 385).

Taxonomically, Deseadan faunas are more similar to Colhuehuapian faunas than they are to those from the Mustersan. Nine genera are known from both Deseadan and Colhuehuapian faunas — *Palaeothentes, Parabderites, Stenotatus, Peltephilus, ?Scotamys, Argyrohippus, Proadinotherium, Cochilius,* and Parastrapotherium (tables 7, 8). But the Mustersan fauna is inadequatly known.

Colhuehuapian mammal faunas of Patagonia are very similar to those from the Santacrucian of Patagonia, more so than to those faunas from the Deseadan. The following genera are recorded from both the Colhuehuapian and Santacrucian: *Microbiotherium, Acrocyon, Arctodictis, Borhyaena, Cladosictis, Sipalocyon, Abderites, Palaeothentes, Parabderites, Pichipilus, Peltecoelus, Proeutatus, Prozaedius, Stegotherium, Stenotatus, Peltephilus, Propalaehoplophorus, Acaremys, Perimys, Luantus, Steiromys, Licaphrops, Theosodon, Adianthus, ?Homalodotherium, Protypotherium, Hegetotherium, Pachyrukhos,* and *Astrapotherium* (tables 8, 9). Colhuehuapian faunas include the first record of platyrrhine monkeys in Patagonia (they are first known from the Deseadan of Bolivia — Hoffstetter, 1969) and of the last record of Leontiniidae in Patagonia (they survive into the Friasian of Colombia — Hirschfeld & Marshall, 1976).

Perhaps the richest and best known of all South American Tertiary faunas is from the Santa Cruz Formation of southern Patagonia. Faunas of this age are characterized by the predominance and diversity of rodents and edentates; by the first and last record of the enigmatic burrowing mammal *Necrolestes*; by the first record of the most primitive Megatheriidae ('Planopsinae') with forms similar to their megalonychid ancestors; by the last certain record of the marsupial subfamilies Abderitinae and Palaeothentinae, and of platyrrhine monkeys in Patagonia; by the marked diversity of Megalonychidae; by the last record of the litoptern family Adianthidae and of a tendency toward monodactylism in the family Proterotheriidae (finally acquired by *Thoatherium*); by the last occurrence of the notoungulate family Notohippidae only in early beds of this age (*Notohippidense* fauna of Ameghino — see Marshall & Pascual, 1977); by the first record of Xotodontinae, Toxodontinae, and Haplodontheriinae; and by the extraordinary quantity of Hegetotheria (Pascual & Odreman Rivas, 1971, p. 395-396) (table 18).

Friasian faunas of Patagonia are similar to those from the Santacrucian, but are less well known. Friasian age faunas in Argentina and Chile are characterized by the first record of the rodent families Caviidae and Dinomyidae, and of typical Megatheriidae; and by the last record of Astrapotheria (table 18).

Santacrucian and Friasian faunas of Argentina are known to share the following genera: ***Proeutatus, Prozaedius, Stenotatus, Propalaehoplophorus, Eucinepeltus, Pseudhapalops, Hapalops, Eucholoeops, ?Stichomys, Prolagostomus, Neoreomys, Eocardia, Thoatherium, Diadiaphorus, Theosodon, Homalodotherium, Adinotherium, Nesodon, Interatherium, Epipatriarchus, Protypotherium, Hegetotherium, Astrapotherium***, and possibly ***Abderites, Borhyaena***, and ***Prepotherium*** (tables 9, 10).

The Friasian La Venta fauna of Colombia is particularly significant because it provides a sample of an aequatorial environment during the middle Miocene. Much of this fauna is distinct, representing genera and species unknown in Argentina or Chile at that time or elsewhere in South America. The fauna also contains taxa representing late survival of essentially early Tertiary mammals such as a didolodont condylarth (*Megadolodus*), a leontiniid, an isotemnid-like notoungulate (McKenna, 1956), and mylodontid ground sloths (Hirschfeld, 1971) which have their closest affinities with Oligocene forms in Argentina.

During the late Miocene and Pliocene the principal Argentine continental sedimentation centers shifted from Patagonia to the pampas and northwestern regions (Pascual, 1961, p. 64; Patterson & Pascual, 1972, p. 251; Yrigoyen, 1969, p. 319, 320, 325). The sediments changed from predominantly pyroclastic (*i.e.* tuffs and bentonitic clays) that characterize pre-Chasicoan units, to predominantly clastic (*i.e.* silts, sands, loess) which predominate post-Friasian units of the pampean region (Pascual, 1961, 1965b; Pascual & Odreman Rivas, 1971, p. 399). This change of sediment type coincided with a post-Friasian phase of Andean orogeny that resulted in elevation of the Andean Cordillera (Herrero-Ducloux, 1963; Farrar & Noble, 1976). With the orogenic movement (***Tercera Fase del Segundo Movimiento de la Orogenia Andina*** of Groeber, 1951, p. 275) there culminated a sedimentary process largely in Patagonia. A major period of orogenic activity occurred between 4.5 and 2.5 Ma (Van der Hammen *et al.*, 1973, p. 101) and resulted in an increase in elevation of 2000 to 4000 meters (B. Simpson, 1975). Elevation of the Andean Cordillera acted "as a barrier to moisture-laden Pacific winds" (Patterson & Pascual, 1972, p. 251). The southern South American habitat changed from primarily savanna-woodland (which predominated during the early to middle Tertiary — Eocene through Miocene) to drier forests and pampas, ranging from forests in the northern parts of the continent to grasslands in the south (Pascual & Odreman Rivas, 1971). There was initiated the desertization of Patagonia, caused by the rain shadow effect of the newly elevated Andes. Precocious pampas environments, predecessors to those prevailing today, "probably came into prominence at about this time, [and] many of the subtropical savanna-woodland forms retreated northward, and new opportunities arose for those mammals able to adopt to a plains environment" (Patterson & Pascual, 1972, p. 251).

