Review

Pleistocene Mammals from Pampean Region (Argentina). Biostratigraphic, Biogeographic, and Environmental Implications

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Abstract: The Pampean Region contains sedimentary sequences with abundant mammal fossil records, which constitute the chronological outline of the Plio–Pleistocene of South America. These classic localities have been used for more than a century to correlate with other South American regions. Throughout this time, a series of misinterpretations have appeared. To understand the stratigraphic significance of these localities and the geochronological situation of each unit referring to the Pleistocene, a critical historical study of the antecedents was carried out, evaluating the state of each unit. The biostratigraphic studies of the Pampean Region's mammalian faunas improved the understanding of biogeographic changes taking into account the environmental fluctuations of the Pleistocene.

1. Introduction

In 1833, Charles Darwin explored the Pampas of southern Argentina. His annotations, as well as those of D'Orbigny [1], were developed within the framework of the ideas of his time that proclaimed a scheme of the Earth's past in which the rest of the regions of the world were incorporated [2]. Darwin visited a large part of the Pampas landscape. He was surprised by the vast extension and abundance of fossil remains, which were the most significant aspects that he mentioned when summarizing the Argentine. These notes were the basis that Ameghino [3,4] used to develop a stratigraphic scheme.

The surface sediments that cover most of the Pampas Region were originally called "terrains pampéenes" and "argile pampéenes" [1], "pampean formation" [5], and "pampa formation" [6]. Ameghino [3] proposed a subdivision of the "Pampean formation" into three units: Lower Pampean, Upper Pampean, and Lacustrine Pampean. These deposits are characterized by presenting a lithological homogeneity, which added to the observed discontinuities and led to the search for other criteria to order them. One of these criteria for separating the deposits into different stratigraphic units was the content of fossil mammals. A significant case was the classic localities between Mar del Plata and Miramar, which present laterally continuous exposures and allowed subdivision based on their paleontological content [4]. Another fact to highlight is that the first stratigraphic analyses of the Pampean deposits were favored by large excavations due to the construction of the ports of Buenos Aires and La Plata, which provided new sections for the analysis [7]. This unit scheme is based on the content of fossil mammals derived from the South America Land Mammals Ages (SALMA) [8], a stratigraphic arrangement widely accepted among paleontologists. We use the evolutionary degree of the faunal assemblages in the stratigraphic ordering of the Pampean deposits.

Recently, a new contribution with different locations and more precise records, a biostratigraphic scheme, was designed in Pleistocene Pampean deposits [7,9–17]. Through this scheme, appropriate relationships of superposition of first and last appearance of mammalian record can be established, and thus a relative chronology can be established.

In this paper, we summarize the main biotic and abiotic events that occurred in Pampean Region in the Pleistocene: glaciations; diastrophism, marine regressions, and transgressions; marked replacements of distribution and quality of the vast southern plains; a geographical connection between the Americas; and the Great American Biotic Interchange (GABI) and the Quaternary Megafauna Extinction (QME) modified the landscape of the region, and strongly influenced its present status.

