



REVISITING THE EVOLUTIONARY HISTORY AND PALEOBIOGEOGRAPHY OF FOSSIL HORSES FROM SOUTH AMERICA

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ABSTRACT: Horses are a conspicuous group of immigrant mammals from North America that arrived in South America during the late Pliocene and no survived the megafaunal extinction, approximately ten thousand years ago. Two main equids lineages are found in South America. The first lineage is the species assigned to *Equus*, which appears during the middle Pleistocene and shows horse-like anatomical features. The second lineage is the genus *Hippidion*, which were horses with very distinctive anatomical features are recorded for the first time during the late Pliocene. The predominance of the dispersal events over vicariant ones is consistent with the migratory habits of horses. The global biogeographic distributions of horses explain the mode of dispersal and their migration from North America to another continent. The dispersal and the diversification process in small to middle size species (*Equus andium*, *Equus insulatus*, *Hippidion devillei*, and *Hippidion saldiasi*) occurred through the Andes corridor; whereas the large species (*Equus neogeus* and *Hippidion principale*) mainly traveled using the eastern plain route. The pathway of dispersion in each species reflects its adaptive change and habitat preference. The present study aims to provide a synthesis of already published data on the phylogeny, systematics, palaeobiogeography and palaeoecology of both the lineages recorded in South America, updating some taxonomic data.

Keywords: Equidae, macroevolution, South America, Quaternary.

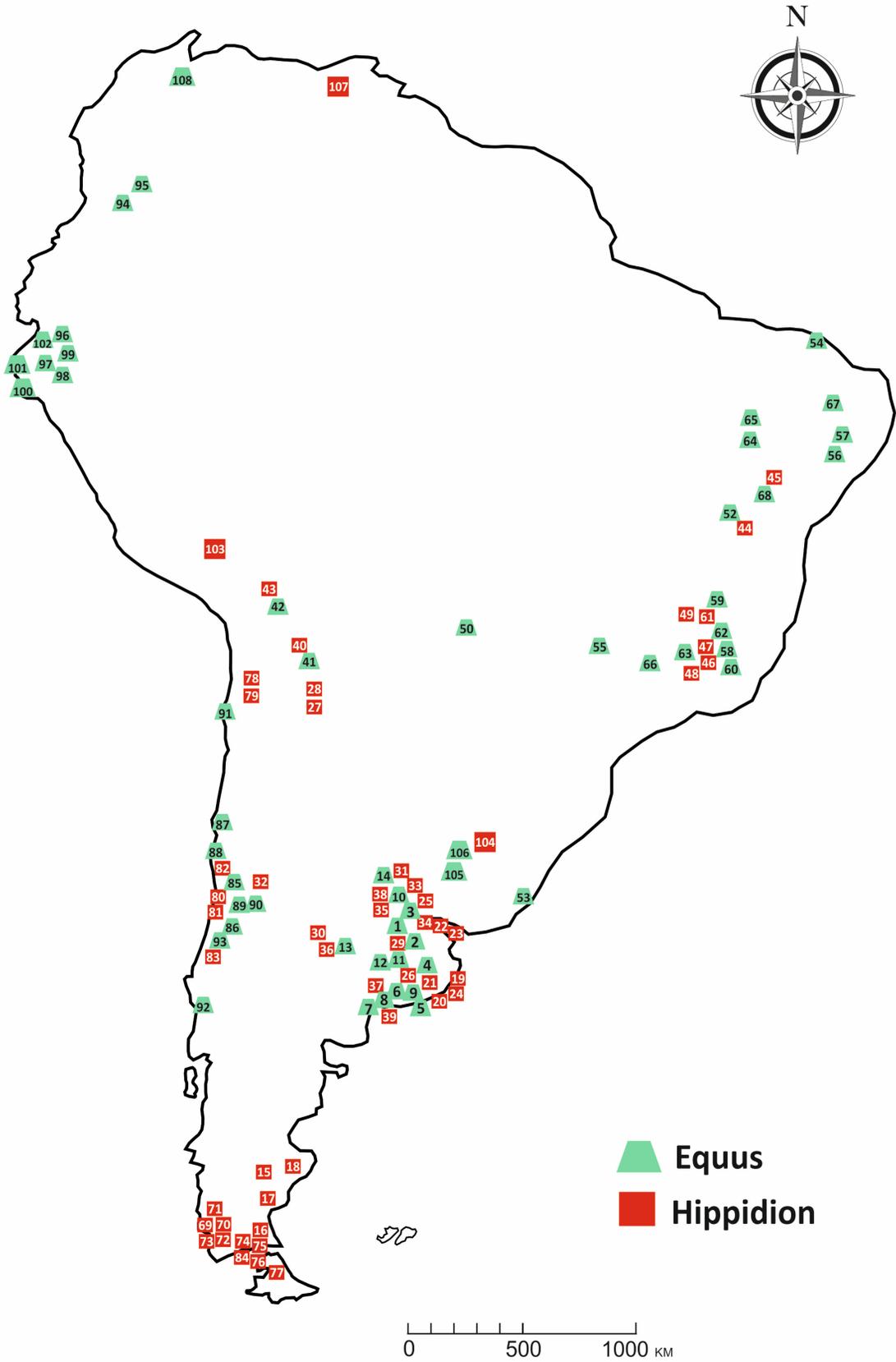
1. INTRODUCTION

The fossil record of horses is one of the best known and provides an exceptional example of large-scale morphological change (Simpson, 1951). The radiation of equids during the Neogene in North America has been cited as a textbook example of adaptive radiation for more than a century (Marsh, 1874), as it is crucial in the development of evolutionary theory, linking trait evolution and adaptive success (Simpson, 1953; MacFadden, 1992; Cantalapiedra et al., 2017). In this study, we present an update on the information of fossil horses in South America, providing a synthesis of already published data on the evolutionary history, phylogeny, systematics, palaeobiogeography, and palaeoecology of two key equid lineages (*Hippidion* and *Equus*) recorded in South America.

