



New records of *Hippidion principale* and *Equus neogeus* from Salado River (Buenos Aires Province, Argentina)

José L. Prado, María T. Alberdi, Ricardo Bonini, and Héctor Crispiani †

With 6 figures and 5 tables

Abstract: This study describes several remains referred to *Hippidion principale* and *Equus neogeus* from a classic locality in Buenos Aires Province: the Salado River. For taxonomic identification of the appendicular remains was performed a multivariate analysis that included the metacarpals and phalanges described and several remains recorded in various locations in Argentina and Brazil. For determination of the skull remains was made a comparative study with other skulls from different localities. These data increasing the record of Equidae in South America and provide new evidence about the chronological distribution. Radiometric data was obtained by the AMS method and dating the site between 12 to 14 KYBP. In general, bearing sediments are referable to the Lujanian Age and the Biozone of *Equus neogeus*.

Key words: Equidae, late Pleistocene, Buenos Aires Province, Argentina.

1. Introduction

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. The most recent papers of Equidae in South America (ALBERDI 1987; ALBERDI & PRADO 1992, 1993, 2004; PRADO et al. 1987, 1998, 2000, 2005, 2013a, b; ALBERDI et al. 1989, 2001a, b, 2003; PRADO & ALBERDI 1994, 1996, 2012; among others) distinguish two genera: *Equus* and *Hippidion*. Each genus has specific dental morphology, with a clear intraspecific variability. *Hippidion* has a more primitive morphology than *Equus*, and its body structure is most robust (PRADO 1984; ALBERDI 1987; ALBERDI et al. 1986, 1987; PRADO & ALBERDI 1994, 2014, 2016; DER SARKISSIAN et al. 2015, among others). The *Hippidion* genus was defined by OWEN (1869) based on a molar from the Lagoa Santa (Brazil) and figured by LUND (1846). ALBERDI & PRADO (1993) and PRADO & ALBERDI (1996) recognized this genus as endemic from

South America, where it is recorded from the Pliocene to the late Pleistocene mainly in Argentina, Bolivia, Brazil, Chile, Peru, and Uruguay. ALBERDI & PRADO (1993) reviewed this group and recognized three species: *Hippidion principale* (LUND), *Hippidion devillei* (GERVAIS), and *Hippidion saldiassi* (ROTH).

The earliest appears of *Equus* in South America record corresponds to the middle Pleistocene of Tarija (Bolivia), dated by MACFADDEN et al. (1983) and MACFADDEN (2013) around 1.0–0.8 Ma. Many articles have been published to arrange the knowledge of the *Equus* species in South America. 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.

The *Amerhippus* subgenus was created by HOFFSTETTER (1950) to include all different species of *Equus* genus from South America. Recently, PRADO & ALBERDI (2017) questioned the use of subgenus *Amerhippus*. The new molecular data increases the known phenotypic

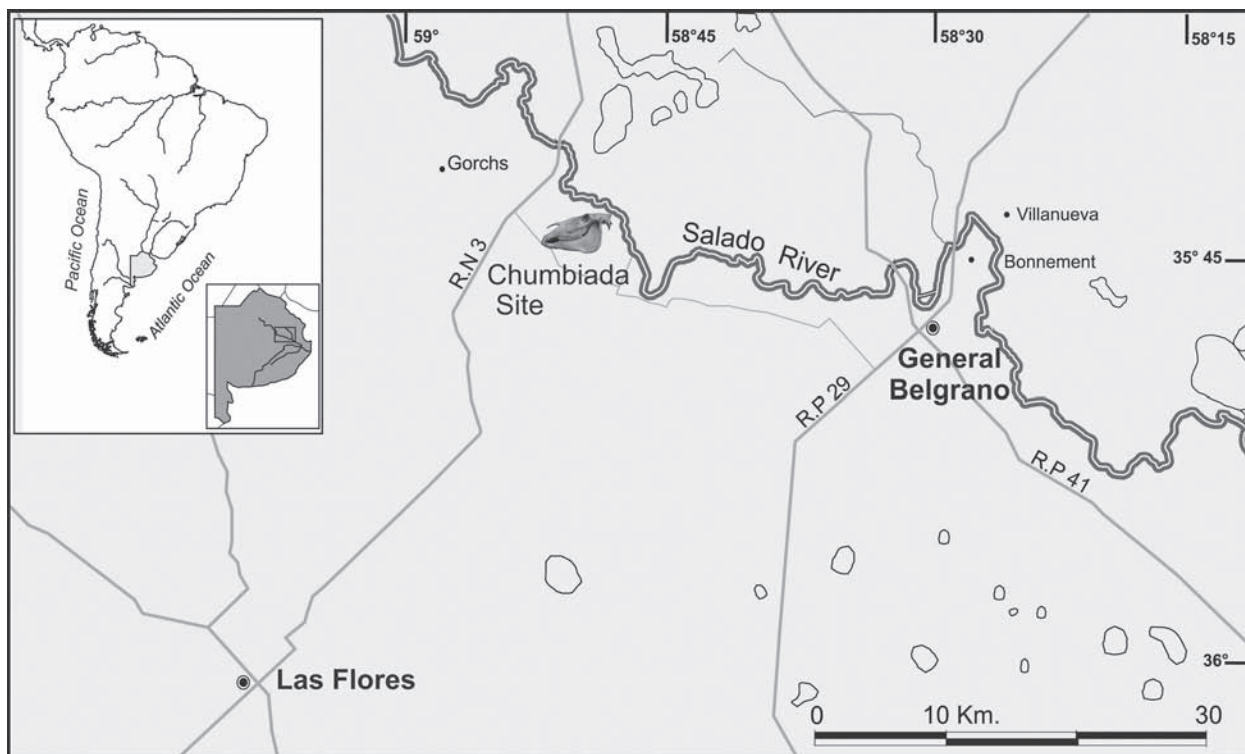


Fig. 1. Location map with sampling site.

plasticity of horses and consequently cast doubt on the taxonomic validity of the subgenus *Amerhippus* (ORLANDO et al. 2008).

The new remains of horse analyzed here come from the fossiliferous locality called La Chumbiada, General Belgrano town, in the Salado River near the city of Las Flores in the Buenos Aires Province (Fig. 1). Dr. CRISPIANI and OTEGUI recorded the fossils. These specimens constitute a new record of horses in South America that complete the description of these species. The aim of this paper is to present a detailed description of this material, its precise taxonomic status, and stratigraphic location. In addition, through the morphological and biometric analysis of the remains described, the paleoenvironmental adaptations of these findings are analyzed.

2. Stratigraphical and chronological context

Fossils equids described in this contribution came from several points along Salado River, close to La Chumbiada locality ($35^{\circ}43'34.39''$ S, $58^{\circ}46'33.56''$ W). In

recent years, different authors proposed several geological schemes (FIDALGO et al. 1973; DILLON & RABASSA 1985; DANGAVS & BLASI 2002; DANGAVS 2009; DANGAVS & REYNALDI 2008; Fig. 2). FIDALGO described for the lower sector of the Salado River basin, the Lujan Formation (upper Pleistocene-Holocene in age) composed by two members: Guerrero, of the fluvial origin, and Río Salado, lacustrine (FIDALGO et al. 1975, 1991). In addition, this author describes the edaphostratigraphic units Puesto Callejón Viejo and Puesto Berrondo, developed at the top of Guerrero and Río Salado members, respectively; and crowned this sequence, the current alluvial deposits. DILLON & RABASSA (1985) proposed a new stratigraphic unit from the basal deposits of the Guerrero Member, which called La Chumbiada Member (late Pleistocene in age). In this way, the Lujan Formation recognized on the banks of Salado River, would be comprised since base to top by La Chumbiada, Guerrero and Río Salado members. Moreover recently, new stratigraphic, geomorphological, chronological and paleontological studies reveal lithological and temporal differences with respect to the original descriptions (FUCKS et al. 2007, 2012; MARI et al. 2013;

	Fidalgo et al. (1973)		Dillon & Rabassa (1985)		Dangavs (2009)		Fucks et al. (2015)		Age (Ka)		
Lithostratigraphic units	modern alluvium		Luján Fm.	Río Salado Mb.	Alluvium		Luján Fm.	Puente Las Gaviotas Mb. Frig. Belgrano Soil La Pelada Soil Gorch Mb.	Holocene		
	Luján Fm.	La Pelada Soil			Río Salado Mb.	Río Salado Mb.				Luján Fm.	La Chumbiada Mb.
		Río Salado Mb.			Guerrero Mb.	Lobos Mb.					
		Puesto Callejón Viejo Soil				La Chumbiada Mb.			La Chumbiada Mb.		
Guerrero Mb.						11.7					

Fig. 2. Stratigraphic schemes of the study area (modified from DANGAVS & REYNALDI 2008).

