

**Chronostratigraphy of the Mammal-Bearing Paleocene of South America**

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Abstract — Land mammal faunas of Paleocene age in the southern Andean basin of Bolivia and NW Argentina are calibrated by regional sequence stratigraphy and magnetostratigraphy. The local fauna from Tiupampa in Bolivia is ~59.0 Ma, and is thus early Late Paleocene in age. Taxa from the lower part of the Lumbra Formation in NW Argentina (long regarded as Early Eocene) are between ~58.0–55.5 Ma, and thus Late Paleocene in age. A reassessment of the ages of local faunas from the Río Chico Formation in the San Jorge basin, Patagonia, southern Argentina, shows that the local fauna from the Banco Negro Inferior is ~60.0 Ma, making this the most ancient Cenozoic mammal fauna in South America. Critical reevaluation of the Itaboraí fauna and associated geology in SE Brazil favors the interpretation that it accumulated during a sea-level lowstand between ~58.2–56.5 Ma. All known South American Paleocene land mammal faunas are thus between 60.0 and 55.5 Ma (i.e. Late Paleocene) and are here assigned to the Riochican Land Mammal Age, with four subages (from oldest to youngest: Peligran, Tiupampian, Itaboraian, Riochican *s.s.*). Based on the fact that notable taxonomic reorganization of Riochican faunas begins ~58.2 Ma, an Early (Peligran, Tiupampian; 60.0–58.2 Ma) and Late (Itaboraian, Riochican *s.s.*; ~58.2–55.5 Ma) subdivision for this land mammal age is formally recognized. An interchange event for continental taxa between North and South America is identified between 58.2 and 56.5 Ma, which correlates with a sea-level lowstand and was probably enhanced by a major tectonic event beginning ~59.5 Ma that uplifted the Andean margin. © 1997 Published by Elsevier Science Ltd. All rights reserved

INTRODUCTION

Paleocene land mammal faunas in South America are known from the San Jorge basin in Patagonia, southern Argentina; the Andean basin in SE Peru, southern Bolivia and NW Argentina; and at Itaboraí in SE Brazil. The absolute and relative ages of the various local faunas are currently debated, and in recent years they have been arranged, in various combinations, into four Land Mammal Ages (see Pascual and Ortiz-Jaureguizar, 1991; Bonaparte *et al.*, 1993; Marshall and Sempere, 1993). Existing controversies stem from a lack of secure geochronologic age control of the vast majority of the local faunas, and the difficulty of correlating them over long distances based on "stage of evolution" of the taxa. Until recently, only local faunas from two localities in the San Jorge basin have been calibrated by magnetostratigraphy (Marshall *et al.*, 1981), the data for which have been interpreted in different ways by some workers (e.g. Bonaparte *et al.*, 1993).

In this paper, we provide a new calibration for the Paleocene land mammal local faunas in the southern part of the Andean basin using refined knowledge of regional sequence stratigraphy and magnetostratigraphy (Sempere *et al.*, 1997). We also reassess ages of local faunas from the San Jorge basin of southern Argentina and Itaboraí of Brazil. Based on this study, we propose a refined zonation for Paleocene land mammal faunas of South America. We also identify an interchange event between North and South America in the Late Paleocene (between ~58.2 and 56.5 Ma) which helps explain aspects of change in faunal composition in the Americas during this time interval.

We begin with an overview of the regional geology of Paleocene mammal-bearing rocks in the Andean basin of

Bolivia and NW Argentina (Fig. 1), which is the foundation for correlating the various local faunas.

**CHRONOSTRATIGRAPHY OF
MAMMAL-BEARING PALEOCENE STRATA IN
BOLIVIA AND NW ARGENTINA**
Geological Setting

The Late Cretaceous-Paleogene stratigraphy of Bolivia is reviewed by Sempere *et al.* (1997). The lithologic units discussed below (Fig. 2) belong to the upper part of the Upper Puca supersequence and to the lower part of the Corocoro supersequence (Sempere, 1990, 1995). This mainly continental Senonian-Oligocene succession was deposited in the axial to distal part of the Andean under-filled foreland basin, under a warm subtropical climate (Sempere, 1994; Sempere *et al.*, 1997).

The Maastrichtian-middle Paleocene uppermost part of the Puca Group comprises the El Molino and Santa Lucía (Fig. 2) formations and their lateral equivalents. Thickness of this succession generally ranges from 200 to 800 m. Sequence-stratigraphic methods enable recognition of numerous sequences in the El Molino and Santa Lucía formations. Grouping of these sequences permits formal recognition of guide units of regional stratigraphic value, respectively called Lower, Middle and Upper El Molino, and Lower, Middle and Upper Santa Lucía (Sempere *et al.*, 1997).

The late Paleocene-Oligocene part of the Corocoro supersequence comprises the Cayara, Potoco and Camargo formations and their lateral equivalents (Fig. 2). The Santa Lucía/Cayara contact separates the Upper Puca and Corocoro supersequences. This contact is a significant unconformity (Figs. 2–4) generally erosional and locally angular

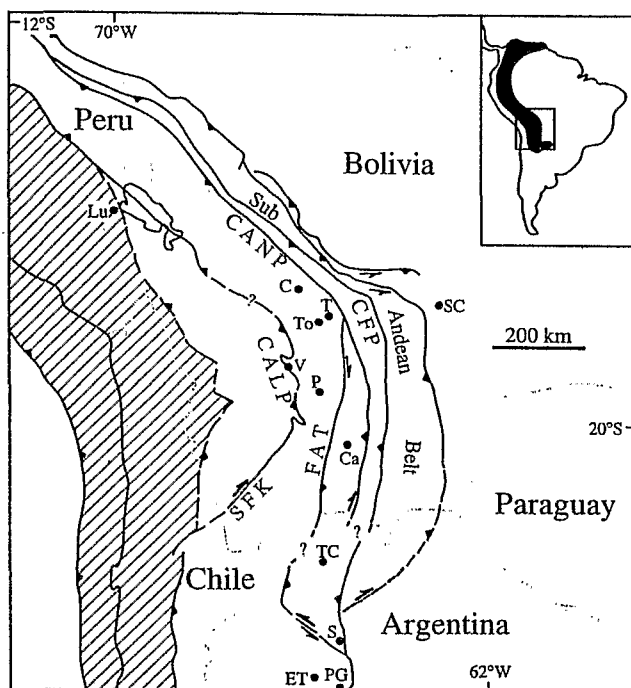


Fig. 1. Neogene structural sketch map of the central Andes (simplified after Sempere, 1994, 1995) showing localities mentioned in text. C = Cochabamba, Ca = Camargo, ET = Estrecho del Tonco, LU = Laguna Umayo, P = Potosí, PG = Pampa Grande, S = Salta, SC = Santa Cruz, T = Tiupampa, TC = Tres Cruces, To = Torotoro, V = Vilcapujio. Hatched = western Andean belt; Spanish abbreviations for faults: CANP = Main Andean Thrust, CFP = Main Frontal Thrust, FAT = Aiquile-Tupiza Fault; SAB = Sub-Andean belt; dotted segments = Khenayani-Turuchipa paleostructural corridor (CPKT). Fine dashed lines are political borders. Insert: Late Cretaceous Andean basin (black) and location of map (box) within South America.

(Marocco *et al.*, 1987), which post-dates a tectonic event initiated at ~ 59.5 Ma (Sempere *et al.*, 1997). This unconformity is dated ~ 58.2 Ma (Sempere *et al.*, 1997) and records in Bolivia a major modification of the tectonic setting, including forebulge uplift (generating the Cayara sandstones) and westward migration of the axis of subsidence. The Cayara Formation marks the onset of the functioning of Andean Bolivia as a continental, external, "classic" foreland basin, resembling the present-day Beni-Chaco basin (Marshall and Sempere, 1991). The overlying, partly equivalent, Potoco and Camargo formations represent the thick latest Paleocene-Oligocene infilling of this foreland basin.

Santa Lucía Formation (~ 60.0 – 58.2 Ma)

The Santa Lucía Formation overlies the El Molino (Maastrichtian-Danian, ~ 73 – 60.0 Ma; Sempere *et al.*, 1997) with a slight discontinuity, which can be traced throughout the basin and is expressed in northwest Argentina by the contact between the Yacoraite-Tunal-Olmedo set of formations and the overlying Mealla Formation. The Santa Lucía and overlying units were deposited in alluvial to lacustrine environments.

The Lower and Middle Santa Lucía Formation form a coarsening and thickening-upward succession, which is interrupted by the abrupt appearance of coarser deposits at their common boundary (Fig. 2). This succession is equivalent to the Mealla Formation of northwest Argentina (Sempere *et al.*, 1997).

The Lower Santa Lucía Formation begins with red-brown mudstones deposited in a lacustrine environment. Thin white to pink tuffaceous beds occur in this unit, especially in its basal portion, as in the Mealla Formation (Salfty and Marquillas, 1981). At Tiupampa, towards the basin margin, the Lower Santa Lucía Formation consists of orange-brown bioturbated siltstones with common gastropod molds.

Somewhat coarser facies mark the base of the Middle Santa Lucía Formation. In the margin areas, medium-grained to conglomeratic sandstones are intercalated with red-brown mudstones and paleosols, and were deposited in meandering fluvial environments. These sandstones yield vertebrate remains in many localities, as at Tiupampa (Gayet *et al.*, 1991).

The Upper Santa Lucía Formation was also deposited in a lacustrine, to alluvial, environment. It consists of red-brown mudstones, which may show some thin green bands. The top of this member is truncated by the erosional unconformity at the base of the Cayara Formation. Southeast of the Khenayani-Turuchipa paleostructural corridor (CPKT, Fig. 1), the time-equivalent of the Upper Santa Lucía is the Impora Formation.

Impora Formation (~ 58.5 – 58.2 Ma)

The Impora Formation exists only in the Camargo syncline (Fig. 1, Ca). It consists of purple to green lacustrine mudstones and marls, and violet to white fluvial sandstones and conglomerates. Fossil vertebrates (fishes, turtles, crocodiles) are abundant (Gayet *et al.*, 1991). Although it displays different facies, the Impora appears to be a time-equivalent of the Upper Santa Lucía Formation (Fig. 4) and was deposited in a distinct lacustrine basin separated from the Potosí region by contemporaneous reactivation of the CPKT (Fig. 1) (Sempere, 1994).

The Maíz Gordo Formation of northwest Argentina (Fig. 4A–C) shows greenish to purple, mudstone-dominated, vertebrate-rich (mostly turtles, crocodiles and fishes) facies, and appears very similar to the Impora Formation, of which it is a distal equivalent (Sempere, 1994). The Maíz Gordo is dated as Late Paleocene on the basis of palynology (Volkheimer *et al.*, 1984), and the Impora is thus of the same age.

Cayara Formation (~ 58.2 – 57.8 Ma)

The Cayara Formation overlies an erosional unconformity in all Andean Bolivia (see Sempere *et al.*, 1997). It consists of whitish sandstones and minor mudstones and conglomerates which were deposited under a warm and