2. Characteristics of the Pampean Region

The Pampean Region (Figure 1) is located approximately between latitude 30–39° S and longitude 57–66° W and occupies a large area (~ 600,000 km^2). The prevailing climate in this region is temperate to subtropical and humid. The annual average temperature can oscillate between 13 and 18 °C, and the annual precipitation records are between 600 and 1200 mm. The climate of the region is controlled by the Atlantic Anticyclone, whose effect decreases in influence from the northeast to the southwest [18]. In the Pampean Region, two subregions are recognized: the Humid Pampa in the northeast and the Dry Pampa in the southwest [19,20]. This division of the region enables the differentiation of three different ecoregions: Pampa (same extent as the Humid Pampa), Espinal, and Low Monte (the Dry Pampa includes both Espinal and Low Monte) [19]. From a biogeographic approach, the study area is within the Pampean zoogeographic domain of the Guayano–Brazilian subregion [21] and the phytogeographic Pampean province of the Chaqueño domain [22]. Recent reviews of the biogeography of South America include the Region Pampeana in the province called Pampa [23]. The vegetation is predominantly herbaceous steppe or pseudo-steppe, although communities of grass prairies and psammophytic and halophytic steppes are registered [24].
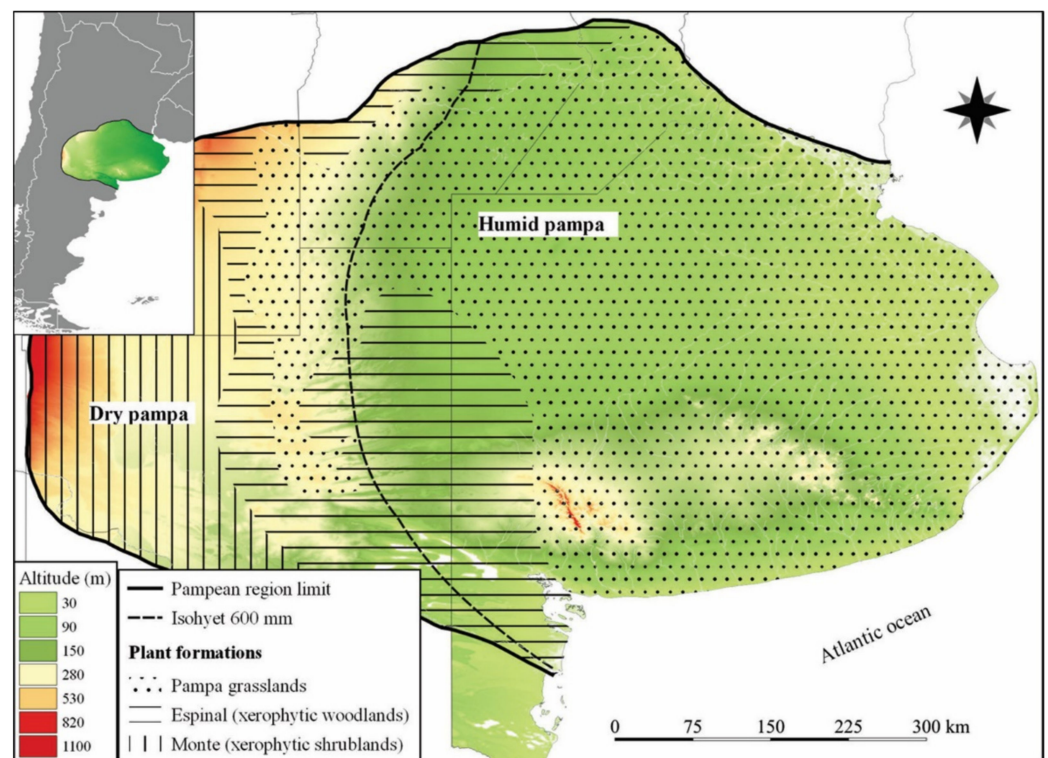
Figure 1. Location of the Pampean Region in Argentina.

The region presents a mainly flat landscape with some slight undulations. A deep mantle of loess and loessic silts is interrupted by the relatively low hills called a system of Ventana and Tandil [25]. The Pleistocene sediments of the Pampean Region were deposited mainly under arid to semi-arid climatic conditions, alternating with indicator levels of more humid conditions [26]. The paleoclimate record indicates that this fluctuation results from the interaction between the air masses of the Pacific and Atlantic anticyclones [27]. At present, Pacific Anticyclone loses its humidity when crossing the Andes Mountains and arrives cold and dry in the Pampean Region. For its part, the winds of the Atlantic Anticyclone are frequently warm and humid.

3. Geology

The Pampean Region includes a large sedimentary basin whose strata date back from the Cretaceous to the Holocene [28]. The younger strata are loess deposits dating back to the Late Cenozoic. For this reason, some authors have included these sediments in a single lithostratigraphic unit, called the Pampeana Formation [26,29,30]. For their part, Riggi et al. [31] and Tonni et al. [32] recognized the Early–Middle Ensenada Formation and the Middle–Late Pleistocene Buenos Aires Formation [33]. Most of these deposits correspond to aquatic facies and a few correspond to primary eolian facies [34]. Moreover, Kraglievich [35] proposed other units based on other correlated deposits in the coastal cliffs between Mar del Plata and Miramar. The Ensenada and Buenos Aires Formations are assignable to the Ensenada and Bonaerian–Lujanian Stage, respectively.

Several hypotheses have been put forward on the genesis of the Pampean sediments. González Bonorino [36] proposed that the Pampean sediments come mainly from the weathering, transport, and erosion of tertiary formations (tertiary basalts of the Patagonian region and crystalline basalt of the Pampean mountain ranges) and Pleistocene volcanism in the Andes Mountains. More recently, it was proposed that there are several loess contribution zones (in addition to the classic ones) that are located to the north and west of the Pampean Region and involve different stages [37]. Rabassa et al. [38] attribute the Pampean loess deposit to the wind activity generated by the climatic conditions derived from the glacial advance, which influences the Pacific's marine anticyclonic centers, shifting their axis to the north. The development of paleosol is widespread in the Pampas sediments. Overlapping paleosols, resulting from the succession of pedogenetic processes, are found in Pliocene and Pleistocene sediments at different regional locations.

