

CHRONOLOGICAL CORRELATION, PALEOECOLOGY, AND PALEOBIOGEOGRAPHY OF THE LATE CENOZOIC SOUTH AMERICAN RIONEGRAN LAND-MAMMAL FAUNA: A REVIEW

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ABSTRACT

The rise and fall of the Rionegran land-mammal fauna of the Río Negro Formation (northern Patagonia), are related to the regression of the "Paranean" sea (Middle to Late Miocene), and to the environmental changes brought about by the Andean diastrophic Diaguíta Phase (Late Pliocene). A new fission track age of 4.41 +/- 0.50 Ma has been obtained for the volcanic ash horizon in the upper part of the Río Negro Formation at the mouth of the Río Negro river. This places its mammal fauna at the beginning of the Montehermosan Land-Mammal Age (Pliocene), with a time range of c. 6 to 3 Ma. Geological and biological evidences show that the Rionegran sediments exposed in the western areas are older than the eastern ones, and can be assigned to the Huayquerian Land-Mammal Age (Late Miocene), ranging approximately from 9 to 6 Ma. Outside South America, the Rionegran fauna can be correlated with the Hemphillian and early Blancan North American faunas, and with the Turolian and earliest Ruscinian faunas of Europe. Rionegran mammals lived in flood-plain environments characterized by pools and swamps, alternated with woodland and grassland. Similarities of the Rionegran fauna with the apparently coeval ones of central, NE, and NW Argentina, indicate that subtropical environmental conditions spread from northern Argentina to northern Patagonia during the Late Miocene-Pliocene.

Keywords: Mammals, biochronology, paleoecology, paleobiogeography, Río Negro Formation, late Cenozoic, Patagonia, Argentina.

RESUMEN

Los orígenes y la desaparición de la fauna de mamíferos rionegrenses de la Formación Río Negro (Patagonia septentrional), han estado relacionados con la retracción del "mar Paranense" (Mioceno Medio a Superior) y con los cambios ambientales ocasionados por la Fase Diastrófica Diaguíta (Plioceno Superior). Una edad de 4,41 +/- 0,50 Ma obtenida recientemente con el método de las trazas de fisión, a partir de un nivel con ceniza volcánica de la porción superior de la Formación Río Negro, en la desembocadura del río homónimo, sitúa esta fauna de mamíferos en los comienzos de la Edad-mamífero Montehermosense (Plioceno), extendida aproximadamente entre 6 y 3 Ma. De acuerdo con las evidencias geológicas y biológicas, los sedimentos rionegrenses expuestos en las áreas occidentales son más viejos que aquellos de las áreas orientales, y pueden ser asignados a la Edad-mamífero Huayqueriense (Mioceno Superior), extendida aproximadamente entre 9 y 6 Ma. Por otra parte, la fauna rionegrense puede ser correlacionada con las faunas hemphilienses y las del inicio del Blancuense de América del Norte, así como con las faunas turolenses y las del inicio del Rusciniense de Europa. Los mamíferos rionegrenses habitaron ambientes de planicies aluviales, caracterizados por lagunas y pantanos alternados con bosques y pastizales. Desde un punto de vista biogeográfico, las similitudes de la fauna rionegrense con las faunas aparentemente coevas del centro, NE y NO de Argentina, indican que durante el lapso

Mioceno Superior-Plioceno las condiciones ambientales subtropicales se extendieron desde el norte de la Argentina hasta el norte de la Patagonia.

Palabras clave: Mamíferos, biocronología, paleoecología, paleobiogeografía, Formación Río Negro, Cenozoico superior, Patagonia, Argentina.

INTRODUCTION

South America has been an island continent for most of the Cenozoic, yielding highly endemic continental biota. The radiation of a peculiar array of endemic mammals (e.g., marsupials, edentates, "ungulates", caviomorph rodents) has made biochronological correlation to other continents extremely difficult. However, conversely, this radiation has been exceedingly useful for developing a detailed sequence of South American Land-mammal Ages (SALMAs), involving most of the Cenozoic (and a small part of the Cretaceous), but with marked gaps (Fig. 1; Marshall and Cifelli, 1990; Pascual and Ortiz Jaureguizar, 1990, 1991, 1992; Marshall and Sempere, 1993; and references therein).