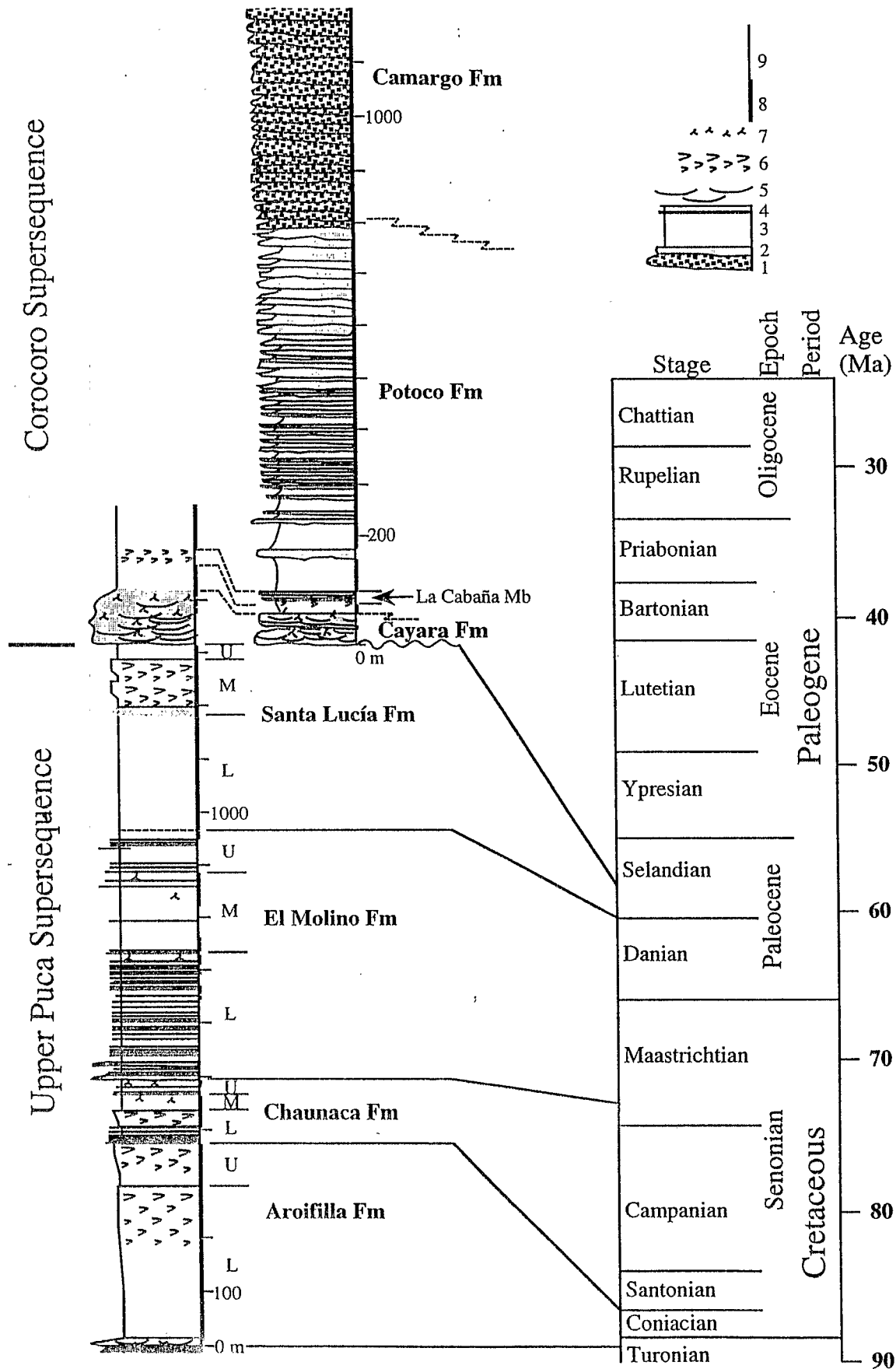


Fig. 2. Stratigraphic columns illustrating lithologies and thicknesses (same scale for both) of the Late Cretaceous to Eocene strata from parts of the Potosí basin. Data concerning the Aroifilla to Cayara formations are from the classic Miraflores syncline near Potosí. Most of the Potoco-Camargo set being absent from the Miraflores syncline, data concerning these units are from the Camargo syncline (modified after Ponce de León, 1966). Abbreviations: Fm = formation, L = Lower, M = Middle, U = Upper. Lithologic symbols: 1 = conglomerates and conglomeratic sandstones, 2 = sandstones, 3 = mudrocks, 4 = carbonates, 5 = channels, 6 = evaporites, 7 = rooting, 8 = predominant brown-reddish color, 9 = predominant greenish, greyish, or whitish, color. Time scale follows Cande and Kent (1992, 1995).

rainy climate. The sandstones are fine to coarse-grained and somewhat saccharoid, frequently finely bioturbated by roots, and distributed in channels which usually show trough cross-bedding. They intercalate with subordinate red-brown mudstones, forming a thinning and fining-upward succession which grades into the red-brown mudstones and siltstones of the lower Potoco Formation. The age of the Cayara-Potoco transition is diachronous (Sempere *et al.*, 1997).

Because the Cayara Formation overlies a conspicuous sequence boundary and generally displays characteristic whitish cross-bedded sandstone facies, it can be recognized throughout the central Andean basin. In this context, the Cayara is equivalent to at least the basal part of the Muñani Formation of southern Peru (Jaillard and Sempere, 1989), the light-colored cross-bedded sandstones generally occurring in the basal part of the Lumbrera Formation of northwest Argentina (see stratigraphic section by Carbajal *et al.*, 1977), the Geste Formation of the Argentine Puna (see Jordan and Alonso, 1987), and the fluvial sandstones assigned to the Maíz Gordo Formation by Donato and Vergani (1988) in the Argentine Puna. Some authors (see Fernández, in Pascual *et al.*, 1978; Gómez-Omil *et al.*, 1989) recognize a disconformity between the Lumbrera and the underlying Maíz Gordo formations, which supports the view that the Cayara and its equivalent strata were deposited irregularly on an erosional surface. However, apart from its basal sandstones, the Lumbrera Formation of northwest Argentina correlates with the lower part of the Potoco Formation of Bolivia.

Lowermost Potoco Formation and La Cabaña Member (~58.0–55.5 Ma)

The Potoco Formation transitionally overlies the Cayara Formation. Its lower part consists of thick red-brown mudstones deposited in a broad, flat, low-energy alluvial environment. The lower Potoco was long mistaken for the upper part of the Santa Lucía Formation in some areas of the Cordillera Oriental. In northwest Argentina, its equivalents are the Lumbrera Formation in the east, and probably the lower part of the Pozuelos Formation in the west (Sempere *et al.*, 1997).

The La Cabaña member is a light-colored intercalation in the lowermost Potoco in most sections. This generally thin member consists of green, yellow-green, gray to violet or whitish mudstones and fine-grained sandstones of lacustrine to alluvial origin. It contrasts with the dominant red-brown lower Potoco. The northwest Argentine equivalent of the La Cabaña member is the "Faja Verde" (= green belt) present in the lower portion of the Lumbrera Formation (see Salfity and Marquillas, 1981, 1994). The Faja Verde is generally up to 25 m-thick (Gómez-Omil *et al.*, 1989), but may be twofold ("Faja Verde Superior" and "Faja Verde Inferior") and collectively ~90 m-thick in the local subsident part of the basin (Carbajal *et al.*, 1977), where palynology indicates a late Paleocene or early Eocene age (Quattrocchio, 1978a, b).

The La Cabaña member commonly includes evaporites,

which formed in playa-lakes scattered over the basin. A few major rivers continued to flow toward the NW or NNW. Lacustrine facies are also known from the Faja Verde in several localities of northwest Argentina. It is thought that deposition of the La Cabaña member and the Faja Verde occurred during a relatively dry climatic period, which induced a reduction in fluvial drainage. Because of this climatic control, they apparently represent a synchronous sedimentary period and hence a potential guide-unit in the southern part of the Andean basin (Sempere *et al.*, 1997).

Geochronology and Biostratigraphy

The geochronology of the mammal-bearing Paleocene units in the Andean basin of Bolivia and NW Argentina is based on a composite of four magnetostratigraphic sections which collectively include the El Molino, Santa Lucía, Cayara and lowermost Potoco formations as summarized in Figure 3 (Sempere *et al.*, 1997).

The Upper El Molino, the entire Santa Lucía and the Cayara were deposited during chron 26r, which spans the 60.9–57.9 Ma interval (Cande and Kent, 1992, 1995) (Fig. 3). The regression marked by the El Molino/Santa Lucía contact is correlated with the Danian/Selandian boundary (60.0 Ma; Haq *et al.*, 1987; Cande and Kent, 1992, 1995; Fig. 2) because it marks the end of marine influence at a time when no decrease in subsidence is perceptible, and this change is therefore apparently due to a eustatic effect. The Lower Santa Lucía/Middle Santa Lucía contact is marked by an increase in grain size, which may be of eustatic or tectonic origin. The age of this sequence boundary is estimated to be ~59.5 Ma (Fig. 3). It coincides with initiation of a sea-level lowstand between 60.0 and 59.0 Ma (Haq *et al.*, 1987).

The erosional base of the Cayara, near the end of chron 26r, is ~58.2 Ma and correlates with initiation of the first major sea-level lowstand in the Cenozoic (Haq *et al.*, 1987). The position of the Cayara in the top of chron 26r is controlled by only one polarity site at Tiupampa. At Pampa Grande, the polarity data suggest that it occurs below the base of chron 26n, although the sampling is sparse in this part of the section and the top of the Cayara apparently continues into chron 26n. Preliminary results from two Cayara sites near Camargo yield normal polarities at ~30 and ~45 m above the base of the Cayara (Sempere *et al.*, 1997). As noted above, the Cayara-Potoco transition is diachronous, which means that its age will vary according to its position in the basin.

The two normal polarity zones in the lower part of the Lumbrera Formation are correlated with chrons 26n and 25n; the Faja Verde Inferior (FVI) occurs at the base of a reversed polarity zone correlated with chron 24r; and the Faja Verde Superior (FVS) occurs higher within the same reversed polarity zone. Assuming that depositional rates were constant for the lower Lumbrera, the predicted age of the FVS would be ~54.5 Ma (Fig. 3).

In summary, the ages of the mammal-bearing units in

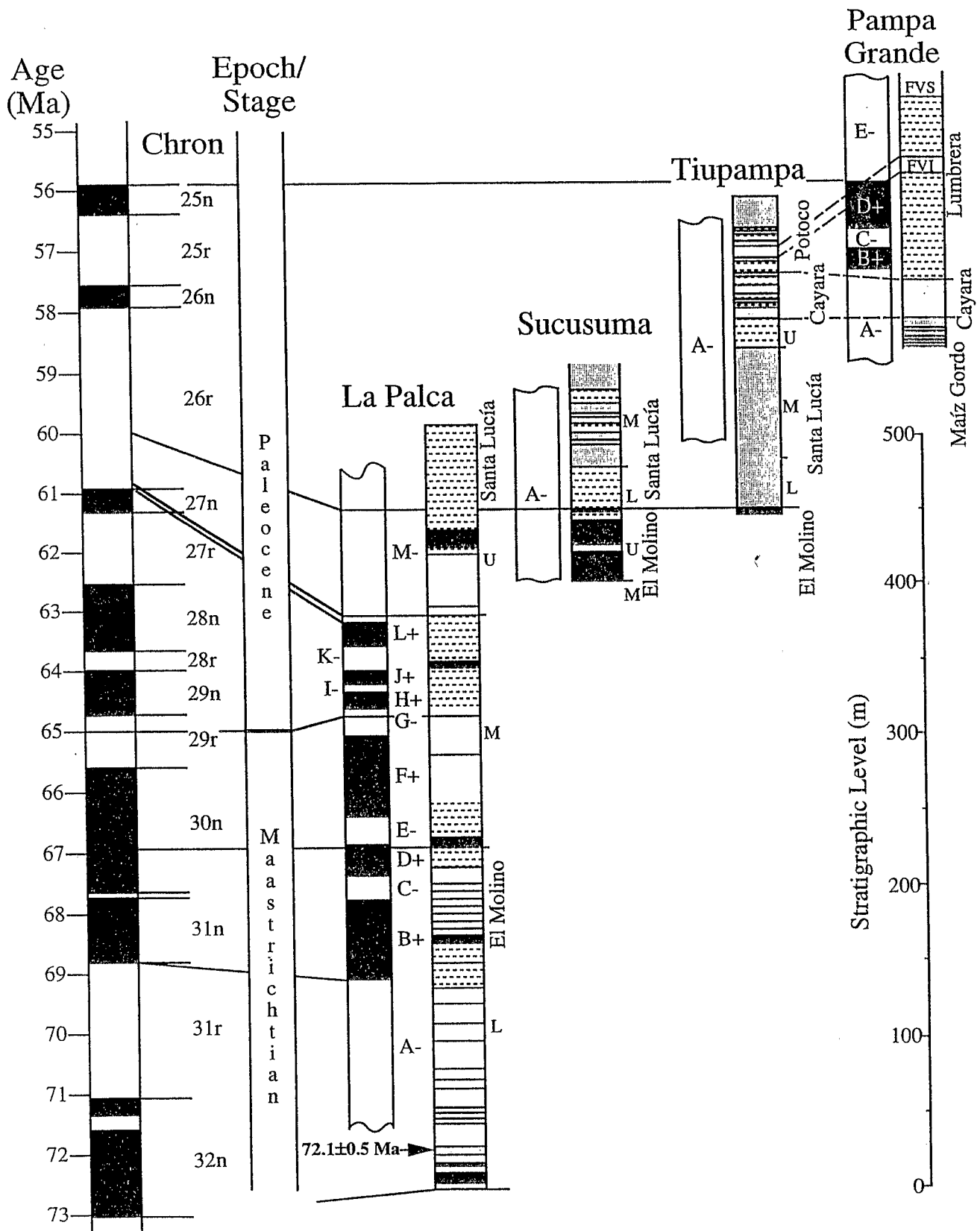


Fig. 3. Correlation of magnetic polarity columns with geomagnetic polarity time scale (after Sempere *et al.*, 1997). Isotopic date from within El Molino Formation is indicated in La Palca magnetic polarity column. Preferred correlations are indicated by dashed lines. Upper dashed line indicates the stratigraphic level of the contact between the El Molino and Santa Lucía formations. Locations of sections are shown in Figure 1. Sucusuma is located ~6 kms north of Torotoro. Geomagnetic polarity timescale (GPTS) follows Cande and Kent (1992, 1995). Chrons 26n and 25n are not recorded at Tiupampa, a feature we attribute to sparse sampling sites in the upper part of this section. FVI = Faja Verde Inferior; FVS = Faja Verde Superior.

