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ARTÍCULO

DIVERSITY OF THE FOSSIL EQUIDS FROM SOUTH AMERICA

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Abstract. The contemporary mammalian communities of South America were defined by the rise of the Isthmus of Panama and by the deep climatic oscillations during the Pleistocene. Horses are a conspicuous group of North American immigrant mammals that came to South America during the Late Pliocene and did not survive the Quaternary megafauna extinction approximately twelve thousand years ago. The present study compiles updated data on the phylogeny, systematics, and ecology of this group in South America. The first lineage is represented by the genus *Equus*, which appears in the Middle Pleistocene and presents anatomical features similar to those of a current horse. The second lineage is the species included in the genus *Hippidion*, which includes horses with highly distinctive anatomical features that were first recorded in the Late Pliocene. Both genera of horses include small (*H. devillei*, *H. saldiasi*, *E. andium*, and *E. insulatus*) and large (*E. neogeus* and *H. principale*) forms, which dispersed in South America using two different routes. The possible model for this dispersal indicates that the small forms used the corridor of the Andes, while the larger horses dispersed along the eastern route and some coastal areas.

Key words. Perissodactyla. Equidae. Pliocene. Pleistocene. South America.

Resumen. DIVERSIDAD DE LOS ÉQUIDOS FÓSILES DE AMÉRICA DEL SUR. Las comunidades de mamíferos contemporáneas de América del Sur estuvieron definidas por el surgimiento del Istmo de Panamá y por las profundas oscilaciones climáticas durante el Pleistoceno. Los caballos son un grupo conspicuo de mamíferos inmigrantes norteamericanos que llegaron a Sudamérica durante el Plioceno Tardío y no sobrevivieron a la gran extinción de la megafauna hace aproximadamente doce mil años. El presente estudio recopila datos actualizados del Cuaternario tardío sobre la filogenia, sistemática y ecología de este grupo en América del Sur. El primer linaje está representado por el género *Equus*, que aparece en el Pleistoceno Medio y presenta rasgos anatómicos parecidos a los de un caballo actual. El segundo linaje son las especies incluidas en el género *Hippidion*, que eran caballos con características anatómicas muy distintivas que se registraron por primera vez a finales del Plioceno. Ambos géneros de caballos incluyen formas pequeñas (*H. devillei*, *H. saldiasi*, *E. andium* y *E. insulatus*) y grandes (*E. neogeus* y *H. principale*), que se dispersaron en América del Sur utilizando dos rutas diferentes. El posible modelo de esta dispersión indica que las formas pequeñas utilizaron el corredor de los Andes, mientras que los caballos más grandes se dispersaron por la ruta oriental y por algunas zonas costeras.

Palabras clave. Perissodactyla. Equidae. Plioceno. Pleistoceno. América del Sur.

THE WORKS carried out by Eduardo P. Tonni on the Quaternary mammals of the Pampean Region have fundamentally contributed to this record being considered one of the best in South America. Tonni was interested in increasing the knowledge of these faunas and consequently encouraged his fellows to focus on updating his systematic knowledge of the different groups. So, in the year 1984, José Luis Prado (J.L.P.) began to review the fossil horses, a task that he continued from 1985 in collaboration with María Teresa Alberdi (M.T.A.) when she visited the Museum of La Plata. This uninterrupted collaboration grew and allowed the development of a project financed by the European community under the co-direction of Tonni.

Horses are the only living members of the Equidae family, which today comprises seven species in the genus *Equus* (including zebras, asses, and caballine horses). In contrast, the equid fossil record shows that extraordinarily more diversity existed in the past. This record provides multiple examples of highly dynamic evolution marked by various waves of explosive radiation and extinctions, intercontinental migrations, and local adaptations (Simpson, 1951, 1953; MacFadden, 1992; Cantalapiedra *et al.*, 2017).

Fossil horses played a crucial role in providing evidence for Darwin's theory of evolution and, later, in what came to be called the modern synthesis (Simpson, 1951). Marsh (1874) had made a considerable collection of fossil horses in

North America. He also began to study the horse's record and ordered them according to the size of the teeth, the height of the dental crown, and the number of fingers of the extremities, and thus, laid the foundations for the future of macroevolution studies.

Charles Darwin, first discovery one tooth of a horse, during the Beagle expedition, in the Pampa at "Bajada de Santa Fé" (Entre Ríos Province); this material is stored at Natural History Museum in London. Owen (1840, p. 109) confirmed its membership to an extinct species indicating "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". After this discovery, many notes and articles took place without clearly demonstrating the diversity of this group in South America. Recently, several papers admitted the presence of two genera: *Equus* Linnaeus, 1758 and *Hippidion* Owen, 1869 (Alberdi & Prado, 1993; Prado & Alberdi, 1994, 2008, 2012, 2016; Machado & Avilla, 2019). Each genus has characteristic dental morphology and an evident intraspecific variability. The morphology in *Hippidion* is more primitive than *Equus* and has a most robust body structure (Prado, 1984; Alberdi *et al.*, 1986, 1987; Alberdi, 1987; Prado & Alberdi, 1994, 2014, 2016; Der Sarkissian *et al.*, 2015, among others).

