Article

Fossil horses from the Late Pleistocene of Tapalqué Creek (Buenos Aires Province, Argentina)

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With 10 figures and 4 tables

Abstract: A comparative study was made with the known record of equids species in South America, identifying the remains as *Equus neogeus*, *Hippidion devillei*, and *Hippidion principale*. These data increase the record of Equidae in South America and provide new evidence about the chronological and geographical distribution. The sedimentary deposits of the Lujan Formation outcropping at Tapalqué creek (4 to 120 ky) were accumulated through fluvial processes. This Formation comprises a rich vertebrate fauna corresponding to the Lujanian South American Land Mammal Age, which includes numerous and diverse vertebrate remains. The taphonomic analysis indicates that the faunistic assemblage was formed and was subject to diagenetic processes without distinction of its action in the fossiliferous levels, that can be recognized as fluvial deposits.

Key words: Equidae, paleoecology, late Pleistocene, taphonomy, Argentina.

1. Introduction

The Mammal faunas from the Pleistocene of Argentine Pampas are among the richest and most diverse of South America (Pascual et al. 1996). Particularly, the Equidae (Perissodactyla), an immigrant from the North America group, are a major component of many local faunas (e.g., Alberdi et al. 1989; Prado et al. 1987; Bargo et al. 1986; Alberdi et al. 2006; Prado & Alberdi 2008; Prado et al. 2012). Equidae is a large family that actually includes horses, wild asses, and zebras. The oldest known fossils assigned to Equidae date from the early Eocene of North America, ca. 55 million years ago. The family became relatively diverse during the Miocene, where there is evidence of great adaptive radiation (Cantalapiedra et al. 2017).

The first fossil horses in South America were discovered by Darwin in Argentina (Owen 1840). Since this publication, notes and articles proliferated, which in most cases do not reflect the global diversity of this group. The several papers of Equidae in South America (Alberdi 1987; Prado et al. 1987; Alberdi et al. 1989; Alberdi & Prado 1993; Prado & Alberdi 1994; Prado & Alberdi 1996; Prado et al. 1998; Prado et al. 2000; Alberdi et al. 2001a; Alberdi et al. 2001b; Alberdi et al. 2003; Alberdi & Prado 2004; Prado et al. 2005; Prado & Alberdi 2012; Prado et al. 2013a; Prado et al. 2013b; García et al. 2018; Prado et al. 2018; among others) distinguish two genera: *Equus* and *Hippidion*. Each genus has a specific dental morphology, with a clear intraspecific variability. *Hippidion* has a more primitive morphology than *Equus*, and its body structure is more robust (Prado 1984; Alberdi et al. 1986; Alberdi 1987; Alberdi et al. 1987; Prado & Alberdi 1994; Prado & Alberdi 2014; Prado & Alberdi 2016; Der Sarkissian et al. 2015; among others).

The genus *Equus* first appeared during the Plio-cene and was once widespread in grassland and des-ert habitats through North America, Asia, Africa, and Europe (MacFadden 1992). The current distribution is over open habitats of eastern and southern Africa and regions of Asia. The earliest appearance of *Equus* in South America record corresponds to the middle Pleistocene of Tarija (Bolivia), dated by MacFadden et al. (1983) and MacFadden (2013) around 0.99 to 0.76 Ma. Many articles have been published to arrange knowledge of the *Equus* species in South America (Machado et al. 2017). Prado & Alberdi (2017) re-viewed this group and recognized three valid species: *Equus andium*, *Equus insulatus*, and *Equus neogeus*.

The *Hippidion* genus was defined by Owen (1869) based on a molar from Lagoa Santa (Brazil) and ap-peared in the publication by Lund (1846). Alberdi & Prado (1993) and Prado & Alberdi (1996) recog-nized 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 princi-pale*, *Hippidion devillei*, and *Hippidion saldiasi*.

The new remains of horse analyzed here come from two fossiliferous localities called Salto de Pie-dra (36° 56′ 54.6″ S; 60° 22′ 19.9″ W) and Avellane-da profiles, along the Tapalqué creek (36° 54′ 05″ S, 60° 20′ 36″ W) near the city of Olavarría, in the Buenos Aires Province. These specimens constitute a new record of horses in South America that completes the descrip-tion of these species. The aim of this paper is to present a detailed description of this material, its precise taxonom-ic status, taphonomic context, and stratigraphic location.