PRADO et al. 2013b; SCANFERLA et al. 2013; PISANO & FUCKS 2016). Since this new data, FUCKS et al. (2015) propose a new stratigraphic scheme to the sedimentary sequences outcropping along of the lower sector of the Salado River basin. While it is a new proposal, the researchers keep the name of the formational unit (i.e. Lujan Formation) given the tradition of this name for fluvial deposits of the region; as well as the lower subdivision. In La Chumbiada we can observe a typical sequence described by FUCKS et al. (2015). In the base, we can recognize La Chumbiada Member, which lies unconformably on the Pampean Fm. (*sensu* GONZÁLEZ BONORINO 1965). This unit is composed by brown to pinkish gravel muds to sandy muds, homogeneous to very stratified, compact but friable (FUCKS et al. 2015), and their origin is related to floodplains deposits. SCANFERLA et al. (2013) recognized a muddy gray and black deposit 1.5 m thick is inserted in the La Chumbiada Member and associated with a paleo-lake, in which found remains of fossils mammals like *Hippidion principale*, *Smilodon populator*, *Doedicurus clavicaudatus*, and *Megatherium americanum*, among others. This level was dated between 12 to 14 KYBP (Table 1). Also, are recognized the overlying deposits to La Chumbiada Member that were reconsidered by FUCKS et al. (2015) and PISANO & FUCKS (2016). This authors recognized the Gorch Member from the grayish sandy mud deposits of the basal part (which could correspond to part of Guerrero Member *sensu* FIDALGO et al. 1973), to gray to pale yellow sands mud slightly gravely to slightly gravely sands grayish, in the upper

part (it would correspond to the Río Salado Member). In addition, a large amount of pulverulent calcium carbonate and gypsum, which can also appear as small rosettes are present. The age of this member is bounded by the approximately 11.6 to 5.6 KYBP. At the top of Lujan Formation, FUCKS et al. (2015) and PISANO & FUCKS (2016) recognized the Puente las Gaviotas Member, which is represented by grayish to brownish sands, dated between approximately 3 KYBP to 600 YBP.

The profile presented in Fig. 3 illustrates the sedimentary succession exposed on the right bank of the Salado River near the La Chumbiada site. It is represented by a succession of approximately seven meters of thickness, sediments of mainly fluvial-lacustrine origin. The level A it is represented by a dark gray edaphised level 0.3 to 0.5 m thick and corresponds to the current soil. Level B it is characterized by light grayish siltstones, with a slight horizontal lamination. In this level, in some cases, freshwater mollusks are recognized. Level C it is composed by light grayish to yellowish and, in some case, pale green-yellow sands to silty sands deposits. These deposits generally are massive in which canaliculus; bioturbations and carbonate concretions are evident. This level should be assigned to the Gorch Member (*sensu* FUCKS et al. 2015). Level D it constitutes the base to the relieved sequence. This is composed by brown, reddish to gray pinkish sandy siltstones sediments with canaliculus and in some cases carbonate concretions. This unit could be associated with the La Chumbiada Member.

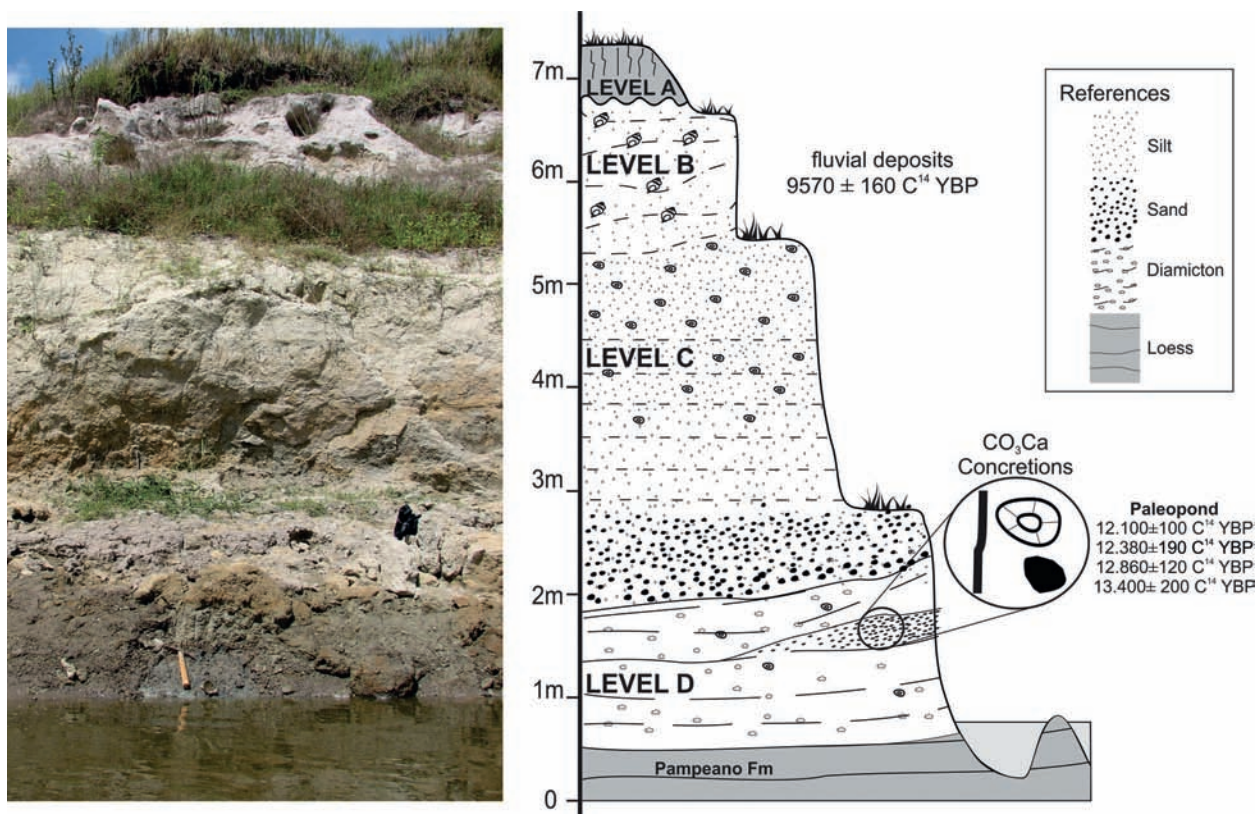


Fig. 3. Stratigraphic section at the studied locality, near to the “La Chumbiada” location, Salado River, Buenos Aires.

3. Material and methods

The fossil remains belong to the collection of Dr. HÉCTOR G. CRISPIANI, which are stored at the paleontological collection of the Museum of the city of Las Flores and the Museum of the city of Rauch kindly ceded by Dr. E. OTEGUI (cited below).

For morphometric and comparative analysis we used data on South American horses described by PRADO & ALBERDI (1994, 2008, 2012), ALBERDI & FRASSINETTI (2000), ALBERDI et al. (2003), ALBERDI & PRADO (2004), PRADO et al. (2005), and RINCÓN et al. (2006). For determination of the skull remains was made a comparative study with other skulls from different localities. The nomenclature and measurements are based on the recommendations and rules elaborated by the “*Hipparion* Conference” (EISENMANN et al. 1988). All dimensions are in millimeters.

For comparative analysis new remains are incorpora-

ted into the large database already used in previous works (PRADO & ALBERDI 2016). Specifically, the remains of the metapodials and phalanges from different localities (MCIII, MTIII, 1PHIII and 2PHIII) were analyzed through principal component analysis (PCA) in order to examine the relationships between the different groups of equids known in South America. The PCA of *Hippidion* skeletal measurements are based on 74 1PHIII and 67 2PHIII and the PCA of *Equus* skeletal measurements are based on 65 MCIII, 75 MTIII, 149 1PHIII and 101 2PHIII.

To explore which group of these new data are associated we used the discriminant analysis (AD) that allowed us to know the affinity of the new remains with one of the known groups. In this analysis, we included all the variables together leaving the group under study in order to observe with which group of those already known have a greater relationship and the degree of it. The statistical package SPSS 15.0 was used for these analyzes.

Fig. 4. Principal Component Analysis (PCA) of MCIII, MTIII, 1PHIII and 2PHIII of *Equus* and 1PHIII and 2PHIII of *Hippidion*.

