

## Neogene Vertebrates from Argentine Patagonia: Their Relationship with the Most Significant Climatic Changes

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### 1. Introduction

Pascual and Odreman Rivas (1973) made an excellent update of the mammal-bearing units of the Patagonian Cenozoic and their relationships with diastrophic processes. In what these authors called “Patagonic area”, they distinguished two regions with mammal-bearing sediments, belonging to two different basins limited southward by the Patagonian massifs: (1) the region between the Macizo de Somun Cura or North Patagonian Massif and the Macizo del Deseado (Deseadan Massif), and (2) south of the Deseadan Massif. Both regions correspond mainly to the San Jorge Gulf Basin and the Austral Basin, respectively (Fig. 1).

In the San Jorge Gulf Basin, sediments with faunas pertaining to the Paleogene prevail, while in the Austral Basin the beginning of the Neogene is best represented with the outstanding exposures of the Santa Cruz Formation, already known since the end of the twentieth century through the fieldwork of Carlos Ameghino and the paleontological descriptions of his brother Florentino (see Ameghino, 1889, 1906).

According to Pascual *et al.* (2002), the oldest Cenozoic mammals recorded in southern Patagonia (Santa Cruz Province) belong to the Paleogene, the Casamayoran (Late Eocene) and Deseadan (Late Oligocene) stages. In turn, the Neogene is represented by the Santacrucian (the latest Early Miocene) stage, followed by younger units up to the Mayoan stage of the “Estratos del Guenguel” (late Middle Miocene) in the northwest of the province (Dal Molin and Franchi, 1996). The Santacrucian stage is undoubtedly the richest of these Neogene units in mammal remains within the Argentine territory, and probably the entire South American continent (Pascual *et al.*, 2002), whereas in Chubut Province there are also older sediments assigned to the Peligran and Riochican (Paleocene) stages.

The continental vertebrate-bearing units are interfingered with marine sedimentary rocks rich in paleontological content, both invertebrate and vertebrate remains. Among the latter, abundant and diverse remains of condrichthyan fish with significant biostratigraphic value (Arratia and Cione, 1996) and spheniscid birds (Simpson, 1972; Cione and Tonni, 1981; Acosta *et al.*, 2004) are recorded. For the Late Paleogene and the Neogene, several marine units have been recognized. The “Patagoniano”, “Patagoniense” or “Patagonia Formation” (including the

San Julián, Monte León and Gaiman formations, see Zinsmeister, 1981; Cione and Cozzuol, 1990; Cione, 2002) ranges from the Late Eocene to the Early Miocene; in northeast Patagonia, it is represented by the Puerto Madryn Formation which is Middle–Late Miocene in age (Arratia and Cione, 1996; Cione *et al.*, 1996).

In the Patagonian region, no mammals that may be clearly correlated with those characterizing the uppermost Miocene–Pliocene units of the extra-Patagonian area (Montehermosan, Chapadmalalan and Marplatán stages; Cione and Tonni, 1999, 2005) have been recorded. The single exception are the few reports of the Puerto Madryn Formation (Dozo *et al.*, 1999, 2002) or those of the Cerro Azul Formation at the northern boundary of the studied area (Montalvo, 2000, 2001, 2003; Urrutia and Scillato-Yané, 2003; Montalvo and Verzi, 2004; among others). Those of the Early Pleistocene (Ensenadan stage) are not present either.

The remains of the Late Pleistocene are relatively frequent, but almost restricted to those representing approximately the last 15,000 yrs, many of which are directly or indirectly associated with archeological sites. Tonni *et al.* (1982: 149) pointed out that during the Pleistocene “... gran parte del territorio patagónico estuvo habitado por megamamíferos de las mismas especies o muy cercanamente emparentadas a las que habitaron el área pampeana” [“... a large portion of the Patagonian territory was inhabited by megamammals of the same species or very close related to those inhabiting the Pampean region”].

The successive faunas recognized since the Neogene in Patagonia will be described, as well as their contribution to the chronology of the host sediments and their relationships to climatic and environmental changes. Given that the vertebrate record in Patagonia is very scarce since the Late Miocene, it was necessary to base the analysis on the northern extra-Patagonian faunas (Pampasian), which are highly diversified and better known, to interpret the changes of the Patagonian region more precisely.

### 2. Climate

The entire Patagonian territory was essentially an oceanic peninsula during the Tertiary and Quaternary periods, since a short distance has always separated the two