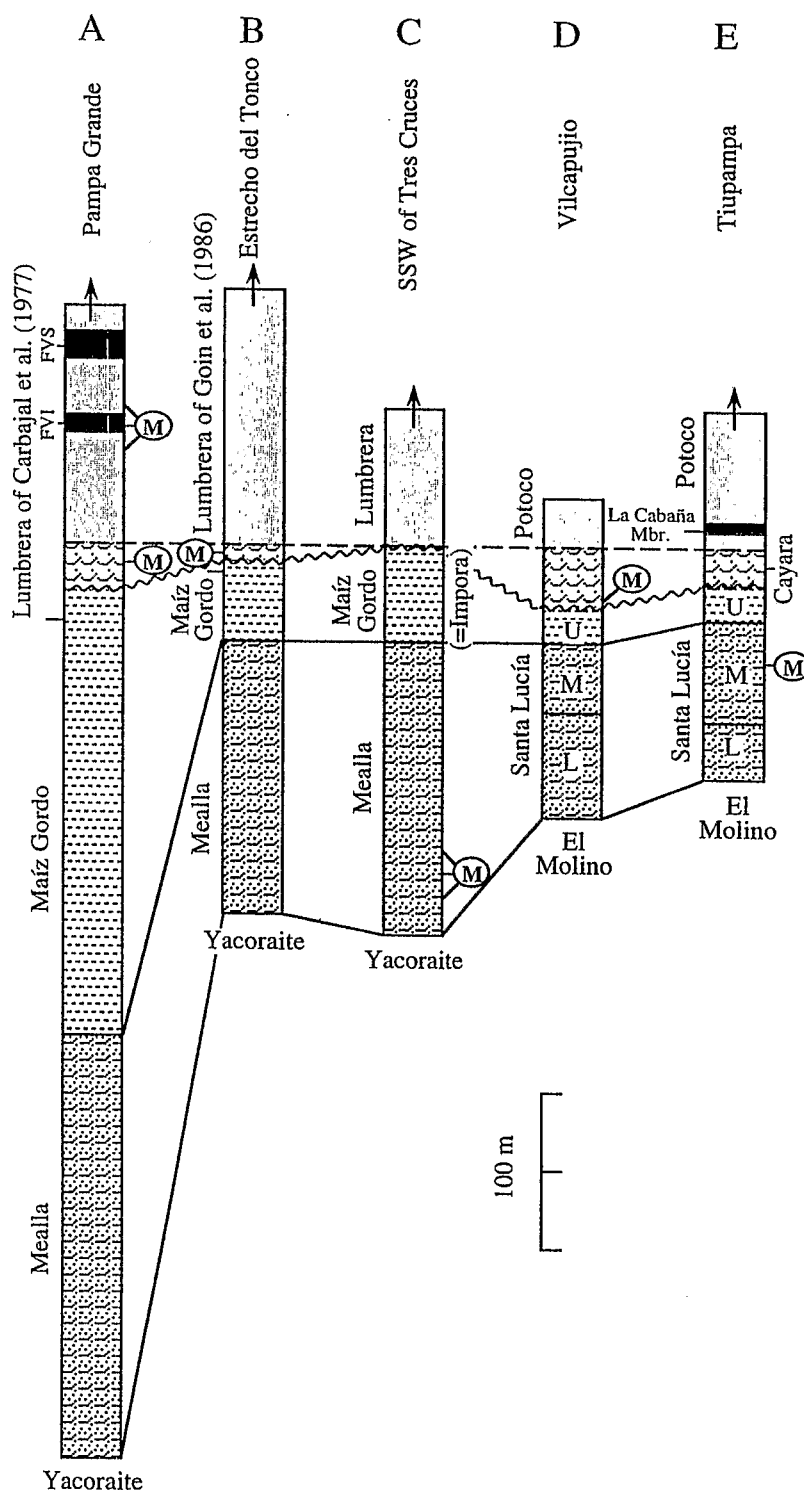


Fig. 4. Stratigraphic sections of mammal-bearing localities in the Santa Lucía and Cayara formations in the southern part of the Andean basin of southern Bolivia and stratigraphic equivalent units containing mammal faunas in northwest Argentina (for localities see Figure 1). Fossil mammals have been described from levels marked by a M, and a detailed account of the stratigraphic positions of the taxa is given in Table 1. The sections are, from left to right, arranged from south to north which approximates their position of most subsidence (A) to most onlap (E) within the Andean basin. Correlation of rock units are justified in the text. Note that the sections are compiled from eight different authors who had different approaches for measuring units or identifying their boundaries. The important points are identification of the units used in this paper and of the relative position of fossil levels within them. FVI = Faja Verde Inferior; FVS = Faja Verde Superior. A. Pampa Grande, Salta Province, NW Argentina ($25^{\circ} 47'S$, $65^{\circ} 25'W$). Stratigraphic section after Carbajal *et al.* (1977), and fossil levels after Carbajal *et al.* (1977), Pascual (1980a, b, 1981), Vucetich (1980), Bond (1981), Vucetich and Bond (1982), Bond and Vucetich (1983), and Bond and López (1993). B. Estrecho del Tonco, Salta Province, NW Argentina ($25^{\circ} 30'S$, $65^{\circ} 55'W$). Upper part of section (top of Maíz Gordo-lower Lumbra) after Goin *et al.* (1986), lower part (Mealla and Maíz Gordo) after Salfity and Marquillas (1994). C. SSW of Tres Cruces, Jujuy Province, NW Argentina ($23^{\circ}-23^{\circ} 15'S$, $65^{\circ} 30'-65^{\circ} 45'W$). Stratigraphy and fossil levels after Pascual *et al.* (1978). D. Vilcapujio, southern Bolivia ($19^{\circ} 04'S$, $66^{\circ} 29'W$). Stratigraphy and fossil level after Sigé *et al.* (1984) as amended by T. Sempere. E. Tiupampa, southcentral Bolivia ($18^{\circ} 02'S$, $65^{\circ} 35'W$). Section measured and lithologies independently recorded by T. Sempere and C. Winker; stratigraphic units and fossil level after Sempere *et al.* (1997) and this study.

the southern part of the Andean basin are as follows: Lower and Middle Santa Lucía (= Mealla), ~60.0–~58.5 Ma; Upper Santa Lucía (= Impora and Maíz Gordo), ~58.5–~58.2 Ma; Cayara (= basal sandstones of Lumbrera), ~58.2–~57.8 Ma; lowermost Potoco and La Cabaña member (= lower Lumbrera and Faja Verde Inferior), ~58.0–~55.5 Ma (Fig. 3).

CHRONOLOGY OF SOUTH AMERICAN PALEOCENE LAND MAMMAL FAUNAS

Andean Basin, Bolivia and Northwest Argentina

The geochronologic and sequence stratigraphic data summarized above permit refined calibration of Paleocene land mammal faunas in the Andean basin of southern Bolivia and northwest Argentina. Stratigraphic sections of the five principal mammal-bearing localities in the Andean basin showing the rock units and fossil levels are given in Figure 4, and a list of the taxa is presented in Table 1. The geochronology of the units and levels in Figure 4 follows that of Figure 3, and the data in these figures are collectively used to estimate the ages of the fossil land mammal local faunas as discussed below.

The notoungulates (*Simpsonotus praecursor* and *S. major*) from 18, 30 and 43 m above the base of the Mealla Formation (= Lower Santa Lucía) at Tres Cruces (Fig. 4C) are between 60.0 and 59.5 Ma in age.

The taxonomically diverse fauna from Tiupampa (Fig. 4E) was originally assigned to the El Molino Formation and believed to be Maastrichtian in age (Muizon *et al.*, 1983). This age assignment was subsequently contested and debated, and by the early 1990s a consensus prevailed that the fauna was Early Paleocene (see Marshall and Sempere, 1993, for a review). As first demonstrated by Gayet *et al.* (1991), the Tiupampa mammal level occurs in the Santa Lucía Formation and lies in the middle part of the Middle sequence (Sempere *et al.*, 1997), ~150 m above the base of our section (Fig. 10). Based on the magnetostratigraphy (Fig. 3), this level is ~59.0 Ma in age (early Late Paleocene). A detailed description of the stratigraphy of the post-Paleozoic strata in the Tiupampa area, with indication of the fossil levels and recorded taxa, is provided in the Appendix.

The notoungulate (cf. *Camargomendesia* sp.) from the base of the Cayara Formation at Vilcapujio (Fig. 4D) is ~58.2 Ma, and the marsupial (*Patene simpsoni*) from the middle part of the basal sandstones of the Lumbrera Formation (= Cayara sandstones) at Estrecho del Tonco (Fig. 4B) is ~58.0 Ma in age.

A notoungulate (*Pampahippus arendesi*) from the upper part of the basal sandstones of the Lumbrera Formation (= Cayara sandstones) at Pampa Grande (Fig. 4A) is ~58.0 Ma, while the numerous other taxa collected from just above, in the base of and from 1 to 10 m below the Faja Verde Inferior of the Lumbrera Formation (= Lower Potoco) are 56.0 to 55.5 Ma.

In summary, all fossil mammals described from the

lower part of the Lumbrera Formation (*s.l.*) of northwest Argentina and previously assigned to the Casamayoran Land Mammal Age (conventionally Early Eocene) are clearly Late Paleocene and date between ~58.0 and 55.5 Ma.

Laguna Umayo, Southeastern Peru

Sigé (1972) described a mammal fauna from a red bed succession at Laguna Umayo near the NE edge of Lake Titicaca in SE Peru (Fig. 1). The fossil level is located ~205 m above the base of a magnetostratigraphic section described by Sigé *et al.* (in prep.). This succession was assigned to the Maastrichtian age Vilquechico Formation, but is now called the Umayo Formation because of its distinct facies, consisting of a homogeneous red bed sequence with a tuffaceous clay component in its upper part (Laubacher and Marocco, 1990; Jaillard *et al.*, 1993; Sigé *et al.*, in prep.). The Maastrichtian age assignment of the Laguna Umayo local fauna was based primarily on the association of egg shell fragments identified as dinosaur (Kérourie and Sigé, 1984), on reputed Maastrichtian age charophytes (Jaillard *et al.*, 1993), and on stage of evolution of the mammals (Sigé, 1972). The magnetostratigraphic section of the Umayo Formation is entirely of reversed polarity, and, in the absence of associated radioisotopic dates, secure correlation with the geomagnetic polarity time scale (GPTS) is not possible. We are therefore unable to confidently constrain the age of this local fauna. The ~500 m-thick Umayo Formation is apparently overlain by the Muñani Formation, the basal part of which is regarded as an equivalent of the Cayara (Jaillard *et al.*, 1993; Sempere *et al.*, 1997). Sigé *et al.* (in prep.) provide alternatives for correlating the reversed polarity zone of the Umayo Formation with the GPTS. It may correlate with chron 29r which crosses the K/T boundary if the identity of the dinosaur egg shells is uncontested and given preference. Or, it may correlate with part of chron 26r, which would make it a time equivalent of the Santa Lucía Formation, as suggested by aspects of its faunal content (see Gayet *et al.*, 1991). The latter alternative leaves open the possibility that the "dinosaur" egg shells may prove referable to some group of large ground birds, such as phorusrhacoids (the earliest record of this group is from the Late Paleocene fissure infillings at Itaboraí in SE Brazil; Sigé *et al.*, in prep.), for which egg shells are presently unknown or unstudied. Regional knowledge of stratigraphic positions of red bed sequences and tuffs as discussed by Sempere *et al.* (1997) suggests that both alternatives are viable, although the second is currently preferred because of the preponderance of paleontological data. Alternatively, correlation of the reversed sequence from Laguna Umayo with chrons 27r and 28r cannot be dismissed. Recently, Crochet and Sigé (1993) reported a new mammal local fauna, from ~200 m stratigraphically above the first in the upper part of the Umayo Formation, which they assigned to the Maastrichtian or Paleocene.

Table 1. List of Paleocene age fossil mammal localities and taxa from the Andean basin of northwest Argentina and southern Bolivia with indication of the stratigraphic units and levels where the fossils were collected as shown in Figure 4. The classification of marsupials follows Marshall *et al.* (1989).