Fidalgo et al. [29,30,39] reviewed the Late Quaternary nomenclature and stratigraphy of the Pampean Region. With new geomorphological data, plus analysis of texture and composition of Late Pleistocene and Holocene deposits, they defined two stratigraphic units: the Luján Formation, which includes the Guerrero and Río Salado members; and the La Postrera Formation. The first is of fluvial-lake origin, and the second is eolian (Figure 2).

Figure 2. Stratigraphy correlation. Local biozones after Cione et al. [40] and Verzi et al. [15].

The La Postrera Formation that covers the entire region includes loess and very fine stratified sands [41]. The sedimentological analysis of eolian material [42] suggests that volcanism in the Andean region was the predominant source of the contribution, specifically, as a contribution of pyroclastic deposits that are made by erosive fluvial and wind processes. Iriondo [43] described a Pampean Wind System based on geomorphological evidence, which would partly explain the origin of these sediments in the central region of Argentina. He proposed that the sediments were redistributed from the Colorado River system. This hypothesis partially fits with the interpretation proposed by Zárate and Blasi [41,42]. For these authors, the sandy loess that covers the southeastern Pampean region would have its origin in the alluvial plains of Colorado, and Negro and the southwesterly winds are predominant in the area today [18,44]. On the other, geomorphological data, such as the orientation of lunettes and dunes, indicate westerly winds in the past [45]. Gardenal [46] proposed four main groups of aeolian sediments in the Pampean region's western part. However, the calibration of these depositional episodes is complex. According to Zárate and Blasi [42], the first and second episodes correspond to the late Pleistocene, the third to the Middle Holocene, and the last to historical times.

Likewise, the Luján Formation is made up of highly developed alluvial plain deposits together with a wide fluvial system of the province of Buenos Aires [29]. The lower levels of this formation correspond essentially to alluvial deposits, such as the La Chumbiada and Guerrero members. In contrast, the upper levels are mainly lacustrine, such as the Río Salado member. In two localities (Paso Otero and Empalme Querandies), the Guerrero member has two facies (one predominantly brown, the other green), among which an ecological succession is evidenced, as its faunas indicate environmental deterioration [47]. The lower brown stratum (members of La Chumbiada, sensu Dillon and Rabassa [48]) is characterized by a fauna of mammals with a high frequency of browsers. On the other hand, the upper green levels (Guerrero member) show an abundance of large herbivores and a decrease in browsing forms [47].

Two pedostratigraphic units are also recognized. The first one, called Puesto Callejón Viejo Soil occurs in the superior part of the Guerrero Member. The other, known as Puesto Berrondo Soil, developed in the Río Salado Member [39]. The latter soil indicates a

decrease in humidity at a regional scale with the fluvio-lacustrine environments' desiccation corresponding to the Rio Salado Member [49].

In the southern coastal zone of the Pampean Region, there are two marine transgressions assigned to the last interglacial and the Middle Holocene [50]. The Pascua Formation is made up of Late Pleistocene marine deposits [29] and occurs in different locations along the coast [51–53]. They are also correlated with the Chuy Formation recognized in Uruguay [54] and the transgression event described for the Late Pleistocene of Brazil [55].

4. Paleoclimatic History and Mammal Diversity

The Late Neogene in South America was marked by active diastrophism and a high frequency of sea-level changes [56]. Both events are related and connected to the various causes of cyclical and climate changes. The sea level's successive descents are connected to the progressive events of diastrophism called the Diaguita Phase. Thus, the most apparent event of this diastrophic phase was the establishment of the Panamanian Land Bridge that interrupted communication between the Atlantic and Pacific oceans. This event radically changed both oceans' circulation, facilitating the emergence of the Arctic ice cap [57]. The cold Circum–Antarctic Current of the Southern Hemisphere was established, and the ice sheet formation in Antarctica began [58].

The main differences between the climatic–environmental conditions of the Tertiary and the Quaternary are linked to the amplitude and frequency of environmental changes. In the Tertiary, geological and paleontological records show long intervals of uniform environmental conditions, sporadically interrupted by geologically short but highly disruptive change intervals. On the other hand, the climatic changes of the Quaternary had greater amplitude and frequency. Both types of changes have different effects on biota. Environmental changes during the Tertiary significantly altered the taxonomic and ecological composition of mammalian communities, operating through cladogenetic processes, extinction, and immigration from other areas. The changes that occurred during the Quaternary are responsible for chorological variations, expanding or contracting the distribution areas of species, communities, and biomes [59–61]. The successive retreat and advance of the glaciers produced, in non-engulfed areas such as the Pampeana Region, an alternation of arid (savanna, steppes) and humid (subtropical forests) biomes. This particularity favored high extinction rates as a consequence of the reduction of favorable areas [62]. During the coldest and driest periods, there was a retraction of the subtropical areas, which facilitated the expansion and interconnection of open biomes [63,64].