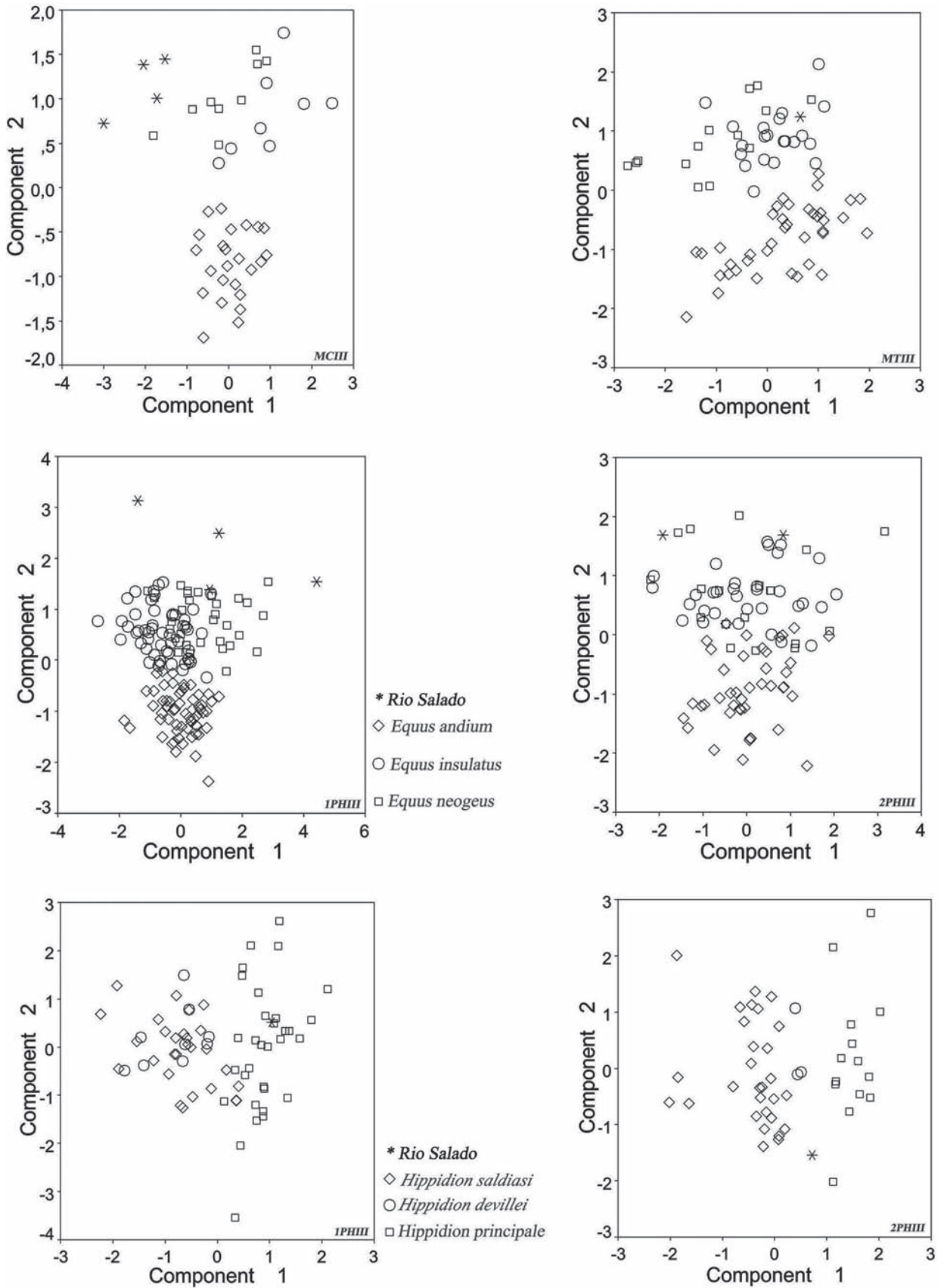


Fig. 4.

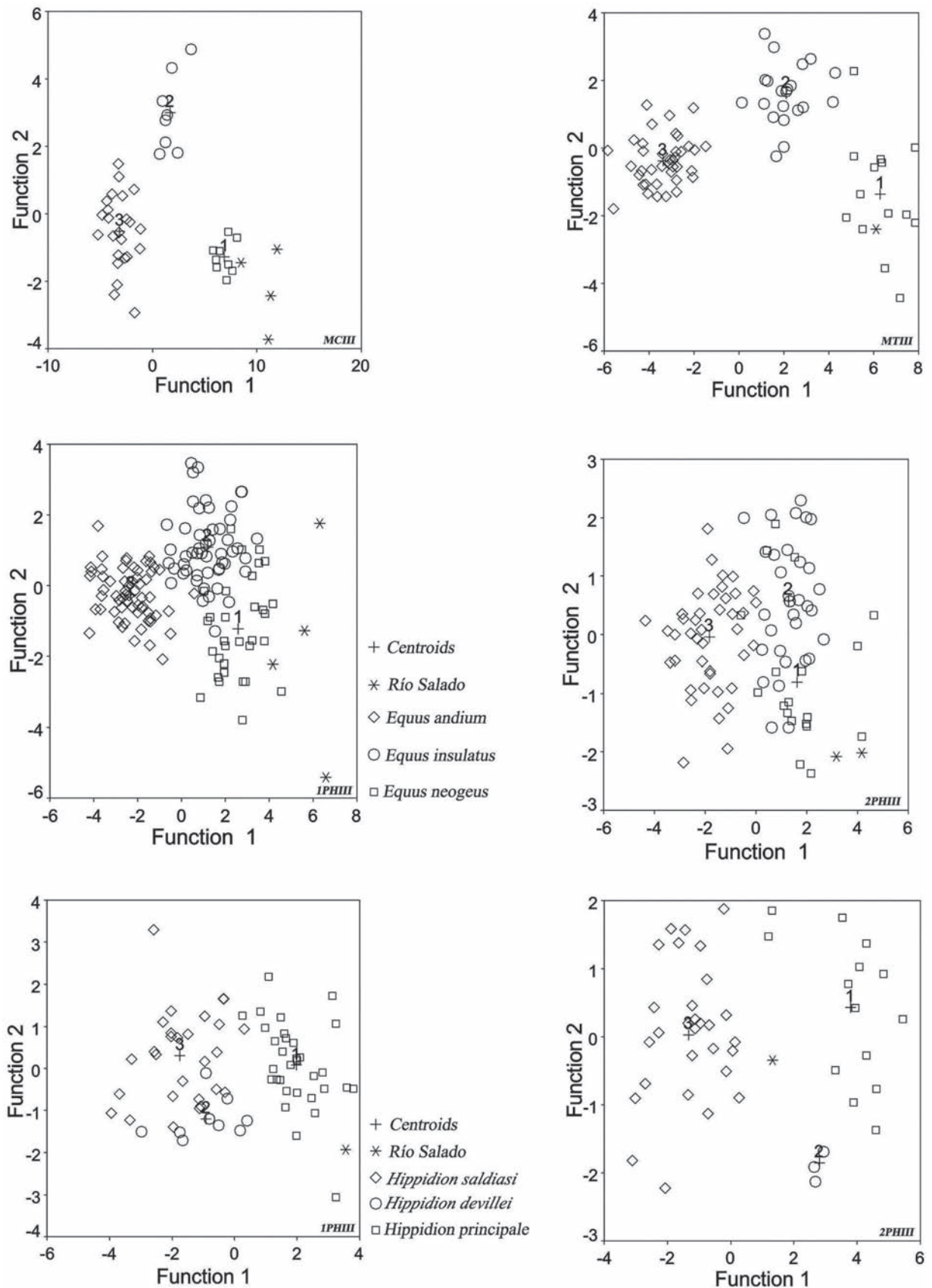


Fig. 5. Discriminant Analysis (DA) of MCI, MTIII, 1PH and 2PH of *Equus* and 1PH and 2PH of *Hippidion*.

4. Results

The PCA distinguished two main groups, one small in size and another large in size, between them an intermediate size overlapping in different degree. In the PCA of 1PHIII the explanation of the cumulative variance of the first three components reaches 87.08% and that of the 2PHIII is 96.78%. In Fig. 4 we see how both elements are distributed between rather large, although 2PHIII is also close to those of intermediate size. The characters that most influence the first three components are indicated in Table 2. In the case of the PCA of the MCIII, the cumulative variance of the first three components reaches a percentage of 89.59%; in the case of the MTIII, the cumulative variance reaches 89.97%; in the 1PHIII, the cumulative variance reaches 95.38%; and in the 2PHIII the cumulative variance reaches 96.23%. In Figure 4 we see how all these elements are distributed among the largest known shapes. The characters that most influence the first three components are indicated in Table 2. The DA analyses based on the PCA groups can provide a correct identification and its significance degree. Results of DA indicate that among the analyzed specimens of MCIII the four specimens from Salado River were correctly identified (100%) into the *Equus neogeus* group (Table 5). In case of MTIII (75) were correctly identified in 100% of cases originally classified (one specimen, Table 5). In case of 1PHIII and 2PHIII were correctly identified in 100% of cases originally classified (4 and 2 specimens respectively). In the case of the genus *Hippidion* the remains are even smaller since we only have one 1PHIII and one 2PHIII. The results of the discriminant analysis of the 1PHIII indicate that this specimen is clearly included among the remains of *Hippidion principale* already known with a correct previous classification of 89% of the cases (Fig. 5). The 2PHIII is grouped with *Hippidion devillei* but this element is not significant because they are very similar and do not clearly discriminate the groups.

5. Systematic paleontology

Order Perissodactyla OWEN, 1848

Family Equidae GRAY, 1821

Subfamily Equinae GRAY, 1821

Tribe Equini GRAY, 1821

Subtribe Plihippina PRADO & ALBERDI, 1996

Equus neogeus LUND, 1840

Synonymy: See PRADO & ALBERDI (2017).

Holotype: Right metacarpal III, number 866, stored in Zoologisk Museum, PETER W. LUND Collection. Copenhagen, Denmark.

Geographic distribution: Main remains came from the Pampean Region, Argentina; others from Lagoa Santa (LUND 1840), Corumba (CUNHA 1981), Sao Raimundo Nonato, Piaui (GUÉRIN 1991), Chique-Chique and Aguas do Araxa (PAULA COUTO 1979), and Cota dos Ossos (ALBERDI et al. 2003) in Brazil; and Arapey Grande creek and Sopas Creek in the Sopas Formation, Uruguay; Cerro Gordo (PORTA 1960) and Tibitó (CORREAL URREGO 1981), Colombia.