2. Physiography, climate, and environmental settings

Traditionally, the terms Pampas (from Quechua pam-pa, meaning plain) or Pampean Region were assigned to the plains encompassing central-eastern Argentina. These vast land plains constitute a natural region (about 750,000 km^2) and are interrupted by the low hills of the Ventana and Tandil system. The region has a flat to gently undulating landscape, characterized by a deep mantle of loess and loessic silts. The Pampas grasslands include the dry steppes of the moderate continental cli-mate (Dry Pampa) to the east, and the humid temper-ate prairies (Humid Pampa) to the west (Mancini et al.

2005). This climatic pattern reflects the dominant ef-fects of the ocean in the southern half of South America (Iriondo & García 1993).

The Pampa Area is considered to have constituted an ecotone (Ringuelet 1961) between two major biogeo-graphic areas; the Brazilian, and Patagonian subregions. Past faunal associations included shifting mixtures of taxa from both subregions at different times during the late Pleistocene and Holocene. During the cold-dry cli-matic phase, there was a reduction of the subregions which was occupied by subtropical and tropical faunas, resulting in the expansion and interconnection of open environment faunas. Later, when the open areas re-treated during the interglacial periods of the warm-wet climatic phase, the rainforest expanded (Tonni et al. 1992). The arid and semiarid conditions are related to a general decline of mean annual temperatures.

Today, the winds from the South Pacific Anticy-clone lose their humidity on the western side of the Andes, and are cold and dry on arriving at the Pampas from the SW and the S, whereas the winds of the South Atlantic Anticyclone are warmer and more humid and arrive in the Pampas from the NE. Tonello & Prieto (2008, 2010) inferred that the arid conditions during the Late Pleistocene in Pampas Region (ca.16.000 to 12.000 yrs BP) were associated with more continental conditions due to the expansion of the land-mass as a result of a lower sea level in the Atlantic coast. Based on sedimentological (Muhs & Zárate 2001), paly-nological (Tonello & Prieto 2010; Quattrocchio et al. 2008), isotopic (Bonadonna et al. 1999) and faunal evidence (Tonni et al. 1999; Prado & Alberdi 1999; Tonni et al. 2003), the climate for the Late Pleis-tocene in the southern Pampas is characterized by a dry climate with ca. 100 mm lower precipitation levels than at present. This is likely related to the influence of maritime polar air masses, triggered by the northward displacement of the polar front, and the intensification of the westerlies from ice cover in Antarctica and the extent of sea ice, as suggested by Heusser (1989) for high latitudes (Quattrocchio & Borromei 1998).

3. Stratigraphic and chronological context

3.1. Regional framework

Fidalgo et al. (1973, 1975, 1991) reviewed the stratigraphic nomenclature of the Quaternary of the Pampean Region. Geomorphological evidence en-

ables two stratigraphic units to be distinguished for the Late Pleistocene and Holocene deposits: the Luján and the La Postrera formations. The former is of fluvial-lacustrine origin, and the latter is of eolian origin. The wind deposits of La Postrera Formation that cover the entire Pampean Region include loess, very fine stratified sands (ZÁRATE & BLASI 1993). The sedimentological analysis of wind material (BIDART 1988; ZÁRATE & BLASI 1991) suggests that volcanism in the Andean region was the predominant process of particle formation, specifically, as a generator of pyroclastic deposits that were reworked by erosive fluvial processes, wind, and glaciers. GARDENAL (1986) describes four main groups of wind geoforms in the western part of Buenos Aires province. The calibration of these episodes is difficult. According to ZÁRATE & BLASI (1991), the first two episodes correspond to the end of the Pleistocene, while the third occurred in the middle Holocene, and the last during historical times. On the contrary, the Luján Formation is represented mainly by floodplain deposits that are widely developed along with the main river systems in Buenos Aires province (FIDALGO et al. 1973). The lower layer of the Luján Formation corresponds largely to the fluvial deposits (the La Chumbiada and Guerrero members), while the upper layers are essentially lacustrine (the Río Salado Member). Two edaphic stratigraphic units are recognized. The first one called the paleosoil Puesto Callejón Viejo that develops in the upper part of the Guerrero Member, and the second, known as paleosoil Puesto Berrondo, developed in the upper part of the Río Salado Member (FIDALGO et al. 1991; BONADONNA et al. 1995). The last paleosoil indicates a higher moisture regime that could coincide with a higher sea level moment, manifested by the marine ingression recorded around 5000–6000 yrs BP (SCHNACK 1987; ZÁRATE & FLEGENHEIMER 1991). Prior to this, another marine transgression associated with MIS 5e, called Pascua Formation, was described for the coastal zone (FIDALGO et al. 1973; ISLA et al. 2000; SCHNACK et al. 2005).