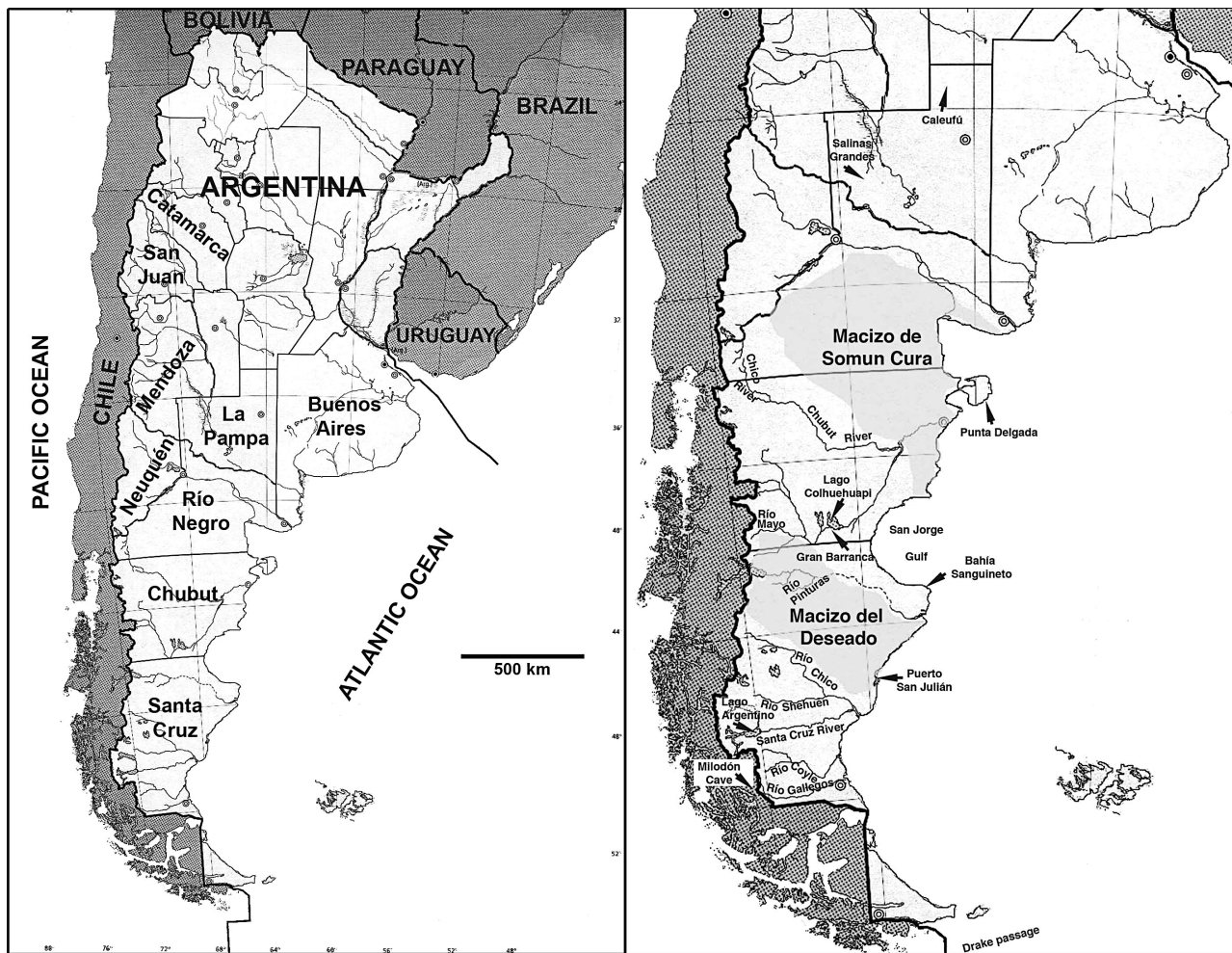


Fig. 1. Map of Patagonia, Argentina, showing main localities and local names used in the text.

large oceanic masses that border it east and west, the Pacific and Atlantic oceans. Moreover, after the complete opening of the Drake Passage, farther south of insular Patagonia, Patagonia became completely surrounded by the sea. In addition, immediately after the climatic optimum of the late Early Miocene (Pagani *et al.*, 1999; Zachos *et al.* 2001), the Antarctic continent became permanently covered by ice (Flower and Kennett, 1994; Shevenell *et al.*, 2004), and the Circum-Antarctic current certainly acted decisively on the climatic ruling of Patagonia. We are considering here the main climatic changes reflected on the fauna; notwithstanding, if we consider changes on partial groups of vertebrates that are better known for local fauna assemblages (i.e. rodents), we would be able to give a more accurate view. It is impossible to do it in Patagonia as a whole, but in a few localities (see Kramarz and Bellosi, 2005). The whole period considered in this contribution, from the Middle Miocene to the end of the Pleistocene (or the beginning of the Holocene), is characterized by a continuous decrease of mean marine temperatures (Zachos *et al.*, 2001) (Fig. 2). This constant temperature decrease certainly defined the climate in most of the Patagonian peninsula, which suffered, in addition to the changes of temperature, its own changes derived from the rising of the Andean Cordillera, all along the western part of its

territory, with the consequent modification of the moisture supply from the Pacific Ocean. Hence, the mountain rise that affected the path of wetter winds from the Pacific eastward forced the precipitation of most of the discharge almost at the beginning of its way over Patagonian territory, and led the extra-Andean area to progressive desiccation. Changes toward lower mean temperature and humidity were gradual and largely determined the faunal changes in different mammal groups and at different moments according to their specific sensitivity (Ortiz Jaureguizar *et al.*, 1993; Pascual *et al.*, 1996).

Quattrocchio *et al.* (1988), on the basis of palynomorphs and vertebrate remains, stated that a marked climatic deterioration occurred by the end of the Miocene in the Colorado Basin (northern Patagonia). Scillato-Yané *et al.* (1993) analyzed the variation of the xenarthran diversity during the Friasian sst-Mayoan lapse and determined that the shift toward colder and drier conditions was a gradual process that occurred during this lapse, resulting in the conditions that prevailed since the Chasicuan stage. This change of climatic conditions influenced the xenarthran diversity selectively and progressively, while tardigrades were the first group showing a taxonomical change, followed by the cingulates. The new environmental conditions are compatible with open areas of grasslands developed during dry

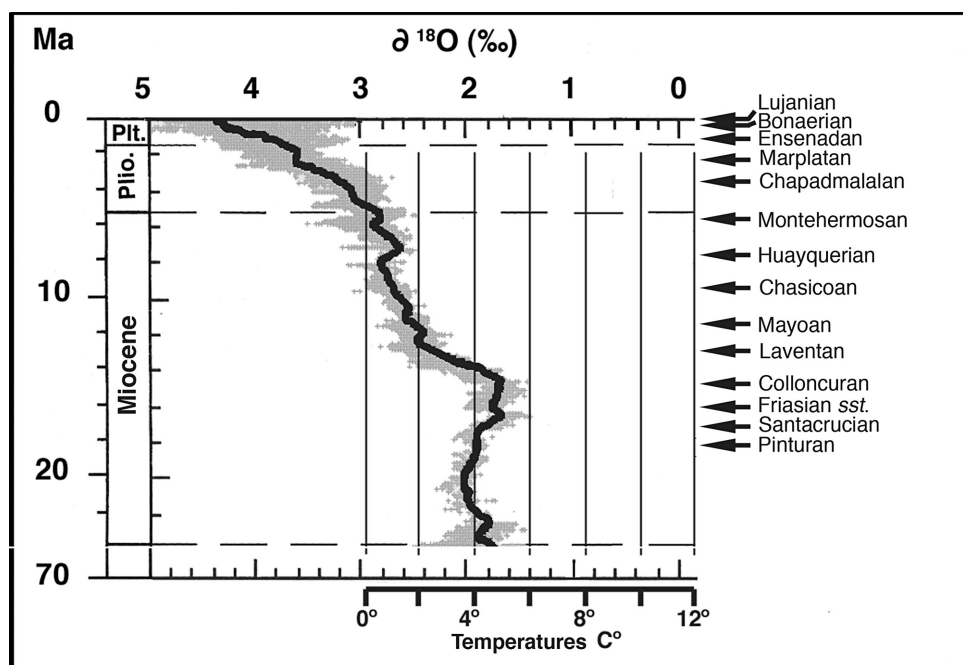


Fig. 2. Miocene to Recent variation of sea temperature and the approximate chronology of the main stages analyzed in the text (temperature curve modified from Zachos et al., 2001).

seasons. Montalvo and Verzi (2004) arrived to similar conclusions based on octodontoid rodents for the following lapse, the Huayquerian–Montehermosan stages, reinforcing the idea that the trend of the climatic–environmental change had a defined directionality since the Middle Miocene.