Since the Pampean Region can currently be considered an ecotone between two important biogeographic areas (Brazilian and Patagonian), the fauna associations included mixtures of taxa from both areas at different times during the Pleistocene. In cold and dry climatic conditions, a contraction of the areas occupied by tropical and subtropical fauna was observed, which resulted in the interconnection of the open environment fauna. On the other hand, when open areas retreated during interglacial periods, the forest expanded. The arid and semi-arid conditions allowed the expansion of the Patagonian and Central mammals (*Lestodelphis*, *Microcavia,* and *Zaedyus*) into areas occupied by the subtropical mammals (i.e., echimyids, procyonids, and tayassuids), which presently inhabit warmer and more humid environments [9,65].

Paleoecological studies by Fariña [66] and Croft [67] suggest that savanna and grassland habitats expanded under dry climates in the Pampean Region. In those times, the steppes were well developed, favored by cold and arid or semi-arid conditions. Some typical mammals of the current Patagonian and Central subregions (i.e., *Microcavia australis* and *Pediolagus salinicola*) are also recorded during the Late Pleistocene in the Pampean Region [9]. Tonni and Cione [10] pointed out that there are also some hot and humid climatic periods, of short duration, interspersed between more extended periods with cooler and more arid conditions.

The range of δO^{18} calculated for the Equidae of the Pampean Region corresponds to a variation of 4.2 °C in the mean annual temperatures throughout the Pleistocene [68]. As a

reference, the current temperature ranges between 13.4 °C in Mar del Plata (38 °S), 16.4 °C in Buenos Aires (34 °S), and 19.2 °C in Santa Fé (32 °S).

According to Sánchez et al. [68], carbon isotope analyses in Equidae from the Pampas Region suggest a change in the pasture: Early Pleistocene horses consumed predominantly C3 plants, and then consumed a C3–C4 mixture in the Middle–Late Pleistocene; towards the Late Pleistocene, they returned to a strict diet of C3 plants.

Cione and Tonni [10] point out that the mammal communities of the Marplatan stage suggest warm and humid conditions. In the Early Ensenada stage, recorded mammals suggest the beginning of a cold, semi-arid period [9]. Mammal records from the Late Ensenadana stage indicate the return of warm and humid conditions [10].

The record of Echimyidae, Dasyproctidae, and Noctilionidae [69] in the Early Bonaerian stage indicates the beginning of a new warm event. The presence of *Ctenomys kraglievichi* and Tayassuidae suggests a strong warm pulse around 0.5 Ma [15,70]. Evidence from other continents also suggests a warm pulse in the Middle Pleistocene, between 0.7 and 0.3 Ma [71].

The interglacial conditions of MIS5e (130 ka) can be inferred from records of mammals of the Lujanian stage [72]. It also happens that during the Last Glacial Maximum (18 ka), mammalian indicators of arid and cold conditions predominated [73]. The pollen record indicates that Late Pleistocene environments were arid, associated with more continental environments and lower sea levels [70]. Isotopes found in terrestrial gastropods indicate a change to a more humid environment in the Pleistocene–Holocene transition [74].

5. The Land Mammals Ages and Biostratigraphy

Ameghino [75,76] proposed a stratigraphic scale that was a reference standard for continental Cenozoic South America. It is a sequence of stages grouped in higher-order units [75,76]. This Ameghino proposal, based on biostratigraphic criteria, is still partly valid today. He proposed a subdivision of the "Pampean formation" into three units: Lower Pampean, Upper Pampean, and Lacustrine Pampean. Ameghino's stratigraphic conception does not differ from that which was developing in Europe at the same time. Ameghino [75] introduced terms such as "formation" and "floor", which are currently used to refer to units of the lithostratigraphic and chronostratigraphic classification. However, for Ameghino, a "formation" was a unit of time that was inferred based on its fossil content, where lithology was not a necessary element for its name, and even less the only one. Later, when Frenguelli [77,78] proposed his stratigraphic scheme, he used Ameghino's names but with another connotation.