I. Pampa Grande, Salta Province, NW Argentina:

- Order Polydolopimorphia
 - Family Bonapartheriidae
 - Bonapartherium hinakusijum* — 1 to 8 m below Faja Verde Inferior (FVI) in lower part of Lumbrera Formation (Pascual, 1980a, 1981)
 - Family Prepidolopidae
 - Prepidolops didelphoides* — 4 to 10 m below FVI (Pascual, 1980b)
 - Prepidolops molinae* — 1 to 5 m below FVI (Pascual, 1980b)
- Order Notoungulata
 - Family Notostylopidae
 - Boreastylops lumbrerensis* — just below FVI (Vucetich, 1980)
 - Family Isotemnidae
 - Pampatennus infernalis* — 4 m below FVI (Vucetich and Bond, 1982)
 - Pampatennus deuterus* — just below FVI (Vucetich and Bond, 1982)
 - Family Notohippidae
 - Pampahippus arenalesi* — one specimen from just above an unprecised Faja Verde, and another specimen from lower third of section of Carbajal *et al.* (1977) below the FVI, which places it in the basal sandstones that we equate with the Cayara Formation (Bond and López, 1993)
 - Family Oldfieldthomasiidae
 - Colbertia lumbrerense* — immediately below FVI (Bond, 1981)
- Order Notopterna
 - Family Indalecidae
 - Indalecia grandensis* — below FVI (Bond and Vucetich, 1983); family and ordinal arrangement follows Soria (1989)
- Order Astrapotheria
 - Family Astrapotheriidae
 - Albertogaudrya? carahuasensis* — from base of FVI (Carbajal *et al.*, 1977)

II. Estrecho del Tonco, Salta Province, NW Argentina:

- Order Sparassodonta
 - Family Hathliacynidae
 - Patene simpsoni* — from middle part of basal sandstones of Lumbrera Formation (*sensu* Goin *et al.*, 1986) which we equate with the Cayara Formation

III. SSW of Tres Cruces, Jujuy Province, NW Argentina:

- Order Notoungulata
 - Family Henricosborniidae
 - Simpsonotus praecursor* — 30 m above base of Mealla Formation (Pascual *et al.*, 1978)
 - Simpsonotus major* — 18 m and 43 m above base of Mealla Formation (Pascual *et al.*, 1978)

IV. Vilcapujio, southwestern Bolivia:

- Order Notoungulata
 - Family Henricosborniidae
 - cf. *Camargomendesia* sp. — from base of Cayara Formation (Sigé *et al.*, 1984, amended by T. Sempere)

V. Tiupampa, southcentral Bolivia:

Mammal level located ~150 m above base of Santa Lucía Formation. Faunal list after Marshall *et al.* (1995) as modified by L. G. Marshall:

- | | |
|--|---|
| Order Peradectia | Family indet. |
| Family Peradectidae | Gen. and sp. indet. |
| <i>Peradectes</i> cf. <i>austrium</i> | Order Pantodonta |
| <i>Roberthoffstetteria nationalgeographica</i> | Family Alcidedorbignyidae |
| Order Microbiotheria | <i>Alcidedorbignyia inopinata</i> |
| Family Microbiotheriidae | Order Condylarthra |
| <i>Khasia cordillerensis</i> | Family Mioclaenidae |
| Order Didelphimorphia | <i>Tiuclaenus minutus</i> |
| Family Didelphidae | <i>Molinodus suarezi</i> |
| <i>Pucadelphys andinus</i> | <i>Pucanodus gagnieri</i> |
| <i>Incadelphys antiquus</i> | <i>Andinodus boliviensis</i> |
| <i>Mizquedelphys pilpinensis</i> | Family ?Periptychidae |
| <i>Tiulordia floresi</i> | aff. ? <i>Mimatuta</i> sp. |
| Order Sparassodonta | Order Condylarthra <i>incertae sedis</i> |
| Family Hathliacynidae | Family Kollpaniidae |
| <i>Allgokirus australis</i> | <i>Kollpania tiupampina</i> |
| <i>Mayulestes ferox</i> | Order Notoungulata |
| Orders indet. | Family cf. Henricosborniidae or Oldfieldthomasiidae |
| Families indet. | gen. et sp. indet. — this specimen, MNHN VII 123, described and |
| <i>Jaskhadelphys minutus</i> | figured by Muizon <i>et al.</i> (1984), needs to be restudied; thin sections of the |
| <i>Andinodelphys cochabambensis</i> | enamel may confirm suspicions that it is in fact an upper tooth of a |
| Order Leptictida | monotreme (Ornithorhynchidae) |
| Family Palaeoryctidae? | |
| cf. <i>Cimolestes</i> sp. | |

San Jorge Basin, Patagonia, Southern Argentina

The only previously published magnetostratigraphic sections for the entire mammal-bearing Paleocene of South

America are from two localities of the Río Chico Formation (*sensu* Legarreta *et al.*, 1990) in the San Jorge basin of Patagonia, southern Argentina (Marshall *et al.*, 1981; Fig. 5). The section at Cerro Redondo included all of the

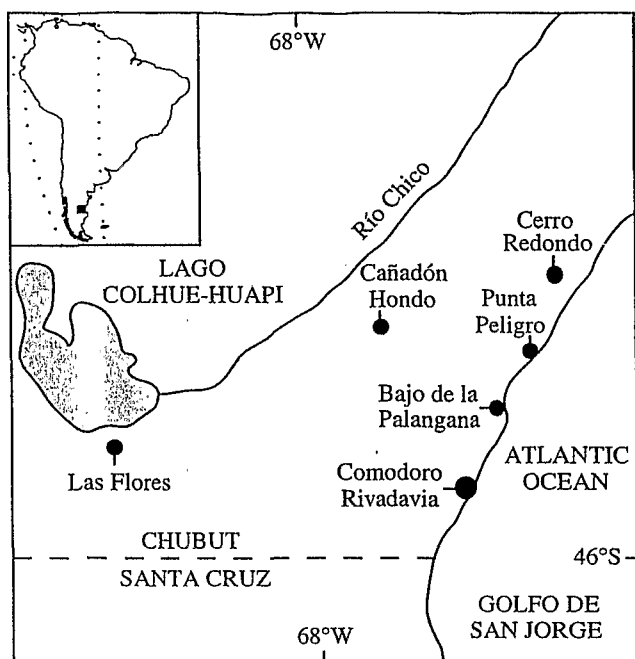


Fig. 5. Map of mammal localities in the Río Chico Formation, San Jorge basin, Patagonia, southern Argentina discussed in the text.

Río Chico Formation at that locality beginning with the "Banco Negro Inferior" (BNI) as its basal unit, while the magnetostratigraphic section at Punta Peligro included only the BNI. The resultant composite magnetostratigraphic section (see Fig. 6) showed that the upper part included two normal polarity zones which correlate with chrons 25n and 26n. The lower portion is a relatively thick reversed polarity zone correlative with chron 26r. No direct age constraint is available for the base of this section, but it must be younger than the ~60.9 Ma age on the young boundary of chron 27n (Cande and Kent, 1992, 1995).

In an attempt to refine the age of the basal part of this paleomagnetic section, and hence to constrain the age of the BNI, we have restudied all published sections of the Río Chico Formation and, following the example of Legarreta *et al.* (1990), attempt to correlate the lithologic changes with the transgressive-regressive cycles proposed by Haq *et al.* (1987). This approach is reasonable because of the proximity of these units to the marine realm and apparently negligible local tectonics. Furthermore, we were able to identify several guide levels in the detailed sections of Simpson (1935) and Feruglio (1949) which permit refined correlation of these sections and of the mammal-bearing levels, and hence a tentative correlation of the faunas with the geomagnetic polarity time scale, using Cerro Redondo as the reference section.

Simplified stratigraphic sections of five mammal-bearing localities of the Río Chico Formation along with the fossil levels are shown in Figure 6, and a list of taxa from each level is given in Table 2. The base of the sections begin with the BNI (our unit 1) which is the principal guide unit. The BNI overlies a marine succession of Danian age

which culminates with the glauconite-rich Banco Verde (Marshall *et al.*, 1981; Legarreta and Uliana, 1994). The BNI is a 5 to 8 m-thick bentonitic claystone which has yielded a mammal fauna from a remnant tuff level at Punta Peligro (Marshall *et al.*, 1981; Bonaparte *et al.*, 1993). The associated vertebrate fauna (crocodiles, turtles) and palynologic assemblage combined with lithologic studies indicate that the BNI was deposited in a marginal lagoon to mangrove environment (Legarreta *et al.*, 1990; Bonaparte *et al.*, 1993; Legarreta and Uliana, 1994). Our unit 2 includes glauconitic sandstones which document a marine influence, whereas our unit 3 (the "Banco Negro Superior", BNS) is a gray to black bentonitic claystone suggesting an origin similar to that of the BNI. Collectively, the contact between the Danian marine succession and the BNI through BNS (our units 1–3), represents a regression which we equate with the one identified by Haq *et al.* (1987) between 60.5 and 60.0 Ma. The base of the BNI thus equates with the Danian/Selandian boundary (60.0 Ma) and with the base of the Santa Lucía Formation. Furthermore, the BNI-BNS succession is a time equivalent of the Lower Santa Lucía Formation. The mammal fauna from the BNI at Punta Peligro is thus ~60.0 Ma.

Our unit 4 extends from the top of the BNS to the base of a 5 to 10 m-thick bed of conspicuous white sandstone. In the middle of unit 4, mammals are known from Bajo de la Palangana (*Carodnia* zone, *sensu* Simpson, 1935) and Cerro Redondo. These two local faunas are ~59.0 Ma (Fig. 6).

The distinct 5 to 10 m-thick white sandstone in the base of our unit 5 occurs between 66 and 73 m above the base of the BNI in the four sections (Fig. 6). A mammal fauna from Las Flores, south of Lago Colhue-Huapi (for which no stratigraphic section is yet published) is recorded 60 m above the BNI, which suggests that it occurs in a stratigraphic position approximately equal to the white sandstone in the base of our unit 5. The Las Flores local fauna was originally discovered by a field team that included two of the authors (RFB and LGM) who recall that the fossils did in fact come from a distinct white sandstone level. The age of the Las Flores local fauna thus appears to be ~58.0 Ma.

The base of our unit 6 begins with a ~15 m-thick cross-bedded sandstone level, which begins 95 to 110 m above the base of the four measured sections (Fig. 6). Fossil mammals are known from this cross-bedded sandstone level at Cañadón Hondo (*Kibenikhoris* zone), from ~14 m above its base at Bajo de la Palangana (*Ernestokokenia* zone), from ~27 m above its base west of Punta Peligro, and ~38 m above its base at Cerro Redondo (the latter level occurs in chron 25n) (Figs. 6, 7). The local fauna from Cañadón Hondo would thus correlate within chron 26n (~57.7 Ma), that from Bajo de la Palangana within chron 25r (~57.0 Ma), and those from west of Punta Peligro and at Cerro Redondo within chron 25n (~56.0 Ma) (Fig. 7). In support of our proposed correlation of the upper faunal levels in the Río Chico Formation, the local fauna from Cañadón Hondo is regarded as older than that from Bajo de la Palangana based on "stage of evolution" of the taxa