From the latest Pliocene to the Early Pleistocene (ca. 2.5–1 Ma), frequent glaciations were recorded in southern Patagonia, with a remarkable increase of the continental ice sheet between 1.5 and 1.2 Ma (Singer et al., 2005).

In the latest Pleistocene (ca. 13–11 <sup>14</sup>C ka BP), a new glacial advance in southern Patagonia under humid conditions (McCulloch et al., 2000; see also Strelin and Denton, 2005) generated a favorable environment for herbivores, including megaherbivores and their predators (Tonni et al., 2003); these conditions seem to have favored also the southern expansion of the running bird *Rhea americana* (see Tambussi and Tonni, 1984).

In summary, from the Santacrucian to the Late Lujanian, within the territory of the present Patagonian region, the faunal associations that were developed correspond to a variety of climatic changes. These changes may be summarized in four successive climatic scenarios (see Fig. 3 for explanations; Figs 4–7):

1. the climatic optimum of the late Early Miocene (Fig. 4), with a well-developed tree vegetation, with full- and semi- tree-dwelling forms (e.g. Primates, Eretizontidae and various Xenarthra, Phyllophaga);
2. later, during the “Friasian” stage (Friasense sst., “Colloncurense” and Mayoense stages), more open environments become predominant, allowing the occurrence of more cursorial and larger forms. The forested areas would have been restricted to the valleys of the rising cordillera, hosting a few

tree-dwelling species (e.g. the last record of Primates and Eretizontidae) (Fig. 5). This changes occurs progressively along the “Friasian” stage, and affected selectively different mammalian lineages (i.e. among the Xenarthra, the Pansantacrucian Tardigrada were more sensitive than Cingulates, and were replaced by the beginning of the Friasian sst. for the lineages that became dominant during the Panaraucanian period);

3. partially in coincidence with the tectonic Quechua phase, neatly open environments with at least one dry season developed, including extensive savannas with Attini (Formicidae) mounds (see Laza, 1982) (Fig. 6). In several mammalian lines, a tendency toward size increase and the beginning of the Pampean lineages are observed. For the first time, Holarctic taxa are recorded (e.g. Procionidae);
4. during the last glacial advance in Late Glacial times (13 to 11 <sup>14</sup>C ka BP), favorable conditions (higher moisture) were recorded in southern Patagonia to support a high diversity of large mammals corresponding to Pampean lineages that dispersed toward the south (e.g. Milodontidae, Tremartidae bears, Machrauquenidae, smilodons) (Fig. 7).

### 3. The Santacrucian Stage

As it has been pointed out in the Introduction, the best-known land-mammal faunas south of the Río Chico of Santa Cruz Province were found in lithostratigraphic units included in the Santa Cruz Formation, the Santacrucian stage. This formation was originally recognized for its exposures at the southern end of the Atlantic coast (see Tauber, 1997) whose radiometric dating yielded a

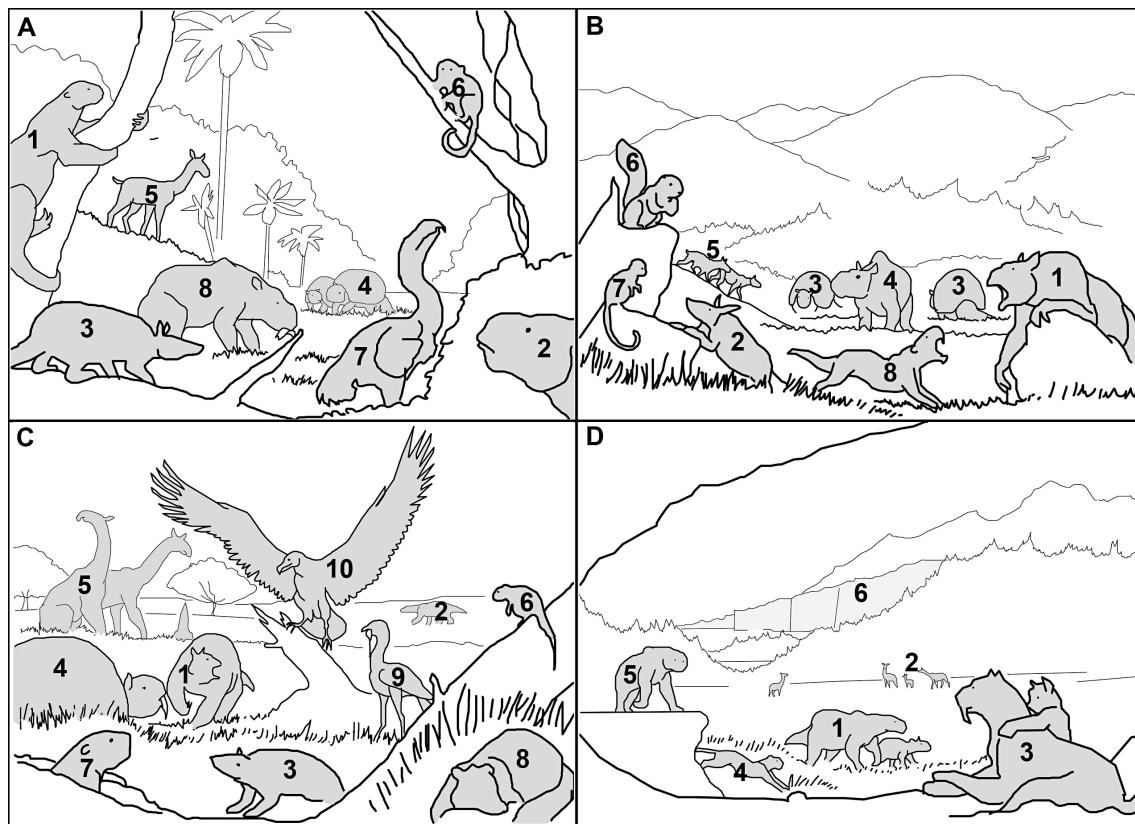


Fig. 3. **A**, Explanation Figure 4: 1, scansorial Megatheriidae; 2, medium size ground sloth; 3, Armadillo; 4, Glyptodonts; 5, Protherotheid native ungulate; 6, Platirhyne monkey; 7, Phororacoid ground bird; 8, Toxodontid native ungulate. **B**, Explanation Figure 5: 1, Megatheriinae; 2, Armadillo; 3, Glyptodonts; 4, Toxodontid; 5, Protherotheid native ungulate; 6, Rodent; 7, Platirhyne monkey; 8, Thylacosmiliid marsupial. **C**, Explanation Figure 6: 1, Mylodontid ground sloth; 2, Sclidotheriine ground sloth; 3, Armadillo; 4, Glyptodonts; 5, Macrauchenid native ungulate; 6, small rodent; 7, large rodent; 8, Inmigrant racoon carnivore; 9, Small Phororacoid ground bird; 10, Giant flying bird, Argentavis. **D**, Explanation Figure 7: 1, Mylodontid; 2, Camelids; 3, Sabertooth carnivore; 4, Large felid Panthera; 5, Large bear Arctotherium; 6, Glacier.

mean of 16.53 Ma (Fleagle *et al.*, 1995), that is the latest Early Miocene.