A recognizable change occurred in the mammal fauna between the Friasian and Chasicoan which was coincident with these environmental changes. Although some ancestral forms for typical Chasicoan taxa are recognizable in known beds of Friasian Age, these are generally distinguished at the generic level (Pascual & Odreman Rivas, 1971); only six genera (*Cardiomys*?, *Vetelia*, ?*Palaehoplophorus*, *Xyophorus*, *Theosodon*, and *Protypotherium*) are known from both faunas (tables 10, 11). Recently, some transitional faunas have been found near Salina Gualicho in Río Negro Province in northeastern Patagonia (Bondesio & Pascual, unpublished).

Chasicoan faunas record the last appearance of typical Friasian forms (*e.g.* *Xyophorus*, Peltephilinae, *Vetelia*, *Theosodon*, Homalodotheriidae, Interatheriidae), and the first appearance of Caviinae, Cardiatheriinae, *Tetrastylus*, *Gyriabrus*, *Diaphoromys*, *Carlesia*, *Typotheriopsis*, *Paedotherium*, and *Tremacyllus* (Pascual & Odreman Rivas, 1971, p. 399) (tables 11, 18).

Sometime during the late Miocene a limited, but important interchange of mammalian taxa between North and South America took place. Procyonids (racoons and their allies), a group of North American origin, first appear in South America in beds of Huayquerian Age, while members of the extinct South American ground sloth families Megalonychidae and Mylodontidae first appear in North America in early Hemphillian time (tables 18 and 19). [Megalonychid sloths are first recorded in North America near the beginning of Hemphillian time (9.0-9.5 Ma). *Pliometanastes* is recorded at about the same time as the first mylodontid, *Thinobadistes* toward the end of the early Hemphillian (7.0-8.0 Ma) (Marshall *et al.*, 1979) (table 19).] It is now generally agreed (*e.g.* Webb, 1976; Marshall *et al.*, 1979) that these groups dispersed along island arcs before the appearance of the Panamanian land bridge in the Pliocene (ca. 3.0 Ma, see below).

The following genera are recorded in both Chasicoan and Huayquerian faunas: *Plesiomegatherium*, *Cercomys*, *Lagostomopsis*, *Diaphoromys*, *Potamarchus*, *Tetrastylus*, *Cardiomys*, *Orthomyctera*, ?*Cardiatherium*, *Procardiatherium*, *Pisanodon*, *Typotheriopsis*, *Hemihegetotherium*, and *Paedotherium* (tables 11, 12).

During the Huayquerian a major change occurred in the mammalian fauna. Many lineages present during the Colhuehuapian, Santacrucian, Friasian, and Chasicoan (the *pan-Santacrucian* faunal groups of Simpson, 1940) [these faunal groups are equivalent to *chronofaunas* and are recognizable on the basis of major relay events], became extinct and others [the *Araucanian* faunal groups of Simpson (1940, p. 682) or *pan-Araucanian* faunal groups of Hoffstetter (1961, p. 495)] which characterize Huayquerian and Montehermosan faunas, became well established.

Table 19. First records of South American immigrants in North America (largely after Webb, 1976)

North American Land Mammal Age	**Taxa**	**Fauna**	**Reference**
Irvingtonian	*Didelphis*	Coleman IIA, Florida	Martin (1974)
Irvingtonian	*Pampatherium* (= *Chlamytherium*) (incl. *Holmesina*)	Coleman IIA, Florida	Martin (1974)
Early Irvingtonian	*Hydrochoerus*	Inglis IA, Florida	Webb (1974)
Early Irvingtonian	*Eremotherium*	Inglis IA, Florida	Webb (1974)
Early Irvingtonian	*Nothrotheriops**	Vallecito Creek, California	Opdyke, Lindsay, Johnson and Downs (1977:316)
Late Blancan	*Titanis***	Santa Fe River I, Florida	Webb (1976:220; pers. comm.)
Late Blancan	*Dasypus* (incl. *Propraopus*)	Haile XVA; Santa Fe River IA, Florida	Robertson (1976:111)
Late Blancan	*Kraglievichia****	Santa Fe River IB; Haile XVA, Florida	Robertson (1976:111); Webb (1974)
Late Blancan	*Glossotherium* (incl. *Paramylodon*)	Haile XVA, Santa Fe River I, Florida; Cita Canyon (*ca.* 2.7 Ma), Texas	Lindsay, Johnson and Opdyke (1976:111); Robertson (1976:111)
Late Blancan	*Glyptotherium*	Cita Canyon (*ca.* 2.7 Ma) and Mt. Blanco, Texas	Lindsay, Johnson and Opdyke (1976:111); Gillette (1974); Gillette and Ray (1981)
Late Blancan	*Neochoerus*	111 Ranch, Flat Tire Fauna, Arizona	Lindsay and Tessman (1974:3)
Late Blancan	*Erethizon*****	Wolf Ranch, San Pedro Valley, Arizona	Johnson, Opdyke and Lindsay (1975:5); Frazier (1981)
Early Hemphillian	*Thinobadistes*	Mixon's Bone Bed, Florida	Hay (1919:106)
Early Hemphillian	*Pliometanastes*	McGehee Farm, Florida	Hirshfeld and Webb (1968:213)
Early Hemphillian	megalonychid	Oshkosh, Nebraska	Schultz and Stout (1948:553)

*Generic arrangement follows Paula Couto (1971:499). Golz, Jefferson and Kennedy (1977) report a ground sloth, the size of *Nothrotheriops*, from a Late Blancan fauna from the Temecula Arkose, Riverside County, California.