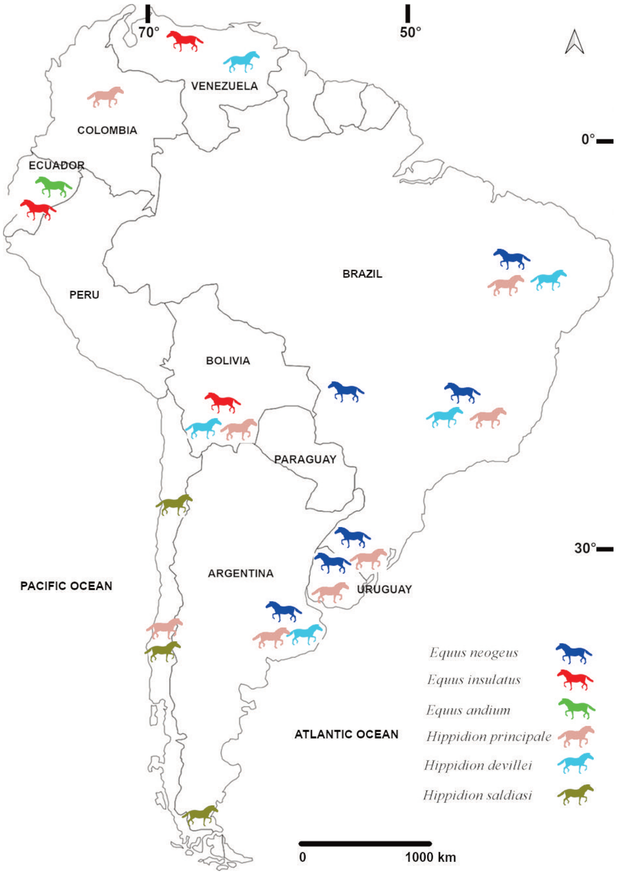

Figure 1. Main distribution of *Hippidion* and *Equus* genera in South America. The drawings of the horses were made Mauricio Antón.

Equus genus arose in the Pliocene of North America and dispersed in Eurasia, Africa, and South America (MacFadden, 1992). Hoffstetter (1950) created the subgenus *Amerhippus* to comprise all species of *Equus* genus from South America, based on "the absence of infundibulum marked on the surface of the lower incisors", that is, in our opinion, the loss of enamel on the occlusal surface. Posteriorly, Hoffstetter (1952), in his revision of the Ecuador mammals, indicated that the ulna is strongest in this subgenus than other *Equus*, except *Equus andium* due to its small size. The distinguishing of *Amerhippus* subgenus from this originality is controversial. Orlando *et al.* (2008) using the DNA-based phylogenetic analyses showed that all Pleistocene South American *Equus* species belonged to the caballine horse lineage, not a different subgenus as he indicates (Hoffstetter, 1950). We questioned the employment of *Amerhippus* subgenus and chose to suppress its use (Prado & Alberdi, 2017).

The first records of South American horses came from the Middle Pleistocene sequence of Tarija (Bolivia), which was dated about 1.0–0.8 Ma by MacFadden *et al.* (1983) and MacFadden (2013). Recently, Prado and Alberdi (2017) reviewed the horses' group and specified that there were three valid species, *Equus andium* Branco, 1883 (ex Wagner, 1860), *Equus insulatus* Ameghino, 1904, and *Equus neogeus* Lund, 1840 (Fig. 1). Machado *et al.* (2017) considered a continuum of gradual variation of autopodial dimensions in which these species partially overlap. Consequently, *Equus* species from South America represent a species cline in which *Equus andium* and *Equus neogeus* represent the diagnostic metapopulations, considering the presence of a single species in South America. In Machado and Avilla (2019), the analysis includes most of the dental data, but does not take into account the degree of wear, which produces an overlap in the data. Consequently, they suggested *Equus neogeus* as the only species in South America. In our opinion, comparing their data and ours (are practically the similar data and equal analysis and result), we interpreted that the differences in size and weight are sufficiently marked to include the three forms corresponding to three species "in a single genus" (Prado & Alberdi, 2017).

In 1869, based on the description of a single molar from Brazil, Owen created the genus *Hippidion*. Later, Moreno (1891) studied a complete skull and several postcranial remains from the Pleistocene of Lobería locality (Argentina) and named it *Onohippidium munizi*. MacFadden and Skinner (1979) indicated the presence of both genera (*Hippidion* and *Onohippidion*) in North America. Alberdi and Prado (1993, 2004) recognized the presence of a single genus, *Hippidion*, endemic in South America and considered the remains from North America, but belonging to *Dinohippus* related to him (Prado & Alberdi, 1996; Alberdi & Prado, 1998). Lately, Avilla *et al.* (2015) created a new genus (*Boreohippidion*) for the material described as *Onohippidium galushai* by MacFadden and Skinner (1979) from North America. We think this taxon should be named *Dinohippus galushai* (not only does it have a minor naso-incisival notch retraction, but its extremities are similar to those of the *Dinohippus* species). The record shows that *Hippidion* is present in Argentina, Bolivia, Chile, Brazil, Peru, and Uruguay from the Pliocene to the Late Pleistocene (Fig. 1). The revision of this genus by Alberdi and Prado (1993) identified three species: *Hippidion principale* (Lund, 1845), *Hippidion devillei* (Gervais, 1855), and *Hippidion saldiasi* (Roth, 1899). The most important differential characteristics of these species are in their body size. The deep nasal notch characterizes this genus, which can make us think about the presence of a proboscis, and has distal extremities with robust metapodials. The upper teeth show an oval protocone, with simple enamel plication, more or less rounded. The lower teeth have a deep ectoflexid, penetrating the isthmus, and paraconid and hypoconid rounded. *Hippidion principale* is the largest, and the shortening metapodials characterize both *Hippidion saldiasi* and *Hippidion devillei*. In the present study, we supply a state-of-the-art about the diversity of Equidae from South America.