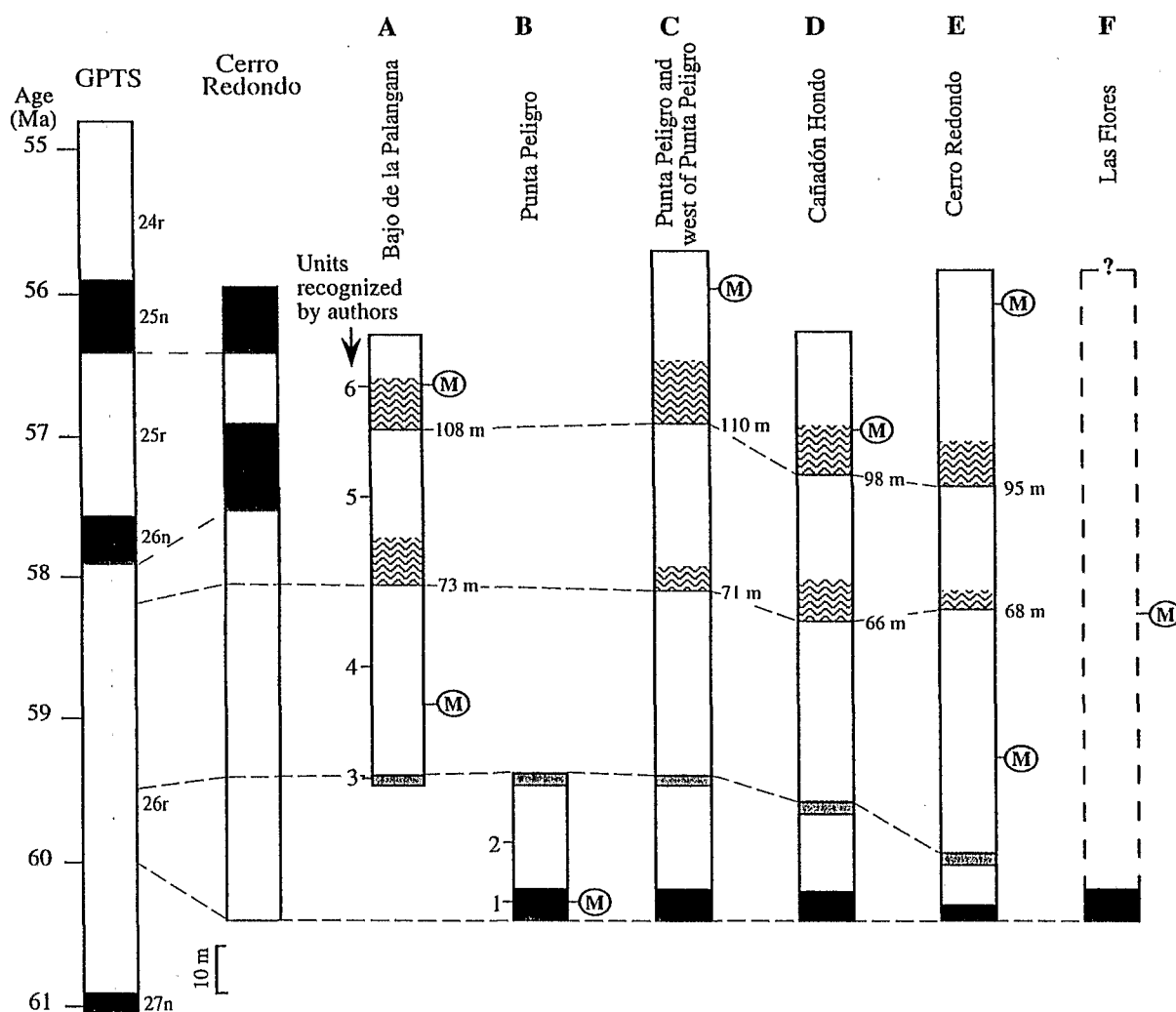


Fig. 6. Stratigraphic sections of five localities (A-F) of the Río Chico Formation in the San Jorge basin, Patagonia, southern Argentina showing general lithologies and levels where fossil mammals have been collected (for locations see Fig. 5). Fossil mammals have been described from levels marked by a M, and a detailed account of the stratigraphic positions of the faunas is given in Table 2. The paleomagnetic section for Cerro Redondo is after Marshall *et al.* (1981) and the GPTS follows Cande and Kent (1992, 1995). The sections can be correlated based on recognition of six guide levels or sequences: (1) the Banco Negro Inferior (BNI), a black bentonite with remnants of tuffaceous material containing fossil mammals; (2) a succession composed of glauconite-bearing sandstones and bentonitic mudstones; (3) the Banco Negro Superior (BNS), a light gray to black bentonitic horizon, above which no marine influence is recognized before the Eocene; (4) a succession composed of fluvial sandstones and mudstones; (5) an alluvial sequence which begins with a 5 to 10 m-thick coarse sandstone (= unit "i" of Simpson, 1935); (6) an alluvial succession which begins with ~15 m of hard-cemented, white to pink, coarse cross-bedded sandstones (= unit "k" of Simpson, 1935). The positions in meters of the base of units 5 and 6 above the base of the BNI are recorded to facilitate correlation with the Cerro Redondo reference section.

- A. Bajo de la Palangana. Lithologies and fossil levels after Simpson (1935) and Feruglio (1949, Figure 90).
- B. Punta Peligro. Lithologies after Feruglio (1949, Figure 90), and fossil level after Marshall *et al.* (1981).
- C. Punta Peligro and west of Punta Peligro. Lithologies and fossil level after Feruglio (1949, Figure 87).
- D. Cañadón Hondo. Lithologies and fossil level after Simpson (1935) and Feruglio (1949, Figure 102).
- E. Cerro Redondo. Lithologies and fossil levels after Simpson (1935, Figure 3).
- F. Las Flores. Stratigraphic level, 60 m above Banco Negro Inferior (Pascual and Ortiz-Jaureguizar, 1991) and ~105 m below rocks containing Casamayoran mammals (Marshall, 1985).

(Simpson, 1935), and this is corroborated by the stratigraphic data and inferred age difference suggested by our study.

Itaboraí, Brazil

The only other significant mammal fauna of Paleocene age in South America is from Itaboraí, about 25 km east of

Niterói, state of Rio de Janeiro, Brazil. The Itaboraí fauna comes from fissure fillings in the lacustrine limestones of the early Paleocene (?) age São José de Itaboraí Formation. A taxonomic list of this exceptionally diverse fauna is provided in Table 3. The vertebrates were recovered from numerous karst cavities in a lower limestone unit and pre-date an upper limestone unit (Brito *et al.*, 1972). For most specimens, their association among themselves and/or with

Table 2. List of fossil mammals from six localities of the Río Chico Formation in the San Jorge basin, Patagonia, southern Argentina, with indication of the levels where the fossils were collected as shown in Figure 6. The classification of marsupials follows Marshall *et al.* (1989).

I. Bajo de la Palangana:

1. Lower mammal level, in fine red sandstone 14 to 20 m above Banco Negro Superior (Simpson, 1935), or 46 m above base of Banco Negro Inferior (Feruglio, 1949, Figure 90). Faunal list after Marshall *et al.* (1983):

Order Xenungulata

Family Carodniidae

Carodnia feruglioi

2. Higher mammal level, in coarse gray to pink sandstone 85 to 88 m above Banco Negro Superior (Simpson, 1935), or 117 m above base of Banco Negro Inferior (Feruglio, 1949, Figure 90). Faunal list after Marshall *et al.* (1983):

Order Sparassodonta

Family Borhyaenidae

?Nemolestes sp.

Order Polydolopimorphia

Family Polydolopidae

Polydolops winecage

Order Condylarthra

Family Didolodontidae

Ernestokokenia chaishoer

Ernestokokenia ?yirunhor

Order Notoungulata

Family Henricosborniidae

Henricosbornia ?lophodonta

?Othnielmarshia sp.

Family Isotemnidae

Isotemnus sp.

Family Interatheriidae

Notopithecus sp.

Family Archaeohyracidae

?Eohyrax sp.

Family indet.

Brandmayria simpsoni

Order Litopterna

Family Macrauchenidae

Victorlemoinea sp.

Family Proterotheriidae

Ricardolydekkeria sp.

Josepholeidia sp.

Order Trigonostylopoidea

Family Trigonostylopidae

Trigonostylops sp.

II. Punta Peligro, from a tuffaceous level in the Banco Negro Inferior:

Fossil list after Scillato-Yané and Pascual (1985), Pascual *et al.* (1992) and Bonaparte *et al.* (1993):

Order Multituberculata

Family Sudamericidae

Sudamerica ameghinoi

Order Monotremata

Family Ornithorhynchidae

Monotrematum sudamericanum

Order Condylarthra?

Family Peligrotheriidae

Peligrotherium tropicalis

Order Condylarthra

Family Mioclaenidae

Raulvaccia peligrensis

Escribania chubutensis

III. West of Punta Peligro:

Fossil level is 135 to 140 m above base of Banco Negro Inferior (Feruglio, 1949, Figure 87):

Order Condylarthra

Family Didolodontidae

Ernestokokenia chaishoer

IV. Cañadón Hondo:

Fossil level is 98 to 108 m above base of Banco Negro Inferior (Feruglio, 1949, Figure 102). Faunal list after Marshall *et al.* (1983):

Order Sparassodonta

Family Hathliacynidae

Patene sp.

Order Polydolopimorphia

Family Polydolopidae

Polydolops kamektsen

Order indet.

Family indet.

Gashternia ctalehor

Order Condylarthra

Family Didolodontidae

Ernestokokenia yirunhor

Order Notoungulata

Family Henricosborniidae

Henricosbornia waitehor

?Peripantostylops orehor

Family ?Notostylopidae

Seudenius cteronc

Family Isotemnidae

?Isotemnus ctalego

Family Interatheriidae

?Transpithecus sp.

Family Oldfieldthomasiidae

Kibenikhoria get

Order ?Litopterna

gen. et sp. indet.

Order Trigonostylopoidea

Family ?Trigonostylopidae

Shecenia ctimeru

V. Cerro Redondo:

1. Lower mammal level, from a clay and sandstone horizon, base of level "h", Figure 3 in Simpson (1935), 37 to 38.5 m above base of Banco Negro Inferior. Faunal list after Marshall *et al.* (1983):

Order Sparassodonta

Family ?Borhyaenidae

gen. et sp. indet.

Order Polydolopimorphia

Family Polydolopidae

Seumadia yapa

Order Litopterna

Family Proterotheriidae

Wainka tshotshe

2. Higher mammal level, in lenses of hard cross-bedded gray sandstone, weathering reddish, level "m", Figure 3 in Simpson (1935), 85 to 86 m above lower mammal level and about 117 to 118 m above top of Banco Negro Inferior. Faunal list after Marshall *et al.* (1983):

Order Xenarthra

Family Dasypodidae

gen. et sp. indet.

Order Notoungulata

Family Isotemnidae

gen. et sp. indet.

Family ?Interatheriidae

gen. et sp. indet.

VI. Las Flores, south of Lago Collhue-Huapi:

Fossil level is 60 m above Banco Negro Inferior (Pascual and Ortiz-Jaureguizar, 1991) and ~105 m below rocks containing Casamayoran mammals (Marshall, 1985). No extensive faunal list is available, although numerous marsupials, condylarths and notoungulates are represented. This is apparently the most taxonomically diverse local fauna known in the Río Chico Formation.

Order Polydolopimorphia

Family Polydolopidae

Epidolops sp. (Pascual and Bond, 1981)

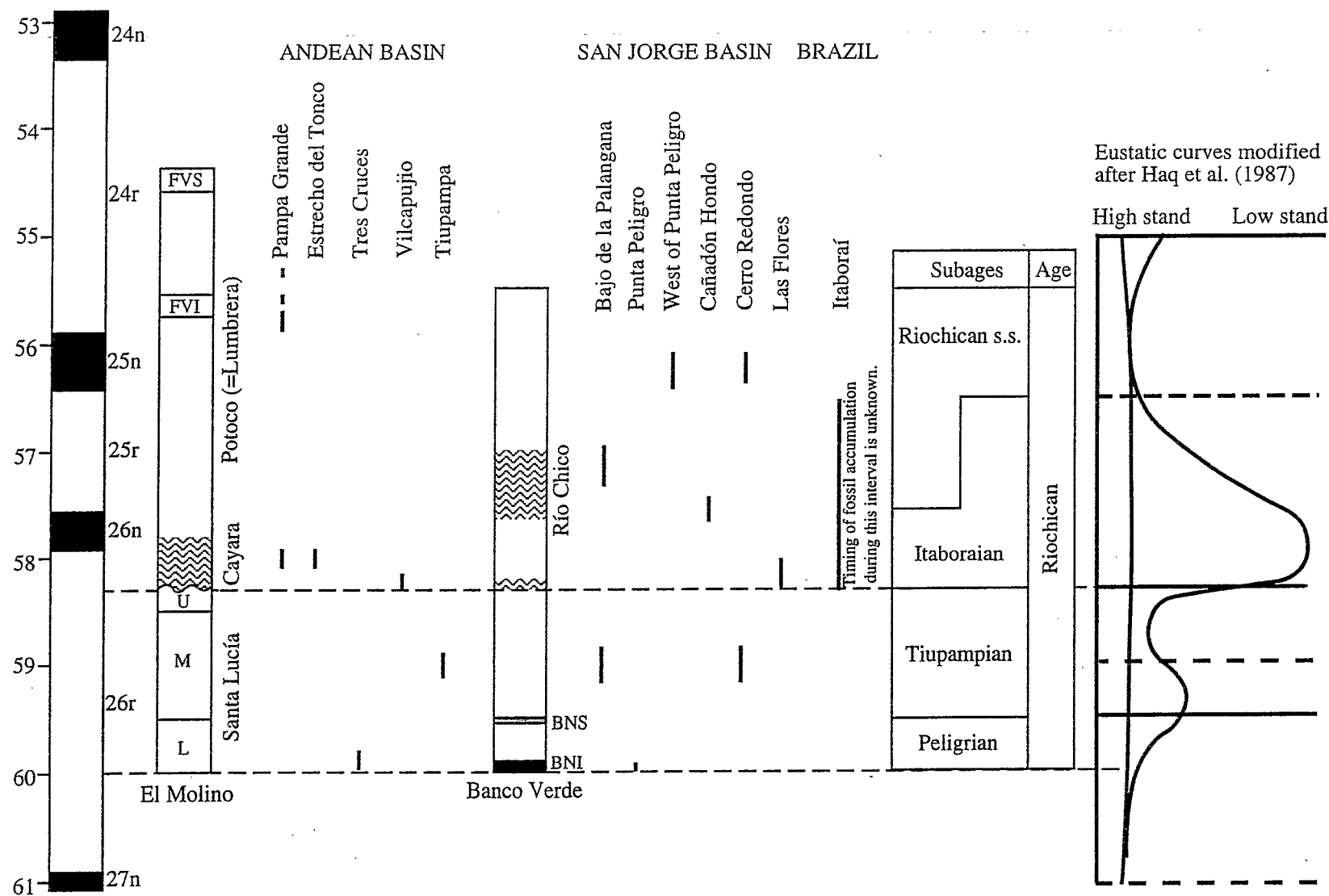


Fig. 7. Summary figure showing chronology of South American Paleocene land mammal faunas based on collective data and correlations presented in Figures 3, 4 and 6, and discussions in text. GPTS follows Cande and Kent (1992, 1995). The eustatic curve of Haq *et al.* (1987) is adjusted to fit the new time scale of Cande and Kent (1992, 1995) and the refined geochronological data presented in this paper.