This formation extends all along the southern territory of Santa Cruz Province, often with quite scattered outcrops, up to the foot of the southern Patagonian Andes, especially along the larger rives such as the Gallegos, Santa Cruz, Shehuen or Chalia and Chico. For many years, the outcropping sediments at the foot of the southern Patagonian Andes were identified as the Santa Cruz Formation; an example are those units surrounding Lago Argentino that were referred to the Santa Cruz Formation, more because of their fossil mammals than for their lithological features. These sediments included a high number of taxa apparently similar to those of the typical Santa Cruz Formation, from the coastal locality between the Coyle and Gallegos rivers. However, Ameghino (1900–1902) had already proposed that this fauna (collected by his brother Carlos in 1889) was older than previously assumed, and identified it as representative of a chronologically different unit that he named as *Étage Notohippidien* (see Marshall and Pascual, 1977). In addition, he outlined that his brother collected the most representative fossils in Karaikén, near Lago Argentino and a little farther north of the sources of the Río Santa

Cruz. In 1930, L. Kraglievich recognized this unit as *horizonte Karaikense* of the “Formación Santacruceña”, stating its greater antiquity within the “Formación Santacruceña” of Ameghino (Kraglievich, 1934).

Another locality bearing “Santacrucean” fossils and known for more than a century is located along the streams of the Río Pinturas Basin, at the northwestern sector of Santa Cruz Province. Following the tradition, these sediments were also assigned to the Santa Cruz Formation. The first mammals were also collected by Carlos Ameghino, and described by his brother Florentino in 1906, but the precise locality was never published. However, after the study of these fossils, Ameghino considered them as intermediate between those somewhat older from the Colhuehuapian and those somewhat younger from the Santacrucean of the coast. He considered them as representing a different biozone, which he named as “Astrapothericulense Zone” (*sic*). In 1931, J. Frenguelli made additional collections in Arroyo Feo and agreed with Ameghino that they were intermediate between the Colhuehuapian and Santacrucean faunas; this argument was followed more recently by De Barrio *et al.* (1984). In turn, Pascual and Odreman Rivas (1971) considered that the mammals from the Río Pinturas should not be separated in a



Fig. 4. Climax scenario of the climatic optimum of the upper Early Miocene, well-developed tree vegetation, with full- and semi- tree-dwelling forms (e.g. Primates, Eretizontidae and various Xenarthra, Phyllophaga).

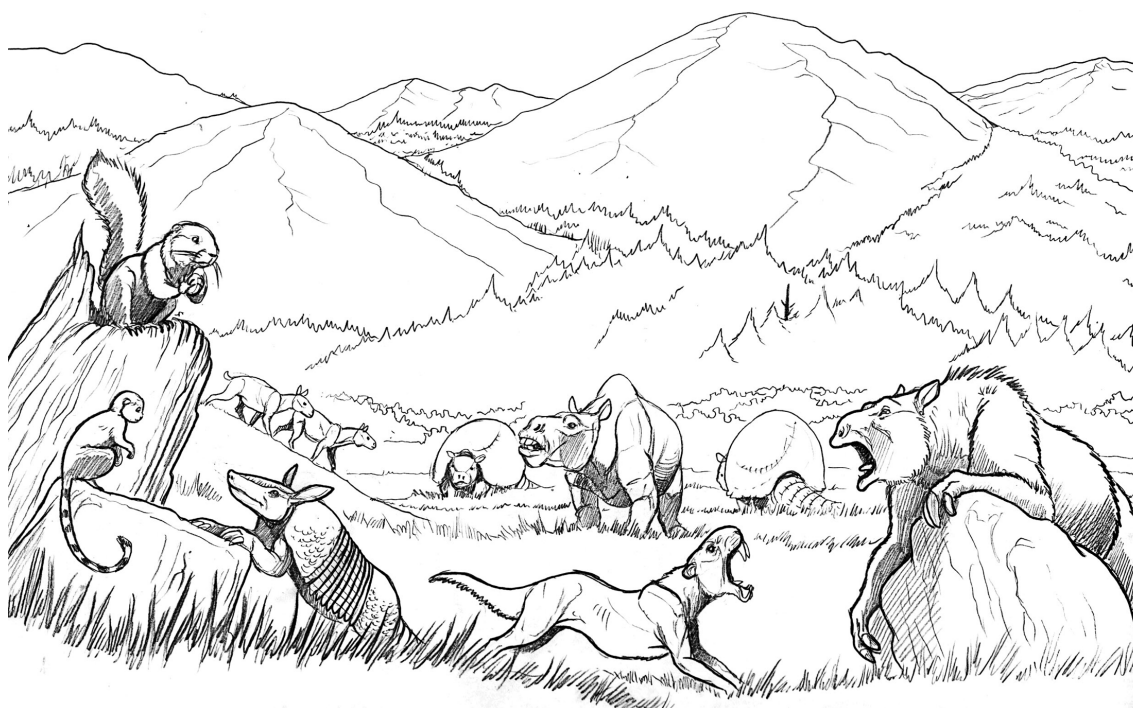


Fig. 5. Climax scenario during the "Friasian" stage (Friasian sst., "Colloncuran" and Mayoan stages), more open environments become predominant, allowing the occurrence of more cursorial and larger forms. The forested areas would have been restricted to the valleys of the rising cordillera, hosting a few tree-dwelling species (e.g. the last record of Primates and Eretizontidae).

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Fig. 6. Climax scenario partially coincident with the tectonic Quechua phase, neatly open environments, including extensive savannas with Attini (Formicidae) mounds. Several mammal lineages show a tendency toward an increasing body size. For the first time, Holarctic taxa are recorded (e.g. Procyonidae).