PHYLOGENY

Early studies suggest that equids were a single assemblage that gradually evolved from *Hyracotherium*, with low crown teeth and four toes on the forefoot and three on the hind leg, up to the more recent *Equus*, that has high crown teeth and a single toe (Simpson, 1951). This classic hypothesis involves a progressive increase in body mass, a gradual finger reduction, and slenderness of the limbs to better evade predators in open habitats and the development of more complex teeth to overcome abrasive grasses. Later studies indicate more complicated radiation and divergent lineages characterized by consecutive evolutionary radiations.

Earliest Equidae shares many characters with primitive representatives of other perissodactyl lineages (*i.e.*, they all share a small size, four-toed forefeet, and brachydont dentition). But they are lacking many of the highly derived characters of the latter species common traits to all Equidae. This family is divided into three subfamilies: a basal Hyracotheriinae (Eocene), late Eocene to Late Miocene Anchitheriinae, and Early to Late Miocene Equinae (Fig. 2).

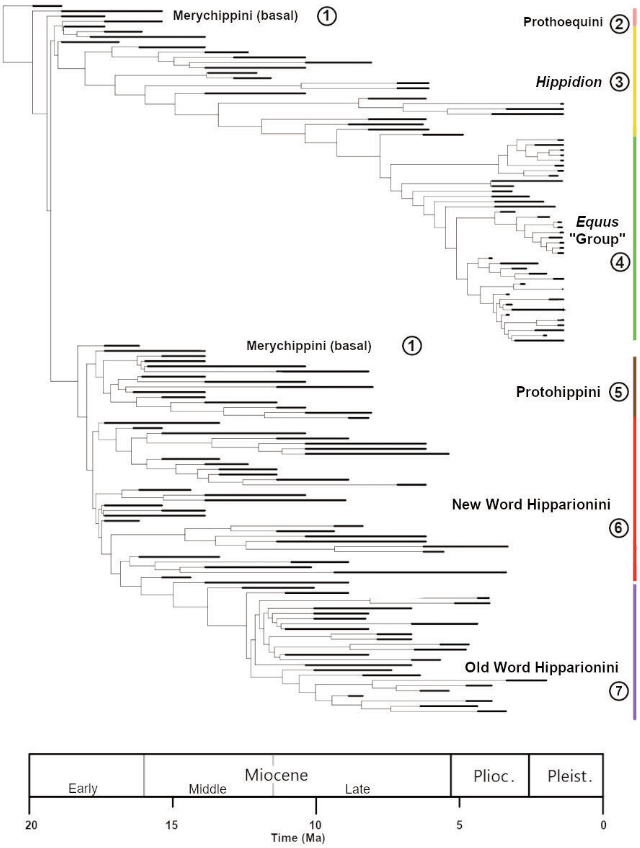

Figure 2. Phylogeny of Subfamily Equinae (Modified from Prado & Alberdi, 2017 and Cantalapiedra *et al.*, 2017). **1,** Merychippini (basal); **2,** Prothoequini; **3,** *Hippidion*; **4,** *Equus* "Group"; **5,** Protohippini; **6,** New World Hipparionini; **7,** Old World Hipparionini. Time scale= 20 Ma.

Both the Anchitheriinae and the Equinae originated in North America, and the lineages of both subfamilies migrated to the Old World (Froehlich *et al.*, 2002).

The late Eocene saw a new type of horse featuring three toes and ectolophodont teeth void of cement. These forms (*Mesohippus* and *Miohippus*) are the first representatives of the subfamily Anchitherinae (MacFadden, 1992), which later were involved in the first relevant event of horse diversification in Miocene times. The anchitheres were the first known horses to venture outside North America.

During the late Early Miocene, between 19 to 16 Ma, the fossil record shows a second radiation. From the genus *Merychippus*, three tribes evolved: Hipparionini, Protohippini, and Equini, all of them widely distributed in North America. The Hipparionini tribe, broadly represented by the genus *Hipparion*, migrated to the Old World in the Late Miocene (Woodburne & MacFadden, 1982). It was a dominant equid in the Neogene record of the Palearctic, Ethiopian, and eastern, coexisting in some places with *Equus* (Eisenmann & Brunet, 1973; Lindsay *et al.*, 1980). This second radiation occurred around 15–12 Ma ago. It brought the development of hypsodonty influenced by climate and vegetation changes (Hulbert, 1993). Around 3.0–2.5 Ma, *Equus* also emigrated to the old world favored by the decrease in temperatures and the increase in polar caps that led to the drop in sea level through the Bering Strait on the one hand; and on the other hand, the dispersion of *Equus* to South America was favored by the rise of the Isthmus of Panama. Both migrations developed widely both in the Old World and in South America. The results of Cantalapiedra *et al.* (2017) indicated that morphological changes are not only faster during moments of group diversification but may be slower. They suggested a scenario where radiation produced very similar species in ecology and shape, and therefore niche differentiation was not the engine of species multiplication. The authors argued that the numerous climatic conditions are responsible for the diversification of horses during the last 18 Ma, either by population fragmentation associated with more significant habitat heterogeneity or by favoring the colonization of new, inaccessible geographic areas until that moment. It is a complex evolutionary process, detailed by statistical and macroevolutionary analyzes.

Living horses belong to the genus *Equus*, the only persisting branch of the horses' evolutionary tree. Molecular analysis supports this hypothesis (Vilstrup *et al.*, 2013). The current horse's diversity dwarfs compared to the more than 200 species defined in the fossil record. The ancestor of *Equus* lived in North America around 4.0–4.5 Ma before displacing into another continent. The ancestors of South American equids reached South America across Panamanian Isthmus (MacFadden, 1997). The descendants of the *Equus* genus in South America appeared approximately 0.99 Ma (MacFadden, 2013) and presented horse-like genetic trait affinities (Orlando *et al.*, 2009). The descendants of the *Hippidion* genus appeared around 2.5 Ma and involved two genetically very much alike generalists (*Hippidion principale* and *Hippidion saldiasi*) and one genetically distinctive high-altitude specialist (*Hippidion devillei*) (Prado & Alberdi, 1996; Orlando *et al.*, 2009).