Table 3. Taxonomic list of fossil land mammals from the fissure fillings at Itaboraí, SE Brazil (after Marshall *et al.*, 1983, 1989; Marshall, 1987; Cifelli, 1983).

Order Microbiotheria	Order Xenarthra
Family Microbiotheriidae	Family Dasypodidae
<i>Monodelphopsis travassosi</i>	<i>Prostegotherium</i> aff. <i>P. astrifer</i>
Order Didelphimorphia	Order Condylarthra
Family Didelphidae	Family Didolodontidae
<i>Derorhynchus singularis</i>	<i>Lamegoia conodonta</i>
<i>Didelphopsis cabrerai</i>	<i>Paulacoutoia protocenica</i>
<i>Eobrasilia coutoi</i>	Order Notoungulata
<i>Itaboraidelphys camposi</i>	Family Henricosborniidae
<i>Gaylordia doelloi</i>	<i>Camargomendesia pristina</i>
<i>Gaylordia macrocynodonta</i>	Family Oldfieldthomasiidae
<i>Marmosopsis juradoi</i>	<i>Colbertia magellanica</i>
<i>Minusculodelphis minimus</i>	<i>Itaboraitherium atavum</i>
<i>Mirandatherium alipioi</i>	Family incertae sedis
<i>Sternbergia itaboraiensis</i>	<i>Palaeocladosictis mosesi</i>
Family Protodidelphidae	Order Litopterna
<i>Bobbschaefferia fluminensis</i>	Family Macraucheniiidae
<i>Guggenheimia brasiliensis</i>	<i>Victorlemoinea prototypica</i>
<i>Procaroloameghinia pricei</i>	Family Proterotheriidae
<i>Protodidelphis vanzolinii</i>	<i>Paranisolambda prodromus</i>
<i>Robertbutleria mastodontioidea</i>	Family Protolipternidae
<i>Zeusdelphys complicatus</i>	<i>Asmithwoodwardia scotti</i>
Order Sparassodonta	<i>Miguelsoria parayirunhor</i>
Family Hathliacynidae	<i>Protolipterna ellipsodontoides</i>
<i>Patene simpsoni</i>	Order Trigonostylopoidea
Family Borhyaenidae	Family Trigonostylopidae
cf. <i>Nemolestes</i> sp.	<i>Tetragonostylops apthomasi</i>
Order Polydolopimorphia	Order Xenungulata
Family Polydolopidae	Family Carodniidae
<i>Epidolops ameghinoi</i>	<i>Carodnia vieirai</i>

specific cavities was never recorded, which impedes location of this fauna in a stratigraphic succession. This local fauna served as the basis for recognition of the Itaboraian Land Mammal Age (Paula Couto, 1952a) which was regarded by Marshall (1985) as approximating middle Paleocene time, while Riochican s.s. was restricted to late Paleocene time.

Soria (1987) reported that some Itaboraí fossils have reputed similarities with both Riochican and early Casamayoran taxa from Patagonia and with reputed early Eocene taxa from northwest Argentina (i.e. the Lumbrera Formation). He interpreted his observations to indicate that the Itaboraí fauna is time transgressive and accumulated during middle Paleocene through early Eocene time (Soria, 1987). He further recommended that usage of the Itaboraian Land Mammal Age be abandoned. A history of the debated age of Itaboraí is provided by Marshall and Semper (1993). The principal controversies result from the erroneous age assignments of some Argentine faunas, particularly the Lumbrera Formation, as well as an uncritical geological evaluation of the age of Itaboraí itself (see below).

Gayet *et al.* (1991) noted that although a hydrothermal origin has classically been favored for the São José de Itaboraí lacustrine limestones, water level in the near-shore lake where the limestones were deposited may have been controlled by the level of the nearby Atlantic Ocean through adjustment of marine and continental phreatic levels. If so, the lacustrine episodes evidenced by the lower and upper Itaboraí limestones were coeval with marine highstands, and the karst formation and the infilling of its

cavities, which occurred between deposition of these limestones, was coeval with a major sea-level lowstand. We propose that karst formation and infilling at Itaboraí coincided with the significant sea-level lowstand between 58.5 and 56.5 Ma as recorded by Haq *et al.* (1987). This is the most significant period of marine lowstand recorded in the Paleocene. The model of karst formation associated with lowstand is consistent with observed geologic processes. Furthermore, the age of the mammal fauna from Itaboraí relative to those elsewhere in the Paleocene of South America, based on the new chronology presented in this paper, is now consistent with observed taxonomic similarities and differences. Thus, the two limestone units apparently formed during Paleocene sea-level highstands which correlate with the maximum inundations which peaked at 61.0 and 56.5 Ma (following Haq *et al.*, 1987) (Fig. 7).

This new age assessment for Itaboraí and the refined ages for Paleocene faunas in the Andean and San Jorge basins, show that correlations of the local faunas are now reasonable. These conclusions are illustrated by the following examples. (1) *Patene simpsoni* is known from Itaboraí and a Cayara-equivalent level of the Lumbrera Formation at Estrecho del Tonco, and *Camargomendesia* from Itaboraí is represented by cf. *Camargomendesia* sp. from the Cayara at Vilcapujio. The Cayara Formation has a basal age of ~58.2 Ma which is coeval in age with the onset of the marine lowstand and hence karst formation and infilling at Itaboraí. The faunas from these three localities are thus very close in age, hence they share the same taxa. (2) The marsupial *Epidolops* from Itaboraí is recorded in Patagonia only from the Las Flores local fauna (Pascual and

Bond, 1981) which appears to be ~58.0 Ma. (3) *Colbertia lumbrerense* from immediately below the Faja Verde Inferior of the Lumbrera Formation (i.e. ~56.0 Ma) is regarded (Bond, 1981) as more advanced in some structures than *C. magellanica* from Itaboraí. The relative stage of evolution of these taxa is supported by our proposed age relationships of the faunas. (4) *Carodnia feruglioi* from Bajo de la Palangana (~59.0 Ma) is more primitive than *C. vieirai* from Itaboraí (Paulo Couto, 1952b).

In a more general context, the younger age of Itaboraí as recognized in our study helps explain some observations about faunal similarities with late Riochican and early Casamayoran (i.e. Vacan subage *sensu* Cifelli, 1985) taxa in the San Jorge basin as proposed by Soria (1987). For example, cf. *Tetragonostylops* sp. occurs in the early Casamayoran at Cañadón Vaca; *Victorlemoinea* sp. is recorded from the upper Riochican level at Bajo de la Palangana and in the early Casamayoran; and *Asmithwoodwardia* sp. occurs in the early Casamayoran. These three taxa were originally described from Itaboraí. Pascual (in Marshall *et al.*, 1983, p. 12) reports that the upper Riochican fossil level at Bajo de la Palangana contains species which have been considered to be typically Casamayoran, and that many genera are shared in common, indicating that there is little time lapse between the uppermost Riochican fauna at Bajo de la Palangana and early Casamayoran. Thus, the Riochican/Casamayoran boundary is ~55.5 Ma (Fig. 7). Since the upper Riochican level at Bajo de la Palangana (~57.0 Ma) appears to overlap Itaboraí in time, and Casamayoran begins only ~1.0 m.y. after inferred termination of infillings at Itaboraí, the observed faunal similarities are understandable (Fig. 7). Our study also cautions that at least some early Casamayoran land mammal age faunas in Patagonia may prove to be latest Paleocene in age.

In summary, reassessment of the age of the taxa from the lower part of the Lumbrera Formation of northwest Argentina shows that they are Late Paleocene (~58.0–55.5 Ma) and not Early Eocene as long believed. The erroneous Early Eocene age assignment for the Lumbrera taxa was largely responsible for the conclusions reached by Soria (1987) that the Itaboraí fauna included taxa of Early Eocene age and was thus markedly time transgressive. Our study suggests that the infillings of Itaboraí occurred sometime between ~58.2 and ~56.5 Ma, although the exact timing(s) of these infillings during this interval remains unknown.

CONCLUSIONS

A Reappraisal of Paleocene Land Mammal Ages

The geochronologic and biostratigraphic data and interpretations presented in Figures 3, 4 and 6 are summarized in Figure 7. The latter permits a refined age estimate and revised correlation of land mammal local faunas between the Andean basin, San Jorge basin and Itaboraí. In this context, the known Paleocene age land mammal faunas of South America range from 60.0 to 55.5 Ma, span ~4.5 m.y., and encompass a more restricted period of time than previously envisioned.

The faunas from the Río Chico Formation were originally placed by Simpson (1935) in the Riochican Land Mammal Age. Simpson (1935) arranged these local faunas into "faunal zones" based on the relative stage of evolution of the taxa. These faunal zones included, 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 *Ernestokenia* faunal zone (fauna from upper level at Bajo de la Palangana). Based on this arrangement, Simpson (1948, p.29) later noted that the Riochican (then tentatively regarded 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 this age encompasses a lapse of time probably great enough to include both middle and late Paleocene. The magnetostratigraphic study of Cerro Redondo (Marshall *et al.*, 1981) confirmed Simpson's view.

During the last ten years, three new land mammal ages have been erected (or resurrected) for Paleocene faunas in South America. Itaboraian for the middle Paleocene (i.e. early part of Riochican *s.l.*), Tiupampian for the early Paleocene (*s.l.*), and most recently Peligran (for the Banco Negro Inferior local fauna, including only five taxa) which is regarded, in part, as middle Paleocene. Riochican *s.s.* has been retained for the upper fauna at Bajo de la Palangana (i.e. to represent late Paleocene time). Usage, age assignments and inclusion (or exclusion) of local faunas within these ages has been chaotic (see Marshall and Sempere, 1993; Bonaparte *et al.*, 1993). Secure correlations of local faunas are possible only when they are made on firm chronostratigraphic inferences based on available radioisotopic, magnetostratigraphic, robust biostratigraphic and detailed sequence stratigraphic observations. Subjective long-distance correlations of local faunas should be avoided. Precise knowledge of the ages of local faunas — not which land mammal age they reputedly can be pigeonholed into — is the critical issue. Liberal application of land mammal age names to uncalibrated local faunas, which is now done widely for South America, gives a false impression of knowledge of evolutionary events that can lead to erroneous interpretations.

In the context of our study, the four "Paleocene Land Mammal Ages" retain their identity (Fig. 7). The only obvious conflict is apparent temporal overlap between upper Itaboraian and lower Riochican. However, given their restricted time span, these "ages" are operationally more equivalent to subages, which are all included within a broad Riochican age spanning 60.0–55.5 Ma (Fig. 7). Thus, the Riochican Land Mammal Age as defined in this study is Late Paleocene *sensu* Cande and Kent (1992, 1995).

Faunal Interchanges with North America

Numerous continental vertebrate groups in Late Cretaceous and Paleocene rocks of South America are also recorded in North America, and these faunal "links" were

used by paleontologists to postulate the existence of a trans-Caribbean land bridge(s) during part of this time interval (i.e. Rage, 1978; Gingerich, 1985; Estes and Baez, 1985). These predictions have only recently been corroborated by geodynamic data (see Pitman *et al.*, 1993; Marshall and Sempere, 1993).

The Caribbean plate began its east-northeastward migration in Campanian time (~80 Ma), and the now submerged Greater Antilles and Aves Ridge formed a subaerial volcanic arc established on the northeastern edge of this plate until possibly the mid-Eocene. It is likely that this arc was the land bridge that provided the pathway for dispersal of continental vertebrates. However, since this land bridge was at a convergent margin, it was constantly subjected to tectonism, magmatic activity, and sea-level fluctuations. Magmatic-tectonic quiescence and/or sea-level highstand periods would have promoted relative subsidence of part of the arc below sea-level. For these reasons, the land bridge "may therefore have frequently been impaired — passing from a pure corridor to a filter corridor to an impasse. Furthermore, species migrating from the north or the south may have reached some of the islands only to be cut off from behind or ahead and become isolated" (Pitman *et al.*, 1993, p. 25).