In his first voyage to South America (1832), Darwin made a series of observations on the extinct fauna that were key in many of his later conclusions. During October 1833, Darwin found a horse tooth in the red argillaceous earth in the Pampas, at “Bajada de Santa Fé”, in the province of Entre Ríos, Argentina. Later, the paleontologist Richard Owen (1840: 109) confirmed the tooth

was from an extinct species and remarked “This evidence of the former existence of a genus, which, as regards South America, had become extinct, and has a second time been introduced into that Continent”. Since this publication, notes and articles proliferated which in most cases do not reflect the general diversity of this group. Recent papers on the Equidae from South America recognize two genera: *Equus* and *Hippidion* (Prado & Alberdi, 2008, 2012, 2016, 2017). The dental morphology of *Hippidion* (oval protocone, rounded protoconid, and hypoconid, reduced metaconid-metastylid double knot) is more primitive than *Equus*, and its body structure is more robust (Prado, 1984; Alberdi, 1987; Alberdi et al., 1986, 1987; Cerdeño et al., 2008; Prado & Alberdi, 1994, 2014, 2016; among others).

The genus *Equus* originated in North America during the Pliocene and subsequent dispersal to Eurasia, Africa and South America (MacFadden, 1992). In 1950, the French paleontologist Robert Hoffstetter created the subgenus *Amerhippus* to include all species of genus *Equus* from South America. The author justifies this subgenus by a single character: the absence of infundibulum along the surface of the lower incisors and, therefore, the loss of enamel on the chewing surface. In a



later work on the revision of mammals of Ecuador Hoffstetter (1952) indicated that the ulna is stronger in the South American horses than other *Equus*. In the literature, the recognition of the subgenus *Amerhippus* is controversial. Recently Prado & Alberdi (2017) questioned the use of subgenus *Amerhippus*. Orlando et al. (2008) conducted DNA-based phylogenetic analyses revealing that all Pleistocene South American species of *Equus* were members of the caballine horse lineage, not a distinct subgenus as first suggested by Hoffstetter (1950). Therefore, the validity of the subgenus *Amerhippus* is questionable, and is not employed herein. The dispersal of the horse *Equus* into South America represents an important event (MacFadden, 2013). There is some controversy about the timing of this dispersion. Several studies have asserted that the age of this dispersal event is late Pleistocene, 0.125 Ma (Lujanian South American Land Mammals Age, SALMA), during a late phase of the Great American Biotic Interchange, GABI 4 (Cione & Tonni, 1999; Coltorti et al., 2010; Woodburne, 2010). However, Tonni et al. (2009) point out that in comparison with the Pampean standard, the Tarija fauna is not exclusively Ensenadan or Lujanian SALMA, given that, although the bulk of the fauna is comparable to that of the Pampean Lujanian, there are some exclusive taxa of the Pampean Ensenadan. New biostratigraphic evidence documents that *Equus* occurs from 15 superposed faunal horizons or zones throughout the Tolomosa Formation at Tarija, Bolivia. This biostratigraphic sequence is independently calibrated to occur between 1.07 to <0.76 Ma (Ensenadan SALMA) and coincident with GABI 3 (MacFadden, 2013).

Many articles have been published of the *Equus* species in South America (Fig. 1). Prado & Alberdi (2017) reviewed this group and recognized three valid species: *Equus andium* Branco 1883, ex Wagner (1860), *Equus insulatus* Ameghino, 1904, and *Equus neogeus* Lund, 1840 (Figs 2 and 3). Recently, Machado et al. (2017) proposed reducing the number of *Equus* species in South America to one, *Equus neogeus*. We do not share this proposal. This proposal may be due, in our opinion, to the fact that species from North and South America are mixed in the analysis, possibly by

the alleged affinity of *Equus occidentalis* with South American forms. The infundibulum in its lower incisors is shared by South American species, for which Hoffstetter (1950, 1952) proposes the new subgenus *Amerhippus*, in which he also included the Rancho La Brea equid, *Equus occidentalis*. The latter species, however, diverges from the other South American species in various characteristics. Beside the cornets in the lower incisors, South American equids, according to Hoffstetter, are characterized by a ventral rotation of the occiput, with a strong deflection of the braincase relative to the face, a broad supraoccipital crest, the vomer joining the palatal processes of the maxillaries well in front of the palatines, and a massive jaw and short limbs. It is true that not all elements of the appendicular skeleton of South American horses are equally diagnostic. For example, when the first phalanges of the third finger are mixed (anterior and posterior), the limits overlap. In the case of metapodes, the metacarpal is more diagnostic than the metatarsals. This is partly because the former limbs are where the weight of the body and the head are most affected (Eisenmann, 1984). Limb morphometric studies have been useful for discriminating *Hipparion* and monodactyl horse species (Eisenmann, 1979). This approach offers a comprehensive view of the material studied. However, in some cases, there are some overlaps, as in the case of the morphometric data between the metapodes of horses, hemiones, asses and *Equus hydruntinus* (Eisenmann & Beckouche, 1986). The latter do not alter the correlation between all the variables analyzed. In our opinion, it is a mistake to interpret these partial overlaps as continuity. The distal limb of horses is closely related to the adaptation to different environments, type of substrates, body weight, and locomotion. The adaptive nature of metapodials and phalanges variation can be explained by the differential success of lineages in macroevolution. Lineages with more advantageous patterns of regulated variation are likely to produce more species (Sharov, 2014). This is in relation to the epigenetic mechanisms that provide organisms with opportunities for rapid adaptive change (Gokhman et al., 2016). The epigenome is viewed today as a collection of regulatory layers that control when, where, and how genes