The Pampian stages of Frenguelli are the Chapalmalense, Ensenadense, and Bonaerense. The post-Pampa stages are the Lujanense, Platense, Querandinense, Cordobense, and Aimarense. The three stages of Pampian are assigned to the Pleistocene, and the five stages after Pampian represent the Holocene (Figure 2).

Kraglievich [35] established another stratigraphic scheme for the southeast of the Pampean Region, where he recognized several formations based on some of the classic names of Ameghino, which were redefined; for example, the "Chapalmalense horizon" or "Chapalmalense stage" became the "Chapadmalal formation". Although Kraglievich described the lithological characters somewhat, the discrimination between the units rested fundamentally on the paleontological content.

Until the 1940s, there was considerable confusion because the same names were often used to distinguish rock, time, and faunal units. Simpson's [79] study brought order to this vast body of information. Later, Wood et al. [80] proposed a new scheme based on several Land Mammals Ages (LMA) for North American records. LMA was a valuable scheme to order and establish a relative age of the Cenozoic terrestrial deposits on this continent. Woodburne [81] used the term North American Terrestrial Mammal Ages (NALMAs) as a schema of formal biochronological units, which was later taken as the basis for the proposed schema of Archibald et al. [82], among others. Pascual et al. [8,83] proposed a new synthesis, based on the criteria of Ameghino (evolutionary grade of the faunas),

that closely corresponds with the LMA concept proposed by Savage [84]. The SALMA arrangement comprises unique taxon associations that are inferred to have existed during a restricted time interval (Table 1). These Ages were established using knowledge of the faunas' evolutionary grade, in the same way that Ameghino did, by noting the times of first and last taxa appearances in the fossil record and other related changes in faunal assemblages over time [59]. The LMA are stratigraphic units that, for the moment, have not been formally recognized by the stratigraphic code of nomenclature of Argentina. However, as a classifying scheme, they have been very useful in evolutionary and biogeographic mammal studies [84,85]. Pascual et al. [59], among others, have underlined its usefulness in establishing intra- and intercontinental correlations of Cenozoic time.

Table 1. The main stratigraphic schemes proposed for the Pampean Region.

| Doering (1882)	Ameghino (1908)		Kraglievich (1952)	Frenguelli (1957)	Fidalgo et al. (1973)	Riggi et al. (1986)
Fm Querandina	Post pampeano	Platense	Fm de Loberia	Serie postpampeano	Fm La Postrera/Fm Luján	Fm Buenos Aires
		Lujanense				
Fm Tehuelche		Bonaerense	Fm de Arroyo Seco	Bonaerense		
		Ensenadense	Fm de Miramar Fm de San Andrés	Ensenadense		
Fm Pampeana	Fm Pampeano		Fm de Vorohué Fm de Barranca de los Lobos		Fm Pampiano	Fm Ensenada
	Fm Araucano	Chapadmalense	Fm de Chapadmalal	Chapadmalense		
		Monte-hermosense				

6. Mammal Biozone Scheme for the Pampas Region

In recents years, four types of regional stage were distinguished, namely (1) alternative regional stages; (2) concurrent regional stages; (3) biogeographical regional stages; and (4) regional land stages [40]. All regional stages are essentially incomparable with the global stages, established with Global Boundary Stratotype Section and Point (GSSP).

In South America, the regional land stages (type 4) are the South American Land Mammal Ages, defined by Pascual et al. [8] and are alternatives to the chronostratigraphic units developed from the terrestrial record. These land mammals ages are used widely. Some can be confidently linked to global chronostratigraphic divisions whereas the correlation of some others is not so clear. These alternative regional stages should be abandoned and, where possible, replaced by biozones or lithostratigraphic units since they make no contribution in the development of chronostratigraphy. For example, Cione and Tonni [86] has demonstrated the efficacy of the Neogene mammal zones in Europe in contrast to the European Land Mammal Ages. In the last decades, Cione and Tonni [10] recommended the substitution of the LMA by a chronostratigraphic/geochronological classification based on biostratigraphy, according to the stratigraphic code of Argentina. In successive presentation, these authors identified five biozones (Association Zones, or Interval Zones) for the Pleistocene [87,88]. These biozones are those of *Ctenomys chapadmalensis*, *Mesotherium*

cristatum, *Megatherium americanum* and *Equus neogeus*. They constitute the biostratigraphic base that sustains the Marplatan, Ensenadense, Bonaerense, and Lujanense Stages/Ages. Considering that the "International Commission on Stratigraphy" [89] established the Plio-Pleistocene boundary in 2.58 Ma, the Sanandresense Sub-Stage of the Marplatan represents in the Pampean Region the beginning of the Quaternary (Table 1).