**A bird of the group Phororhacoidea.

****Kraglievichia s.l.*, after Robertson (1976) includes *Plaina* and *Vassalia*.

****Frazier (1981) refers specimens, called *Coendu* by early workers, to *Erethizon*.

Diaphoromys and *Typotheriopsis* are last recorded during Huayquerian time. Sparassocynidae, Argyrolagidae (= Microtragulidae), Thylacosmilidae, *Eleutherocercus, Phtoramys, Pseudoplataeomys, Brachytherium, Eoauchenia, Promacrauchenia, Pseudotypotherium*, Abrocomidae, and Procyonidae are first recorded in beds of Huayquerian Age from Argentina (table 12). Other notable features of Huayquerian faunas include an incredible diversity of Glyptodontidae marking the "evolutionary climax" of this group; a decrease in the diversity in southern latitudes of Megalonychidae and a progressive replacement by their collaterals, the Megatheriidae and Mylodontidae; and among the Mylodontidae, the Mylodontinae are rare and the Scelidotheriinae abundant in the Pampean region of Buenos Aires Province, while in the foothills of the Andes (like the Valle de Santa María) and in the Mesopotamian region (between the Ríos Paraná and Uruguay) Mylodontinae are more common than Scelidotheriinae.

Among rodents, the Octodontidae and Echimyidae began to develop features and distributions that characterize living representatives; the first record of gigantic forms of Dinomyidae (*e.g.*, *Telicomys*); and the first record in southern latitudes of large Erethizontidae (*i.e.*, *Neosteiromys*).

Among notoungulates, three lineages of Toxodontidae become well established — the Xotodontinae, Haplodontheriinae, and Toxodontinae. There is an "evolutionary climax" of the Mesotheriidae and the first record in that group and in the Hegetotheriidae of relatively large forms (*e.g.*, *Pseudotypotherium, Hemihegetotherium*) (Pascual & Odreman Rivas, 1971, p. 401).

The following mammal genera have been recorded in both Huayquerian and Montehermosan faunas: *Hyperdidelphis, Thylatheridium, Achlysictis, Thylacosmilus, Microtragulus, Doellotatus, Chorobates, Eleutherocercus, Urotherium, Pronothrotherium, Plesiomegatherium, Phtoramys, Pseudoplateomys, Cercomys, Eumysops, Lagostomopsis, Telicomys, Cardiomys, Caviodon, Orthomyctera, Palaeocavia, Protabrocoma, Cyonasua, Brachytherium, Eoauchenia, Promacrauchenia, Xotodon, Pseudotypotherium, Paedotherium,* and *Tremacyllus* (tables 12, 13).

Montehermosan faunas are, as in the Huayquerian, dominated by *pan-Araucanian* groups. In southern latitudes the marsupial family Borhyaenidae, the hydrochoerid rodents *Anchimysops* and *Neoanchimys*, the octodontid rodent *Phtoramys*, and the toxodont subfamily Haplodontheriinae are recorded for the last time, while the rodent family Myocastoridae is recorded for the first time (table 13).

The earliest recorded cricetine rodents (tribe Sigmodontini) in South America are known from the "Banco N° 3" (*sensu* Bonaparte, 1960) of the Monte Hermoso Formation along the Atlantic coast, approximately 60 kilometers east of Bahía Blanca, Buenos Aires Province, Argentina. One species each of *Auliscomys* and *Bolomys* are represented (Reig, 1978). These taxa, as well as those from the younger Chapadmalal Formation (see below), are specialized pastoral (grazing) forms which differ little from living species inhabiting the same area today (Reig & Linares, 1969, p. 643; Reig, 1978). They are too advanced and diversified to be considered the first invaders of this group into South America. It is believed by some workers (*e.g.* Hershkovitz, 1972; Reig, 1981) that these rodents arrived possibly in the late Miocene or earlier, by waif dispersal from North America. The Sigmodontini are now thought to have evolved in North America before 7.0 Ma (Baskin, 1978, p. 125), long before their first record in South America or before completion of the Panamanian land bridge during Pliocene time.

The following fossil genera have been recorded from both Montehermosan and Chapadmalalan faunas: *Hyperdidelphis, Thylatheridium, Sparassocynus, Argyrolagus, Microtragulus, Chaetophractus, Doellotatus, Macroeuphractus, Plaina, Chrorobates, Tolypeutes, Ringueletia, Palaeodaedicurus, Urotherium, Proscelidodon, Actenomys, Eucoleophorus, Pithanotomys, Pseudoplataeomys, Cercomys, Eumysops, Isomyopotamus, Telicomys, Cardiomys, Caviodon, Orthomyctera, Palaeocavia, Lagostomopsis, Chapalmatherium, Protohydrochoerus, Protabrocoma, Chapalmalania, Cyonasua, Brachytherium, Promacrauchenia, Xotodon, Pseudotypotherium, Paedotherium*, and *Tremacyllus* (tables 13, 14).