There is no consensus about the origin of the three *Hippidion* species. Prado and Alberdi (1996) observed apparent affinities between *Hippidion* and *Pliohippus* in their cladistics analysis. This latter genus lived between 6 and 14.5 Ma in North America. According to them, *Hippidion* could have derived from the line that gave rise to modern Equidae until about 10 Ma, similar result proposed Barrón-Ortiz *et al.* (2019). These authors used the divergence time criterion, which states that species should be regarded as distinct genera if they diverged well before the Miocene–Pliocene boundary. Based on this criterion, they proposed the assignment of a new genus to "*Dinohippus*" *mexicanus*, and the synonymy of *Haringtonhippus* with *Equus*. They represent too much time before the entry of the hippidiformes in South America. In contrast, the partial sequences of ancient mitochondrial DNA suggest a relatively more recent derivation, whit *Hippidion* among modern equids. Weinstock *et al.* (2005) indicated that, unlike the models elaborated with the morphology, *Hippidion* was phylogenetically close to the horses *sensu stricto*, with clearly more recent onset than the date of around 10 Ma. Furthermore, their demonstration that the stilt-legged horses, often regarded as Old World migrants correlated with the Asses hemionus from Asia, affected an endemic line in North America. Orlando *et al.* (2009) noted that *Hippidion devillei* joins a paraphyletic ensemble based on *Hippidion principale* and *Hippidion saldiasi*. However, nuclear data remains to establish whether the latter represents two different morphospecies. Lately, Der Sarkissian *et al.* (2015) determined eight entire mitochondrial genomes of *Hippidion*. They indicated that the two sequenced morphospecies (*Hippidion saldiasi*, *Hippidion principale*) formed a monophyletic clade, original to current and extinct *Equus* lines.

BIOGEOGRAPHY

Gould and Eldredge (1977) postulated that climate change could contribute to cladogenetic speciation by isolating populations within the species' geographic range. However, it is not always clear the role of the climate in evolution. Several studies indicate that climate changes can represent a powerful mechanism to force speciation due to: introducing vicarious barriers as climatic zones change across the Earth's surface; can promote dispersal due to the search for the climatic space preferred by the different populations; can force isolation of small community by the above conditions, and can act as selective pressure when populations inhabit a new climatic space. For this reason, many authors consider it an essential motor in evolution (Janis, 1989, 1993, 1997; Janis & Wilhelm, 1993; Vrba, 1993, 1995; Janis *et al.*, 2000; Vrba & DeGusta, 2004; among others).

In North America, the climate varied from hot and humid to cold and dry from the Miocene to the Pliocene, with fluctuations. Savanna and grassland habitats increased during the Miocene due to the shallow effects of rain and cooling. Thus, geographic and climatic differences between regions formed various habitats that supported a diverse group of mixed-browsing, grazing, and foraging mammals (Hulbert & MacFadden, 1991). During the Early Miocene, tiny horses that inhabit more covered (leafy) environments begin to develop or diversify, exhibiting body size plasticity and tooth morphology alterations (MacFadden, 2005). At this time, the Equinae subfamily undergoes a significant radiation event. *Parahippus* (the last genus in which side toes were critical for mechanical support) marks the basis of the adaptive radiation of herbivores that lived contemporaneously with browsing forms (MacFadden, 1992). Most speciation events were via dispersal into new regions (Maguire & Stigall, 2008). This diversification took place in various stages and different geographic areas, from North America to the rest of the New and Old World. Classically, this radiation has been related to climate and environment as the evolution of grassland habitats in North America during this time (Matthew, 1912; Stirton, 1947; Shotwell, 1961; Webb, 1977, 1983; Stebbins, 1981; Janis, 1989; MacFadden & Cerling, 1994; Webb *et al.*, 1995; Stigall, 2013). This diversification would bring with it the development of the hypsodonty linked to the presence of abrasive grasses richer in silica or a more significant amount of dust in suspension as a consequence of high volcanic activity (Osborn, 1910; Matthew, 1926; Simpson, 1951; Janis, 1988; Wang *et al.*, 1994; MacFadden, 1997, 2000).

As grasslands spread throughout the Miocene and Pliocene in North America, the Equini tribe experienced significant adaptive radiation, achieving larger body sizes and increased skull and jawbones to accommodate the larger size of their premolars and molars. Around 13 Ma, during the Clarendonian, the trend towards colder and drier climates resulted in a mosaic of open deciduous forest and grasslands in the Great Plains region. The interval also saw a global increase in the biomass of plants using C4 photosynthesis, as indicated by changes in carbon isotope ratios of tooth enamel from fossil herbivores around the world (MacFadden *et al.*, 1996; Cerling *et al.*, 1997). The new extensive grasslands and steppes (deciduous trees, boreal forests, tundra, and desert biomes) replaced the savanna during the Pliocene and the Early and Middle Pleistocene. Plant communities were significantly affected by climatic changes linked to glacial cycles throughout the Late Pleistocene. During cold spells, continental ice sheets supplanted the boreal ecosystems, and tundra vegetation replaced forests in areas not covered by glaciers. Boreal communities supplanted temperate ones in mid-latitudes. On the contrary, the cold communities withdrew towards the north during the interglacial intervals. North America experienced increased aridity and decreased temperature throughout the last 10 Ma of the Cenozoic due to global changes, with a warm pulse around 3 Ma (Graham, 1999).