SALMAs sequence was originally justified on the basis of "stage-of-evolution" arguments, and it remains relatively poorly constrained geochronologically in spite of growing radioisotopic and magnetostratigraphic studies over the past twenty years. Today, seven (i.e., Alamitian, Casamayoran, Mustersan, Divisaderan, Colhuehuapian, Chapadmalalan, and Lujanian) of the eighteen undisputed Late Cretaceous-Cenozoic SALMAs lack either radioisotopic dating or magnetic polarity stratigraphies (Marshall and Sempere, 1993; Flynn and Swisher, 1995).

On the basis of SALMAs sequence, most of the South American Cenozoic continental mammal faunas have been slotted in biochronologically, and, subsequently,

correlated with intra and extra continental coeval faunas (Marshall *et al.*, 1983, 1984; Savage and Russell, 1983). However, some of the South American faunas, like the Mesopotamian fauna and the Rionegran fauna, do not have a precise chronological correlation.

On the basis of its edentates, "ungulates" and caviomorph rodents, the land-mammal fauna of the "Rionegran" (Río Negro Formation; Andreis, 1965; Franchi *et al.*, 1984; and Fig. 2) have been correlated with the "Mesopotamian" one, and biochronologically with the Huayquerian-Early Montehermosan SALMAs (Marshall *et al.*, 1983; Pascual *et al.*, 1984; Pascual and Bondesio, 1985). These correlations suggest that the Rionegran fauna represents the last Tertiary mammal fauna of Patagonia.

Recently, Bigazzi *et al.* (1995) published several fission track data obtained from volcanic ash bands intercalated in sediments exposed along the southern coastal area of Buenos Aires province, and at the mouth of the Río Negro in northeastern Patagonia. In the latter locality, a very pure rhyolitic volcanic glass located in the upper part of the Río Negro Fm. yielded an age of 4.41 +/- 0.50 Ma (Fig. 3). Consequently, these sediments fall into the Montehermosan SALMA, approximately between 6 to 3 Ma (Fig. 1; but see Flynn and Swisher, 1995).

In this paper, considering the new fission track data, previous radioisotopic and magnetostratigraphic data obtained in correlated continental sequences, and the land-mammal faunal composition, the geochronology, biochronology, palaeoecology, and biogeography of the Rionegran fauna are reexamined.

TIME (Ma)	CHRONOSTRATIGRAPHY	EPOCHS	SALMAs	NALMAs	ELMAs
-	TERTIARY (LATE)	PLIOCENE	CHAPADMALALAN		
-			MONTEHERMOSAN	BLANCAN	RUSCIAN
5		MIOCENE (MIDDLE-LATE)	HUAYQUERIAN	HEMPHILLIAN	TUROLIAN
-			CHASICOAN		
-			FRIASIAN		
15			SANTACRUCIAN		

Figure 1. Standard Late Cretaceous and Cenozoic Epochs, and correlated South American (SALMAs), North American (NALMAs) and European (ELMAs) Land-mammal Ages. Based on Pascual *et al.* (1996) and Steininger *et al.* (1990).

GEOLOGY OF THE RÍO NEGRO FORMATION

Rionegran mammals have been recovered principally from the continental Río Negro Formation (Andreis, 1965; Franchi *et al.*, 1984; Pascual *et al.*, 1984), exposed in northern Patagonia (Fig. 2). This formation overlies the marine sediments which correspond to the transgression of the so-called "Paranean Sea" or "Enterrrian" or "Rionegrense marino" (Fig. 4). These sediments, which are assigned Late Miocene-Early Pliocene ages, are composed of olive green to greenish ochre clays and sandy clays and contain banks of molluscs (Andreis, 1965; Zinsmeister *et al.*, 1981; Franchi *et al.*, 1984).

Gravels of the Tehuelche Fm. have been found overlapping the Río Negro Fm. These deposits range from dark greyish brown to bluish grey with bands that vary between 8 and 15m thickness. The Tehuelche Fm. has been

assigned to the Plio-Pleistocene by Lizuaín (1983) and to the Pleistocene by Sepúlveda (1983).