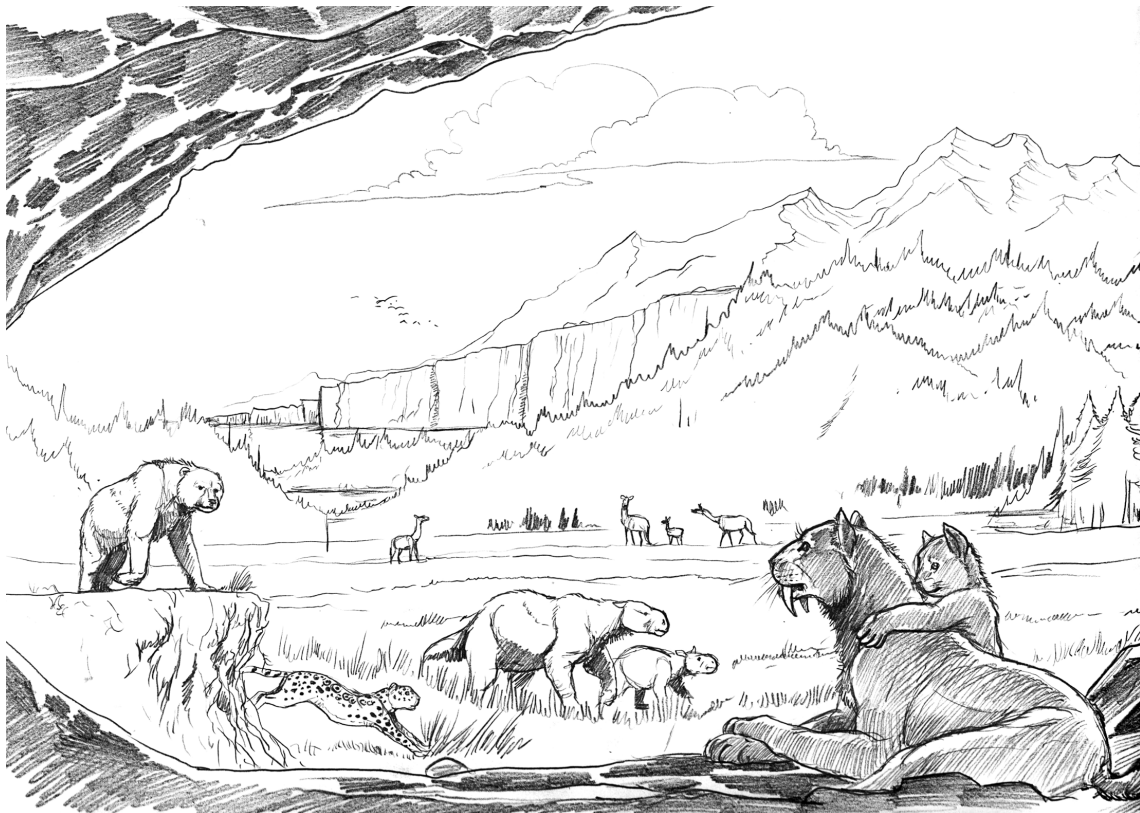


Fig. 7. More favorable conditions (higher moisture) were recorded in southern Patagonia which supported a high diversity of large mammals corresponding to Pampean lineages which dispersed southward (e.g. Mylodontidae, Tremarctinae bears, Machrauchenidae, Smilodons) during the last glacial advance in Late Glacial times (13 to 11 <sup>14</sup>C ka BP).

different “Land-mammal Age” from the Santacrucian, but later Fleagle *et al.* (1995: 129) did not share this argument and concluded that the “Pinturan” fauna should be considered as “... a separate faunal zone”. Probably both the Pinturan mammals and the Notohippidian mammals from Lago Argentino have not such a taxonomic and ecological differentiation to justify a clear separation from the Santacrucian; however, the span of time between both deposits is quite short (see also Kramarz and Bellosi, 2005). This was supported by Patterson and Wood (1982) and Marshall (1976). Notwithstanding, Kramarz and Bellosi (2005) considered that in the Pinturas Formation there are two different assemblages of rodents, the lower and middle with affinities with both Colhuehuapian and Santacrucian genera, and the upper bearing the typical Santacrucian species.

Multivariate similarity analyses among different mammal units, taking them as units, and considering the families of Cenozoic mammals as “characters”, revealed a hierarchical organization of the “Land-mammal Ages” (see Pascual *et al.*, 1996). According to this criterion, the Patagonian Faunistic Cycle includes the Deseadan Subcycle (older), and the PanSantacrucian Subcycle (younger). This latter includes the Colhuehuapian and Santacrucian “Land-mammal Ages” being the “Notohippidian” and the “Pinturan” part of the Santacrucian. According to the evolutionary degree of their mammals, they represent a succession of very close communities which immediately precede the mammal communities of the Santa Cruz Formation of the coast. The well-known degree of taxonomical identity between the communities of the “Notohippidian” with those typically Santacrucian of the coast could be explained because “... el período de subsidencia del mar “Patagoniano” (= Formación Cerro Centinela en la región del Lago Argentino y Formación Monte León en la costa Atlántica) haya sido más corto que en la costa actual del Atlántico, y que el movimiento regresivo haya comenzado en el Oeste para extenderse gradualmente hacia el Este” [“... the subsidence period of the “Patagonian” Sea (= Cerro Centinela Fm. in the Lago Argentino region and Monte León Fm. at the Atlantic coast) had been shorter along the present Atlantic coast and that the regressive movement had begun toward the west to move gradually eastwards”; Feruglio, 1944: 99; 1949: 181]. The “Notohippidense” of Lago Argentino (Santa Cruz Formation *auct.*) and the Santa Cruz Formation of the Atlantic coast represent the continental facies after the regression of the “Patagonian” sea; and probably this is the reason of the minor difference between the evolutionary degrees of their communities. Besides, the mammal communities characterizing the Colhuehuapian present an evolutionary degree immediately preceding that of the “Notohippidian” and “Pinturan” of the cordilleran foot. Radiometric dating approach the age of the sediments bearing Colhuehuapian fauna of the Sarmiento Formation at Gran Barranca, south of Lago Colhué Huapi, Chubut (ca. 19 Ma; Kay *et al.*, 1999, Madden *et al.*, in press), to that of the Monte León Formation of the Atlantic coast (ca. 19.35 Ma; Fleagle *et al.*, 1995). Although radiometric dating of the “Notohippidian” sediments are available, the mean dates of the Santa Cruz Formation at the Atlantic coast (16.53 Ma) and the “Pinturan” of Río Pinturas (17.08 Ma) explain the degree of taxonomic identity and

compositional similarity of the Colhuehuapian communities (ca. 19 Ma *vide* Kay *et al.*, 1999), “Pinturan” (ca. 17 Ma) and Santacrucian (ca. 16.5 Ma). These two were estimated from those obtained by Fleagle *et al.* (1995).