This new scheme, the sequence of names proposed by Ameghino is used with few modifications for the Quaternary of Pampean Region. Consequently, the use of a term must be associated with its definition in the classification system; otherwise, it will generate confusion and incorrect interpretations. In this proposal, the biostratigraphic units are based on characters, such as the spatial location of the taxa, which are verified in the field; however, there is still a certain level of abstraction in their recognition (Figure 3).
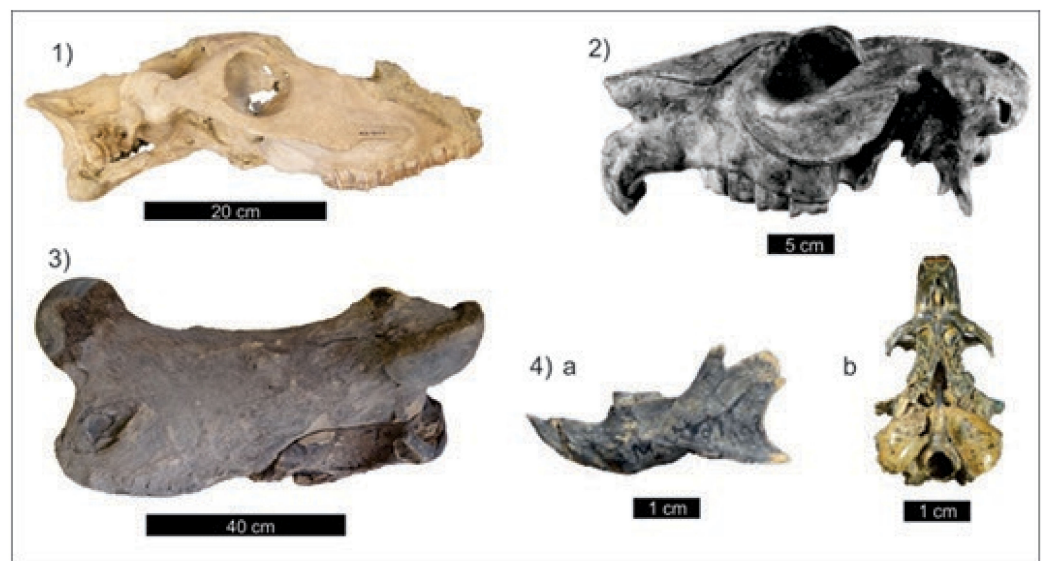
Figure 3. Four taxa from Argentinian Pampa that define the biozones. 1, Skull in lateral view of *Equus neogeus*; 2, Skull in lateral view of *Mesotherium cristatum*; 3, Femur of *Megatherium americium*; 4(a,b), Skull in ventral view and mandible in lateral view of *Ctenomys chapalmalensis*.

6.1. Ctenomys chapalmalensis Biozone

This biozone coincides with the Upper Marplatan (Early Pleistocene), particularly with the San Andrés Formation. *Ctenomys chapalmalensis* is an exclusive taxon from the San Andrés Formation, and it represents the oldest record of Ctenomys in this region. The deposit of this formation and its fauna content was correlated with Patagonia's glacial advances to MIS82 to 78 [90]. This biozone is characterized by the last record of *Eumysops*, whose species were widespread during the Pliocene and Early Pleistocene. [91].

6.2. Mesotherium cristatum Biozone

This biozone coincides with the Ensenadan (Lower to Middle Pleistocene), particularly with the Ensenada Formation in the Pampean Region [32] and with Miramar Formation [35], in the southeast. Numerous taxa of biostratigraphic importance are recorded in the Ensenadan, some exclusive to this stage (*Panochthus intermedius*, *Glyptodon munizi*, *Neosclerocalyptus pseudornatus*, *Neosclerocalyptus ornatus*, *Megatherium gallardoi*, *Scelidotherium bravardi*, *Antifer ensenadensis*, *Catagonus metropolitanus*, *Theriodictis platensis*, *Arctotherium angustidens*, and *Mesotherium cristatum*).

As the type profiles in which the fossils used by Ameghino [74] as the basis for his Ensenadan (Puerto de La Plata, Ensenada) were found are not currently available, Tonni et al. [32] suggest as a new type locality a quarry located in Hernández (La Plata County), whose sequence includes characteristic fossils of the *Mesotherium cristatum* biozone [88].