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Fig. 1 - Geographic distribution of different taxa of *Hippidion* and *Equus* from South America. In Argentina: 1-35, Arrecife; 2-34, Mercedes (Luján); 3-25, Arenero Spósito y Venta Obligado (San Pedro); 4, Ayacucho; 5, Necochea; 6, Arroyo Seco; 7-39, Montehermoso; 8, Río Quequén Salado; 9, Paso Otero 5; 10-33, Arroyo Ramallo; 11, Arroyo Tapalqué; 12, Calera Avellaneda; 13, Anchorena; 14-38, Barrancas de San Lorenzo y Alvear (Santa Fé province); 15, Los Toldos; 16, Las Buitreras; 17, Cerro Bombero; 18, Piedra Museo; 19, Voruheé; 20, Mar del Sur; 21, Lobería; 22, Olivos; 23, Canal de Conjunción en puerto La Plata; 24, Mar del Plata; 26, margen izquierda del Río Quequén Grande (Buenos Aires); 27, Barranco Negro (Jujuy); 28, Esquina Blanca in Uquía; 29, Río Salado; 30, San Luis; 31, Carcaraña; 32, Uspallata; 36, Anchorena; 37, Quequén Salado; in Bolivia: 40-42, Tarija; 41-43, Ulloma; in Brazil: 44, Santana (Estado de Bahia); 45-68, Toca dos Ossos (Estado de Bahia); 46-63, grutas de la región de Lagoa Santa; 47, Confins (Lapa do Galinheiro); 48, Lapa Come Não bebe; 49, Lapa de Bahu and Lapa de Escribania (Estado de Minas Gerais); 50, Rio Paraguai in Corumba (Estado de Mato Grosso do Sul); 52, Curaçaba (Estado de Bahia); 53, Santa Vitoria do Palmar (Rio Grande do Sul); 54, Tanque 2 de Itapipoca (Estado Ceará); 55, Curimatás (Estado de Paraíba); 56, Lage Grande (Alagoinha); 57, Pesqueira (Estado de Pernambuco); 58, Lapa do Cavalo; 59, Lapa de Escribania 5 and 11; 60, Lapa da Lagoa do Sumidouro; 61, Lagoa Santa Flere Hule Lapa dos Coses; 62, Lapa do Galinheiro; 64, Sao Raimundo Nonato; 65, Piaui; 66, Aguas do Araxa; 67, Chique-Chique; in Chile: 69, Cueva del Milodón (Ultima Esperanza); 70, Cueva Lago Sofia 1; 71, Cueva Lago Sofia 4; 72, Cueva de la Ventana; 73, Cueva del Medio; 74, Cueva de los Chinges; 75, Cueva Fell; 76, Cerro Sota; 77, Alero Tres Arroyos 1; 78, Betecsca 1; 79, Kamac Mayu (Atacama Desert); 80, Chacabuco; 81, Santa Rosa de Chena; 82, Tierras Blancas; 83-93, Taguatagua; 84, Cueva Pali Aike; 85-86, Calera, Lo Aguirre; 87, Valle de Elqui; 88, Los Vilos; 89, Conchalí; 90, Colina; 91, Punta Rieles; 92, Huimpil; in Colombia: 94, Cerrogordo; 95, Tibitó; in Ecuador: 96, Quebrada Otón; 97, Riobamba; 98, Punín (Quebrada Chalán, Quebrada Colorada, Quebrada Grande, Quebrada El Colegio, etc); 99, Alangasí; 100, La Carolina; 101, Salinas Oil Fields (Santa Elena Peninsula); 102, Río Chiche (Andes Ecuadorian); in Perú: 103, Tirapata; in Uruguay: 104, Formación Sopas, Artigas Department; 105, Arapey Grande creek; 106, Sopas Creek in the Sopas Formation; in Venezuela: 107, Breal de Orocual; 108, Inciarte (Estado de Zulia). Modified from Prado & Alberdi (2017).



Fig. 2 - Skull of different *Equus* species. 1: *Equus neogeus* from Luján, Buenos Aires province, Argentina; 2: *Equus insulatus* from La Carolina, Santa Elena Peninsula, Ecuador; 3: *Equus andium* from Chalan Punín, Ecuador.

are turned on and off. The promising new high-coverage genome of horses (Schubert et al., 2014; Gaunitz et al., 2018; Librado et al., 2017) will enable paleoepigenetic reconstruction in the near future.

The other group of horses in South America is the hippidiforms. Owen (1869) created the genus *Hippidion* based on only one molar from Brazil. In 1891, Moreno described one complete skull and some postcranial remains from the Pleistocene of Lobería (Argentina), and assigned it to *Onhippidium munizi*. The uncertainty began after the nomination and description of both genera in North America by MacFadden & Skinner (1979). Alberdi & Prado (1993, 2004) recognized just one genus, *Hippidion*, which is endemic to South America, and that the materials from North America assigned to both genera were not hippidiforms, but closer to *Dinohippus* (Prado & Alberdi, 1996; Alberdi & Prado, 1998). Avilla et al. (2015) proposed a new genus (*Borehippidion*) for the remains described as *Onhippidium* in North America. *Hippidion* is recorded from the Pliocene to the late Pleistocene mainly in Argentina, Bolivia, Brazil, Chile,



Fig. 3 - Upper and lower cheek teeth length of different *Equus* and *Hippidion* species. 1: P2-M3 left of *Hippidion saldiasii* from Betecsa 1, Calama (II Región, Chile); 2: P2-M3 left of *Equus neogeus* from Arroyo Tapalqué at level of Avellaneda street, Olavarría (Buenos Aires province, Argentina); 3: p2-m3 right of *Hippidion principale* from Monte Hermoso (Buenos Aires province, Argentina); 4: p2-m3 right of *Equus neogeus* from Monte Hermoso (Buenos Aires province, Argentina).

Peru, and Uruguay (Figure 1). Prado & Alberdi (2017) recognized three species: *Hippidion principale* (Lund), *Hippidion devillei* (Gervais), and *Hippidion saldiasii* (Roth) (Figures 3 and 4). These species differ mainly by their body size. *Hippidion principale* is much larger than others, and the differences between *Hippidion saldiasii* and *Hippidion devillei* are based on the shortening metapodial (Fig. 5). *Hippidion* is characterized by a retracted nasal notch, which has been interpreted as an adaptation to the presence of a proboscis and limbs with robust metapodials (Figures 4 and 5). The upper teeth present an oval protocone, more or less rounded, with simple enamel plication, and the lower teeth have a deep ectoflexid, penetrating the isthmus, and a rounded paracoid and hypoconid.