The emergence of the Panama Isthmus locked communication between the Atlantic and Pacific oceans and altered both water circulations, facilitating the Arctic polar ice cap installation. The cool Circum Antarctic Current was established (Pascual *et al.*, 1996). The Pliocene in South America is marked by the apogee of the Age of the Southern Plains (Ortiz Jaureguizar & Cladera, 2006). In northern South America, the Pliocene flora changed successively from tropical lowland to high-elevation vegetation due to the developing Andes. On the contrary, grasslands and steppes were dominant in southern South America. The most evident changes between Tertiary and Quaternary climatic conditions correlate to the environment's amplitude and frequency. Throughout the Pleistocene, glaciers' repeated advance and retreat produced coincident expansion and retraction of arid and humid climates. A savannah corridor developed along the eastern margin of the Andes, offering a corridor that connected the grasslands of Argentina and Colombia, continuing northward across the Panamanian land bridge to North America. Equally, when open areas withdrawal through interglacial periods of warm wet climates, rainforests increased and favored a second corridor to expand across eastern South America (Sánchez *et al.*, 2004).

The uplift of the Isthmus of Panama about 3.0 Ma favored the dispersion of horses into South America (Simpson, 1950, 1980; Patterson & Pascual, 1972; Webb, 1976, 1985, 1991; Morgan, 2002, 2005). The latest studies indicated that this exchange was complex and began before the Pleistocene, probably during the Miocene, but the main phase of the GABI took place around 2.7–1.8 Ma (Cione & Tonni 1995a, 1995b; Ortiz Jaureguizar, 1997, 2001; Scillato-Yané *et al.*, 2005; Woodburne *et al.*, 2006; Reguero *et al.*, 2007; Carlini *et al.*, 2008). Some authors considered that this bridge acted as a selective environmental filter (Webb, 1978; Simpson, 1980). Biogeographic data shows three fundamental habitats in the Panamanian bridge: mesic tropical forest, mesic savanna, and xeric scrub savanna (Webb, 1978). During the Pleistocene, the rise and fall of glaciers led to an increase and decrease in arid and humid biomes. While in times of cold climates, there was a decrease in subtropical and tropical biomes, leading to the rise and interconnection of open spaces.

The first record of the Equini tribe corresponds to the genus *Hippidion* in Esquina Blanca (Jujuy, Argentina): *Hippidion devillei* in sediments dated around 2.5 Ma (Prado *et al.*, 1998, 2000; Reguero *et al.*, 2007) and the first record of *Equus* is in Tarija, Bolivia (MacFadden & Azzaroli, 1987; MacFadden, 2013), were the evidence documents that *Equus* occurs from 15 superposed faunal horizons throughout the Tolomosa Formation. This biostratigraphic sequence is calibrated between 1.07 to <0.76 Ma, coincident with phase 3 of the "Great American Bioestratigraphical Event" (GABI, *sensu* Webb, 1976).

The amplitude and frequency of environmental changes during the Pleistocene in South America are related to the cyclical expansion and retreat of glaciers, leading to increased and reduced arid zones. This event gave rise in the Andes to a north-south corridor for animals and plants that connected the steppes and grasslands of southern Argentina with the grasslands of Colombia, continuing north through the Panamanian land bridge to southeastern North America. On the other hand, during interglacial periods of hot and humid climates, open areas decreased, and tropical forests expanded, representing a second corridor through eastern South America (Sánchez *et al.*, 2004). According to Prado and Alberdi (2014), gave rise to two possible dispersal routes, one through the Andes corridor (the smaller species *E. andium*, *E. insulatus*, *H. devillei*, and *H. saldiasi*) and the other by the route of the eastern plains (the larger forms, *E. neogeus*, and *H. principale*). Despite these species' wide dispersal and richness, horses disappeared from South America at the end of the Pleistocene (Prado *et al.*, 2011). In the Late Pleistocene of Chile there are few but significant data on the coexistence of *H. saldiasi* and *H. principale*. One explanation could be that *H. principale* has crossed the range through some valleys from the east, as was also proposed for *Notiomastodon*.

FEEDING ECOLOGY AND BODY MASS

Recently, carbon isotope analysis indicates that these horses had different dietary adaptations (Sánchez *et al.*, 2006; Prado *et al.*, 2011). Their high-crowned teeth traditionally suggested that horses ate abrasive grasses. However, the carbon isotopes in this region indicate that the horses were both mixed-grass eaters and more specialized C_3 grasses. Late Pleistocene horses show a wide range of $\delta^{13}C$ values ranging from closed forests to C_4 grasslands. This variability in their diet and extension in their occupied biome follows the habitat theory postulated by Vrba (1992), according to which North American generalists and open biome specialists experienced successful radiation throughout South America (Vrba, 1992; Moreno Bofarull *et al.*, 2008). In general, *E. insulatus* from Santa Elena (Ecuador) exhibit high $\delta^{13}C$ values indicative of an exclusive diet of C_4. High values of $\delta^{18}O_{CO3}$ in this horse are related to the ingestion of meteoric waters in a tropical environment. *E. neogeus* has a wide range of $\delta^{13}C$ values. The sample from Pampas has $\delta^{13}C$ values typical of open C_3 forests and grasslands. In contrast, samples from northeastern Argentina yielded $\delta^{13}C$ values from C_4 areas, with very few C_3-C_4 mixture samples. Surprisingly, $\delta^{18}O_{CO3}$ does not reflect this latitudinal variation, and the variability in oxygen isotope values is lower than that observed in $\delta^{13}C$. The entire sample of *E. insulatus* from Tarija has $\delta^{13}C$ values from a mixture of C_3-C_4. The high altitude of Tarija explained the low value of $\delta^{18}O_{CO3}$. *Equus andium* has $\delta^{13}C$ values indicative of a mixed C_3 to C_3-C_4. Recently, the stable isotope analyses on *E. andium* from several Late Pleistocene locations in the northwestern Chilean Patagonia indicated the presence of C_3 vegetation ranging from forestal to woodland areas (González-Guarda *et al.*, 2017). Low $\delta^{18}O_{CO3}$ values are also due to the effects of high highs. *Hippidion* shows significantly lower $\delta^{13}C$ values, indicating a more restricted diet to C_3 wooded forests or open areas. *Hippidion devillei* and *H. saldiasi* have lower $\delta^{18}O_{CO3}$ values than *H. principale*. This is due to high elevation effects in the case of *H. devillei* and high latitude effects *H. saldiasi* (52° S).