According to Andreis (1965), Fidalgo *et al.* (1975), and Franchi *et al.* (1984), the Río Negro Fm. mainly consists of bluish to violet-blue psammities, defined as volcanic and pyroclastic sandstones. There are also some pinkish and yellowish siltstones, and a few thin, lenticular conglomerate bands. In between the siltstones, the sporadic presence of volcanic glass is noted, and a thin intercalation of white tuffs is found in the Punta Mejillón area. The probable origin of the sediments is fluvial, but there are a few eolian intercalations as well. The most common outstanding sedimentary structure is cross-bedding, which shows a preferential orientation to ESE, reaching 110°. Considering both surface exposures and information from the subsoil, the Río Negro Fm. in its type area (*i.e.*, in the mouth of the Río Negro), a total thickness of 200 m may be computed. A marine intercalation, named "Facies Balneario La Lobería" by Angulo and Casamiquela (1982), occurs in an area from the type locality to the latitude of Bahía Rosas.

TAXONOMIC COMPOSITION AND BIOCHRONOLOGY OF THE RIONEGRAN FAUNA

According to Pascual *et al.* (1984) and Pascual and Bondesio (1985), the mammal fauna of the Río Negro Fm. is of scarce occurrence, and is composed by edentates, litopterns, notoungulates, and caviomorph rodents. There are also several ichnofossils (Casamiquela, 1974; Angulo and Casamiquela, 1982; Pascual *et al.*, 1984).

Only a few of the "Rionegrán" taxa have been used for biochronological correlations. The cf. *Pliomorphus* sp. (Megalonychidae) found in the "Bajo de Santa Rosa" (Fig. 2), is structurally intermediate between *Eucholoeops* (Santacrucian SALMA; Fig. 1) and *Pliomorphus* ("Mesopotamian"), although it is more closely related to the latter genus (Scillato Yané *et al.*, 1976). Accordingly, these authors suggest that this taxon indicates an early to middle Pliocene age for the Río Negro Fm. at the "Bajo de Santa Rosa". However, since the "Mesopotamian" is presently correlated with the Huayquerian-Montehermosan time span (Marshall *et al.*, 1983) or the Chasicoan-Montehermosan interval (Bondesio, 1986), cf. *Pliomorphus* sp. more probably indicates a Late Miocene-Pliocene age for the mammal-bearing sediments of the "Bajo de Santa Rosa".

The aff. *Tyotheriopsis* sp. (Mesotheriidae), recovered from the "Gran Bajo del Gualicho" (Fig. 2), shows dental characters which are more advanced than those of the Friasian taxa, and very similar to those of *Tyotheriopsis chasicoensis* Cabrera and Kraglievich, 1931, a characteristic species of the Chasicoan SALMA (Fig. 1). Pascual *et al.* (1985) conclude that aff. *Tyotheriopsis* sp. indicates a post-Friasian (Chasicoan?) age for the mammal-bearing sediments of the Río Negro Fm. at the "Gran Bajo del Gualicho".