Chapadmalalan faunas are characterized by the first record of a number of *Pampean* faunal groups of Simpson (1940) which came to dominate Pleistocene (*e.g.* Uquian, Ensenadan, Lujanian) faunas. During the Chapadmalalan, the Ctenomyinae reached their major known diversification; the Caviidae were varied; the Cardiomyinae (*Cardiomys, Caviodon*), the hydrochoerid *Cardiatherium*, and the dinomyid (Eumegamyinae) *Telicomys* make their last known record, and some of these groups are represented by a number of specialized cursorial taxa (*e.g. Protohydrochoerus, Chapalmatherium*). The bear-like procyonid *Chapalmalania*, first recorded in the Montehermosan, makes its last record in the Chapadmalalan. The litoptern family Proterotheriidae, and the notoungulate subfamilies Xotodontinae and Haplodontheriinae undergo a marked reduction in diversity during the Chapadmalalan and are unknown in later faunas. The notoungulate genus *Tremacyllus* (Hegetotheriidae) is last recorded during Chapadmalalan time.

Establishment of the Panamanian land bridge in the Pliocene provided a direct dry land connection between the two Americas (Webb, 1976). Across this portal an extensive interchange of terrestrial faunas occurred. The beginning of this interchange in South America is marked by the appearance, in the Chapadmalal Formation in the southeast corner of Buenos Aires Province, Argentina, of mammals which evolved from North American emigrants (fig. 2). These include a mustelid (*Conepatus*, Reig, 1952), a tayassuid (*Argyrohyus*, J. L. Kraglievich, 1959), and four genera (*Akodon, Dankomys, Graomys, Reithrodon*) of Sigmodontini rodents (Reig, 1978, 1980). The appearance of this contingent of northern animals favors the existence of the Panamanian land bridge by this time. A marked increase in mammals of North American origin occurs between the Chapadmalalan and Uquian (late Pliocene - Early Pleistocene - see Marshall, Butler, Drake & Curtis, 1982) in which 18 genera are recorded for the first time (Patterson & Pascual, 1972, p. 287; Marshall, Berta, Hoffstetter, Pascual, Reig, Bombin & Mones, 1984).

A large number of terrestrial vertebrates of South American origin appear in North America in beds of late Blancan Age dated around 2.7 Ma (table 19). These include *Neochoerus, Erethizon, Glyptotherium, Glossotherium, Kraglievichia*, and *Dasypus* among the mammals, and the phororhacoid ground bird *Titanis*. Numerous other South American mammals, including *Nothrotheriops, Eremotherium, Hydrochoerus, Pampatherium*, and *Didelphis*, appear slightly later in the Irvingtonian (Webb, 1976).

RADIOISOTOPE DATES

Argentina

The unique nature of the South American Tertiary land mammal fauna and absence of two-way interchanges of continental faunas with North America deterred precise biostratigraphic intercontinental correlations by early workers. Despite these drawbacks a *relative* time scale for mammalian faunal succession within South America is agreed upon (Patterson & Pascual, 1972; Feruglio, 1949; Pascual & Odreman Rivas, 1971, 1973; Simpson 1940, 1948) (table 1). The time scale used by these workers was based largely upon stratigraphic tie-ins of the mammal-bearing beds with the marine "Patagonian" beds (tentatively assigned a latest Oligocene or earliest Miocene Age by early workers). The mammal-bearing beds above and below the marine deposits were correlated with geochronological time units largely on the basis of *stage of evolution* and overall distinctness, or similarity, between the contained faunas. Lack of extensive interdigitations of fossiliferous marine and non-marine strata in South America deterred further refinement.

Recently, Argentine beds and faunas of Riochican through Uquian (latest Pliocene — early Pleistocene) Age have been partially calibrated in terms of a radioisotope time scale (Marshall *et al.*, 1977, 1979, 1981, 1982; Marshall & Pascual, 1978). These geochronologic data, along with some radioisotopic dates from Bolivia (see below) permit refined intra- and intercontinental paleontologic-stratigraphic correlations (fig. 10).

At places the Rio Chico Formation is conformably underlain by the marine Salamanca Formation, the late Danian (early but not earliest Paleocene) Age of which is established on various independent lines of evidence (see p. 9). Basalt flows are intercalated between the late Cretaceous, dinosaur bearing Bajo Barreal Formation (= *Chubutense* of Feruglio, 1949, p. 335) and the Salamanca Formation along the upper course of the Río Chico del Chubut, just east of Lago Colhué-Huapí. A sample of one of these basalt flows capping the Bajo Barreal and regarded by Feruglio (1949, p. 335, fig. 157) as the base of the Salamanca Formation, was collected 3 kilometers east of Lago Colhué-Huapí on the south side of the Río Chico, and gave a whole-rock age of 64.2 ± 0.8 Ma (KA 3575). A second sample of a flow 7 kilometers east of Lago Colhué-Huapí on the north side of the Río Chico gave a whole-rock age of 62.3 ± 0.4 Ma (KA 3576). These dates provide basal ages for the Salamanca Formation at these localities (Marshall, Butler, Drake & Curtis, 1981). An early Paleocene Age for the Salamanca Formation is supported by a date of 61 ± 5 Ma of a vitric tuff [measured by E. Linares, INGEIS, Buenos Aires] reported from the upper Hansen Member at Cañadón Hondo along the east side of the Río Chico (Andreis, 1977). The age of this tuff was recalculated by R. Drake (University of California, Berkeley) to be 62.5 ± 5.0 Ma. Dr. Gualter Chebli, YPF, Argentina, believes (personal communication) that this tuff is from the base of the Río Chico Formation and probably from the *Toba cinerítica* level of the profile in fig. 102 of Feruglio (1949).