In view of the probable fragility of the Aves Ridge connection, faunal interchange is likely to have occurred in "pulses" beginning in the Campanian until at least the

southern part of the arc became fragmented after the early Eocene (Pitman *et al.*, 1993). This "pulse-hypothesis" would have permitted opportunities for endemic evolution of first-wave immigrants and for subsequent dispersal of these same stocks during a later "pulse". For this reason, and because the timing of the "pulses" have yet to be identified and calibrated, the direction of dispersal of most groups is not clear (Gayet *et al.*, 1991, 1992). As is the case with the Great American Faunal Interchange beginning ~2.5 Ma and for which four "pulses" have been identified (Marshall *et al.*, 1982; Marshall, 1985), a continuous land route would predictably permit an interchange "pulse" to be reciprocal and balanced.

The data presented in this paper permit identification of a dispersal event between North and South America, and hence a "pulse" when the land bridge was operative. The sea-level lowstand recorded by Haq *et al.* (1987) between 58.5 and 56.5 Ma would have provided a geodynamic opportunity for total emergence of the land bridge. This opportunity was probably enhanced by the late Paleocene tectonism and uplift related to change in plate convergence that affected at least the western margin of South America. This event (~58.2 Ma) marks the boundary between the Upper Puca/Corocoro supersequences in Bolivia (Sempere, 1990; Sempere *et al.*, 1997), and correlates with the Zuni/Tejas sequence boundary in North America (Sloss, 1963; Leighton and Kolata, 1991). A reconstruction of the

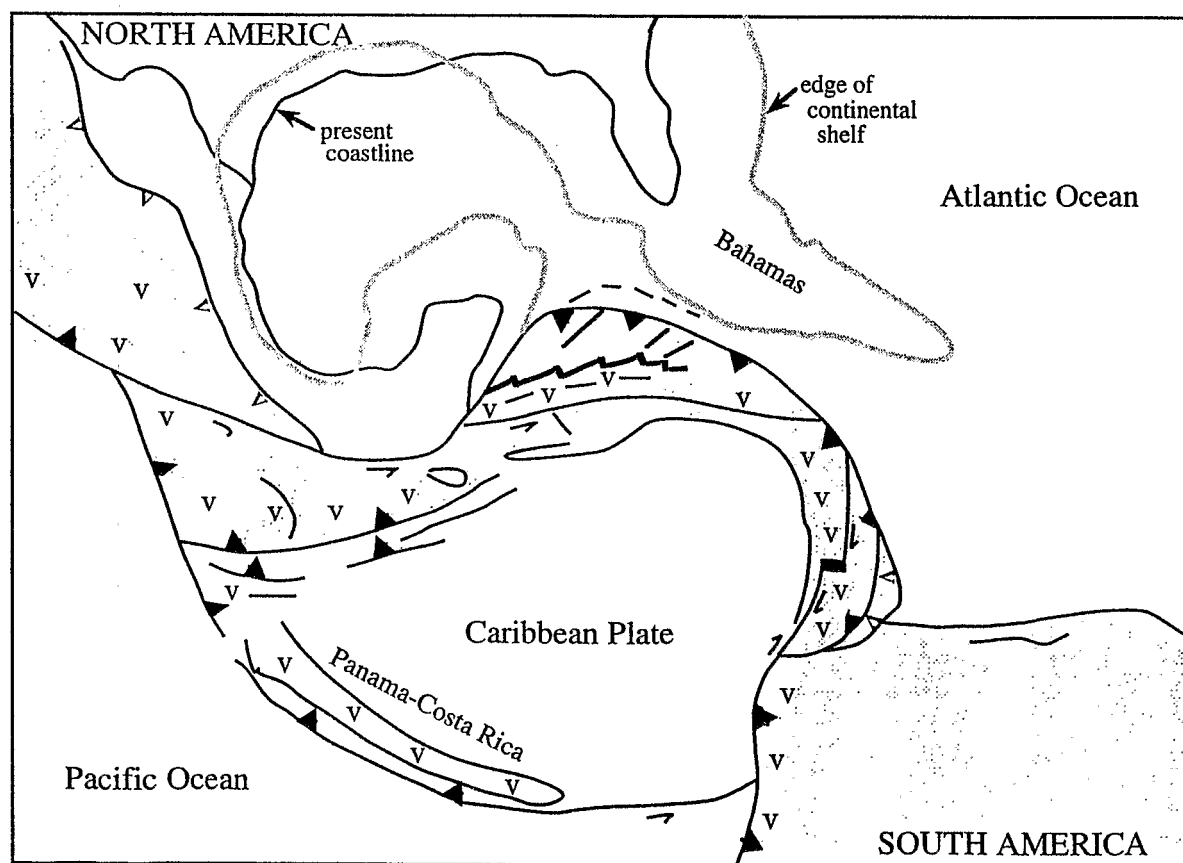


Fig. 8. Configuration of Caribbean region ~59 Ma showing position of land bridge (shaded) along the eastern edge of Caribbean plate that permitted the reciprocal dispersal of North and South American continental taxa between ~58.2 and ~56.5 Ma (modified after Pitman *et al.*, 1993, Fig. 2.5E).

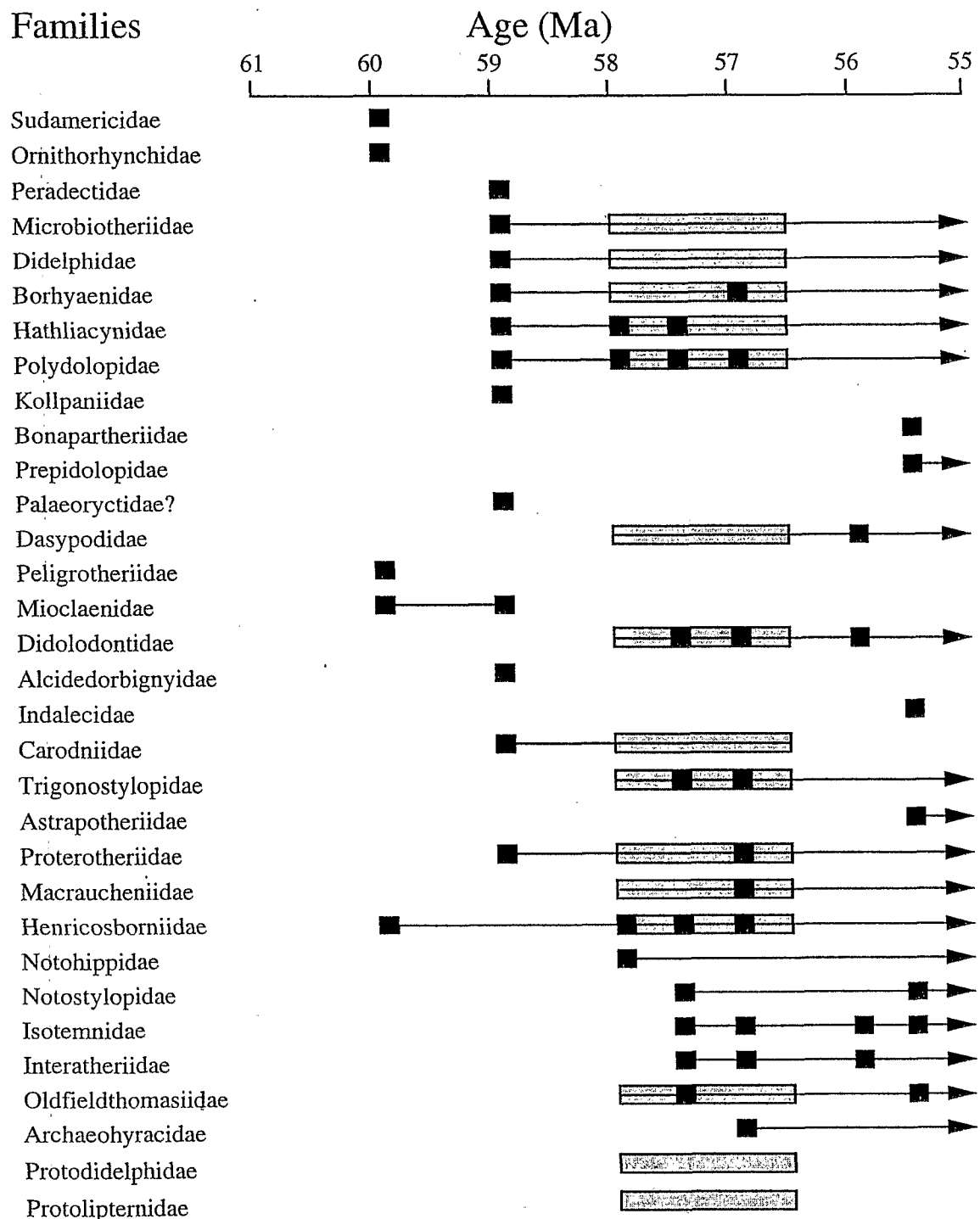


Fig. 9. Chronostratigraphic ranges of mammal families in Riochican Land Mammal Age local faunas showing major change in faunal composition beginning ~58.2 Ma. Data for the Andean basin are presented in Table 1, for the San Jorge basin in Table 2, and for Itaboraí in Table 3. Taxa from the Andean and San Jorge basins are in solid square boxes, and those from Itaboraí are in elongated stippled rectangles; both are arranged on basis of correlations presented in Figure 7. The data for Itaboraí indicate only the potential "window" during which karst infilling occurred, and should not be inferred to indicate that all taxa are represented during this entire time span. Arrows indicate that taxa continue into younger faunas.

geology of the Caribbean region at this time (Fig. 8) documents the existence of a continuous land bridge between northwest South America and the Yucatán area of North America (Pitman *et al.*, 1993).

Four mammal groups that apparently participated in an interchange during this time are (we list only earliest

known records in North America and Europe for which the faunas are well dated): Xenarthra (armadillos at Cerro Redondo and Itaboraí in South America; palaeonodons in the late Tiffanian [~57 Ma] of North America; anteater in early middle Eocene [~50 Ma] of Europe); Didelphidae (Tiupampa and Itaboraí in South America; Clarkforkian [~55 Ma] in North America; earliest Eocene [~55 Ma] in

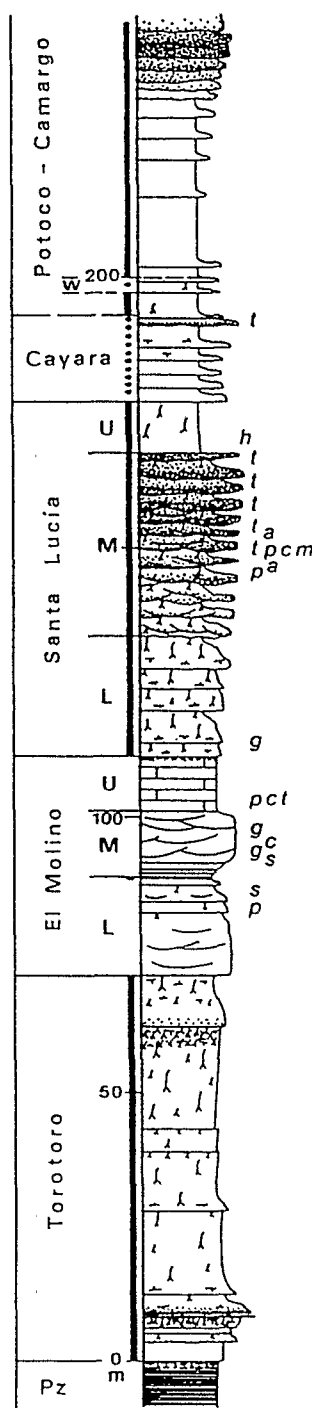


Fig. 10. Stratigraphic section of the post-Paleozoic strata at Tiupampa. Abbreviations: Pz = Paleozoic (Ordovician); L = Lower, M = Middle, U = Upper, w = La Cabaña member (see text). Fossil content (see Appendix Table 1): a = amphibians and squamates, c = crocodiles, g = gastropods, h = charophytes, m = mammals, p = fishes, s = selachians, t = turtles. Lithologic symbols same as in Fig. 2.

Europe); apparent sister groups Xenungulata (Bajo de la Palangana and Itaboraí in South America) and Dinocera (late Tiffanian of North America); and possible sister groups Notoungulata (appear ~60.0–59.5 Ma in South America) and Arctostylopoida (late Tiffanian in North America) (data after Gingerich, 1985; Marshall and Mui-

There thus exist strong faunal ties between late Riochican (to include the Itaboraian and Riochican subages) of South America and late Tiffanian faunas of North America, which based on the geochronology summarized in this paper are, in total or large part, time equivalents.