3.2. Local framework

Fossil equids described in this paper came from two stratigraphic profiles along the Tapalqué creek. One of these is the outcrop at Avellaneda Bridge locality, located in the center of the Olavarría City, and the other is the Salto de Piedra locality, about 8 km outside the city (Fig. 1). At Salto de Piedra locality, six depositional unit separated by discontinuities (alounits) have been recognized. They represent the Late Quaternary stratigraphic sequence that outcrops along the upper basin of the Tapalqué creek (see also ORGEIRA et al. 2001).

– Depositional Unit I comprise very pale brown (10YR 7/3) silty sand deposit with subordinate gravel (rounded fragments of calcium carbonate composition). A well-developed calcrete (about 25 cm thick) crowns the top of the unit. Below this calcrete, matrix-supported massive gravel (diamict), horizontal layers of gravel and fine sand and irregular carbonate nodules predominate. Vertebrate remains are relatively abundant as well as crotovinas. This unit corresponds to the Middle Pleistocene (> 120 ky BP) colluvial and fluvial deposits and broadly correlate with the upper level of the Pampiano Formation (FIDALGO et al. 1973).

– Depositional Unit II to IV are brownish yellow to very pale brown (10YR 6/6 to 10YR 7/3) sandy silt to sandy gravel deposits, with trough cross and horizontal bedding structure. Vertebrate remains and small freshwater gastropods (e.g., *Succinea meridionalis*, *Heleobia parchapii*, *Biomphalaria peregrina*) are abundant in some layers. These species inhabit lotic and lentic environments, adhered to algae or rocks (GAILLARD & CASTELLANOS 1976). *Succinea meridionalis* has hydrophilic habits, related to humid soils or saturated water. These units correspond to Late Pleistocene fluvial deposits (ca. >21 to 11 ky BP), which may be correlated to the Guerrero Member of the Luján Formation (FIDALGO et al. 1973).

– Depositional Unit V comprises a light gray to gray (2.5Y 7/1 to 2.5Y 6/1) silty deposit with horizontally laminated to massive structure and lenticular geometry. The malacological association is characterized by the same freshwater gastropods present in Unit II to IV. This unit corresponds to Early/Mid Holocene fluvial-lacustrine deposits (ca. 11 to 4 ky BP) which may be correlated to the Río Salado Member of the Luján Formation (FIDALGO et al. 1973).