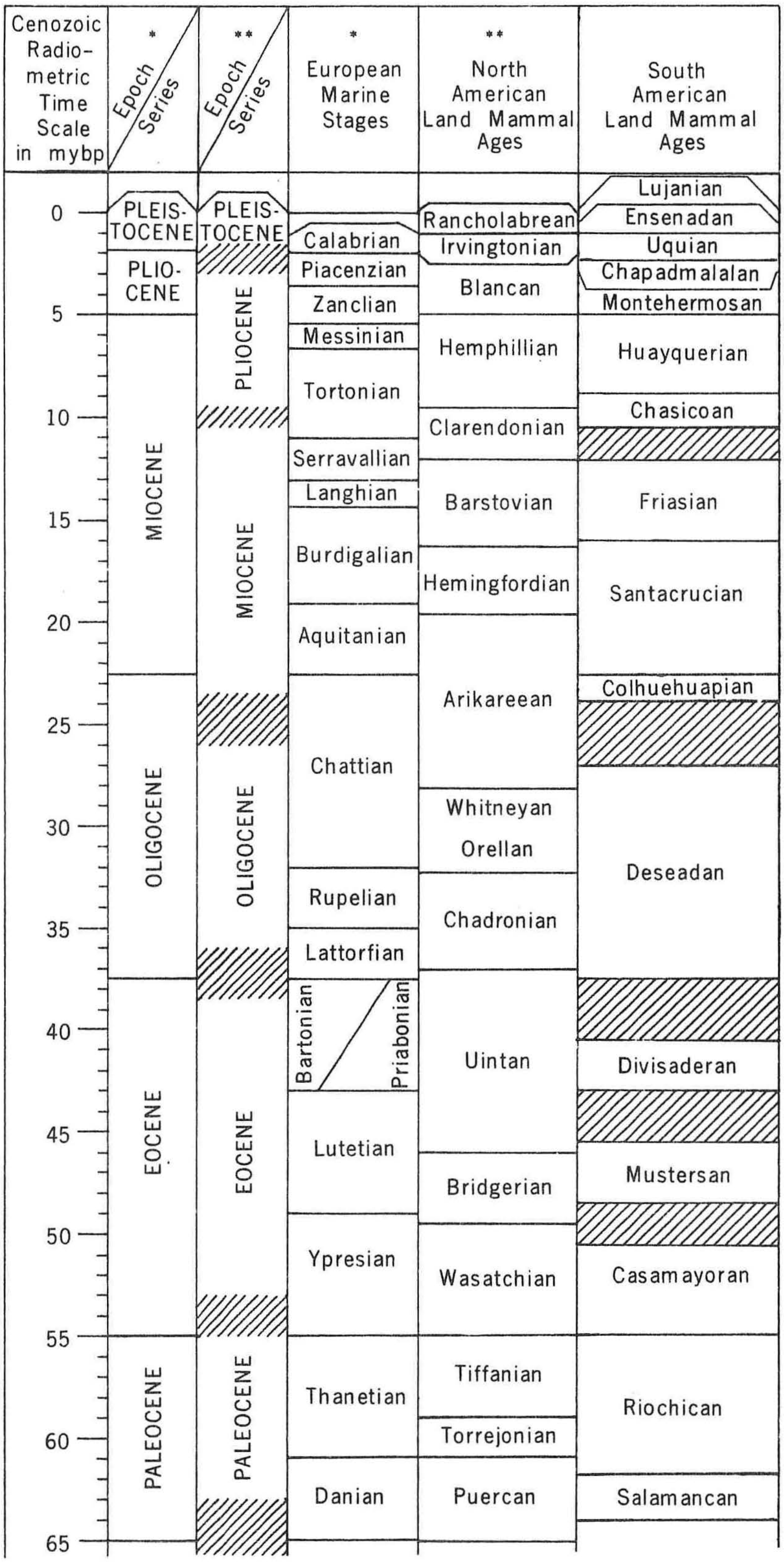
Rock samples suitable for paleomagnetic analysis were collected from 35 sites in a 140 meter section of the Río Chico Formation on the southeast slope of Cerro

Redondo along the Atlantic coast north of Punta Peligro, and from 4 sites in a 5 meter section from the base of the Río Chico Formation (the ***Banco Negro Inferior***) at Punta Peligro. The Banco Negro Inferior was shown to be of reversed polarity at both localities, and at Cerro Redondo no significant unconformity was observed between the Salamanca and Río Chico Formations. These data require that the Salamancan-Riochican boundary be placed near the Danian-Thanetian boundary (~62.0 Ma) (fig. 10). Given this age constraint, the paleomagnetic sequence observed at Cerro Redondo correlates best with the magnetic polarity time scale in the interval from above anomaly 27 chron into anomaly 25 chron. The implied age range of the Río Chico Formation at Cerro Redondo thus encompasses middle and late Paleocene time (Marshall, Butler, Drake & Curtis, 1981).

Many taxa from the upper Riochican level at Bajo de la Palangana occur in typical Casamayoran faunas, indicating that there is little time difference between late Riochican and early Casamayoran (see p. 65). The Río Chico Formation at Bajo de la Palangana is conformably overlain by fossiliferous beds of Casamayoran Age (see p. 12). The exposures at Cerro Redondo terminate below this contact and latest Riochican time is not recorded in that section. Due to absence of geochronologic calibration of latest Riochican, it is convenient and plausible to recognize the Riochican-Casamayoran boundary as the boundary between the Paleocene and Eocene Epochs (fig. 10).