Some non-mammal groups that may have used the land bridge (apparently from South America to North America) at this time include mesosuchian crocodiles (*Sebecus* at Tiupampa and Itaboraí), and ratite (rheas), caracara and phorusrhacoid ground birds (all three groups known at Itaboraí) which are known in early middle Eocene (~50 Ma) rocks in Europe, but are as yet unknown in North America (Storch, 1993).

Several mammal groups appear in both North and South America before the beginning of the ~58.2–56.5 interchange, indicating that they participated in an earlier interchange event. These include pantodonts (Tiupampa [~59.0 Ma] in South America; middle Torrejonian [~63 Ma] in North America); mioclaenid condylarths (Banco Negro Inferior [~60.0 Ma] and Tiupampa in South America; Puercan [~65 Ma] in North America); and *Peraedectes* (Tiupampa and Laguna Umayo in South America; Puercan in North America) (Marshall and Muizon, 1988; Bonaparte *et al.*, 1993). The early tectonic history of the Caribbean region is still too poorly known to provide insights as to whether tectonism maintained or reactivated the land bridge in the Danian. The only eustatic datum that would suggest availability of a land bridge between 65.0 and 58.2 Ma is the global regression recognized by Haq *et al.*, (1987) between 60.5 and 59.0 Ma. An interchange at this time would account for the occurrence of these three groups in South America and suggest that all dispersed from North America where they are known earlier. We emphasize, however, that the evidence for the existence of a land bridge at this time is substantially more speculative than for the one beginning ~58.2 Ma. Nevertheless, a land bridge at this time is possible given the fact that the major tectonic event that uplifted the Andean margin began ~59.5 Ma.

Numerous mammal taxa are first recorded in the South American fossil record between ~58.2 and 55.5 Ma (see Tables 1–3). These “first appearances”, especially of families (Fig. 9), may be attributed to four factors: 1) dispersal from North America (as noted above); 2) sampling bias (i.e. earlier faunas are still poorly known and some of these taxa may be recorded with additional collecting); 3) landscape reorganization and hence changes in ecologies produced by tectonism beginning ~59.5 Ma may have stimulated rapid faunal turnover; and 4) some may be “pseudoextinctions” resulting from the evolution of one taxon into another (e.g. Mioclaenidae–Didolodontidae, see Bonaparte *et al.*, 1993; Alcidedorbignyiidae–Indalecidae, this study and data in Soria, 1989). Unfortunately, the data set for mammal evolution in the Paleocene of South America is still too poorly known to identify which factor(s) best explains each of the first (and last) appearances. However, the available record shows that Riochican faunas undergo notable taxonomic reorganization beginning

it is useful to formally recognize an Early (Peligran and Tiupampian; ~60.0–~58.2 Ma) and Late (Itaboraian and Riochican s.s.; ~58.2–56.5 Ma) subdivision for Riochican time Fig. 7).

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APPENDIX: STRATIGRAPHY OF THE POST-PALEOZOIC STRATA IN THE TIUPAMPA AREA

On the basis of the lithologic descriptions and of successive sequence correlations from the classical area of Potosí presented by Sempere *et al.* (1997), the Torotoro, El Molino, Santa Lucía, Cayara, Potoco and Camargo formations are easily distinguished in the Tiupampa area (Fig. 10). Faunal lists for each sequence in this area are provided in Table 1 of Appendix.

Torotoro Formation (Coniacian-Campanian). At Tiupampa, this unit consists of red, rhizolith-bearing, argillaceous sandstones and siltstones. Where the section was measured, the Ordovician strata are overlain, with no angularity and no conglomerate, by a red-brown siltstone. Some conglomeratic levels are known in the first and last tens of meters of the formation. The two paleosol guide-levels made of coalescent rhizoliths, which are respectively correlated with the early Santonian "basal limestone" and middle Campanian "upper green level" of the Chaunaca Formation, are present. The lower one, which occurs about 8 m above the base of the Cretaceous section, is overlain by a thin, coarse conglomeratic bed, which is thought to represent a reg deposit. The sandstones are very soft, immature, mostly fine-grained, and show no cross-bedding or channels. They are likely to have been deposited in an alluvial plain environment, relatively far from main rivers, under a warm climate with dry and rainy seasons.

El Molino Formation (Maastrichtian-Danian). The three sequences of the El Molino Formation can be recognized in the Tiupampa area. The Lower sequence (early Maastrichtian) is represented by a thinning-upward succession of white sandstone beds intercalated with pink to reddish siltstones and mudstones. The sandstones are rather soft, more mature than the underlying Torotoro sandstones, and show no cross-bedding. The upper part of the sequence shows repeated pinkish paleosols at top of individual sequences. The Lower El Molino shows a regressive evolution and is thought to have been deposited in an estuarine to fluvial environment. A selachian-bearing fossiliferous level mentioned by Muizon *et al.* (1983) near Vila Vila, 6 km northwest of Tiupampa, is located in this sequence (Gayet *et al.*, 1991).

The Middle sequence (late Maastrichtian-Danian) is represented by hard, mature, medium to coarse-grained calcareous sandstones showing pronounced trough cross-bedding and channels, and numerous large gastropod molds akin to *Eocerithium* (*Chemnitzia*) *potosensis* Bonarelli (Cerithiidae). A crocodile bone and teeth of the selachian *Dasyatis* sp. were recovered from this sequence at Tiupampa (Gayet *et al.*, 1991). These sandstones are interpreted to have been deposited in a high-energy estuarine environment, and to represent only the early part of the Middle El Molino depositional interval.

The Upper sequence (latest Danian) is represented by 10 m of gray fine-grained limestones. Its top surface is marked by a dissolution breccia, which indicates immersion and exposure to weathering. A bone bed located in its basal part yielded remains of Siluriformes (catfish), turtles and crocodiles (Gayet *et al.*, 1991). These limestones are interpreted to be of restricted-marine to lacustrine origin.

Santa Lucía Formation (Early Selandian). The three sequences of the Santa Lucía can also be recognized in the Tiupampa area. The Lower Santa Lucía consists of orange-brown bioturbated siltstones with common gastropod molds intercalating with some rooted sandstones, which were deposited in a distal alluvial to lacustrine environment.

The contact between the Lower and Middle Santa Lucía is expressed by the appearance of coarser facies, as in the rest of the basin. The Middle Santa Lucía sandstones are medium-grained to conglomeratic, and are intercalated with commonly rooted red-brown mudstones and some paleosols. This sequence was deposited in a meandering fluvial environment. The main fossiliferous level of the Tiupampa locality is located in the middle part of the Middle Santa Lucía (Fig. 10).

The Upper Santa Lucía underlies the erosional base of the Cayara Formation and is represented by ~10 m of dark brown-red mudstones, which were deposited in a lacustrine environment.

Cayara Formation (Late Paleocene). This unit is characterized by whitish sheet-like sandstones, locally calcareous and/or conglomeratic, which alternate with red-brown mudstones showing some rooting. One turtle-bearing conglomeratic bed is present at the top of the unit. The general color of the Cayara Formation at Tiupampa is rather light, which strongly contrasts with the dark-brown color of the underlying Upper Santa Lucía, and with the red-brown to orange-red color of the overlying Potoco-Camargo set. The Cayara is interpreted to have been deposited here in an alluvial plain environment.

Potoco and Camargo formations (Late Paleocene-Oligocene). The Potoco-Camargo stratigraphic set is the youngest unit to crop out at Tiupampa, since it is found at erosion level and/or is underthrust below Ordovician strata. This explains why its thickness appears reduced when compared with neighboring localities as Torotoro. Thus, only a part of the late Paleocene-Oligocene time span is represented at Tiupampa.

The red-brown to orange-red thick mudstones which transitionally overlie the Cayara sandstones and mudstones are assigned to the Potoco Formation. Within the lower Potoco, the La Cabaña member (here 3 m-thick) is represented by two fine-grained sandstone beds separated by violet mudstones. The Potoco Formation is coarsening and thickening-upward and grades into the Camargo Formation, which consists of conglomeratic sandstones and conglomerates. Clasts, up to 5 cm in diameter, are of Cretaceous calcareous sandstones, Cretaceous or Triassic red medium-grained sandstones, and silicified Jurassic sandstones. They indicate coeval erosion of Mesozoic rocks in an unknown area.

The Potoco-Camargo set includes alluvial plain, meandering to braided river, and possibly distal fan, deposits. It was thus deposited in an alluvial s. l. setting throughout this time span. Transition from the Potoco Formation to the Camargo Formation indicates progradation of coarse facies of proximal alluvial origin upon fine-grained facies of distal alluvial origin, suggesting that an uplift area was actively maintained during deposition of this stratigraphic set.

Table 1. List of fossil taxa described from the Tiupampa (*) and ruVila-Vila (†) localities, according to stratigraphic units (modified after Gayet *et al.* 1991).

El Molino Formation	Santa Lucia Formation
<i>Lower El Molino sequence</i>	<i>Middle Santa Lucia sequence</i>
Class Selachii	Class Osteichthyi
Order Rajiformes	Order Clupeiformes
Family Sclerorhynchidae	Family Clupeidae
<i>Pucapristis branisi</i> †	<i>Gasteroclupea branisai</i> *
<i>Ischyrrhiza hartenbergeri</i> †	Order Osteoglossiformes
Family Rhombodontidae	Family Osteoglossidae
<i>Pucabatis hoffstetteri</i> †	<i>Phareodusichthys tavernei</i> *
Class Osteichthyi	Order Characiformes
Order Pycnodontiformes	Family Characidae
Family Pycnodontidae	<i>Hoplias</i> sp. *
gen. et sp. indet.†	Order Siluriformes
Order Semionotiformes	Family Ariidae
Family Semionotidae	<i>Rhineastes</i> sp. *
gen. et sp. indet.†	Family Andinichthyidae
Order Characiformes	<i>Andinichthys bolivianensis</i> *
Family Serrasalminae	Family incertae sedis
gen. et sp. indet.†	<i>Hoffstetterichthys pucai</i> *
Order Siluriformes	<i>Incaichthys suarezi</i> *
Family Ariidae	Order Perciformes
<i>Rhineastes</i> sp.†	Family Centropomidae
Family Andinichthyidae	gen. et sp. indet. *
gen. et sp. indet.†	Order Dipnoi
Order Dipnoi	Family Ceratodontidae
Family Lepidosirenidae	<i>Ceratodus</i> sp. *
<i>Lepidosiren</i> cf. <i>paradoxa</i> †	Family Lepidosirenidae
Class Cladistia	<i>Lepidosiren</i> cf. <i>paradoxa</i> *
Order Polypteriformes	Class Cladistia
Family Polypteridae	Order Polypteriformes
<i>Dajetella sudamericana</i> †	Family Polypteridae
Class Reptilia	<i>Dajetella sudamericana</i> *
Order Chelonia	Class Amphibia
Family Podocnemididae	Order Anura
? <i>Roxochelys</i> cf. <i>vilavilensis</i> †	Family Leptodactylidae
Order Crocodilia	<i>Estesius boliviensis</i> *
Family indet.	Order Gymnophiona
gen. et sp. indet.†	Family indet.
<i>Middle El Molino sequence</i>	gen. et sp. indet. *
Class Gastropoda	Class Reptilia
Order Caenogastropoda	Order Chelonia
Superfamily Cerithiacea	Family Podocnemididae
Family Cerithiidae	<i>Roxochelys</i> cf. <i>vilavilensis</i> *
cf. <i>Eocerithium</i> (<i>Chemnitzia</i>) <i>potosensis</i>	? <i>Roxochelys vilavilensis</i> †
Bonarelli (d'Orbigny) *	Order Squamata
Class Selachii	Family ?Iguanidae
Order Rajiformes	gen. et sp. indet. *
Family Dasyatidae	Family Aniliidae
<i>Dasyatis schaefferi</i> *	gen. et sp. nov. *
Class Reptilia	Family Boidae
Order Crocodilia	gen. et sp. indet. *
Family indet.	Family Madtsoiidae
gen. et sp. indet. *	gen. et sp. indet. *
<i>Upper El Molino sequence</i>	Family Tropidophiidae
Class Osteichthyi	gen. et sp. indet. *
Order Siluriformes	Order Crocodilia
Family Ariidae	Family Sebecidae
<i>Rhineastes</i> sp. *	<i>Sebecus querejazus</i> *
Class Reptilia	Family Dyrosauridae
Order Chelonia	<i>Sokotosuchus</i> aff. <i>ianwilsoni</i> *
Family indet.	Class Mammalia*
gen. et sp. indet. *	see Table 1 in text
Order Crocodilia	<i>Upper Santa Lucia sequence</i>
Family indet.	Phylum Charophyta
gen. et sp. indet. *	Order Porocharacea
	<i>Feistiella gildemeisteri</i> *
	Cayara Formation
	Class Reptilia
	Order Chelonia
	Family indet.
	gen. et sp. indet. *