Latitude and altitude determine the distribution of vegetation throughout the world. C_4 plants repeatedly evolved from C_3 plants as an adaptation to low CO_2 levels, conditions of water stress, and high rates of insolation and high temperatures. Decreasing stomatal conductance can reduce transpiration and increase water use efficiency compared to C_3 vegetation (Edwards & Smith, 2010). Therefore C_4 plants are frequently found in hot and arid climates and they are more abundant at middle latitudes and low altitudes (Sage *et al.*, 1999). As expected, carbon values experience an increase in decreasing latitude. Sage *et al.* (1999) show that today C_4 grasses are absent in southern latitudes above 46° S. MacFadden *et al.* (1999) viewed the transition between C_4 and C_3 plants around 32°–35° S when considering the $\delta^{13}C$ values of Pleistocene *Equus*.

Specifically, *Hippidion devillei* from the Early Pleistocene fed on C_3 plants. *Hippidion principale* from the Middle Pleistocene fed on C_3 and C_3-C_4 plants mixed diet, while those from the Late Pleistocene fed on all C_3 plants. These data are concordant in part with Bolivia's lower and Middle Pleistocene (MacFadden & Shockey, 1997). These authors suggested that the Tarija horses fed to a greater extent on C_4 plants (*E. insulatus*) and other especially mixed plants (*H. principale* and *H. devillei*), which indicates they could have found their food resources in a wide range of pastures. This pattern suggests that equids from the Middle Pleistocene used different types of opportunistic feeding in the Pampean Region and may have adapted to very varied habitats. However, most of the Middle Pleistocene horses preferred mixed feeding.

In contrast, the Late Pleistocene populations tend to a more selective diet, restricting their habitat preference. In any case, different nutritional hypotheses have been postulated concerning the extinctions of mega mammals at the end of the Pleistocene and the theory of the more significant number of extinct taxa related to specialized diets. The preference of *H. principale* and *E. neogeus* for resource partitioning in the Pampean Region during the Late Pleistocene would confirm these hypotheses.

Body mass estimates built on regression equations between bone measurements and body masses across known modern specimens provide a way to combine body size data obtained from some skeletal dimensions. Alberdi *et al.* (1995), in their work on the study of the body mass of horses, observed a different pattern of chronological changes in body mass for each continent. There is a decreasing trend in body mass in Europe and Africa, while in North America, the general direction is the inverse, with body mass increasing over time. Finally, two different lineages show both trends as evident in South America. Within the *Hippidion* group, the medium-sized *H. devillei* produced two species of body mass: *H. saldiasi*, which has a similar body mass, and *H. principale*, which reaches a larger size (Figs. 3, 4). In the *Equus* group, the medium-sized *E. insulatus* gave rise to two groups of different sizes: *E. neogeus*, which maintains or increases their body mass, and the small *E. andium*. In general, one can make two observations: first, autopodial elements are better predictors of body mass than