Feruglio (1949, p. 40) reports that at the Great Barranca south of Lago Colhué-Huapí (his fig. 105), at Cerro Blanco, and in the barranca on the south side of the Valle Hermoso (his fig. 106, p. 53), basalt flows are intercalated between beds of Deseadan and Colhuehuapian Age. Two of these basalt flows from separate localities at the west end of the Great Barranca south of Lago Colhué-Huapí gave ages of 28.8 ± 0.9 Ma (KA 2919) and 24.3 ± 0.5 Ma (KA 2942). One flow capping beds believed to be of Deseadan Age at the east end of this barranca gave an age of 27.7 ± 0.6 Ma (KA 2943), and one from Cerro Blanco gave an age of 35.4 ± 0.4 Ma (KA 2920). Based on these dates, Marshall, Pascual, Curtis & Drake (1977), and Marshall & Pascual (1978) tentatively concluded that a terminal date of 34.0 Ma be accepted for known Deseadan, while 25.0 Ma be taken to represent a basal age for known Colhuehuapian. This interpretation is supported by the fact that samples of two flows from Pico Truncado gave complementary ages; the first conformably overlies rocks of Deseadan Age and gave an age of 33.6 ± 0.4 Ma (KA 2917), while the second lies 37 meters up section from the first and gave an age of 27.6 ± 0.4 Ma (KA 2918).

Spalletti & Mazzoni (1979, p. 277, fig. 3) published a detailed study of the geology of the Great Barranca south of Lago Colhué-Huapí. They show that the basalt intercalated in the barranca occurs in the lower part of their *Miembro Puesto Almendra* which contains vertebrate faunas of Deseadan Age and which they believe encompasses lower and middle Oligocene time. Thus, contrary to the conclusions reached by Marshall, Pascual, Curtis & Drake (1977), and by Marshall & Pascual (1978), based on the geological observations of Feruglio (1949), it now appears that the dates obtained on these basalts calibrate Deseadan Age faunas directly at this locality. The three basalts sampled may be of the same flow; if that is true the oldest date (28.8 ± 0.9 Ma) from the least weathered of the samples, should be accepted as most closely approximating the age of this flow. Thus, the dated beds of known Deseadan Age apparently


Cenozoic Radiometric Time Scale in mybp
* Epoch Series
** Epoch Series
* European Marine Stages
** North American Land Mammal Ages
South American Land Mammal Ages
0
5
10
15
20
25
30
35
40
45
50
55
60
65
PLEISTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
PALEOCENE
PLEISTOCENE
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MIOCENE
OLIGOCENE
EOCENE
PALEOCENE
Calabrian
Piacenzian
Zanclian
Messinian
Tortonian
Serravallian
Langhian
Burdigalian
Aquitanian
Chattian
Rupelian
Lattorfian
Bartonian
Priabonian
Lutetian
Ypresian
Thanetian
Danian
Rancholabrean
Irvingtonian
Blancan
Hemphillian
Clarendonian
Barstovian
Hemingfordian
Arikareean
Whitneyan
Orellan
Chadronian
Uintan
Bridgerian
Wasatchian
Tiffanian
Torrejonian
Puercan
Lujanian
Ensenadan
Uquian
Chapadmalalan
Montehermosan
Huayquerian
Chasicoan
Friasian
Santacrucian
Colhuehuapian
Deseadan
Divisaderan
Mustersan
Casamayoran
Riochican
Salamancan

encompass early and middle Oligocene time (fig. 10): see Marshall (1982a).

However, according to Hoffstetter (*in* Petter & Hoffstetter 1983), the interpretation of the Great Barranca section published by Spalletti & Mazzoni (1979, fig. 2-3) remains debatable. According to them (*ibid.* p. 274 and 277), the basalt flow of the Puesto Almendra Member is ***intercalated*** in fossiliferous beds ***tentatively*** assigned to the Deseadan; but the fossil mammals have not yet been identified. Moreover, Pascual (pers. com.) observed Colhuehuapian mammals just above the lowest basalt in Great Barranca; also remains of an astrapothere ("muy probablemente *Parastrapotherium* sp., grande como restos de una especie asociada con mamiferos incuestionablemente colhuehuapenses") were "parcialmente digeridos" by this basalt, which could belong then to the Colhuehuapian. In summary, it is certain that the Deseadan fauna was in existence during the early Oligocene, but its persistance into the middle Oligocene does not seem demonstrated.

Andreis (1977) reports a date (determined by E. Linares) on a basalt from the top of the El Sol Formation (Deseadan Age) from Cañadón Hondo. However, the apparent age of this basalt is somewhat uncertain, for Andreis lists its age as 24 ± 3 Ma on p. 77, 29 ± 3 Ma on p. 82, and 28 ± 3 on p. 94.

Two ^{40}K-^{40}Ar age determinations are available for Santacrucian beds and faunas. A plagioclase concentrate of a tuff from the north side of the Río Gallegos gave an age of 21.7 ± 0.3 Ma (KA 1252) (Evernden, Savage, Curtis & James, 1964, p. 170). A second date of 18.5 ± 0.2 Ma (KA 2944) was obtained on a fine grained vitric tuff from a level 116 meters above the base of the Santa Cruz Formation at Monte León (Marshall, Pascual, Curtis & Drake, 1977; Marshall & Pascual, 1978). These dates indicate that a least the greater part, if not all, of the coastal Santa Cruz Formation is of early Miocene Age (fig. 10).

Biotite and plagioclase concentrates from an ignimbrite underlying a mammal-bearing horizon in the Friasian Age Collón Curá Formation along the Río Collón Curá, Neuquén Province gave ages ranging from 14.0 (KA 3006) to 15.4 (KA 3005) Ma, with an average of 14.5 Ma for four dates (Marshall, Pascual, Curtis & Drake, 1977; Marshall & Pascual, 1978). These dates establish a middle Miocene Age for these beds, which is consistent with the somewhat more progressive ***stage of evolution*** of the faunas compared with typical Santacrucian Age faunas (fig. 10).