6.3. Megatherium americanum Biozone

This biozone coincides with the Bonaerian (Middle Pleistocene). Its lower limit coincides with the lower part of the Buenos Aires Formation in the northeast of the Pampean Region [32,33] and probably with Arroyo Seco Formation [35] in the southeast. According to the fauna evidence, it begins with a warm event, with a predominance of pedogenesis and typical Brazilian mammals' registry. Considering these particularities and the stratigraphic situation, Verzi et al. [15] suggest that the Bonaerian begins in the interglacial period corresponding to MIS11, around 0.4 Ma [90,92]. This interglacial event was the warmest and the longest in the last 0.5 Ma, generating a significant rise in sea level, observed in the beach sediments of the southern province of Buenos Aires. [52,88].

Numerous taxa with biostratigraphic importance are recorded for the first time on this stage (*Panochthus tuberculatus*, *Megatherium americanum*, *Glyptodon elongatus*, *Glyptodon reticulatus*, *Lestodon armatus*, *Mylodon darwini*, *Scelidotherium leptocephalum*, *Glossotherium robustum*, *Eutatus seguini*, *Macrauchenia patachonica*, *Toxodon platensis*, *Artotherium bonariense*, *Pecari tajacu*, and *Lama gracilis*).

A biozone based on the micro mammals, the *Ctenomys kraglievichi* biozone, was described based on faunas from the southern Pampean Region [15,93]. It is temporarily limited to the base of the *Megatherium americanum* biozone, and there are micro mammals associated with a warm climate pulse.

6.4. Equus neogeus Biozone

This biozone coincides with the Lujanian (Upper Pleistocene, [12,94]. However, Cione and Tonni [40] suggest that this biozone does not agree with the SALMA Lujanian proposed by Pascual et al. [8], who also include the Bonarian stage.

The guide fossil *Equus neogeus* is recorded from the base of the unit, which is correlated with MIS5e (ca.130 ka BP) [13,87]. This interglacial period is probably represented by the coastal sea levels assigned to the Pascua Formation [29]. Recent dating suggests that a part of the deposits referred to as the Pascua Formation and the "Belgranense" can be correlated with part of the MIS3 [95,96].

Some exclusive taxa are registered (*Doedicurus clavicaudatus*, *Neosclerocalyptus paskoensis*, and *Equus neogeus*). In contrast, others are registered for the first time in the region (*Panochthus greslebini*, *Microcavia australis*, *Dolichotis patagonum*, *Eligmodontia typus*, *Galea musteloides*, and *Lycalopex gymnocercus*).

7. Great American Biotic Interchange

Biogeographic studies have shown that South America was an insular continent, isolated from the rest of the continents, for a period of time that spans much of the Cenozoic [97,98]. Under these particular conditions, South American land mammals evolved in their world until the Isthmus of Panama. By the Late Miocene, the descendants of these autochthonous lineages (condylarths, notoungulates, lithopterns, marsupials and edentates) and immigrants from Africa arriving in the Late Eocene or Early Oligocene (platyrrhine primates and caviomorph rodents), had achieved a balance in their communities. A peculiarity of these faunas is the coexistence of carnivorous and omnivorous marsupials with placental ungulates and edentates [78,98].

The GABI was the most important event from a biogeographical perspective in the Late Cenozoic [99,100]. The earliest appearances of migrating terrestrial animals demonstrate intercontinental dispersals' timings and help to understand when the Isthmus of Panama formed [101]. Recent works on the paleobiology of the mammals from the Argentine Pampas have refined our comprehension of its final formation [102]. Around 2.8 Ma ago, the tectonic activities of the Pacific margin connected the two Americas. A habitat corridor was opened, which helped the dispersal of plants and animals between the Americas, thus producing the GABI [103]. This land corridor functioned selectively [104]. The partial replacement of native South American mammals by North American immigrants is due to three different causes. First, the arrival of new ungulates and carnivores to South America.

The native ungulates suffered pressure from the holarctic placental predators. For its part, there was an imbalance in the diversity of mammalian species on each continent because they are areas of different sizes. Third, global climate changes caused changes in the Isthmus of Panama's environments that lead to an imbalance between the number of South American and North American migrants [103]. It has been suggested that there were three main types of habitat corridors: tropical mesic forest, mesic savanna, and xeric scrub savanna [104]. In the humid interglacial phase, jungle environments dominated the tropics, and the main movement of fauna was from the Amazon to Central America. During the more arid glacial phase, the directional pattern was reversed [103]. Various groups of mammals moved from one continent to another, although the result seems more favorable for North American immigrants. There was a significant change in the structure of the communities in South America [105,106].

This event was complex and began during the Miocene [107]. The main phase of the GABI occurred around 2.7 Ma to 1.8 Ma, and with less intensity until about 1.0 Ma. A late phase occurred from 0.8 Ma until recent times and resulted in enrichment in the south [108].