Stratigraphic distribution: Upper Pleistocene of Buenos Aires province, Argentina, Brazil, Colombia, and Uruguay. PORTA (1960) correlated Cerro Gordo (Colombia) with the Punian in Ecuador (sensu HOFFSTETTER 1952).

Type horizon: Lujanian Land Mammal Age.

Studied material: Fragment of left maxilla with P2-M3 and part of the area of the vomer and part of the distal area of the skull that could correspond to the same individual (no. 5): two jaws quite complete, one is missing only the left p3 (no. 4) and the other is missing the left ascending branch (no. 7); and a fragment of the right jaw with p3-m3 (no. 5). The postcranial skeleton has a right humerus, a right radius-ulna and several carpal bones (1 right magnum, 1 right lunatum, 1 right scaphoid, 1 pyramidal or triquetum, 1 proximal sesamoid, 4 metacarpals, 2 right and 2 left). Three right calcaneus; one left metatarsal; four first phalanges, two second phalanges and three third phalanges of the central finger, only one complete phalanx, all numbered than 4 (Fig. 6).

Description: Two fragments of a skull (no. 5) possibly of the same individual that could reach a length between the occipital part and the P2 around 405 mm. One retains the upper series, P2-M3 left, with the almost complete part of the palate; and the other part corresponds to the occipital area with the back part of the vomer and the part of the left orbit almost complete. The vomer begins at the distal level of the protocone of M2. The triangular protocone except in P2, which is more oval, with a marked caballin fold in the premolars while in the molars, are being lost. The hypocone open and more or less oval except in M3 that is isolated into the lopho. The wide styles in the premolars with a very marked fold in the mesostyle, while in the molars are thinner, narrow and without groove (dimensions of the molars in Table 3).

The jaw (no. 7) is quite complete and preserves the right and left series with p2-m3. Lacks the left ascending branch or ramus and also conserves the complete symphysis with the incisors, i1-i3 right and left in a straight line, and the canines are rather strong. The morphology is typical of *Equus neogeus*: with the double knot metaconid-metastylid elongated and the linguaflexid very open, protoconid and hypoconid with the straight border; the ectoflexid without crossing the isthmus in premolars and practically in contact with the linguaflexid in molars. Protostylid is not observed and it seems



Fig. 6.

to have an advanced wear although it still conserves the well-marked occlusal drawing, except in the m1 that begin to be lost (Table 3).

The dimensions of the jaw (no. 7) are the following: the total length of the jaw from the point between the alveoli of the i1 to the back of the condyle is 421.5 mm; the length of the muzzle is 112 mm; the length of the right premolar series p2-p4 is 84 mm, the molar series m1-m3 is 77.5 mm, and the total length p2-m3 is 161.5 mm. The same data of the left series are 84 / 77 / 160.5 mm, respectively; the straight distance between the back of the alveole of m3 and the posterior edge of the ascending ramus is 127 mm; the distance between the posterior alveolar borders of the i3 is 67 mm; the height of the jaw at the condyle is 221.5 mm; the height of the right ascending ramus is 210 mm; the height of the mandible posterior to m3 is 116 mm; the height of the jaw between p4 and m1 is 77 mm; the height of the jaw in front of p2 is 65.5 mm; length of the symphysis is 89 mm; the minimal breadth of the symphysis is 38 mm.

The other mandible (no. 4) is similar to the previous one, it only differs in that it has the two ascending ramus completes and lacks the left p3, even the symphysis with the previous series (i1-i3 right and left totally straight) and the canines rather strong. In addition, we have a younger jaw fragment, without symphysis neither ascending ramus. Teeth p3-m3 with the figures all well formed and differentiated by the presence on p3 and p4 of a strong pli caballinid in the ectoflexid that does not cross the isthmus; while in molars, m1-m3, it crosses it and is practically in contact with the lingua flexid in m2 and m3 (no. 5). The measurements of the premolars and molars are in Table 3. The remains of the appendicular skeleton present the typical characters of *Equus neogeus*, it seems that they could all correspond to the same individual (all marked with No. 4; see Fig. 6).

Genus *Hippidion* OWEN, 1869
Hippidion principale (LUND, 1846)

Synonyms: See PRADO & ALBERDI (2017).

Holotype: Upper right M2 from the older breccia of the Lagoa Santa cave (Brazil), figured by LUND (1846, pl. 49, fig. 1). PETER W. LUND Collection (ZMK).

Type locality: Lagoa Santa, Minas Gerais State, Brazil.

Geographic distribution: South America, from several localities of the Buenos Aires and Santa Fé provinces (Argentina), Tarija (Bolivia), Artigas Department (Uruguay) and Toca dos Ossos and Lagoa Santa (Brazil).

Stratigraphic distribution: Upper Pleistocene, Lujanian Land Mammal Age.

Studied material: One young mandible (No. 6) that retains the series p2-m3 right and p2-m1 left (i3 and canines come to the surface and the right m3 little worn teeth); one fragment of jaw that conserves only the i2-i3 in the symphysis and the p2 very worn; and one first and a second phalanges of the third finger (the two latter without number).

Description: The jaw No. 6 corresponds to a young animal. This jaw keeps the symphysis complete, narrow and long, the i3 and the canines in germ and lacks the ascending ramus. The right jaw has p2-m3 while the left only p2-m1. Only the following dimensions can be taken: the muzzle length is approximately 150 mm; on the right row: premolar length p2-p4 is 101.5 mm, molar length m1-m3 is 103.6 mm, and total length p2-m3 is 208 mm, in the left series only the premolar length is 104.7 mm; the muzzle breadth between the posterior alveolar borders of the i3 is 62.1 mm; the height of the jaw between p4 and m1 is approximately 90 mm; the height of the jaw in front of p2 is around 67 mm; length of the symphysis is approximately 115 mm; the minimal breadth of the symphysis is 40 mm. The fragment of the right jaw with part of the symphysis with the i2 and i3 and the p2 very worn, possibly correspond to a rather old animal (without No.); and one 1PHIII and 2PHIII from Rauch Museum (without No.) (Fig. 6.6, 6.11). The measurements of the premolar and molar are in Table 3 and bones in Table 4.

6. Discussion

The morphological features of dental and the appendicular skeleton of the remains from Salado River are diagnostic of *Equus neogeus*. We observe in the PCA how both MCIII and MTIII are grouped with larger size remains. The multivariate analyzes of PCA and DA permitted an assignation to the largest and most slender horse in South America, widely distributed in

Fig. 6. Remains of *Equus neogeus* and *Hippidion principale* from Salado River. **1** – Fragment of *Equus neogeus* skull with P2-M3 right (no. 5); **2** – mandible of *Equus neogeus* almost complete with p2-m3 left and right and symphysis (no. 7); **3** – mandible of *Hippidion principale* with p2-m3 right and p2-m1 left and symphysis (no. 6); **4** – mandible of *Equus neogeus* with p2-m3 right and left (in the latter was missing p3; no. 4); **5** – a fragment of hemimandible of *Equus neogeus* with p3-m3 right (no. 5); **6** – a fragment of symphysis with i2 and i3 and jaw with p2 right of *Hippidion principale* (without no.); **7** – MCIII right of *Equus neogeus* (No. 4); **8** – MTIII left of *Equus neogeus* (Rauch Museum, without no.); **9** – two astragali right of *Equus neogeus* (No. 4); **10** – two 1PHIII of *Equus neogeus* (no. 4); **11** – 1PHIII and 2PHIII of *Hippidion principale* (Rauch Museum, without no.). Scales in centimeters.

Brazil, Uruguay, and Argentina: *Equus neogeus*. The PCA analysis on our data in both autopodial remains yielded positive value for the coefficients of component one, indicating that this component described variation in size among the groups. The characters that weigh more in this component permit a good identification of the groups with minor overlapping between them (Fig. 4; Table 2). Which is one more indicator of how the adaptation of this group of animals to the environment is reflected in the distal part of the extremities and fundamentally in the metapodials. In the case of the phalanges there is an overlap due to the fact that both phalanges, anterior and posterior of the same animal, present differences in size and are included in a single analysis (Fig. 5). In the case of DA, the remains of Salado River are grouped directly with the largest species. All this allows us to conclude that the remains of *Equus* horses from Salado River correspond to *Equus neogeus*. In the case of the remains of *Hippidion* from the Salado River, the PCA and DA analyzes of the 1PHIII indicate that it corresponds to *Hippidion principale*. Recently MACHADO et al. (2017) questioned the use of proportions of the bones of the autopodia for distinguishing among different horse species in South America. We believe that this methodology is complementary to studies of traditional morphology and has proven to be a valuable tool in the study of several equid groups (DIVE & EISENMANN 1991; FORSTEN 1998). Several proxies utilized for the study of late Pleistocene paleoclimate indicated arid environmental conditions in the Pampean region, associated with more continental conditions and environments related to a lower sea level (TONNI et al. 1999; QUATTROCCHIO et al. 2008; TONELLO & PRIETO 2010). Nevertheless, SCANFERLA et al. (2013) suggest that the predominance of fluvial and fluvio-lacustrine deposits recognized in Salado basin indicates that around 14 KYBP more humid conditions prevailed than previously suggested. *Hippidion principale* and *Equus neogeus* were found in Salado River in association with other large mammals such as saber-toothed cat (*Smilodon populator*), the giant ground sloth (*Megatherium americanum*), and a large glyptodont (*Doedicurus clavicaudatus*). SCANFERLA et al. (2013) suggest that this faunal association, composed basically of taxa adapted to cold and arid environment present during the late Pleistocene, is compatible with a glacial period, involving the last glacial stage, which also includes the last glacial maximum.