2. PHYLOGENY

The South America species of *Equus*, genus shows horse-like anatomical features and genetic affinities (Orlando et al., 2009). Biochronological data sug-

gests most of these occurrences are late Pleistocene; with one significant exception from the Tarija basin in Bolivia where *Equus insulatus* is recorded between 0.99 to 0.76 Ma (*sensu* MacFadden, 2013).

The *Hippidion* genus was first recorded at around 2.5 Ma, and includes two genetically similar generalists (*Hippidion principale*, *Hippidion saldiasi*) and one genetically distinct high-altitude specialist, *Hippidion devillei* (Prado & Alberdi, 1996; Orlando et al., 2009). Currently, the diversification of *Hippidion* species remains controversial. Prado & Alberdi (1996) proposed, on the basis of a cladistic analysis using morphological data, the affinity of *Hippidion* with *Pliohippus*. The latter is recorded between 6 and 14 Ma in North America. Also, *Hippidion* would have diverged from the lineage that leads to modern Equidae before 10 Ma. This implies a dispersion prior to the time when *Hippidion* is recorded for the first time in South America. On the contrary, a much later divergence date, with *Hippidion* nesting within modern equids, was indicated by the study of partial ancient mitochondrial DNA sequences (Weinstock et al., 2005). This analysis proposed that *Hippidion* was phylogenetically close to the caballine horses, with origins considerably more recent than the accepted date of around 10 Ma. Furthermore, based on analysis of ancient DNA, Orlando et al. (2009) proposed *Hippidion devillei* clusters outside a paraphyletic assemblage con-

sisting of *Hippidion principale* and *Hippidion saldiasi*. Recently, Der Sarkissian et al. (2015) obtained new mitochondrial data and suggested that the two morphospecies sequences (*Hippidion saldiasi* and *Hippidion principale*) formed a monophyletic clade, basal to extant and extinct *Equus* lineages. This contrasts with previous genetic analyses, and supports *Hippidion* as a distinct genus. This new data allowed us to estimate the divergence between *Hippidion* and *Equus* at approximately 5.6 to 6.5 Ma before *Hippidion* entered South America, following the formation of the Panamanian Isthmus 3.0 to 3.7 Ma.

3. PALAEOBIOGEOGRAPHY

The contemporary South American mammalian communities were determined by the emergence of the Isthmus of Panama, and by the profound climatic oscil-

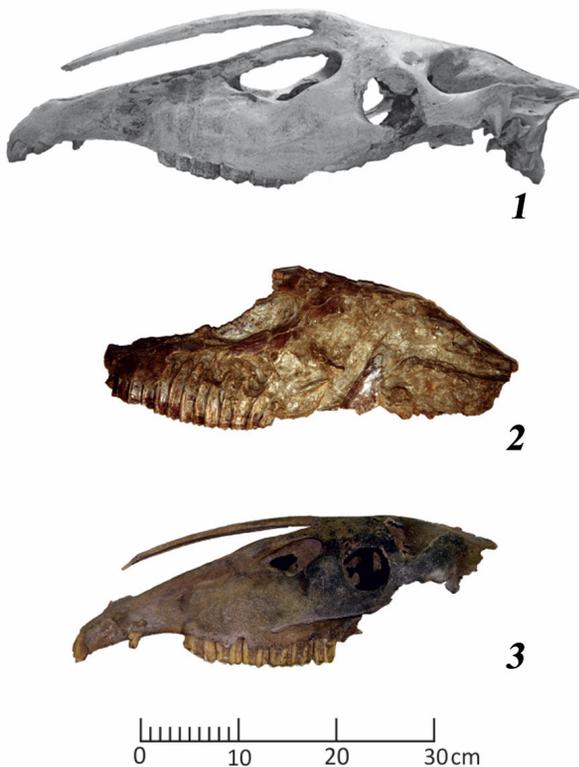


Fig. 4 - Skull of different *Hippidion* species. 1: *Hippidion principale* from Mar del Plata, Argentina; 2: *Hippidion devillei*, incomplete, from Tarija, Bolivia; 3: *Hippidion saldiasi* from Calama, Chile.



Fig. 5 - Metapodials of different *Hippidion* and *Equus* species: 1: MCIII of *Hippidion principale* from Tarija, Bolivia; 2: MCIII of *Hippidion devillei* from Tarija, Bolivia; 3: MCIII of *Hippidion saldiasi* from Última Esperanza, Punta Arenas, Chile; 4: MTIII of *Equus neogeus* from Quequén Salado-Indio Rico, Buenos Aires province, Argentina; 5: MTIII of *Equus insulatus* from Santa Elena Peninsula, Ecuador; 6: MTIII of *Equus andium* from Riobamba, Ecuador.

lations during the late Pliocene and Pleistocene. The emergence of the Isthmus closed communication between the Atlantic and Pacific oceans and changed both water circulations, facilitating the installation of the Arctic polar ice cap. The cool Circum-Antarctic Current was finally established (Pascual et al., 1996). The Pliocene in South America is characterized by the apogee of the Age of the Southern Plains (Ortiz-Jaureguizar & Cladera, 2006). In northern South America, the Pliocene vegetation changed sequentially from tropical lowland to high-elevation vegetation as a result of the developing Andes. On the contrary, in southern South America, grasslands and steppes were dominant. The most evident changes between Tertiary and Quaternary climatic conditions are correlated to the amplitude and frequency of the environment. Throughout the Pleistocene, the repeated advance and retreat of glaciers produced an evident and coincident expansion and retraction of arid and humid environments. A savannah corridor developed along the eastern border of the Andes, offering a corridor that linked the grasslands of Argentina and Colombia, continuing northward across the Panamanian land bridge to North America. Conversely, when open areas withdrawal during interglacial periods of warm-wet climates, rainforests enlarge and favored a second corridor to expand across eastern South America (Sánchez et al., 2004).