Geochronologic studies of Huayquerian and Montehermosan Age beds and faunas are available for two localities yielding rich mammal faunas of those ages in Catamarca Province, northwest Argentina (Marshall, Butler, Drake, Curtis & Tedford, 1979; Marshall & Patterson, 1981). Diverse faunas of Huayquerian Age have been

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Fig. 10. — Cenozoic radioisotope time scale and chronostratigraphy showing approximate chronology of South American Land Mammal Ages correlated with North American Land Mammal Ages and European Marine Stages. The South American time scale is based on radioisotope dates of volcanic rocks associated with faunas in Argentina, (*) largely follows Berggren and Van Couvering (1974); (**) largely follows D.E. Savage (1975).

Note: The extension of the Deseadan to middle Oligocene remains debatable (Hoffstetter, pers. comm.).

collected from units XV-XX of the *Araucanense* of Stahlecker (*in* Riggs & Patterson, 1939; Marshall & Patterson, 1981) from near Chiquimil in the Valle del Río Santa María; and Huayquerian and Montehermosan Age faunas have been collected from units 14-17 of the *Araucanense*, and units 18-32 of the Corral Quemado Formation, respectively, of Stahlecker (*in* Riggs & Patterson, 1939; Marshall & Patterson, 1981) in the vicinity of Corral Quemado (fig. 2).

Rock samples for paleomagnetic analysis were collected from each of 38 sites at Corral Quemado (24 are believed to correlate with units 3-10 of Stahlecker, and 14 with his units 18-28) and 6 sites at Chiquimil are believed correlative with Stahlecker's units XVIII-XIX. The paleomagnetic section from units 3-10, along with an average date of 6.68 Ma for mineral separates of a tuff believed correlative with unit 8, indicate correlation with the greater part (7.4 to 6.5 Ma) of epoch 7 of the magnetic polarity time scale (Marshall, Butler, Drake, Curtis & Tedford, 1979). The short paleomagnetic section from Chiquimil includes an average date of 6.02 Ma on mineral separates from a basal tuff from unit XIX of Stahlecker, and correlates best with the middle of epoch 6 of the magnetic polarity time scale (Marshall, Butler, Drake, Curtis & Tedford, 1979). These geochronologic studies bear directly on the age of Huayquerian faunas.

Fossils assignable to the Huayquerian land mammal age are abundant in unit XVII of the Chiquimil section, some 75 meters below the tuff from unit XIX dated at 6.02 Ma, making the base of the Huayquerian at that locality somewhat older. Accepting an age of 14.5 Ma for the type Friasian (Marshall, Pascual, Curtis & Drake, 1977; Marshall & Pascual, 1978), and the existence of a paleontological hiatus between known Friasian and Chasicoan, the Chasicoan-Huayquerian boundary is tentatively placed at about 9.0 Ma (fig. 10).

The paleomagnetic section of units 18-28 of the Corral Quemado section is capped by a tuff (unit 29 of Stahlecker) which has an average age of 3.54 Ma based on determinations of various mineral separates. This date provides a minimum age for the Montehermosan at that locality. The magnetostratigraphic date indicate that these beds occur at least within the middle part of the Gilbert epoch and provide a maximum age of about 4.4 Ma for the base of the section. These data favor placement of the boundary between known Huayquerian and known Montehermosan at these localities at about 5.0 Ma (Marshall, Butler, Drake, Curtis & Tedford, 1979) (fig. 10).

Refinement of the boundary of known Montehermosan and Chapadmalalan is based on the geochronologic data of the Corral Quemado Formation and on paleontologic data with suggest marked similarity in faunas of these ages (Pascual & Odreman Rivas, 1973, p. 303). These data favor tentative placement of the Montehermosan-Chapadmalalan boundary at about 3.0 Ma (fig. 10; also see below).

The time span of the Chapadmalal Formation and its Chapadmalalan Age faunas can be estimated on various lines of evidence, some of which are circumstantial. First, the Panamanian land bridge probably emerged about 3.0 Ma ago (Hoffstetter, 1981), and, based on an extensive review of pertinent literature, Sloan (1980, p. 523) placed final closure at 2.8±0.2 Ma. The interchange apparently commenced either at that time or shortly following final emergence. Thus, 3.0 Ma may be used as an approximate maximum age for Chapadmalalan beds and faunas. Second, since it is generally conceded that the interchange was a reciprocal and synchronous event, the appearance of seven South American genera in North America in beds of late Blancan Age (*ca.*

2.7 to 2.5 Ma) indicates the existence of the land bridge by that time. Thus, Chapadmalalan predictably ranges from about 3.0 to about 2.5 Ma (fig. 10).