From a biostratigraphy point of view, this faunal association was referred to the Lujanian Age (c. 130–13 KYBP; ALBERDI et al. 2003; CIONE & TONNI 2005;

ZURITA et al. 2005). Stratigraphic unit, La Chumbiada and Guerrero members of the Lujan Formation, as a whole represent the Lujanian, which is biostratigraphically based on the *Equus neogeus* biozone (CIONE et al. 2009). More recently, TOLEDO (2011) reinterpreted the “Piso Lujanense” based on a sequence stratigraphy analysis and AMS, OSL, and ESR dating in the Lujan section. This author proposed that the Pleistocene Pampean valley fill spans from OIS 4 to OIS 2 with sequence boundaries at 75, 55, 30, 17 and 13 KYBP. Hence, this association is consistent with a glacial period, possibly involving the last glacial stage, which also includes the last glacial maximum (c. 18 KYBP).

Recent studies using carbon isotope analyses reveal that these horses had different food adaptations (SÁNCHEZ et al. 2006; PRADO et al. 2011). Due to their high crowned teeth, it has traditionally been thought that horses fed on abrasive grasses. However, carbon isotopic data from the Pampean Region indicate that these horses ranged from mixed feeders to more specialized C₃ grazers. Specimens of *Hippidion principale* from the latest Pleistocene showed a more restricted diet, feeding in primarily wooded C₃ grassland, in comparison to *Equus neogeus* that showed a wider plasticity on its dietary preferences. *Equus neogeus* has a wide range of δ¹³C values. Sample from Pampas has δ¹³C values typical of woodland and open C₃ grasslands, whereas the samples from northeast of Argentina yielded δ¹³C values of C₄ areas, with very few samples falling in a mixed C₃–C₄ environment.

7. Remarks and conclusions

Although the horse remains from Salado River are scarce, they are enough distinctive in morphology and size to be assigned unequivocally to *Equus neogeus* and *Hippidion principale*.

Equus neogeus is the largest and most slender species of the known South American horses (PRADO & ALBERDI 2017), and appears to have predominated at middle and lower latitudes in eastern South America (Argentina, Uruguay, and Brazil). This species occupied savannas or xerophytic grasslands, and consequently would have been better adapted to open and arid landscapes. *Hippidion* were equids characterized by a retracted nasal notch, which has been interpreted as an adaptation to the presence of a proboscis and limbs with robust metapodials. Likewise, *Hippidion principale*, appears to have predominated at middle and lower latitudes in eastern South America. This species

lived in open habitats under a cold and wet climate (ALBERDI & PRADO 1992, 1993; PRADO & ALBERDI 2016, 2017).

Acknowledgements

This paper is dedicated to the memory of HÉCTOR CRISPIANI, for his passion for the fossils and the paleontology, his selflessness will always be remembered. The authors wish to express many thanks to the Las Flores and Rauch Museum, for to make the studied of the material easily. We thank the reviewers (L. AVILLA and other anonymous) for their useful and valuable comments and suggestions which contributed to improve the manuscript. This work has been made possible thanks to Research Project ANPCYT PICT 2015-01512 to JLP and PICT 2015-0724 to RB; DGICYT CGL2010-19116/BOS and CGL2016-79334-P from Spain to MTA; and Grant of the National University of Central Argentina (UNICEN) to JLP and RB. The funders had no role in study design, data collection and decision to publish, or preparation of the manuscript.

References

- ALBERDI, M.T. (1987): La Familia Equidae, GRAY, 1821 (Perissodactyla, Mammalia) en el Pleistoceno de Sudamérica. – IV Congreso Latinoamericano de Paleontología, Santa Cruz de la Sierra, Bolivia, **1**: 484-499.
- ALBERDI, M.T., CARTELLE, C. & PRADO, J.L. (2003): El registro Pleistoceno de *Equus (Amerhippus)* e *Hippidion* (Mammalia, Perissodactyla) de Brasil. Consideraciones paleoecológicas y biogeográficas. – *Ameghiniana*, **40**: 173-196.
- ALBERDI, M.T., FERNÁNDEZ, J., MENEGAZ, A.N. & PRADO, J.L. (1986): *Hippidion* OWEN 1869 (Mammalia, Perissodactyla) en sedimentos del Pleistoceno tardío de la localidad Barro Negro (Jujuy, Argentina). – *Estudios Geológicos*, **42**: 487-493.
- ALBERDI, M.T. & FRASSINETTI, D. (2000): Presencia de *Hippidion* y *Equus (Amerhippus)* (Mammalia, Perissodactyla) y su distribución en el Pleistoceno Superior de Chile. – *Estudios Geológicos*, **56**: 279-290.
- ALBERDI, M.T., MENEGAZ, A.N. & PRADO, J.L. (1987): Formas terminales de *Hippidion* (Mammalia, Perissodactyla) de los yacimientos del Pleistoceno Tardío-Holoceno de la Patagonia (Argentina y Chile). – *Estudios Geológicos*, **43**: 107-115.
- ALBERDI, M.T., MENEGAZ, A.N., PRADO, J.L. & TONNI, E.P. (1989): La Fauna Local de Quequén Salado-Indio Rico (Pleistoceno Tardío) de la provincia de Buenos Aires, Argentina. Aspectos Paleoambientales y Biostratigráficos. – *Ameghiniana*, **25**: 225-236.
- ALBERDI, M.T. & PRADO, J.L. (1992): El registro de *Hippidion* OWEN, 1869 y *Equus (Amerhippus)* HOFFSTETTER, 1950 (Mammalia, Perissodactyla) en América del Sur. – *Ameghiniana*, **29**: 265-284.
- ALBERDI, M.T. & PRADO, J.L. (1993): Review of the genus *Hippidion* OWEN, 1869 (Mammalia; Perissodactyla) from the Pleistocene of South America. – *Zoological Journal of the Linnean Society*, **108**: 1-22.
- ALBERDI, M.T. & PRADO, J.L. (2004): Caballos fósiles de América del Sur. Una historia de tres millones de años. – Universidad del Centro de la Provincia de Buenos Aires, INCUAPA serie monográfica, Olavarría, **3**: 1-269.
- ALBERDI, M.T., PRADO, J.L. & MIOTTI, L. (2001a): *Hippidion saldiasi* ROTH, 1899 (Mammalia, Perissodactyla) at the Piedra Museo site (Patagonia): their implication for the Regional Economy and Environmental. – *Journal of Archaeological Science*, **28**: 411-419.
- ALBERDI, M.T., ZARATE, M. & PRADO, J.L. (2001b): Presencia de *Hippidion principale* en los Acanilados Costeros de Mar del Plata (Argentina). – *Revista Española de Paleontología*, **16**: 1-7.
- AMEGHINO, F. (1904): Recherches de Morphologie Phylogénétique sur les molaires supérieures des Ongulés. – *Anales del Museo Nacional*, **3**: 1-541.
- BRANCO, W. (1883): Ueber eine Fossile Säugethier-Fauna von Punin bei Riobamba in Ecuador. II: Beschreibung der Fauna. – *Palaeontologische Abhandlungen*, **1**: 57-204.
- CIONE, A.L. & TONNI, E.P. (2005): Biostratigrafía basada en mamíferos del Cenozoico superior de la Región Pampeana. – In: BARRIO, R., ETCHEVERRY, R.O., CABALLÉ, M.F. & LLAMBÍAS, E. (Eds.): *Geología y Recursos Minerales de la provincia de Buenos Aires*. – *Relatorio del XV Congreso geológico Argentino*, La Plata, **11**: 183-200.
- CIONE, A.L., TONNI, E.P. & SOIBELZON, L. (2009): Did humans cause the late Pleistocene-early Holocene mammalian extinctions in South America in a context of shrinking open areas? – In: HAYNES, G. (Ed.): *American Megafaunal Extinctions at the End of the Pleistocene*: 125-144; New York (Springer).
- CORREAL URREGO, G. (1981): Evidencias Culturales y Megafauna Pleistocénica en Colombia. – *Fundación Investigación Arqueológica Nacional*, **12**: 1-148.
- CUNHA, F.L. (1981): *Equus (Amerhippus) vandonii* n.sp. um novo cavalo fossil de Corumba, Mato Grosso do Sul, Brasil. – *Boletín del Museo Nacional Geología*, **40**: 1-19.
- DANGAVS, N.V. (2009): Los paleoambientes cuaternarios del arroyo La Horqueta, Chascomús, provincia de Buenos Aires. – *Revista de la Asociación Geológica Argentina*, **64**: 249-262.
- DANGAVS, N.V. & BLASI, A.M. (2002): Los depósitos de yeso intrasedimentario del arroyo El Siasgo, partidos de Monte y General Paz, provincia de Buenos Aires. – *Revista de la Asociación Geológica Argentina*, **57**: 315-327.
- DANGAVS, N.V. & REYNALDI, J.M. (2008): Paleolimnología de la laguna Cerrillo del Medio, Monte, provincia de Buenos Aires. – *Revista de la Asociación Geológica Argentina*, **63**: 29-42.
- DER SARKISSIAN, C., VILSTRUP, J.T., SCHUBERT, M., SEGUIN-ORLANDO, A., EME, D., WEINSTOCK, J., ALBERDI, M.T., MARTIN, F., LÓPEZ, P.M., PRADO, J.L., PRIETO, A., DOUADY, C.J., STAFFORD, T.W., WILLERSLEV, E. & ORLANDO, L. (2015): Mitochondrial genomes reveal the extinct *Hippidion* as an outgroup to all living equids. – *Biology Letters*, **11**: 20141058.
- DILLON, A. & RABASSA, J. (1985): Miembro La Chumbiada, Formación Luján (Pleistoceno, provincia de Buenos