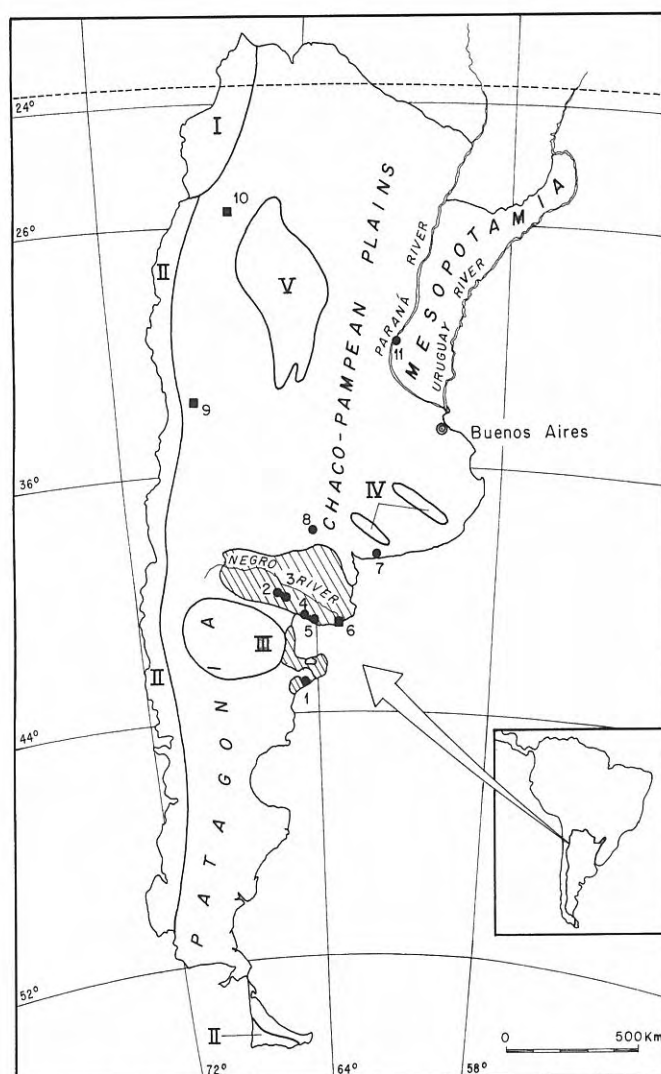


Figure 2. Main Argentinian morphostructural units and geographic situation of the localities cited in the text, with the known geographic extension of the Río Negro Fm. Modified from Andreis (1965) and Pascual *et al.* (1996). 1: Punta Cracker; 2: Bajo de Santa Rosa; 3: Gran Bajo del Gualicho; 4: Bahía Creek; 5: Balneario La Lobería; 6: Mouth of the Negro River; 7: Monte Hermoso Fm. (Montehermosan - early Chapadmalalan SALMAs); 8: Epecuén Fm. (Huayquerian SALMA); 9: Huayquerías (Huayquerian SALMA) and Tunuyán (Montehermosan SALMA) Fms.; 10: Corral Quemado Fm. (Montehermosan SALMA); 11: "Mesopotamian" fauna. ●: Localities without radioisotopic and/or magnetostratigraphic dates; ■: localities with radioisotopic and/or magnetostratigraphic dates. I: "Puna"; II: "Cordillera"; III: Northpatagonin "Masif"; IV: Bonaerean Sierras; V: Pampean Sierras. ■ Río Negro Fm.

The *Kiyutherium* aff. *orientalis* (Hydrochoeriidae) of Bahía Creek (Fig. 2) is very similar to *K. orientalis* Francis and Mones, 1965, a species that ranges from

GEOCHRONOLOGY OF THE "RIONEGRAN" AND CORRELATED SEDIMENTS AND FAUNAS

Only few of the known land mammal-bearing sediments referred to the Huayquerian and Montehermosan SALMAs (see Marshall *et al.*, 1983) are associated to volcanic ash deposits and, consequently, to radiometric ages. From the Huayquerian, a tuff from the top of the Huayquerias Fm. (Fig. 2) yielded a K/Ar date of 5.8 Ma (Marshall *et al.*, 1986; Yrigoyen 1994). A magnetostratigraphic section with associated K/Ar dates from the Andalhualá Fm. (Fig. 2) shows that these rocks and associated faunas range from 7.5 to 6.4 Ma (Butler *et al.*, 1984). In the Bolivian northern Altiplano, Huayquerian faunas have been dated between 9 and 8 Ma (Marshall *et al.*, 1992).

From Montehermosan SALMA, taxonomically diverse faunas are known from the Tunuyán Fm. (Fig. 2), which occurs above a tuff in the top of the Huayquerian Huayquerías Fm., dated 5.8 Ma. Another Montehermosan fauna was recovered from the Corral Quemado Fm. (Fig. 2), for which magnetostratigraphic and associated K/Ar ages range from 6.4 to 3.5 Ma (Butler *et al.*, 1984). Many Montehermosan faunas on the northern Bolivian Altiplano occur between tuffs date from 5.4 to 2.8 Ma using K/Ar (Marshall *et al.*, 1992).