The most recent contributions on vertebrates, especially mammals, recorded in the Santa Cruz Formation, include papers by Tauber (1997, 2000 a, b), Tauber *et al.* (2003, 2004 a, b), Kramarz (1998, 2001), Ribeiro and Bond (1999), Candela (2003) and Vizcaíno *et al.* (2004), among others.

For the Pinturas Formation (the latest Early Miocene) of Santa Cruz Province, see Kramarz (1999, 2004) and Tejedor (2003).

In turn, Tauber *et al.* (1999) described the first group of Santacrucian continental vertebrates for Neuquén Province; in this association, characteristic taxa of this age such as *Astrapotherium*, *Protypotherium*, *Adinotherium* and *Hegetotherium* may be found.

Forasiepi *et al.* (2001) analyzed the carnivorous marsupial *Arctodictis*, recorded in the Santacrucian (Middle Miocene) of Patagonia and La Venta (Colombia), and concluded that quite probably the specimen of Colombia has to be referred to another larger taxon related to *Prothylacynus* or *Dukecynus*.

#### 4. The Friasian and Colloncuran Stages

In the Middle Miocene, the diastrophic movements that uplifted the Patagonian Cordillera (especially the early subphases of the Quechua phase) caused the sediments of this age to be restricted to structural valleys located along the piedmont of the already defined Patagonian Cordillera (Pascual and Odreman Rivas, 1973). Such lithostratigraphic units as the Chimehuín and Rancahue formations (Turner, 1965), and the Collon Cura and Ñorquinco formations (Cazau, 1972) are assigned to these ages.

During the “Friasian” s.l., typical mammals of warm, tropical or subtropical environments that were present during the last climatic optimum of the Santacrucian, even at more southern latitudes, disappeared from the record. This event marked a sharp turnover in the composition of the mammal faunas of the southern tip of South America (Pascual, 1984; Pascual *et al.*, 2002), pointing out the beginning of a new faunistic cycle – the Panaraucanian which replaced the preceding Patagonian cycle (Pascual and Ortiz Jaureguizar, 1990). On the other hand, the withdrawal of marine environments is followed by open environments, named by Pascual and Bondesio (1982) as *Edad de las planicies australes* (“Age of the Southern Plains”), which mainly corresponds to the development of depocenters north of the Patagonian region, in the Chaco-Pampean plains. This *Edad de las planicies australes* is represented by mamma-bearing sediments of the Chasicoan, Huayquerian and Montehermosan stages (Pascual and Ortiz Jaureguizar, 1990).

At the beginning of the Panaraucanian cycle (represented by the transitional “Friasian” s.l. stage (included the Colloncuran, Mayoan and Chasicoan stages), a few members of the Patagonian cycle are still recorded. This is the case of the ungulates Homalodotheriidae and Nesodontinae, and the cingulate xenarthrans

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Pelthephilidae (Bondesio *et al.*, 1980a). These forms disappeared from the record in later units in which cursorial grazers prevailed. However, among the xenarthrans, the changes in the beginning of the Panaraucanian are slow and by groups, the tardigrades being the first group to show a taxonomical change, and the cingulates the last one (Scillato-Yané *et al.*, 1993; Scillato-Yané and Carlini, 1998).

In Río Negro Province, mammals found in the Collón Cura Formation, near Pilcaniyeu Viejo, were assigned to the Friasian stage (Bondesio *et al.*, 1980a, b; Pascual *et al.*, 1984). In addition to the mammals that characterize the sediments of this age, a few specimens of fish, amphibians, anurans, reptiles and birds are present (Pascual *et al.*, 1984).

Later, the contributions of Vucetich *et al.* (1993, and literature therein; Scillato-Yané and Carlini, 1998) showed that the Collón Cura Formation, present in Neuquén and Río Negro provinces, bears a transitional fauna between the older one from the Friasian sst., and the younger from the Mayoan stage. In this way, these authors updated the sequence that had been supported originally by L. Kraglievich (1934). The Collón Cura Formation has an absolute age of 15.4 Ma, dated on the Pilcaniyeu Ignimbrite which occurs within this formation (Rabassa, 1975; Bondesio *et al.*, 1980a; Franchi *et al.*, ms.).

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## 5. The Mayoan Stage

Sediments of the Río Mayo Formation (“Estratos del Guenguel”), exposed in the northwest of Santa Cruz Province, are  $^{40}\text{Ar}/^{39}\text{Ar}$  dated in ca. 11.5 Ma (see Dal Molín and Franchi, 1996). Above the tuffs with this dating, a megatheriine xenarthran assigned tentatively to *Eomegatherium* (Brandoni and Carlini, 2004) was found, in addition to remains of *Megathericulus* and new xenarthrans described by Scillato-Yané and Carlini (1998). In the El Pedregoso Formation and other coeval units (“Estratos del Guenguel”; Franchi *et al.*, ms) of this province, Pascual *et al.* (2002) found transitional mammals between those of the Patagonian and Panaraucanian cycles (Ortiz Jaureguizar, 1986), which means “. . . un cambio ecológico sustancial que hemos tomado como efecto de las primeras subfases de la compleja Fase Quechua” (“. . . a substantial ecological change that we have taken as the effect of the first sub-phases of the complex Quechua Phase”; Pascual *et al.*, 2002: 540).

The Río Mayo Formation is also exposed at the margins of the Río Chico in Río Negro Province and yielded a primitive Thilacosmyliidae (Goin and Carlini, 1993) probably related to the genus described by Goin (1997) for the “Laventan” SALMA, La Venta, Colombia (Kay *et al.*, 1997).

## 6. The Huayquerian Stage

The sediments of the Puerto Madryn Formation, exposed in Península Valdés (Chubut Province) between Punta Delgada and Pico Lobo, include remains of continental vertebrates described by Dozo *et al.* (1999; 2002). The

presence of the pampatherid *Kraglievichia*, as well as certain dolichotine and cardiatherine rodents, certifies the Huayquerian age of the sediments, deposited under temperate-warm climatic conditions (Dozo *et al.*, 2002). From a paleobiogeographic point of view, the southernmost distributions of several mammal taxa are recorded here (e.g. *Kraglievichia* sp.), showing a southern displacement of climatic conditions, at least near the coast.