The GABI is a complex history of multiple dispersal events between the Americas during the Pliocene and Pleistocene. Horses were a conspicuous group of immigrant mammals from North America. Their demographic history was punctuated by major cycles of expansions and collapses, probably related to the major glacial and interglacial cycles.

These dispersal events coincided with the development of two dispersal pathways (Webb, 1991), that ultimately contributed to the distribution of horses (Prado & Alberdi, 2014). Recent biogeography studies based both on phyto- and zoogeographic data, show that South America is composed of two regions with different evolutionary histories and showing closest links with other Austral areas. This pattern is evident in the recent distributions, and in the fossil record dispersion. Compiling numerous sources of information, Morrone (2014), confirmed the Neotropical and Andean regions, separated by the Andean Cordillera, which in turn divides the continent into two different areas: western and eastern.

The dispersal and the diversification process in small to middle size species, *Equus andium*, *Equus insulatus*, *Hippidion devillei*, and *Hippidion saldiasi*, occurred through the Andes corridor, whereas the large species, *Equus neogeus*, and *Hippidion principale* used the eastern plain route, firstly (Fig. 6). The pathway of dispersion in each species reflects its adaptive change and habitat preference (Alberdi & Prado, 1992) and may have occurred during two or three immigration events. Woodburne (2010) described the principal phases of interchange between the Americas as GABI 1 (2.6 to 2.4 Ma), GABI 2 (1.8 Ma), GABI 3 (1.0 to 0.8 Ma) and GABI 4 (0.125 Ma). In this context, MacFadden (2013) suggest that *Equus neogeus* may have originated independently from a North American sister species within

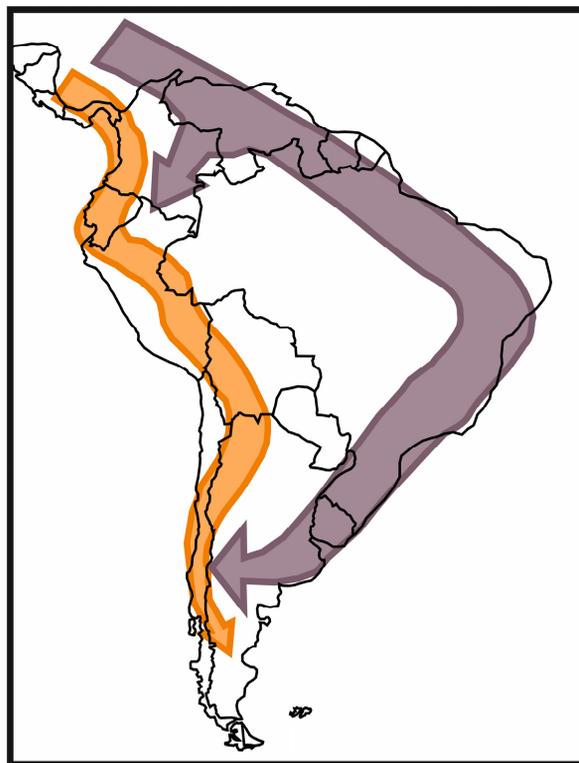


Fig. 6 - The geographic distribution of the Equini tribe from South America and possible migratory routes. Small to middle size species through the Andes corridor (*Equus andium*, *Equus insulatus*, *Hippidion devillei*, *Hippidion saldiasi*) in orange and the large forms (*Equus neogeus*, *Hippidion principale*) used the eastern plain route in violet. Modified from Prado & Alberdi (2017).

the caballine clade, thus suggesting a second dispersal of *Equus* during GABI 4 at 0.125 Ma. The first arrival corresponded to *Equus insulatus* recorded in Tarija (Bolivia) and dispersal through the Andes corridor during GABI 3 (MacFadden & Azzaroli, 1987; MacFadden, 2013). *Equus neogeus* is the largest and most slender morphotype of the South American horses, and occurs in eastern South America, but does not occur outside of lowland Argentina, Uruguay, and Brazil. This species preferred savannas and consequently would have been better adapted to open and arid landscapes (Prado & Alberdi, 1994). The first record of *Hippidion* came from Esquina Blanca (Jujuy, Argentina) were *Hippidion devillei* appears in a sedimentary layer dated around 2.5 Ma (Prado et al., 1998, 2000; Reguero et al., 2007) and corresponds to GABI 1.

4. BIOCHRONOLOGY

The SALMA are stratigraphic units not formally recognized by any code of nomenclature, but as an organizing device. They have proven to be very useful in developing concepts about mammalian stratigraphy and evolution (Savage, 1962; Simpson, 1971). Pascual et al. (1996) suggest that SALMA has proved to be useful for intra and intercontinental correlations and subdividing