Judging from Bigazzi *et al.* (1995) and our own observations, there are two volcanic horizons intercalated in the Río Negro Fm. in its type area. The highest one (MS, Fig. 3) is situated almost at the top of the series, and is formed by alternating layers of volcanic ash and earthy gypsum beds. This horizon does not represent primary deposition since it shows a large amount of terrigenous material mixed with glass. Moreover, the glass shows alteration; in fact it is too much altered to allow an age measurement. The lower horizon (CP, Fig. 3), 10 m below the MS, is intercalated in a fluvio-palustrine level. This horizon consists of very pure rhyolitic volcanic glass, practically free of terrigenous material (Bigazzi *et al.*, 1995). Both samples are stratigraphically well separated and show very different chemical compositions (Bigazzi *et al.*, 1995, p. 110-112). For the lower horizon, an age of 4.41 ± 0.50 Ma was obtained by the fission track method (Bigazzi *et al.*, 1995, p. 115).

According to the standard South American Cenozoic time-chart, the fission track age for the CP level of the Río Negro Fm. correlates these sediments to the Montehermosan SALMA (Fig. 1). This fission track age is in agreement with the geological and paleontological evidence, which suggests a Montehermosan age for the sediments of the Río Negro Fm. in its type area (Angulo and Casamiquela, 1982; Franchi *et al.*, 1984; Pascual and Bondesio, 1985). This agrees with a K/Ar age of 9.41 Ma (*i.e.*, Chasicosan SALMA) for the marine "Paranean" sediments at Punta Cracker (Fig. 2; Zinsmeister *et al.*, 1981), the same sediments that underlie the Río Negro Fm. in its type area.

Considering the biochronological and geochronological information, it is possible to correlate the

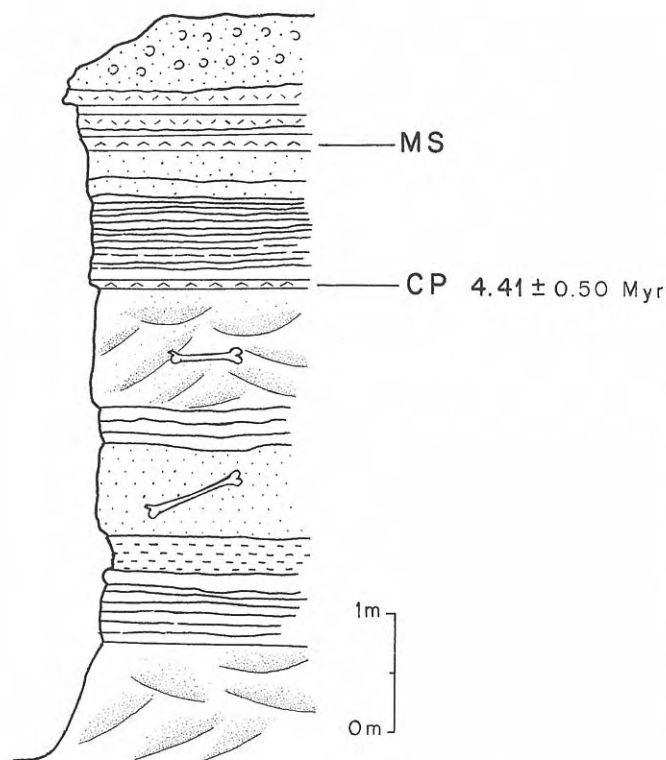


Figure 3. Stratigraphic section of the Viedma "series". MS, CP = volcanic horizons.

Huayquerian to Montehermosan SALMAs (Fig. 1). In turn, *Cardiatherium* aff. *iselli*, another Hydrochoeridae, which has been found at the "Balneario La Lobería" (Fig. 2), is very similar to the Huayquerian *C. iselli* Rovereto, 1914. It shows several dental characters indicative of those of the gigantic and highly cursorial Hydrochoeridae Protohydrochoerinae, a group recorded during Montehermosan SALMA. On the basis of such evidence, Pascual and Bondesio (1985) have referred the Río Negro Fm. to the Huayquerian SALMA, and probably to the beginning of the Montehermosan.

In considering the eastern slope of the Río Negro Fm., Angulo and Casamiquela (1982) proposed to separate the sediments of the type area from the western ones. Consequently, these authors assigned the eastern sediments to the Montehermosan SALMA, and the western ones to older SALMAs (Chasicosan?-Huayquerian). This hypothesis is supported by the fossil mammals, since the taxa recovered from western deposits ("Bajo de Santa Rosa" and "Bajo del Gualicho") are older than eastern ones (Bahía Creek and "Balneario La Lobería"). A similar conclusion was reached by Franchi *et al.* (1984).