In sediments of the Cerro Azul Formation exposed in Salinas Grandes de Hidalgo, La Pampa Province, Urrutia and Scillato-Yané (2003) recorded the dasypodid *Macroeuphractus retusus*, which represents also a western expansion of its known geographic distribution. This species had been previously recorded in the Montehermosan stage of Buenos Aires Province (Farola Monte Hermoso) and the Ituzaingó Formation (in the *conglomerado osífero* [“bone bearing conglomerate”]), Entre Ríos Province, in NE Argentina. The sediments of the Cerro Azul Formation are referred by these authors also to the Huayquerian stage, being another case of southern (and western) extension of fauna.

For 11 sites of La Pampa Province, 10 of which correspond to the Cerro Azul Formation and 1 to *niveles coetáneos de la Formación Río Negro* (“coeval levels of the Río Negro Formation”), Montalvo and Cerdeño (2002) recorded the hegetotherid notoungulate *Hemihegetotherium achathaleptum*, also present in sediments referred to the Huayquerian of Catamarca, San Juan and Mendoza provinces. Montalvo (2000) also assigned a Huayquerian age for the Cerro Azul Formation in Telén, La Pampa Province.

## 7. The Huayquerian–Montehermosan Stages

In Calefú, La Pampa Province, Verzi *et al.* (2003) described a new octodontid rodent of the genus *Xenodontomys*, based on more than 200 specimens. They conclude that it is the most derived chronomorph of the phyletic sequence previously known of *Xenodontomys* and hence the site of Calefú would represent the youngest levels of the Cerro Azul Formation (probably Montehermosan), perhaps coeval with those of the Irene “Formation” of southern Buenos Aires Province. Montalvo *et al.* (2000a, b) and Montalvo (2001) assigned the Calefú exposures to the Late Miocene–Early Pliocene. In the first paper, the presence of the rodents *Phthoromys* and *Neophanomys biplicatus* suggested to the authors an Early Pliocene age (Montehermosan, see Montalvo *et al.*, 2000a, b). For this same site of the Cerro Azul Formation (Calefú), Montalvo and Rocha (2003) cited the presence of the cavid rodent *Neocavia* which would confirm the assignment to the Montehermosan stage (Late Miocene). Similar conclusions were reported by Esteban *et al.* (2003) based on the study of dasypodids found in the Estancia El Recado, located 10 km farther southwest of Calefú, and by Abello *et al.* (2002), with the study of marsupials. For them, the age of the site would be somewhat older than that of Calefú with *Xenodontomys*, and assigned it to the Huayquerian stage (Late Miocene).

## 8. The Lujanian Stage

Among the first findings of Pleistocene mammals are those recovered by Charles Darwin in 1834 in Puerto San Julián, belonging to a large native South American ungulate, described by Owen (1838–1840) as *Macrauchenia patachonica*. Although this author recognized the similarity with the camelids in the length of their cervical vertebrae – hence its generic name – he pointed out that it was an ungulate different from any other known before. In 1889, Ameghino proposed to include this curious genus, together with others from the Neogene, in the Order Litopterna.

Mercerat (1897) mentioned *Tyotherium* (= *Mesotherium*), a guide taxon from the Ensenadan, as collected in Shang Aiken, Río Coig. However, later authors such as Ameghino and Feruglio considered this reference as highly dubious (see Tonni *et al.*, 1982; Pascual *et al.*, 2002).

In Bahía Sanguinetta, Santa Cruz Province, Parodi (1930) cited the record of *Megatherium australis*, *Mylodon "darwini"* and *Glyptodon clavipes* (?). Likewise, Tonni *et al.* (1982) cited several unpublished records on materials housed in the collections of the División Paleontología Vertebrados of the Museo de La Plata. This is the case of *Antifer* sp. (MLP 57-III-7-1) from the confluence of the Limay and Neuquén rivers; *Macrauchenia* sp. (MLP 80-IX-5-1) in central Chubut Province ("Cerro Guacho") and Equidae indet. (MLP 67-XI-7-1) from Cañadón Seco, Santa Cruz Province. Also in Santa Cruz Province (Puerto Deseado), the geologist C.A. Ferrari found remains of *Megatherium* sp. (see Tonni *et al.*, 1982: 149).

In Sierra de Portezuelo (Neuquén Province), Garrido and Álvarez (2004) reported remains of *Equus* in sediments that have been assigned to the Late Pleistocene.

The gomphotherid proboscidean *Stegomastodon* has been found in Río Negro Province, in the Huahuel Niyeu valley, near the city of Ingeniero Jacobacci (Pascual *et al.*, 1984).

During the Late Pleistocene and beginning of the Holocene, there were favorable climatic-environmental conditions in southern Patagonia for the peopling of the territory (Miotti, 1998; Miotti *et al.*, 2003; Massone, 2003). Humans arrived accompanied by a relatively high diversity of mammals, among which there were representatives of the large, later extinct, South American mammals. Open archeological sites, refuges and caves are testimonies of the coexistence of men with many of those large mammals, which certainly were part of their diet. Men have been considered as responsible of the so-called "Megafaunal Extinction" (Martin, 1986). The most representative taxa of Santa Cruz are *Megatherium* sp., *Mylodon* sp., *Lama gracilis*, *Hippidion* sp. From an ecological point of view, the presence in such high latitudes of the Mylodontidae *Mylodon* is quite surprising, since living xenarthrans in general and particularly the Pilosa (e.g. sloths and anteaters) have endothermic mechanisms which led them to having a variable body temperature. It has been assumed that they could not have inhabited cold or temperate-cold environments. Scillato-Yané (1976: 310) proposed the following argument:

... los Mylodontidae de la subfamilia Mylodontinae vivieron durante el Período Cuaternario hasta latitudes

relativamente elevadas, tanto en Norteamérica como en Sudamérica (Patagonia Austral); por lo tanto, tuvieron que soportar temperaturas que, en ese tiempo y lugares, fueron sin duda bastante bajas. Evidentemente pudieron de algún modo adaptarse a condiciones ambientales mucho más rígidas que aquéllas en las que prosperaron los Mylodontidae terciarios. Esta adaptación sólo resulta explicable si consideramos la posibilidad de que los Mylodontinae cuaternarios hayan sido mejores termorreguladores que sus predecesores. Tal hipótesis está avalada por la siguiente circunstancia: el estudio anatómico de las inserciones craneanas y mandibulares revela que se ha verificado un paulatino perfeccionamiento de la musculatura masticatoria de estos tardígrados en el transcurso del Cenozoico; dicho perfeccionamiento se ha de haber visto reflejado en una más adecuada masticación de los alimentos, que a su vez permitió un mejor aprovechamiento energético de los mismos. El metabolismo más intenso resulta imprescindible para el mantenimiento de una temperatura corporal más elevada