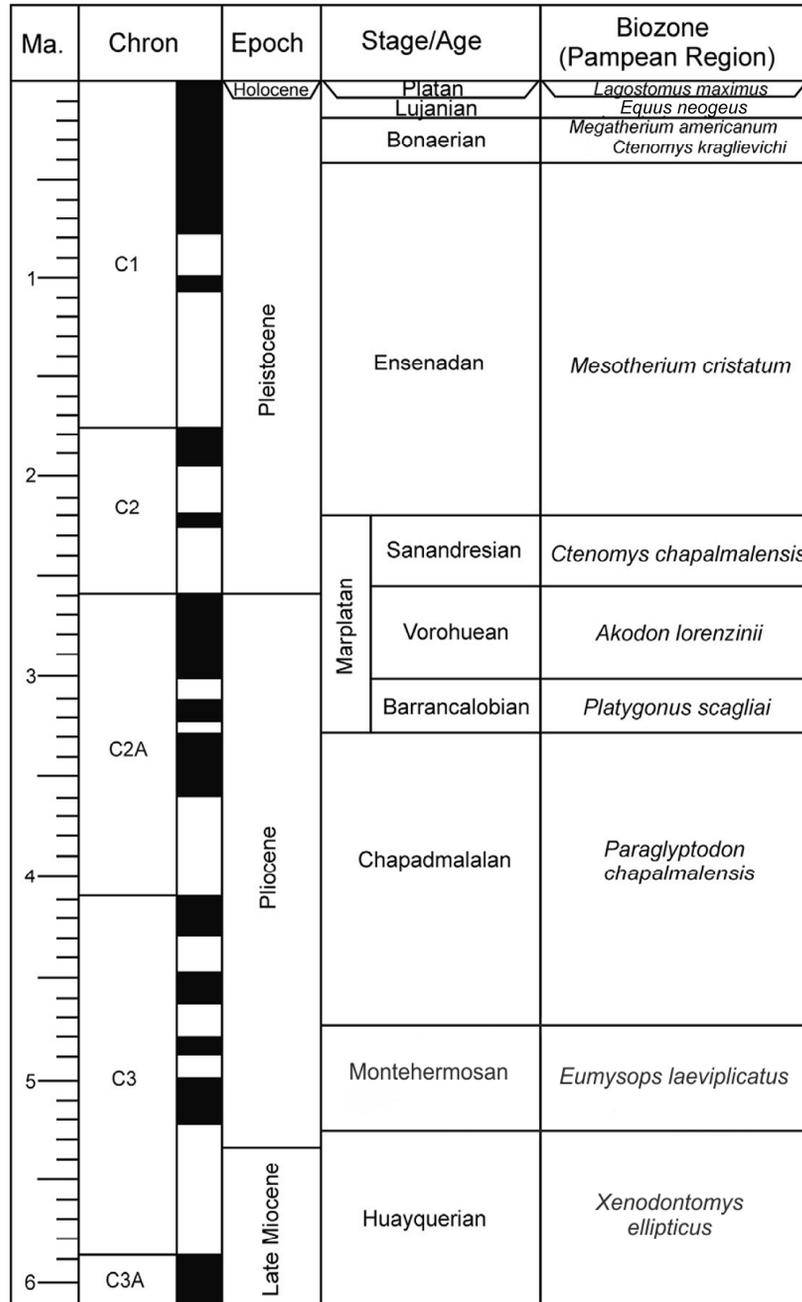


Fig. 7 - The chronological framework of mammalian biochronology of South America modified from Cione & Tonni (1999).

Cenozoic time. The Land Mammals Ages were first proposed by Wood et al. (1941) and characterized by unique mammalian assemblages. Pascual et al. (1965, 1966), Marshall et al. (1983, 1984) and Pascual et al. (1996) among others, used SALMA for South America. Recently, Cione & Tonni (2005) proposed a new biostratigraphic framework involving the continental sediments and faunas of the Pampean region, from the Late Miocene to the present. These authors recognized 13 biozones for this interval, which represent the biostratigraphic basis for the recognition of stages and sub-

stages in the Pampean Region. In this paper, we follow both of these criteria to establish the chronological position of the horses (Figure 7).

According to Alberdi & Prado (2004), *Hippidion devillei* was the first species of the Equini recorded in South America. It is found in land-mammal bearing sediments of the Uquian SALMA in northern Argentina (Prado et al., 1998). *Hippidion principale* was recorded for the first time in sediments of the Ensenadan SALMA in Bolivia. *Hippidion saldiasi* was recorded in sediments of the Lujanian SALMA in Patagonia, Argentina (Alberdi

& Prado, 2004). So far as the biochronology is known, most of these occurrences of *Equus* are late Pleistocene; with one significant exception of *Equus insulatus* from the Tarija basin of Bolivia. In Argentina, Uruguay and Brazil, *Equus* occurred during the latest Pleistocene, and it defines the base of the Lujanian SALMA (*sensu* Pascual et al., 1996). In the Pampean Region, Cione et al. (2009) proposed the *Equus neogeus* biozone based on the "Piso Lujanense" from Ameghino. Nevertheless, if *Equus* is restricted to the Pampean species *Equus neogeus*, then the use of this latter taxon still can be used as an index fossil for the Lujanian Stage within the Pampean region. It is clear that the Lujanian Stage or Biozone of *Equus neogeus* defined by Cione & Tonni (1999, 2005) does not correspond to the Lujanian SALMA of Pascual et al. (1965, 1996). Recently, we recorded remains assigned to *Equus neogeus* from the Campo Spósito site (province of Buenos Aires). This site was referred to the Bonarian Stage, with a base at ~130 ka and top at 10 Ka. The level containing the remains of *Equus* was dated by OSL, ESR and U-Th series between 40 to 200 ky BP (Prado et al., 2012; Toledo et al., 2014, 2015). These findings implied that the status of *Equus neogeus* as an index fossil of the Lujanian Stage, or its lower limit, should be revised as this taxon clearly expanded in the Pampean region before ~130 ka BP. Also, these results reinforce the fact that *Equus* dispersed into South America during GABI 3. Argentina has allowed discussions on the correlation of type sections in the Pampean area with other regions (e.g. Reguero & Candela, 2011; Tauber, 2005). It is necessary to carry out new studies in areas outside the Pampean region to contrast this scheme.

5. PALAEOECOLOGY

The skeleton of the fossils mammals has been the main source of information for interpreting its ecology. Several studies in horses from South America document changes in body size, skull magnitudes, dentition morphology and limb structure (Alberdi & Prado, 1993; Alberdi et al., 1995; Bernardes et al., 2013; Prado & Alberdi, 1994, 2014). Additionally, the use of stable isotopes in fossil horses has been successfully increased (Domingo et al., 2012; Dantas et al., 2013; Prado et al., 2015; among others), and have contributed to understanding the feeding paleoecology of extinct species (MacFadden et al., 2004). Carbon is fixed through plant photosynthesis, which has three different pathways: C_3 (Calvin-Benson), C_4 (Hatch-Slack), and CAM (crassulacean acid metabolism). The C_3 pathway is found mainly in dicotyledonean trees and shrub, and in some temperate grasses. The C_4 pathway is typical of monocotyledonean grasses, as well as some trees and shrubs from warm regions (Cerling et al., 1997) and the CAM pathway is found in succulent plants such as cacti and bromeliads. Several factors, such as saline soils, low light intensity, and a lack of nutrients, affect the abundance of C_3 and C_4 plants in ecosystems. The temperature plays an important role, as localities with temperatures below 25 °C show an increase in C_3 plants while C_4 plants decrease (Ehleringer & Cerling, 2002).