8. Quaternary Megafauna Extinction

The most outstanding feature of the Pleistocene fauna of South America is the extinction of its rich megafauna [20,109]. The extinction event of species and genera of mammals (and in some cases of entire families) is frequently recorded since the Middle Miocene in the Pampean Region. These events are related to the environmental climate changes that occurred in that period time. However, these events can be considered normal, such as background extinction, compared to the Late Pleistocene's extinction. The latter was a particularly extraordinary event where all mega-mammal species (more than 1000 kg) and most large mammals (more than 44 kg) disappeared [110,111]. This QME, whose victims were large mammals, mainly North Americans, South Americans, and Australians, has been attributed to different factors [112]. Various types of theories have been proposed for this extinction. On the one hand, some propose hypotheses related to climatic and ecological changes [113], while another group blames human activity for the disappearance of megafauna [114]. Evidence for meteorites has also been proposed [115]. The most recent approaches to QME suggest a synergy between increased human impacts and rapid climate change [116,117]. The idea of factor synergy in QME originates from the observation that extinction was most intense and rapid in central North America, where the arrival of the first Clovis hunters coincides with climate change at the end of the Pleistocene. It is also well documented that climate change itself caused at least some extinctions. This is true for species that run into impervious barriers while trying to stay in their habitat when climatic zones change. The question is to what extent the combination of rapid climate change and increasing human pressures amplifies extinction compared to the extinctions that result from each cause.

Martin [114] suggested that the extinction of large North American mammals is closely related to human populations' rapid dispersal. This hypothesis, called "Overkill", is based on the synchronism of extinction with this arrival. In contrast, the South American registry does not support this hypothesis. This window of coexistence would represent a less extended period than that of North America [118,119]. Archaeological sites with megafauna are not abundant and there is no evidence of mass slaughter sites in the Pampean Region [120]. In the Pampean registry, it is seen that of the total of 16 extinct genera, only five show evidence of human exploitation [121]. The hypothesis about the human pressure that contributed to the extinction is now stronger than in the past. The appearance of works on chronology, simulations, paleoclimatology, paleontology, and archeology support this debate. However, it is an oversimplification to say that an abrupt hunt in a short period time caused extinction [122,123]. The various evidence show that blitzkrieg in the strict sense can be rejected in South America.

Paleoclimate records do not suggest a unique late Pleistocene transition. Oxygen isotope records indicate that the recent glacial retreat was neither faster nor greater in magnitude than other Pleistocene changes [124]. Climate change has a great influence on the diversity of plants and animals. The question is whether the climatic changes of the late Pleistocene were sufficient to have triggered an atypical ecological response. Three ecological theories were postulated to explain the Pleistocene extinction: (1) the key species model [125], (2) coevolutionary disequilibrium, and (3) the mosaic-nutrient model. Cione et al. [110] have proposed an alternative model called "broken Zig-Zag". This hypothesis proposes an alternation of the megafauna's relative frequency as a consequence of the replacement between the habitats of savannas and forests of the glacial and interglacial intervals. During the last interglacial period, humans entered South America. They broke the zig-zag, hunting large mammals and putting pressure on their populations that were in decline due to changes in environmental conditions.

9. Final Remark

Two factors affecting the diversity of mammals during the Pleistocene in this region. In the first place, the glaciations and the climatic and sea-level changes associated with them. Second, the arrival of immigrants from North America [58,59,88].

Since the Pliocene, these latitudes' climatic conditions changed from hot and humid to colder, drier, accentuating seasonality. The alternation in the advance and retreat of glaciers caused a coming and going of arid (savanna and steppes) and humid (tropical and subtropical forests) biomes. The diversity of mammals shows more variations than in previous times, highlighting the heterogeneity of the habitat. This cyclical pattern allowed the provincialism that characterizes the mammalian faunas of the Pampean Region during the Pleistocene. The evidence suggests that, biogeographically, the Pampean Region is an ecotonal area very sensitive to paleoclimatic changes. Therefore, although some taxa have a wide distribution in South America, their records do not necessarily reflect synchronicity. Consequently, is not easy to establish a precise correlation between distant locations without isotopic or paleomagnetic data.

The Pleistocene from the Pampean Region includes the Sanandresian, Ensenadan, Bonarian, and Lujanian stages, each one of which is the carrier of a specific mammalian fauna that characterizes and defines the following corresponding biozone: *Ctenomys chapalmalensis*, *Mesotherium cristatum*, *Megatherium americanum,* and *Equus neogeus*.

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