– Depositional Unit VI is a dark grayish brown (2.5Y 4/2) sandy silt deposit with granular structure. These sediments were affected by pedogenesis in the form of a dark soil (Mollisol), well-drained, which differentiates an A-AC-C profile (Figs. 2, 3). This unit corresponds to edaphic alluvial Late Holocene deposits.
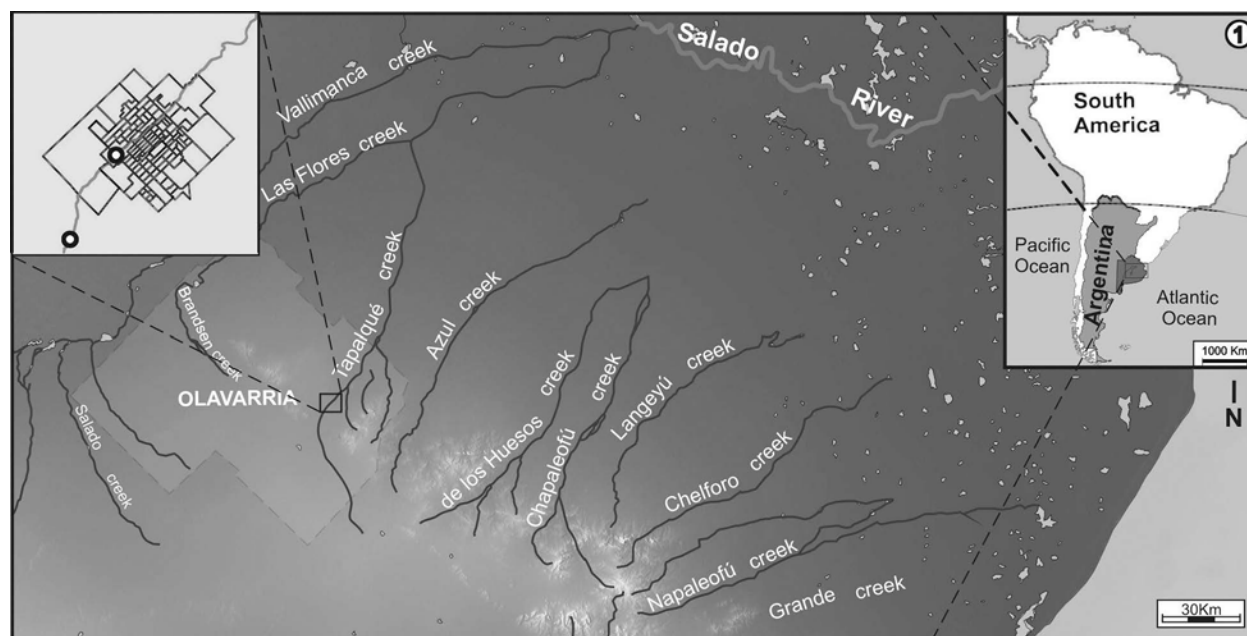
Fig. 1. Location map showing the sampling site.

4. Biostratigraphy

FLORENTINO AMEGHINO established the reference standard for the continental Cenozoic of South America and proposed a sequence of ages grouped into higher-order units (AMEGHINO 1889; AMEGHINO 1906). This scheme, with its subsequent modifications, is still valid today to establish a chronology of the region (CIONE et al. 2007). Until the 1940s there was great confusion, because the same names were used to distinguish rock, time, and faunal units. SIMPSON (1940) and PASCUAL et al. (1965, 1966) established a certain order by proposing a South American Land Mammal Age scheme (SALMA) based on the continental sequences of mammals. These ages were established through the evolutionary degree of the faunas, in part following the same way as AMEGHINO. Although these units have not been recognized by any stratigraphic code, they have proved to be very useful as an organizational method in the development of concepts about the stratigraphy and evolution of mammals (SIMPSON 1971; PASCUAL & ORTIZ JAUREGUIZAR 1990). PASCUAL et al. (1996) suggested that SALMA has proved to be useful for intra- and intercontinental correlations and subdividing Cenozoic time.

Recently, CIONE & TONNI (2005) proposed a new biostratigraphic framework involving the continental sediments and faunas of the Pampean region, from the Late Miocene to the present. These authors recognized 13 biozones for this interval, which represent the biostratigraphic basis for the recognition of stages and substages in the Pampean Region. In this paper, we follow both of these criterions to establish the chronological position of the horses. The sediments attributed to the Lujanian Age that are stratigraphically correlated with the *Equus neogeus* Biozone (*sensu* CIONE & TONNI 2005), would be represented, in the Pampean region, by the lower part of the Luján Formation (Guerrero Member). This unit was deposited during the interval between ca. 21 and 11 ky BP (TONNI et al. 2003), preliminary ^{14}C from both profile extend this interval to 35.3 and 10.1 ky BP (Table 1).