- Aires): una nueva unidad estratigráfica del valle del río Salado. – Actas de las I Jornadas Geológicas Bonaerenses, **1**: 1-27.
- EISENMANN, V., ALBERDI, M.T., DE GIULI, C. & STAESCHE, U. (1988): Studying Fossil Horses: Methodology, **1**: 1-72. Leiden (Brill).
- DIVE, J. & EISENMANN, V. (1991): Identification and Discrimination of First Phalanges from Pleistocene and Modern *Equus*, Wild and Domestic. – In: MEADOW, R.H. & UERP-MANN, H.-P. (Eds.): Equids in the Ancient World II: 278-333. Wiesbaden (Reichert).
- FIDALGO, F., DE FRANCESCO, F. & COLADO, U. (1973): Geología superficial en las Hojas Castelli, J.M. Cobo y Monasterío (Provincia de Buenos Aires). – 5° Congreso Geológico Argentino, Actas, **4**: 27-39.
- FIDALGO, F., DE FRANCESCO, F. & PASCUAL, R. (1975): Geología superficial de la llanura bonaerense. Relatorio: Geología de la Provincia de Buenos Aires. – Sexto Congreso Geológico Argentino: 103-138.
- FIDALGO, F., RIGGI, J.C., GENTILE, R., CORREA, H. & PORRO, N. (1991): Los “Sedimentos postpampeanos” continentales en el ámbito sur bonaerense. – Revista de la Asociación Geológica Argentina, **46**: 239-256.
- FORSTEN, A. (1998): The fossil horses (Equidae, Mammalia) from the Plio-Pleistocene of Liventsovka near Rostov-Don, Russia. – Geobios, **31** (5): 645-657.
- FUCKS, E., HUARTE, R., CARBONARI, J. & FIGINI, A. (2007): Geocronología, paleoambientes y paleosuelos Holocenos en la Región Pampeana. – Revista Asociación Geológica Argentina, **62**: 425-433.
- FUCKS, E., PISANO, M.F., CARBONARI, J. & HUARTE, R. (2012): Aspectos geomorfológicos del sector medio e inferior de la Pampa Deprimida, provincia de Buenos Aires. – Revista de la Sociedad Geológica, España, **25**: 107-118.
- FUCKS, E., PISANO, M.F., HUARTE, R., DI LELLO, C.V., MARI, F. & CARBONARI, J. (2015): Stratigraphy of the fluvial deposits of the Salado river basin, Buenos Aires province: lithology, chronology and paleoclimate. – Journal of South American Earth Sciences, **60**: 129-139.
- GONZÁLEZ BONORINO, F. (1965): Mineralogía de las fracciones arcilla y limo del pampeano en el área de la Ciudad de Buenos Aires y su significado estratigráfico y sedimentológico. – Revista de la Asociación Geológica Argentina, **20**: 67-148.
- GRAY, J.E. (1821): On the natural Arrangement of Vertebrate Animals. – London Medical Repository Review, **15**: 296-310.
- GUÉRIN, C. (1991): La fauna des vertebres du Pléistocène supérieur de l'aire archéologique de Sao Raimundo Nonato (Piauí, Brésil). – Comptes Rendus de l'Académie des Sciences, Paris, **312**: 567-572.
- HOFFSTETTER, R. (1950): Algunas observaciones sobre los caballos fósiles de América del Sur. *Amerhippus* gen. nov. – Boletín Informativo de Ciencias Nacionales, **3**: 426-454.
- HOFFSTETTER, R. (1952): Les Mammifères Pléistocènes de la République de l'Équateur. – Mémoires de la Société Géologique de France, N.S., **31**: 1-391.
- LUND, P.W. (1840): Nouvelles recherches sur la faune fossile du Brésil. – Annales des Sciences Naturelles, **13**: 310-319.
- LUND, P.W. (1846): Meddelelse af det Udbytte af 1844 Undersøgte Knoglehuler Have Avgivet Til Kundskaben Om Brasiliens Dyreverden For Sidste Jordomvæltning. – Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige Og Mathematisk Afhandling, **12**: 57-94.
- MACFADDEN, B.J. (2013): Dispersal of Pleistocene *Equus* (Family Equidae) into South America and calibration of GABI 3 based on evidence from Tarija, Bolivia. – Plos One, **8** (3): e59277.
- MACFADDEN, B.J., SILES, O., ZEITLER, P., JOHNSON, N.M. & CAMPBELL, K.E. (1983): Magnetic Polarity Stratigraphy of the Middle Pleistocene (Ensenaden) Tarija Formation of Southern Bolivia. – Quaternary Research, **19**: 172-187.
- MACHADO, H., GRILLO, O., SCOTT, E. & AVILLA, L. (2017): Following the footsteps of the South American *Equus*: Are autopodia taxonomically informative? – Journal of Mammal Evolution <https://doi.org/10.1007/s10914-017-9389-6>.
- MARI, F., Fucks, E., PISANO, M.F., HUARTE, R. & CARBONARI, J. (2013): Cronología radiocarbónica en paleoambientes del Pleistoceno tardío y Holoceno de la Pampa Deprimida, provincia de Buenos Aires. – Revista del Museo de La Plata, Sección Antropología, **2013**: 51-58.
- ORLANDO, L. MALE, D., ALBERDI, M.T., PRADO, J.L., PRIETO, A., COOPER, A. & HÄNNI, C. (2008): Ancient DNA clarifies the Evolutionary History of American Late Pleistocene Equids. – Journal of Molecular Evolution, **66**: 533-538.
- OWEN, R. (1848): Description of teeth and portions of jaws of two extinct anthracotheriid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the NW coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. – Quarterly Journal of the Geological Society, London, **4**: 103-141.
- OWEN, R. (1869): On Fossil Teeth of Equines from Central and South America, Referable to *Equus conversidens*, *Equus tau*, and *Equus arcidens*. – Proceeding of the Royal Society of London, **17**: 267-268.
- PAULA COUTO, C. (1979): Paleomastozoología. – 590 pp.; Río de Janeiro (Academia Brasileira de Ciências).
- PISANO, M.F. & Fucks, E.E. (2016): Quaternary mollusc assemblages from the lower basin of Salado River, Buenos Aires Province: Their use as paleoenvironmental indicators. – Quaternary International, **391**: 100-111.
- PORTA, J. DE (1960): Los Équidos fósiles de la Sabana de Bogotá. – Boletín de Geología, Universidad Industrial de Santander, Colombia, **4**: 51-78.
- PRADO, J.L. (1984): Fenética de los metatarsianos de taxa fósiles *Hippidion* OWEN, *Onohippidium* MORENO, *Parahipparion* C. AMEGHINO y *Equus (Amerhippus)* LINNÉ (Mammalia, Perissodactyla). – CIPFE Orione Contribuciones en Biología, Montevideo, **11**: 11-15.
- PRADO, J.L. & ALBERDI, M.T. (1994): A quantitative review of the horse *Equus* from South America. – Palaeontology, **37**: 459-481.
- PRADO, J.L. & ALBERDI, M.T. (1996): A cladistic analysis of the horses of the tribe Equini. – Palaeontology, **39**: 663-680.
- PRADO, J.L. & ALBERDI, M.T. (2008): Restos de *Hippidion* y *Equus (Amerhippus)* procedentes de las Barrancas de San Lorenzo, Pleistoceno tardío (Provincia de Santa Fé,