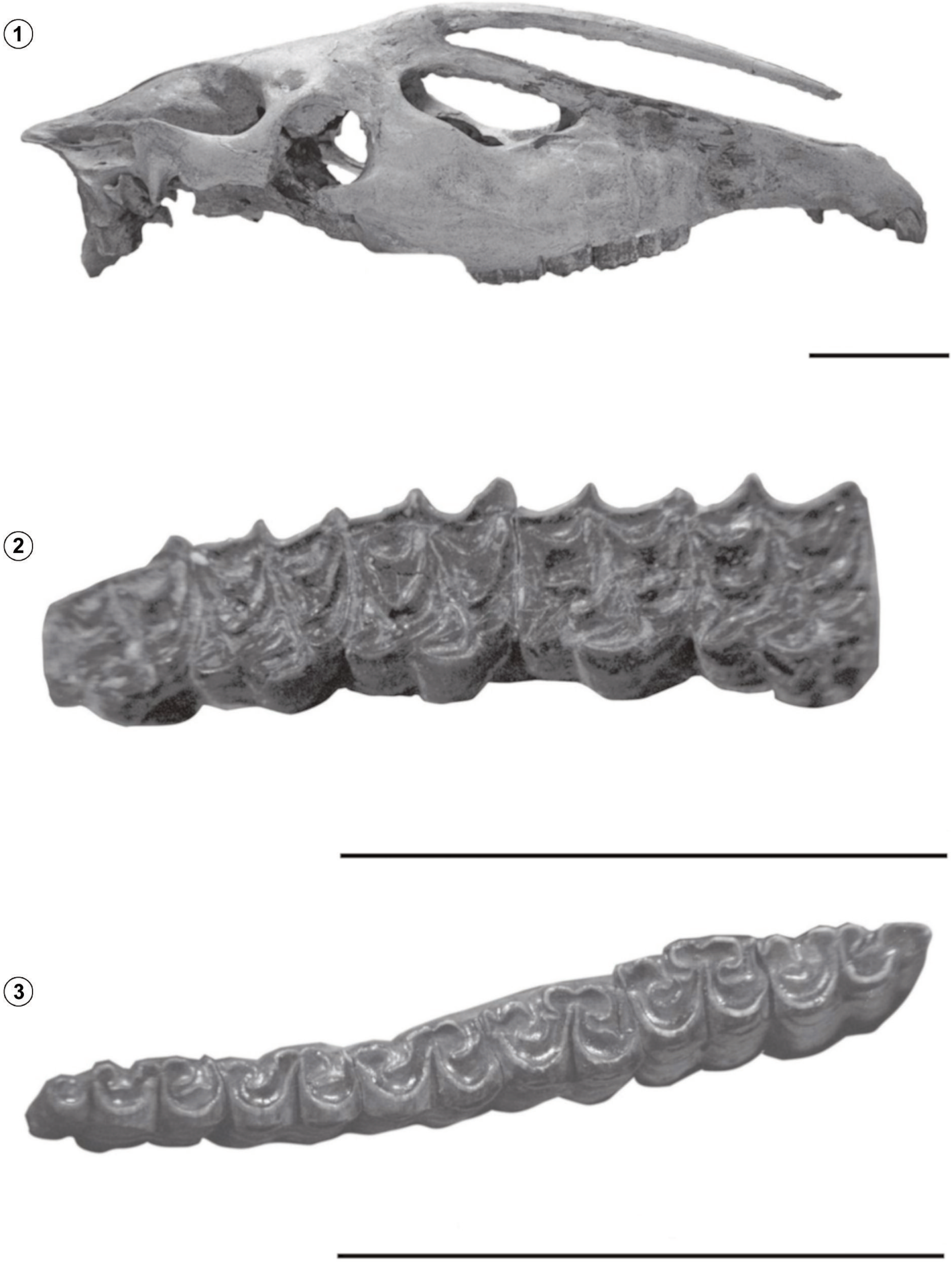

Figure 3. Representation of the ***Hippidion*** genus. From top to bottom: skull of ***Hippidion prinipale*** from Mar del Plata in right side view; P3-M3 right of ***Hippidion principale*** from Quequén Grande, in occlusal view; and p2-m3 right of ***Hippidion principale*** from Tarija, in occlusal view (Modified from Alberdi & Prado, 2004). Scale= 10 cm.

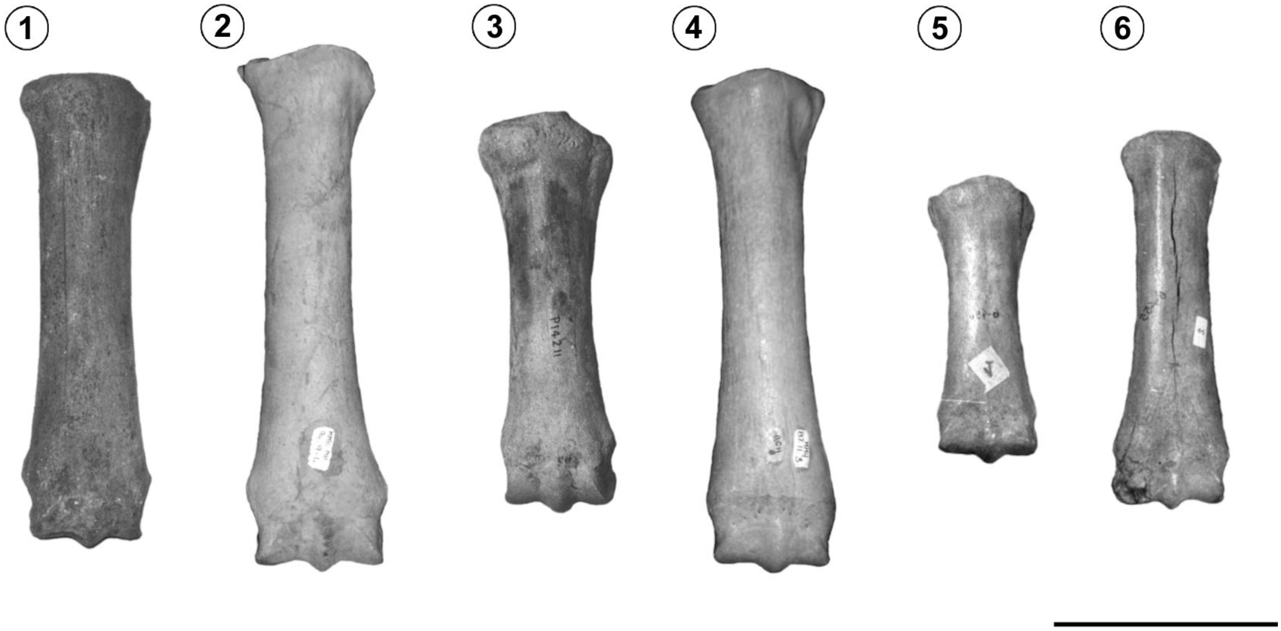

Figure 4. Different metapodials, MCIII and MTIII, of ***Hippidion*** species from South America. **1,** MCIII of ***Hippidion principale*** from Tarija; **2,** MTIII of ***Hippidion principale*** from Tarija; **3,** MCIII of ***Hippidion devillei*** from Tarija; **4,** MTIII of ***Hippidion devillei*** from Tarija; **5,** MCIII of ***Hippidion saldiasi*** from Última Esperanza; **6,** MTIII of ***Hippidion saldiasi*** from Última Esperanza (Modified from Prado & Alberdi, 2017). Scale= 10 cm.

cranial elements, and second, anteroposterior diameters of metapodials and the first phalanx are better predictors of body mass than lengths and widths (Figs. 5, 6). We might expect *a priori* that some skeletal dimensions were closely related to body mass as a logical consequence of the fact that the extremities usually transmitted bodyweight to the substrate (Hylander, 1985; Jungers, 1988). In addition, the highest prediction values of the maximum metacarpal and phalanx depths, such as opposite lengths and widths, can be expected since while the depths change in direct proportion to body mass, the sizes and widths show some variations. There is the same obstacle in comparing our results with other authors because they use different groups of perissodactyls (Janis, 1990; Scott, 1990) or different size ranges for existing *Equus* (MacFadden, 1986).