According to Pascual and Bondesio (1985), another Rionegran mammal has been recovered from the Los Salitrales Fm., Buenos Aires Province (Fidalgo *et al.*, 1978). It is an Octodontidae Ctenomyinae rodent, named *Xenodontomys* (= "*Proctenomys*") *simpsoni* Kraglievich, 1961, which suggests a Huayquerian age for this formation (Pascual *et al.*, 1965; Pascual and Bondesio, 1985, p. 141).

Rionegrans fauna with the Huayquerian and early Montehermosan SALMAs, the Hemphillian and early Blancan NALMAs, and also with the Turolian and earliest Ruscinian ELMAs (Fig. 1).

SOUTH AMERICAN PALEOENVIRONMENTS AND BIOGEOGRAPHY DURING "RIONEGRAN" TIMES

The Northpatagonian Massif (Fig. 2) began to act as a positive structural unit during Middle to Late Miocene times as a result of the tectonic activity of the early subphases of the diastrophic Quechua Phase (Yrigoyen, 1979). Epeirogenic uplifts in its southern region and concomitant subsidence of the northern region, produced the most extensive southern South American post-Paleocene marine transgression (Uliana and Biddle, 1988, and references therein). This seaway, known as the "Paranean sea", separated the terrestrial environments of southern South America from those farther north, spreading over virtually all of eastern Argentina, western Uruguay and southern Paraguay.

The regression of the "Paranean sea" (Fig. 4) was impelled by the late subphases of the diastrophic Quechua Phase. This regression of the widespread "Paranean sea" caused similarly widespread plains, characterizing a temporal interval named "the age of the southern plains (ASP)" by Pascual and Bondesio (1982). ASP covers a time interval from Late Miocene to Late Pliocene, including Chasicoan, Huayquerian, Montehermosan and Chapadmalalan SALMAs (Fig. 1). During this interval, plain environments also existed at lower South American latitudes (Pascual and Gamarro, 1969; Pascual and Bondesio, 1982; Pascual, 1984).

Throughout ASP, the South American fauna was dominated by native taxa ("ungulates", xenarthrans, and caviomorph rodents) which were predominantly grazers and cursorials (Pascual *et al.*, 1985; Ortiz Jaureguizar, 1986, 1989; Pascual and Ortiz Jaureguizar, 1990; Pascual *et al.*, 1996). According to Ortiz Jaureguizar, (1989), this fauna was ecologically similar to the Middle Miocene-Early Pliocene North American Clarendonian Chronofauna (Webb, 1983). Similar to this Chronofauna, there is evidence that the climate became cooler during the ASP, and drier than earlier. Forested biomes were replaced by an expanding savannah.

In northern Patagonia, the ASP was represented by the Rionegrans fauna. According to Pascual and Bondesio (1985), geological and biological evidences suggest that the Rionegrans land-mammal fauna lived in flood-plain environments with pools and swamps (Hydrochoeriidae), alternated with woodlands (Megalonychidae) and grasslands (Mesotheriidae, Hydrochoeriidae).

Biogeographically, the Rionegrans fauna shows similarities with the apparently coeval faunas of central, NE, and NW Argentina. This suggests that subtropical conditions spread from northern Argentina to northern Patagonia during the Late Miocene and Pliocene (Pascual