5. Material and methods

The material under study is deposited in the INCUAPA-CONICET, Faculty of Social Sciences of the National University of Central Buenos Aires. It is an incomplete skull of *Equus* (FCS-P.10.1.1) coming from the Tapalqué creek profile near the bridge of Avellaneda avenue in Olavarría. Several remains assigned to *Hippidion* coming from Salto de Piedra profile, specifically: one M1-2 right (FCS-P.8), one distal epiphysis of
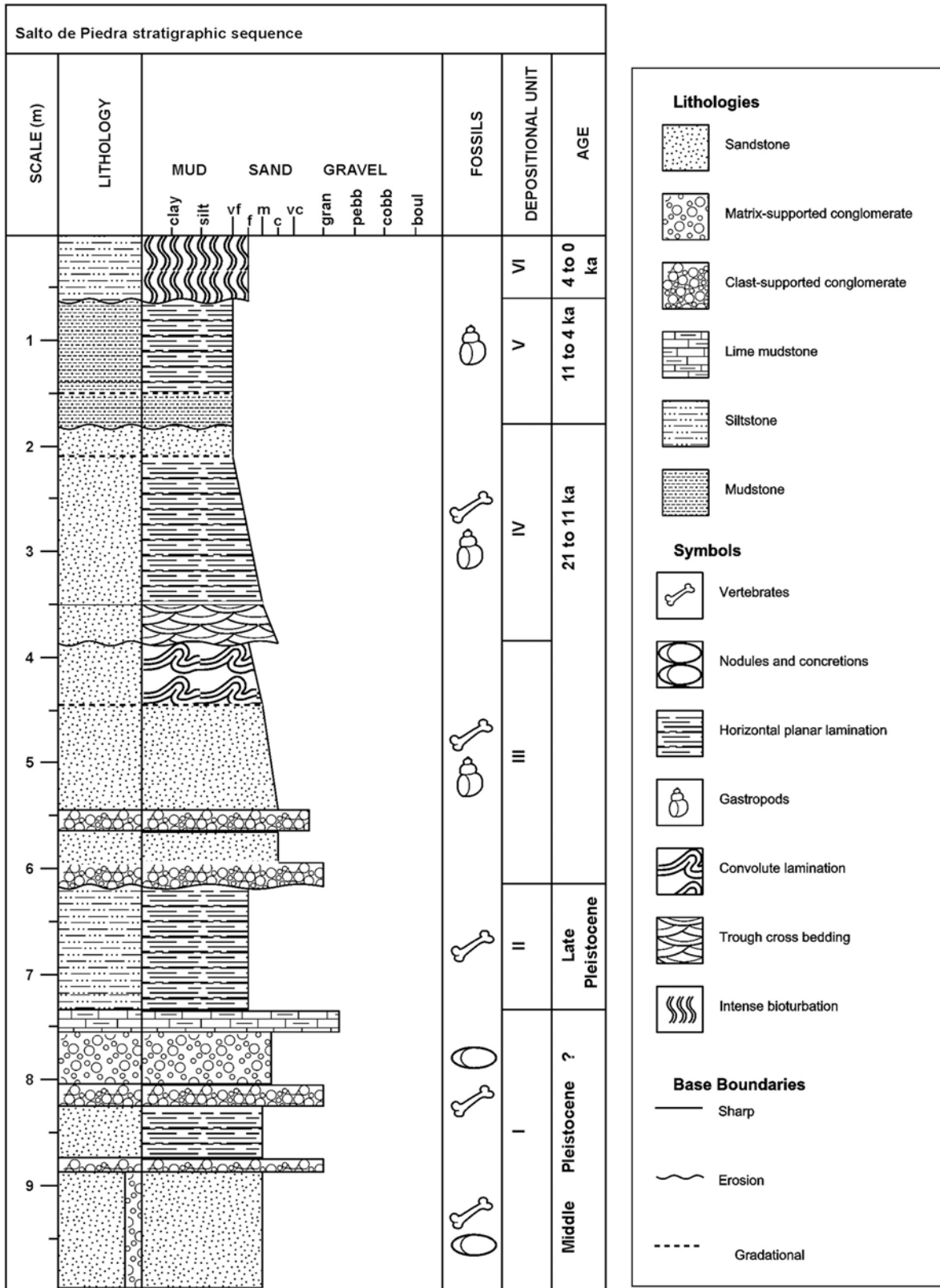
Fig. 2. Profile representing the sedimentary succession exposed on sequences outcropping along of the Tapalqué River.