[“...the Mylodontidae of the Mylodontinae subfamily lived during the Quaternary period up to relatively high latitudes, both in North America and in South America (southern Patagonia); therefore, they had to bear temperatures which in those times and places were undoubtedly quite low. Evidently, they could in some way adapt to environmental conditions much more rigid than those in which the Tertiary Mylodontidae had prospered. This adaptation is only explained if we consider the possibility that the Quaternary Mylodontinae were better thermo-regulators than their predecessors. Such hypothesis is supported by the following circumstance: the anatomical study of the cranial and mandibular insertions reveals a gradual improvement of the masticatory muscles of these tardigrads during the Cenozoic; such improvement has been reflected in a much better chewing of the food, which in turn allowed a better energetic utilization. A more intense metabolism was necessary for the maintenance of a higher body temperature”].

This adaptive possibility could have been favorable when coincident with some of the frequent, more benign climatic pulses that characterized the Finiglacial and Postglacial (Tonni *et al.*, 2003). This seems to be ratified because many other animals lived with mylodonts, most of which still inhabit those latitudes of Patagonia, and others are currently restricted to intertropical regions, like the jaguar (Martin *et al.*, 2005).

Numerous radiocarbon dating of remains of *Mylodon* cf. *M. listai* in one of the caves (“Cueva del Milodón”) yielded a mean age of  $11,200 \pm 170$   $^{14}\text{C}$  yr BP (see also Borrero, 1997; Tonni *et al.*, 2003). In this same “Cueva del Milodón”, remains of a felid, *Panthera onca mesembrina*, has been recorded (see Tonni *et al.*, 2003).

Prevosti *et al.* (2003) reported the southernmost record of a bear, *Pararctotherium*, found in a cave of the Pali-Aike National Park, Magallanes, Chile. In this cave, remains were also found of the extinct equiid *Hippidion* sp., on which a radiocarbon dating yielded  $11,210 \pm 50$   $^{14}\text{C}$  yr BP. *Hippidion* is frequent in several

archeological and paleontological sites referred to the Uppermost Pleistocene of the southernmost tip of Patagonia (Alberdi *et al.*, 1987).

*Smilodon populator* seems to be also present in the “Cueva del Milodón” (southern Chile) on the basis of recently published materials from old collections housed in the Zoological Museum of Amsterdam (Barnett *et al.*, 2005); another reference from the same region (Cueva del Medio) was published by Massone (1996).

In central Chile, remains of the proboscidean *Cuvieronius humboldti* were found in the archeological site of Tagua Tagua, south of Santiago (Casamiquela, 1999), as well as somewhat farther south in the site Monte Verde (Casamiquela *et al.*, 1996).

## 9. Discussion

The Late Miocene and Pliocene vertebrates come from continental and marine formations related to the last geotectonic processes that affected the Colorado Basin and led to the differentiation of the present basins of the Negro and Colorado rivers. In several mammal lineages, chronomorphs grading from west to east can be observed, which display more primitive features in those closer to the modern Cordilleran region. According to Pascual *et al.* (1984), this is related to the displacement of continental environments in this direction. The remains of the most recent Tertiary mammals of the study area are those from the Río Negro Formation, in eastern Río Negro Province, and equivalent levels of the Cerro Azul Formation in La Pampa Province. Remains of rodents such as *Cardiatherium* (including *Kiyutherium*, see Vucetich *et al.* 2005) recorded there suggest a Huayquerian age, which does not contradict the absolute dating (Alberdi *et al.*, 1997).

As it can be seen in Fig. 2, after the Mi-1 glaciation in Antarctica (Zachos *et al.*, 2001), there was a trend toward increasing temperature that reaches the highest point with the climatic optimum of the latest Early Miocene, coinciding with part of the Santacrucian. Notwithstanding, Shevenell *et al.* (2004) clearly stated, “... southwest Pacific sea-surface temperatures (SSTs) cooled 6 to 7°C during the late Early Miocene climate transition (14.2 to 13.8 Myr ago).” (p. 1766); so, part of the Santacrucian could have had a climate cooler than during the climatic optimum. All the Colhuehuapian to Colloncuran mammals of Patagonia have among their components Platyrrhine primates, associated with other modern inter-tropical species. Although the proterotheriid litopterns (convergent with equids) are characteristic of open areas, they coexisted with several species ambulatory-scansorial as megatherioid sloths (ancestors of living tree-sloths) and with fossorial rodents. As Webb (1978) pointed out, the extraordinary diversity of middle- to large-sized mammals suggests an optimum balance between grasslands and forests, as those of the savanna-park. Especially in the west, other mammals (rodents and digging marsupials) are evidence of drier climate events, or a complex of environments represented by dune deposits alternating with higher areas of wet forests (Bown and Lariestra, 1990).

Approximately 11 Ma ago, the development of the ice sheet in Antarctica seems to have caused a remarkable climatic change, seen both in a lithogenesis change (certainly associated with an Andean orogenic phase), and in a mammal-communities turnover since the Mayoan stage of southern Patagonia. With this turnover starts a new faunistic cycle, named by Pascual and Ortiz Jaureguizar (1990) as the Panaraucanian, which had the northern extra-Patagonian area as main setting (Pascual *et al.*, 1996: 290–294). The mean values of  $\delta^{18}\text{O}$  went on rising gradually in the Late Miocene. In this lapse, the Great American Biotic Interchange (the “New Island Hoppers” of Simpson, 1950, 1980) began. In the Early Pliocene or Uppermost Miocene (6 Ma), there was an additional cooling and a little expansion of the ice sheets of Western Antarctica and the Arctic. A little after, the closing of the Panama Isthmus occurred and, consequently, the connection between both Americas started, triggering a massive interchange of biotas. The Early Pliocene is marked by a soft trend of increasing temperature up to ~3.2 Ma, when the  $\delta^{18}\text{O}$  increased again, evidenced by the establishment of a glaciation in the Northern Hemisphere, which seems to have intensified the mammal interchange between both Americas. The scarce mammal remains known of the first part of the Pleistocene belong to taxa that were current inhabitants of the Pampas and the rest of the South American continent. Hence, the climatic-environmental conditions prevailing by those times in the southern end of Patagonia cannot be recognized through them.

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### Chapter 13

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