On all continents, environmental conditions and the type of substrates strongly influence the evolutionary history of Equini. Hot climates and environments with a significant forested component (for example, wooded savannas) and hard substrates correlated with the small body size species. In contrast, large species are related to cold climates, open vegetation (*e.g.*, steppes and grasslands), and soft substrates. Large body size could be associated with open environments primarily to aid the energy efficiency of locomotion (Peters & Wassenberg, 1983). These data for monodactyl equids suggested a correlation between global temperatures and the body sizes of the species. But if we consider the entire record of the Equidae family (56 million years), global temperatures seem to correlate with the taxonomic diversity of horses (Shoemaker & Clauset, 2014). These authors observed that the mechanism called "driving or directional diffusion model", in which the selective effects on the body size of the species vary independently of the state of occupation of the nearby niches, substantially explaining most of the changes observed in the evolution of the body mass of Equidae. These results suggest that increases in disparity are not necessarily driven by macroecological competition for niches, as is commonly assumed. Saarinen *et al.* (2016) indicated that the correlation of body size and vegetation openness is unclear and is likely to reflect the varying effects of population density, ecological adaptations, and environmental conditions on the body size of different species.

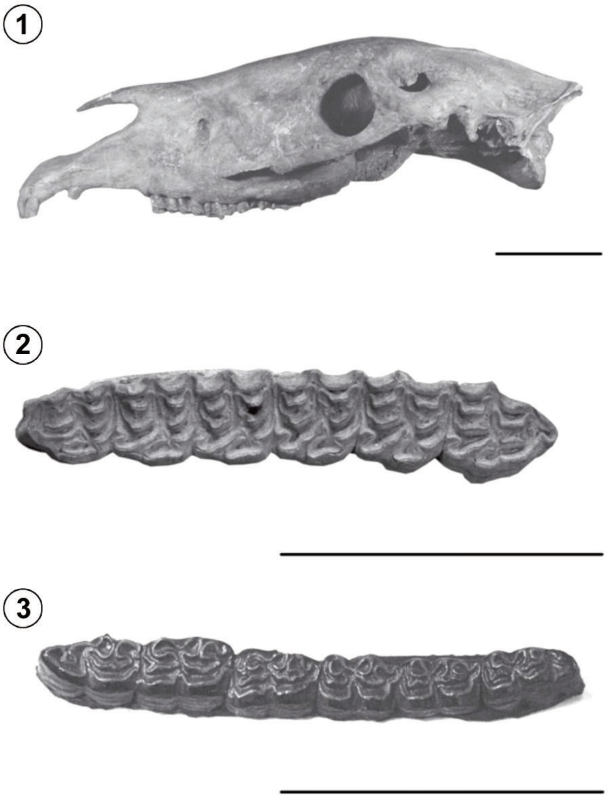

Figure 5. Representation of the ***Equus*** genus. From top to bottom: skull of ***Equus neogeus*** from Luján in left side view; P2-M3 right of ***Equus andium*** from the Chalán, Punín, in occlusal view; and p2-m3 left of ***Equus insulatus*** from Tarija, in occlusal view (Modified from Alberdi & Prado, 2004). Scale= 10 cm.

CONCLUSIONS

The six species of South American Equidae were recorded over much of the continent, from the Andes to the immense plains. However, two possible dispersal routes explain their distribution, one through the Andes corridor (*E. andium*, *E. insulatus*, *H. devillei*, and *H. saldiasi*) and the other by the route of the eastern plains (*E. neogeus* and *H. principale*).

The last record of horses in different regions in South America provides insights into potential causes of their extinction. The data mainly from Pampas and Patagonia regions is sufficiently robust to support the synergy hypothesis interaction among the last appearance records of horses, first appearance records of humans, and the Younger Dryas to Holocene climatic transition in South America. The stable isotopes and dental enamel microwear indicate that horses from South America had different dietary adaptations. This generalist-opportunist alimentary strategy facilitated the dispersal of this group in South America, where they occupied a wide range of environmental conditions from cold and arid to hot and humid habitats. But, the Late Pleistocene populations tend to a more selective diet, restricting their habitat preference. These specialized diets may be another reason to fall these species to extinction at the end of the Pleistocene. However, the evidence is still patchy and we need more information from other regions.

Figure 6. Different metapodials, MCIII and MTIII, of ***Equus*** species from South America. **1,** MCIII of ***Equus neogeus*** from Quequén Salado-Indio Rico; **2,** MTIII of ***Equus neogeus*** from Quequén Salado-Indio Rico; **3,** MCIII of ***Equus insulatus*** from Tarija; **4,** MTIII of ***Equus insulatus*** from Santa Elena; **5,** MCIII of ***Equus andium*** from Riobamba; **6,** MTIII of ***Equus andium*** from Riobamba (Modified from Prado & Alberdi, 2017). Scale= 10 cm.

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