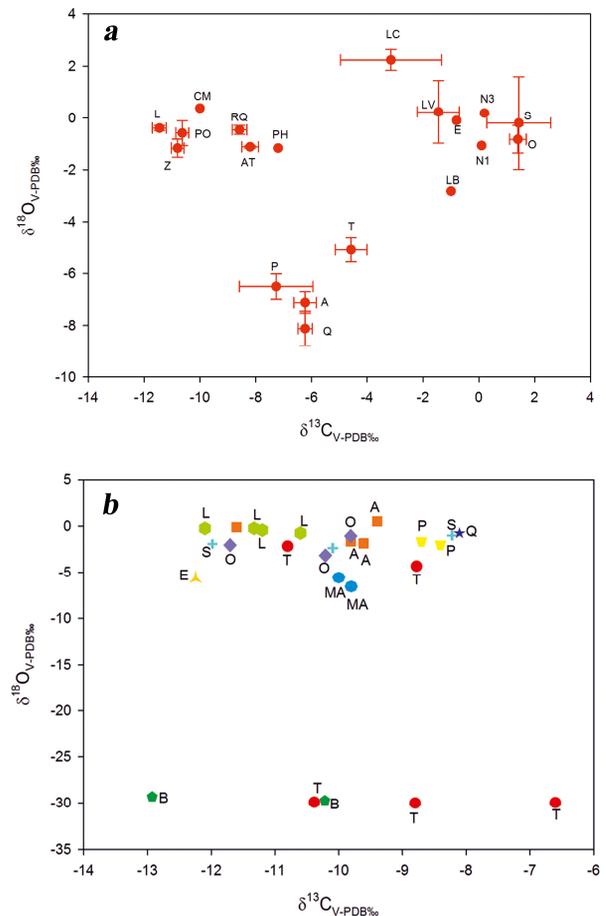


Fig. 8 - Average and standard error of isotopic values from different localities in Argentina, Bolivia, Colombia and Ecuador of *Equus* (a) and *Hippidion* (b). A: Alangasi, AT: Arroyo Talpaqué, B: Buenos Aires, CV: Cantera Vial. Buenos Aires province, CM: Centinela Mar, E: Última Esperanza, LB: La Banda, LC: La Carolina, LV: La Venta, L: Luján, M: Magdalena, N1: Napua-1, N3: Napua-3, O: Oroulandia, PH: Punta Hermengo, PO: Paso Otero, P: Punín, Q: Quebrada Colorada, RC: Río Chiche, RQ: Río Quequén, S: Salinas Oil, T: Tarija, Z: Zajón Seco, MA: Mina Aguilar, O: Olivos, P: Paraná, B: Buenos Aires, L: Luján, S: Río Salado, A: Arroyo Talpaqué, Q: Río Quequén, E: Última Esperanza. Modified from Prado & Alberdi (2017).

In mammals, digested carbon becomes incorporated into the tissue of the consumer; this is the case for dental enamel apatite (Koch, 2007). Herbivores have carbon isotopic values enriched by 14‰ in comparison with plant $\delta^{13}C$ values (Cerling & Harris, 1999). Based on classifications proposed by Hofmann & Stewart (1972) and MacFadden & Cerling (1996), C_4 plant eaters show values from -2‰ to 2‰, C_3 plant eaters have values from -19‰ to -9‰, and C_3/C_4 mixed-diet herbivores show values between -9‰ and -2‰. The $\delta^{13}C$ values of herbivore teeth record a dramatic increase in consumption of C_4 grasses during the late Miocene and provide the first evidence for appearances of C_4 grass in the past (Strömberg, 2004).

Based on mesowear and microwear analyses,

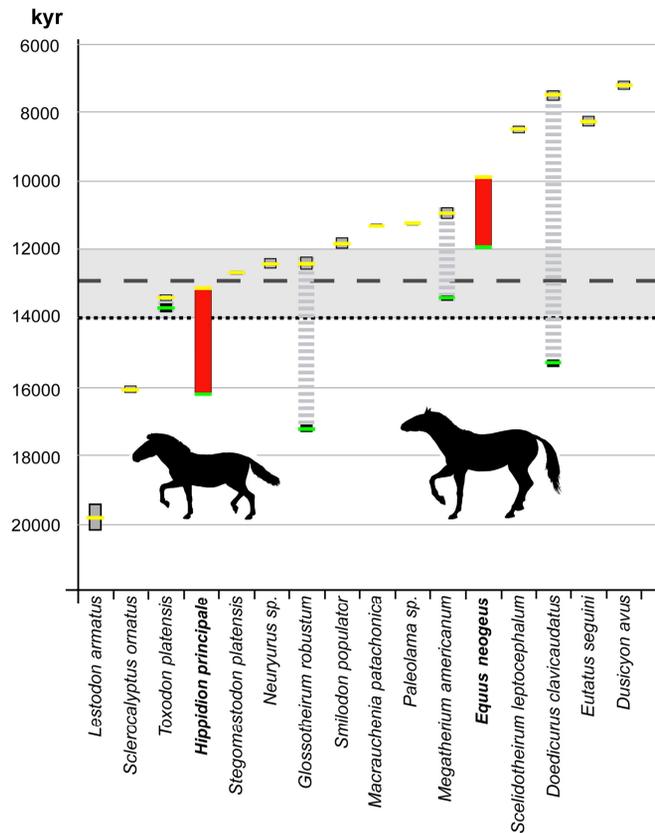


Fig. 9 - Last-appearance dates for megafauna from the Argentine Pampas region, using only robust dates from previous papers and the new dates. The horizontal dashed line indicates a consistent archeological signal. The dotted horizontal line indicates the earliest occupation evidence or minimal human activity. The gray boxes indicate the dates obtained from the literature, the red boxes indicate radiocarbon data of South American horses, and the yellow line is the average of these. Black boxes indicate the new dates and the green line is the average of these. The gray band denotes the timing of Younger Dryas cooling in the Argentine Pampas region (Hajdas et al., 2003; Krohling & Iriondo, 1999) (Modified from Prado & Alberdi, 2017).