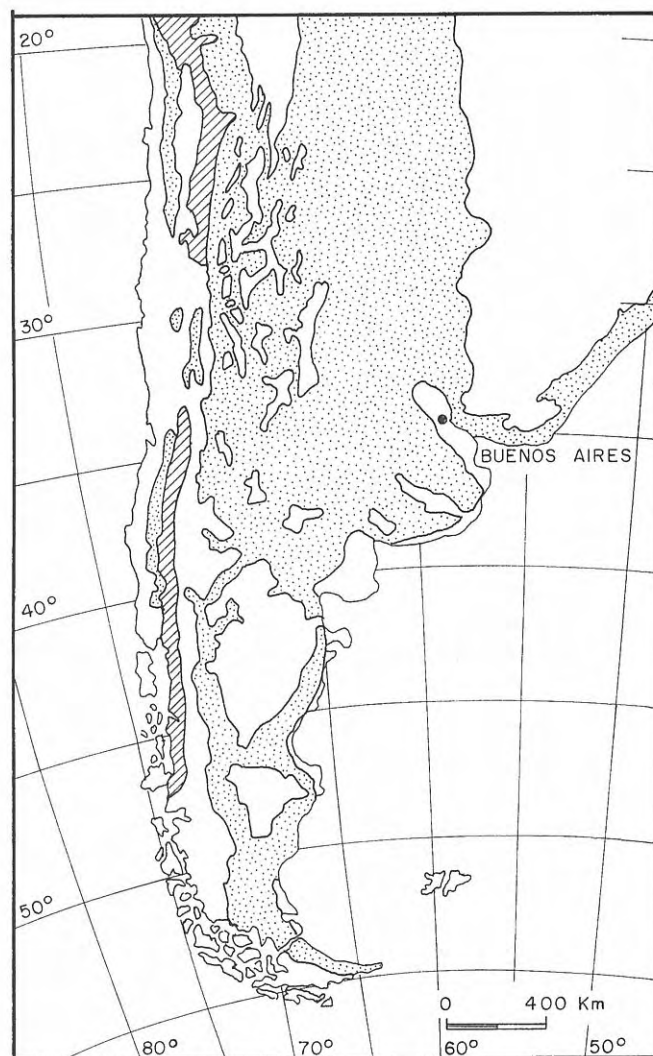


Figure 4. 5 Ma paleogeographic reconstruction showing regression of the "Paranean Sea" in southern South America. ▨ represents areas of nonmarine sedimentation; □ represents areas of marine sedimentation; ▨ indicates regions affected by igneous activity. Modified from Uliana and Biddle (1988).

and Bondesio, 1985; Pascual and Ortiz Jaureguizar, 1990; Pascual *et al.*, 1996). In spite of these overall similarities, there were minor differences between regions. For example, the apparently scansorial Megalonychidae and Nothrotheriinae Megatheriidae edentates were almost exclusively confined to the "Mesopotamian" and "Rionegrans" flood-plain areas, two wetter and more wooded areas alongside the Pampas. In turn, the Myrmecophagidae and Cyclopidae were predominantly confined to the higher-plain alluvial deposits of central-western Argentina (Pascual *et al.*, 1996).

Whilst the rise of the ASP was related to an Andean diastrophic phase, its fall was also related to a later diastrophic phase. This last phase, named Diaguaita (Yrigoyen, 1979), marks the end of the widespread southern plains. From an environmental point of view,

the end of the ASP, as in the Clarendonian Chronofauna, appears related to increased aridity, decreasing temperatures, and an increase in steppe-like environments (Ortiz Jaureguizar, 1989; Pascual and Ortiz Jaureguizar, 1990).

In northern Patagonia, the environmental changes brought about by the Diagueta Phase are represented by the coarser sediments of the Tehuelche Fm. These sediments were deposited in a high energy environment, induced by the uplift of territory north of the Northpatagonian Massif (Fig. 2; Pascual and Bondesio, 1985). Outside Patagonia, the Diagueta Phase was responsible for the uplift of the Central Cordillera and the Argentine oriental orographic systems (*e.g.*, "Puna", Pampean Sierras, Bonaerian Sierras; Fig. 2), the uplift of the Mesopotamian region (Fig. 2), and the subsequent appearance of the Panamanian land-bridge (Pascual *et al.*, 1996). All these events had dramatic consequences for the South American biota. The final uplift of the Pampean Sierras formed a major barrier to moisture-laden Atlantic winds; consequently, the regions situated along the western slopes of these Sierras became severely desiccated, and the Chaco-Pampean plain (Fig. 2) took on its present environmental conditions. Similar uplift of the Central Cordillera (Fig. 2) produced the rain shadows that resulted in the extremely xeric conditions presently existing in the area between this mountain chain and the Pampean Sierras. The subsequent appearance of the Isthmus of Panamá permitted the more massive phases of the "Great American Biotic Interchange" (Stehli and Webb, 1985; Marshall and Cifelli, 1990; Pascual and Ortiz Jaureguizar, 1990; Pascual *et al.*, 1996).

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