- Argentina). – Revista Española de Paleontología, **23**: 225-236.
- PRADO, J.L. & ALBERDI, M.T. (2012): Equidos y gonfoterios del Pleistoceno tardío de San Pedro, provincia de Buenos Aires, Argentina. – Estudios Geológicos, **68**: 261-276.
- PRADO, J.L. & ALBERDI, M.T. (2014): Global evolution of Equidae and Gomphotheriidae from South America. – Integrative Zoologica, **9**: 434-443.
- PRADO, J.L. & ALBERDI, M.T. (2016): Fossil Horses from Argentina. – In: AGNOLIN, F.L., LIO, G.L., BRISSÓN EGLI, F., CHIMENTO, N. & NOVAS, F.E. (Eds.): Historia Evolutiva y Paleobiogeografía de los Vertebrados de América del Sur. Contribuciones Científicas del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, **6**: 303-309.
- PRADO, J.L. & ALBERDI, M.T. (2017): Fossil Horses of South America. Phylogeny, Systematics and Ecology. – 150 pp.; The Latin American Studies Book Series (Springer).
- PRADO, J.L., ALBERDI, M.T. & REGUERO, M.A. (1998): El Registro más antiguo de *Hippidion* Owen, 1869 (Mammalia, Perissodactyla) en América del Sur. – Estudios Geológicos, **54**: 85-91.
- PRADO, J.L., ALBERDI, M.T. & REGUERO, M.A. (2000): Comentarios sobre la Geocronología, Estratigrafía y Paleontología de Vertebrados de la Fm. Uquía en el perfil de Esquina Blanca, Jujuy. Respuesta a E.P. TONNI y A.L. CIONE. – Estudios Geológicos, **56**: 133-137.
- PRADO, J.L., ALBERDI, M.T., DE LOS REYES, M., POIRÉ, D.G. & CONALICCHIO, J.M. (2013 b): New material of *Equus (Amerhippus) neogeus* (Mammalia, Perissodactyla) from the late Pleistocene of Olavarría (Argentina). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **269** (2): 125-134.
- PRADO, J.L., ALBERDI, M.T., MARTÍNEZ, G. & GUTIÉRREZ, M.A. (2005): *Equus (Amerhippus) neogeus* LUND, 1840 (Equidae, Perissodactyla) at Paso Otero 5 site (Argentina): Its implications for the extinction of South America horse. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2005**: 449-468.
- PRADO, J.L., BONINI, R., ALBERDI, M.T., SCANFERLA, A., POMI, L.H. & FUCKS, E. (2013a): Nuevos registros de *Hippidion* (Mammalia, Perissodactyla) en el Pleistoceno tardío de la provincia de Buenos Aires, Argentina. – Estudios Geológicos, **69**: 239-253.
- PRADO, J.L., MENEGAZ, A.N., TONNI, E.P. & SALEMME, M.C. (1987): Los Mamíferos de la Fauna Local Paso Otero (Pleistoceno Tardío), Provincia de Buenos Aires. Aspectos Paleambientales y Bioestratigráficos. – Ameghiniana, **24**: 217-233.
- PRADO, J.L., SÁNCHEZ, B. & ALBERDI, M.T. (2011): Ancient feeding ecology inferred from stable isotopic evidence from fossil horses in South America over the past 3 Ma. – BMC Ecology, **11**: 1-15.
- QUATTROCCHIO, M.E., BORROMEI, A.M., DESCHAMPS, C.M., GRILL, S.C. & ZAVALA, C.A. (2008): Landscape evolution and climate changes in the Late Pleistocene-Holocene, southern Pampa (Argentina): evidence from palynology, mammals and sedimentology. – Quaternary International, **181**: 123-138.
- RINCÓN, A., ALBERDI, M.T. & PRADO, J.L. (2006): Nuevo registro de *Equus (Amerhippus) santaeelenae* (Mammalia, Perissodactyla) del pozo de asfalto de Inciarte (Pleistoceno superior), estado Zulia, Venezuela. – Ameghiniana, **43**: 529-538.
- SÁNCHEZ, B., PRADO, J.L. & ALBERDI, M.T. (2006): Ancient feeding, ecology and extinction of Pleistocene horses from the Pampean Region, Argentina. – Ameghiniana, **43**: 427-436.
- SCANFERLA, A., BONINI, R., POMI, L., FUCKS, E. & MOLINARI, A. (2013): New late Pleistocene megafaunal assemblage with well-supported chronology from the Pampas of southern South America. – Quaternary International, **307**: 97-161.
- TOLEDO, M.J. (2011): El legado lujanense de Ameghino: revisión estratigráfica de los depósitos pleistocenos-holocenos del Valle del Río Luján en su sección tipo. Registro paleoclimático en La Pampa de los estadios OIS 4 al OIS 1. – Revista de la Asociación Geológica Argentina, **68**: 121-167.
- TONELLO, M.S. & PRIETO, A.R. (2010): Tendencias climáticas para los pastizales pampeanos durante el Pleistoceno tardío-Holoceno: estimaciones cuantitativas basadas en secuencias polínicas fósiles. – Ameghiniana, **47** (4): 501-514.
- TONNI, E.P., CIONE, A.L. & FIGINI, A.J. (1999): Predominance of arid climates indicated by mammals in the pampas of Argentina during the late Pleistocene and Holocene. – Palaeogeography, Palaeoclimatology, Palaeoecology, **147**: 257-281.
- WAGNER, A. (1860): Ueber fossile Säugetierknochen am Chimborasso. – Sitzungsberichte der königlich Bayerischen Akademie der Wissenschaften zu München, **1860**: 330-338.
- ZURITA, A.E., SCILLATO-YANÉ, G.J. & CARLINI, A. A. (2005): Palaeozoogeographic, biostratigraphic and systematic aspects of the genus *Sclerocalyptus* AMEGHINO 1891 (Xenarthra, Glyptodontidae) of Argentina. – Journal of South American Earth Sciences, **20**: 120-129.

Manuscript received: March 19th, 2018.

Revised version accepted by the Stuttgart editor: May 25th, 2018.

Addresses of the authors:

JOSÉ LUIS PRADO, RICARDO BONINI, INCUAPA, CONICET-UNICEN, Del Valle 5737, 7400 Olavarría, Argentina; e-mails: jprado@soc.unicen.edu.ar; ricardo.bonin@soc.unicen.edu.ar

MARÍA TERESA ALBERDI, Departamento de Paleobiología. Museo Nacional de Ciencias Naturales (CSIC), Madrid, España; e-mail: malberdi@mncn.csic.es

HÉCTOR CRISPIANI, Museo de Ciencias Naturales “Florentino Ameghino” de Las Flores, Argentina.

Appendix

Table 1. Radiocarbon ages in years BP and calibrated of the taxa recorded in the Salado River profile.

Species	14C Age	Cal BP old	Cal BP young	Cal BP median	Lab number	Material dated	Reference	Collection number
<i>Doedicurus clavicaudatus</i>	14140 ±60	17330	17092	17211	GrA-48480 (AMS)	Bone (vertebrae)	Prado et al. 2015	MACN-2821
<i>Doedicurus clavicaudatus</i>	12860 ±50	15435	15220	15328	GrA-48961(AMS)	Bone (plate)	Prado et al. 2015	MACN-6744
<i>Megatherium americanum</i>	11590 ±60	13473	13348	13411	GrA-49130(AMS)	Tooth (M1)	Prado et al. 2015	MACN-2321
<i>Hippidion principale</i>	14190 ±60	17396	17166	17281	GrA-49323(AMS)	bone	Prado et al. 2015	MHP-without number
<i>Doedicurus clavicaudatus</i>	12380 ±190	14845	14117	14481	LP-2568 (standard)	bone	Scanferla et al. 2013	MHM-P 63
<i>Smilodon populator</i>	13400 ±200	16399	15818	16109	LP-2140 (standard)	bone	Scanferla et al. 2013	MHM-P 53
<i>Hippidion principale</i>	12860 ±120	15560	15176	15368	LP-2259 (standard)	bone	Scanferla et al. 2013	MHM-P 54
<i>Hippidion principale</i>	14120 ±50	17169	16961	17065	Beta-311032(AMS)	Tooth (P3)	Prado et al. 2013a	MHM-P 54

Table 2. Characters most important for Principal Component Analysis (PCA) 1, 2 and 3 components for *Equus* and *Hippidion* species. The numbers correspond to the measurements recommended in the “*Hipparion* Conference” New York 1981 (see EISENMANN et al. 1988). Abbreviations: MCIII, third metacarpal; MTIII, third metatarsal; 1PHIII, first phalanx of the third digit; 2PHIII, second phalanx of the third digit.

Principal components	Character numbers	Eigen value	Principal components	Character numbers	Eigen value
<i>Equus neogeus</i>			Component 3		
MCIII				1PHIII5	0.420
component 1	MCIII13	0.981		1PHIII8	-0.230
	MCIII14	0.976	2PHIII		
	MCIII10	0.973	Component 1	2PHIII4	0.955
	MCIII5	0.971		2PHIII1	0.952
	MCIII11	0.969		2PHIII3	0.945
component 2	MCIII16	0.871		2PHIII5	0.919
	MCIII9	-0.713	Component 2	2PHIII2	0.439
	MCIII3	-0.272		2PHIII3	-0.247
component 3	MCIII8	0.484	Component 3	2PHIII5	-0.364
	MCIII2	-0.440		2PHIII6	0.315
	MCIII1	-0.288	<i>Hippidion principale</i>		
MTIII			1PHIII		
component 1	MTIII11	0.973	Component 1	1PHIII7	0.914
	MTIII10	0.976		1PHIII8	0.897
	MTIII13	0.966		1PHIII1	0.880
	MTIII14	0.954		1PHIII5	0.870
	MTIII12	0.946	Component 2	1PHIII9	0.674
component 2	MTIII8	0.933		1PHIII6	-0.435
	MTIII9	-0.313		1PHIII2	0.353
	MTIII2	-0.280		1PHIII4	-0.340
component 3	MTIII9	0.846	Component 3	1PHIII9	0.586
	MTIII1	-0.300		1PHIII2	-0.316
	MTIII2	-0.295		1PHIII3	0.205
1PHIII			2PHIII		
Component 1	1PHIII6	0.970	Component 1	2PHIII4	0.966
	1PHIII7	0.968		2PHIII3	0.934
	1PHIII4	0.964		2PHIII5	0.917
	1PHIII1	0.960		2PHIII1	0.902
Component 2	1PHIII9	0.440	Component 2	2PHIII6	-0.453
	1PHIII8	-0.316		2PHIII1	0.393
	1PHIII2	0.316		2PHIII2	0.392
			Component 3	2PHIII5	-0.389

Table 3. Measurements of *Equus neogeus* and *Hippidion principale* teeth from Salado River (Buenos Aires Province). All dimensions are expressed in millimeters. Abbreviations: Ls, occlusal length; Bs, occlusal breadth; PrL, occlusal length of the protocone; postfl., occlusal length of the postflexid.