Uquian faunas record the first major contingent of North American participants in the interchange. The Uquian is based on the fauna from the Uquía Formation, Jujuy Province, northwest Argentina and the type locality is at Esquina Blanca (Marshall, Butler, Drake & Curtis, 1982). Recently, rock samples for paleomagnetic analysis were collected from 20 sites in a 215 meter section of the Uquía Formation at Esquina Blanca. The paleomagnetic section best correlates with the magnetic polarity time scale from just below the Gauss-Matuyama boundary up into the lower part of the large reversed zone in the upper half of the Matuyama epoch (Marshall, Butler, Drake & Curtis, 1982). This correlation is corroborated by consideration of the synchronization of timing of the interchange and an average ^{40}K-^{40}Ar date of 2.8 Ma for nearly concordant biotite and glass ages of the *toba dacítica* of Castellanos (1950) from near the base of the Uquía Formation, approximating the true age of the tuff and providing a maximum age for the base of the paleomagnetic section. Thus, the Uquía Formation ranges from about 2.5 Ma at the lowest level exposed to about 1.5 Ma in age at the very top of section (fig. 10). The lowest level from which fossil land mammals have been recorded (see Castellanos, 1950) ranges from about 2.5 to 2.4 Ma (Marshall, Butler, Drake & Curtis, 1982). It is not known whether Uquian Age taxa (*sensu lato*) occur throughout the Uquía Formation.

Bolivia

For Bolivia, a number of radioisotope dates obtained at the Department of Geology and Geophysics, University of California, Berkeley, provide important geochronologic information. However, these dates are sometimes difficult to use because the papers in which these dates were reported (Evernden *et al.*, 1966, 1977) do not always provide sufficient data on the exact lithological nature of the samples nor of the localities from which they came. Moreover, the designations of stratigraphic units from which the dates were obtained are sometimes inaccurate, both in the sections published by Evernden *et al.* (1966, 1977), and in the sheets of the 1/100,000 geological map of the ***Servicio Geológico de Bolivia*** upon which these sections were based.

An important reference point is provided by the ***Toba 76***, with an age of 5.5 Ma (Evernden *et al.*, 1966, section CC'). A visit to this locality by R. Hoffstetter and R. Ascarrunz enabled them to ascertain that the sample was collected at Vituy de Umala, west of Cañaviri. It is a cinerite located in the base of the Umala Formation which lies unconformably on the folded Totora Formation. This date provides a maximum age for the fauna of Pliocene aspect collected in the Umala Formation (at Umala, Ayo Ayo, Vizcachani, etc.) which is overlain by a well-characterized Pleistocene fauna with *Scelidodon* and *Macrauchenia*. But the Montehermosan-Chapadmalalan Age faunal association (Hoffstetter *et al.*, 1971b; Hoffstetter & Villarroel, 1974; Villarroel, 1975, 1977) from the Umala Formation differs from those of Argentina. This difference is explainable on ecological grounds, notably the latitude and altitude of the Bolivian Altiplano. The faunas of the La Paz Formation (Sehuencoma, Gualberto Villarroel, Achocalla) are temporal equivalents to those of the Umala Formation. This is also true of that from Pomata (200 kilometers south of La Paz), where a cinerite occurs in the base of fossil-bearing sediments (which, according to Martinez, would be the ***Toba 76***), lying unconformably on the Totora Formation, or more accurately on its terminal facies, and designated in sections and maps as the ***Conglomerado Pomata*** (= Crucero). The section by Evernden *et al.* (1966) shows, above this conglomerate, a volcanic unit which gave a date of 6.4 Ma, but it is curiously designated as ***Lavas Mauri***, a stratigraphic unit defined far to the northwest. It is difficult to know whether the dated sample corresponds to the cinerite observed under the Pliocene fauna of Pomata, or whether it is another volcanic unit of this region. It should also be noted that the fossil-bearing unit of Pomata (equivalent to the Umala Formation) is mapped erroneously as "***Formación Mauri***" on the geological sheets 6038 Corque and 6039 Choquecota; it is not figured in the section by Evernden *et al.* (1966) in the Pomata area, but seems to have been included, farther to the northwest, in the ***Lavas y sedimentos Mauri***, which is erroneous.

The dates of Evernden *et al.* (1966, section BB') show that the fossil locality of Achiri and its equivalents (Camacho, Rosario, etc.) of the Mauri 6 Formation (here correctly named) are located above two volcanic units dated at 8.0 and 10.5 Ma, respectively. On the other hand, the Mauri 6 Formation is apparently equivalent to the upper part of the Totora Formation, of which the terminal Crucero facies (lateral equivalent of the fossil-bearing section at Achiri — see section BB' in Evernden *et al.*, 1966) is above two cinerites (Toba Callapa ca. 7.5 Ma; Toba Ulloma 9.0 Ma), apparently equivalent to those of Mauri 6. Finally, the Totora Formation s.l. (including Crucero) is unconformably overlain by a volcanic unit (***Lavas Mauri***, dated 5.9 Ma; section CC' *in* Evernden *et al.*, 1966) which would indicate it to be contemporaneous with the ***Toba 76*** of Umala (5.5 Ma). Despite the confusion resulting from the inaccurate use of the term ***Mauri***, it is clear that the Achiri fauna and its equivalents are within the 6.0 to 8.0 Ma interval (*i.e.*, late Miocene) and correspond in time to Huayquerian Age faunas in Argentina (fig. 10).

In Bolivia, the Pliocene Age of faunal associations from the Umala Formation (Umala, Ayo-Ayo, Vizcachani) and La Paz (Sehuencoma, Achocalla, Gualberto Villarroel) Formation, and known also at Pomata, is confirmed by radioisotopic dates. This fauna is later than the ***Toba 76*** which underlies the Umala Formation, and corresponds to 5.5 Ma (see above) and is older than the ***Toba Chijini*** which overlies the fossiliferous beds of the La Paz Formation dated at 3.27 Ma (see Clapperton, 1979). Servant (personal communication), in opposition to Clapperton (1979), maintains his previous conclusion (Servant, 1977; Ballivián, Bles & Servant, 1978) that there is no glacial formation before the ***Toba Chijini***, and that this cinerite occurs in the upper part of the La Paz Formation.

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