Mihlbachler et al. (2011) showed that Pleistocene horses from North America are able to mainly eat not only grass but also leaves off trees or shrubs. MacFadden et al. (1996) suggested the existence of a latitudinal gradient, meaning that above 35° latitude, C₃ plants start to increase while C₄ plants decrease. The South American horses in general were C₃/C₄ mixed feeders and lived in grasslands or prairies. Although there were some populations that exclusively fed on C₃ and occupied forest habitat and other that fed on C₄ plants and living in grassland zones (Pérez-Crespo et al., 2018). The horse populations from Argentina show that they mainly ate C₃ plants, which indicated the presence of C₃ grassland areas (Domingo et al., 2012). On the other hand, horses from Colombia, Brazil, and Perú, located above parallel 35°, were specialized C₄ plants feeders. Domingo et al. (2012) also indicated the presence of a vegetation elevation gradient, where C₄ plants were abundant in lower zones, and C₃ plants were abundant in higher zones, explaining the diet of Bolivian and Ecuadorian populations. The flexibility in their diet and by extension in their occupied biome agrees with the habitat theory (Vrba, 1992) according to which generalists and open biome

specialists from North America accomplished successful radiation throughout South America (Moreno Bofarull et al., 2008).

Hippidion only fed on C₃ plants, although some individuals were C₃/C₄ mixed feeders, but with important ingest of C₃ plants (Prado et al., 2011; Pérez-Crespo et al., 2016). This could be explained by the fact that some individuals inhabited higher elevations, where C₃ plants are abundant, or lower latitude than 35°S on C₃ were predominate grasslands with nearby forests (Domingo et al., 2012). Samples from early Pleistocene show that *Hippidion principale* and *Hippidion devillei* have $\delta^{13}\text{C}$ values typical of wooded C₃ grassland (Figure 8a). *Hippidion devillei* and *Hippidion saldiasi* have lower $\delta^{18}\text{O}_{\text{CO}_3}$ values than *Hippidion principale* (Figure 8b). This is due to high elevation effects in the case of *Hippidion devillei*, and high latitude effects in the case of *Hippidion saldiasi* (52° S).

Another important indicator of horses' ecology is the body size. In all continents, the evolutionary history of the horse was strongly influenced by body size, related with environmental conditions and type of substrates (Shoemaker & Clauser, 2014; Saarinen et al., 2016).

Alberdi et al. (1995) present the body mass predictions for South American fossil horse species. Both genera present different patterns. Within the *Hippidion* group, the middle sized *Hippidion devillei* produced two body mass species: (1) *Hippidion saldiasi*, which has a similar body mass, and (2) *Hippidion principale*, which reaches a greater size. In the *Equus* group, the large-sized *Equus insulatus* gave rise to two different sized groups: (1) *Equus neogeus*, which retain or increase their body mass; and (2) the small *Equus andium*.

6. HORSE EXTINCTION

Late Quaternary megafauna extinctions impoverished mammalian diversity worldwide (Koch & Barnosky, 2006). About 70% of South American large mammal species (animals with an average body size ≥ 44 kg) went extinct at the end of the Pleistocene epoch (Prado et al., 2015). The causes of this extinction - the role of humans versus climate - have been the focus of much controversy (Barnosky & Lindsey, 2010; Prado & Alberdi, 2016, 2017; Villavicencio et al., 2016). Horses have figured centrally in this discussion because it's a species that dominated late Pleistocene faunas in terms of abundance and geographical distribution, but none survived into the Holocene. On a global scale, several species of horses were widespread and common during the middle and late Pleistocene, with a distribution that covered most of Eurasia and northern Africa, as well as North and South America. The late Pleistocene was a period of extraordinarily intense environmental change. By the end of this period, the last glacial maximum (LGM) marked one of Earth's most extreme moments of climatic variability (Clark et al., 2009). The decreased grassland in Eurasia due to of the LGM caused a massive crash in the horse population. However, one formerly wild subspecies (*Equus ferus przewalskii*) had survived, and abundant genetic diversity has been preserved in domesticated forms (Orlando et al., 2009; Weinstock et al., 2005). The new world stilt-legged horses disappeared around 30 ka BP in North America, before the earliest arrival of humans (Weinstock et al., 2005; Vilstrup et al., 2013; Prado & Alberdi, 2017). In South America, *Hippidion* and *Equus* survived no later than 10 ka BP (Prado & Alberdi, 2016, 2017).

The timing of the horse extinctions in each region of South America is poorly known. There are many archaeological sites with recorded horses, but the coexistence with humans is difficult to verify. The taxon dates evidence is very rare and are strictly concentrated in two regions, Pampas and Patagonia (Borrero, 1997; Alberdi & Prado, 2004). The extinction window in Pampas ranges from c. 13.9 and 10.1 ka BP for *Equus neogeus* and c. 11.3 to 15 ka BP for *Hippidion principale* (Prado et al., 2015; Figure 9). The archaeological record from southern Patagonia indicates that the timing of horse extinction was restrained by a complex interaction between climate changes that precipitated vegetation change, associated with growing human impacts (Villavicencio et al., 2016). The data from Pampas and Patagonia are robust enough to consider synergy interaction among

last appearance records of horses, first appearance records of humans, and the Holocene climatic transitions. However, the evidence is still scarce in other regions in South America.

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