Upper tooth	Species	Locality	Tooth	Ls	Bs	Height	PrL
num. 5	<i>Equus neogeus</i>	Río Salado	P2 right	38.0	23.8	48.0	9.5
num. 5	<i>Equus neogeus</i>	Río Salado	P3 right	29.6	27.3	64.5	13.0
num. 5	<i>Equus neogeus</i>	Río Salado	P4 right	28.0	27.6	70.0	12.3
num. 5	<i>Equus neogeus</i>	Río Salado	M1 right	25.6	26.8	63.0	11.9
num. 5	<i>Equus neogeus</i>	Río Salado	M2 right	25.9	26.5	69.5	13.5
num. 5	<i>Equus neogeus</i>	Río Salado	M3 right	25.8	22.8	72.0	14.0
Lower tooth	Species	Locality	Tooth	Ls	Bs	Height	Postfl.
num. 7	<i>Equus neogeus</i>	Río Salado	p2 right	29.8	16.7		
num. 7	<i>Equus neogeus</i>	Río Salado	p3 right	26.9	16.5		11.8
num. 7	<i>Equus neogeus</i>	Río Salado	p4 right	25.5	16.6		10.0
num. 7	<i>Equus neogeus</i>	Río Salado	m1 right	23.5	15.7		6.6
num. 7	<i>Equus neogeus</i>	Río Salado	m2 right	23.0	14.5		6.8
num. 7	<i>Equus neogeus</i>	Río Salado	m3 right	29.0	13.9		8.3
num. 7	<i>Equus neogeus</i>	Río Salado	p2 left	29.0	16.4		
num. 7	<i>Equus neogeus</i>	Río Salado	p3 left	27.1	17.9		11.0
num. 7	<i>Equus neogeus</i>	Río Salado	p4 left	25.5	17.2		10.7
num. 7	<i>Equus neogeus</i>	Río Salado	m1 left	24.1	17.0		5.9
num. 7	<i>Equus neogeus</i>	Río Salado	m2 left	23.5	14.8		6.1
num. 7	<i>Equus neogeus</i>	Río Salado	m3 izq	28.6	13.0		6.1
num. 5	<i>Equus neogeus</i>	Río Salado	p3 right	31.0	18.3		14.5
num. 5	<i>Equus neogeus</i>	Río Salado	p4 right	28.0	18.0		13.2
num. 5	<i>Equus neogeus</i>	Río Salado	m1 right	26.0	16.3		10.5
num. 5	<i>Equus neogeus</i>	Río Salado	m2 right	26.0	15.3		10.2
num. 5	<i>Equus neogeus</i>	Río Salado	m3 right	30.9	13.5		10.0
num. 16	<i>Hippidion principale</i>	Río Salado	p2 right	37.1	20.2		
num. 16	<i>Hippidion principale</i>	Río Salado	p3 right	32.8	22.0		
num. 16	<i>Hippidion principale</i>	Río Salado	p4 right	30.7	21.6		
num. 16	<i>Hippidion principale</i>	Río Salado	m1 right	31.0	18.0		
num. 16	<i>Hippidion principale</i>	Río Salado	m2 right	32.1	17.2		
num. 16	<i>Hippidion principale</i>	Río Salado	m3 right	38.3	14.9		
num. 16	<i>Hippidion principale</i>	Río Salado	p2 left	39.7	20.6		
num. 16	<i>Hippidion principale</i>	Río Salado	p3 left	32.3	20.6		
num. 16	<i>Hippidion principale</i>	Río Salado	p4 left	31.7	20.5		
num. 16	<i>Hippidion principale</i>	Río Salado	m1 left	30.0	20.2	53.0	
without num.	<i>Hippidion principale</i>	Río Salado	p2 right	38.4	19.5		

Table 4. Measurements of *Equus neogeus* and *Hippidion principale* bones from Salado River (Buenos Aires Province). Numbers following EISENMANN et al. (1988). All dimensions are expressed in millimeters. Abbreviation: SI, slender index.

Collect number	Bone	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	SI
Col. HGC-4	MCIII left	<i>Equus neogeus</i>	249	238.7	34	27.7	56	34	42	18.2	9.4	49.6	54	40.7	30.5	32.6	6.5	13.65
Col. HGC-4	MCIII right	<i>Equus neogeus</i>	234	225	36	27	54	32.4	43.3	16	7.2	51	54.3	37	28.7	32	5.2	15.38
Col. HGC-4	MCIII right	<i>Equus neogeus</i>	250	240	34.1	27.9	56	35	46	18.5	7.2	50	54.2	40.3	31.2	32.8	6	13.64
Col. HGC-4	MCIII left	<i>Equus neogeus</i>	242	231	34.2	27.8	49	32	39	17	8.5	47	49.6	37	28.5	30.2	3	14.13
Museo Rauch	MTIII left	<i>Equus neogeus</i>	282	268.5	35	32.5	52	43	45.6	15.1	7.2	50.4	52	38.3	28.7	30		12.41
Col. HGC-4	CAL right	<i>Equus neogeus</i>	120	75	20.1	35.7	55.1	58	56									
Col. HGC-4	CAL right	<i>Equus neogeus</i>	117.1	74.3	18.7	32.6	52	55	53.6									
Museo Rauch	CAL right	<i>Equus neogeus</i>	118.5	74	20.7	33.5	53.2	58	56									
Col. HGC-4	1PHIII	<i>Equus neogeus</i>	96	87	44.9	71.4	46	58.5	53.2	33.5	55.4							
Col. HGC-4	1PHIII	<i>Equus neogeus</i>	98	87.6	41	65	40.7	55	51	29	59							
Col. HGC-4	1PHIII	<i>Equus neogeus</i>	98.3	90.1	35.2	56.8	36.8	45.6	45.6	24	62.2							
Col. HGC-4	1PHIII	<i>Equus neogeus</i>	89	79.2	35	60	40	48.5	45.7	26.2	50							
Col. HGC-4	2PHIII	<i>Equus neogeus</i>	51.2	42.2	46	53	33	52.2										
Col. HGC-4	2PHIII	<i>Equus neogeus</i>	48	38	48.7	57	33	53										
Museo Rauch	1PHIII	<i>Hippidion principale</i>	74	71	46	55.5	39.7	49	48.4	27.5	40.5							
Museo Rauch	2PHIII	<i>Hippidion principale</i>	46	34.5	50	54	33	51										

Table 5. Percentage of correct classification of Discriminant Analysis (DA) of *Equus* and *Hippidion* from Salado River (Buenos Aires province, Argentina).

	Original	<i>Equus neogeus</i>	<i>Equus insulatus</i>	<i>Equus andium</i>	Total	
McIII	<i>E. neogeus</i>	100%	0	0	9	
<i>Equus</i>	<i>E. insulatus</i>	0	100%	0	8	
	<i>E. andium</i>	0	0	100%	24	
	Rio Salado	100%	0	0	4	
MtIII	<i>E. neogeus</i>	92.9%	7.1%	0	14	
<i>Equus</i>	<i>E. insulatus</i>	0	100%	0	21	
	<i>E. andium</i>	0	0	100%	29	
	Rio Salado	100%	0	0	1	
First	<i>E. neogeus</i>	87.5%	12.5%	0	28	
phalanx	<i>E. insulatus</i>	5.9%	92.2%	2%	51	
	<i>Equus</i>	0	1.6%	98.4%	62	
	Rio Salado	100%	0	0	4	
Second	<i>E. neogeus</i>	81.8%	13.6%	4.5%	22	
phalanx	<i>E. insulatus</i>	26.5%	73.5%	0	34	
	<i>Equus</i>	0	7%	93%	42	
	Rio Salado	100%	0	0	2	
		<i>Hippidion principale</i>	<i>Hippidion devillei</i>	<i>Hippidion saldiasi</i>		
First	<i>H. principale</i>	100%	0	0	32	
phalanx	<i>H. devillei</i>	0	90%	10%	10	
	<i>Hippidion</i>	<i>H. saldiasi</i>	3.2%	19.4%	77.4%	31
	Rio Salado	100%	0	0	1	
Second	<i>H. principale</i>	92.9%	7.1%	0	14	
phalanx	<i>H. devillei</i>	0	100%	0	4	
	<i>Hippidion</i>	<i>H. saldiasi</i>	0	0	100%	48
	Rio Salado	0	100%	0	1	