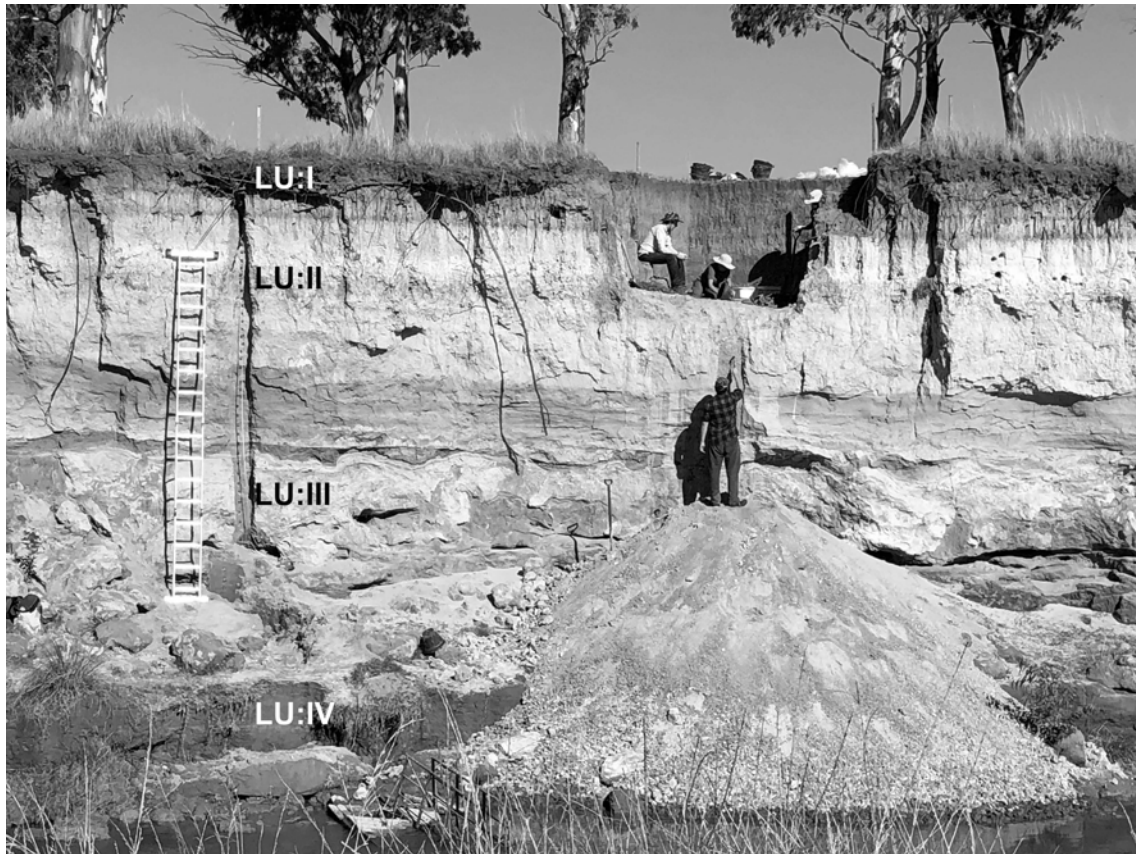
Fig. 3. Detail of the excavation and profile at the Salto de Piedra site.

Table 1. ¹⁴C ages from the studied profiles. *Calibrated age with Calib 7.1 with two sigma, curve SHCal04 (HOGG et al. 2013; STUIVER et al. 2019).

Lab number	Sample	Profile	14C age (14C ka BP)	14C age cal. AP*	Median	Unit	Reference
LP-395	*S. meridionalis*	Salto de Piedra	8810 ± 140	9535–10,187	9830	V	Figini et al. 1995
LP-379	*S. meridionalis*	Salto de Piedra	9710 ± 110	10,693–11,256	10,993	V	Figini et al. 1995
	Biomphalaria sp.	Salto de Piedra	9,850 + 350–340	10,296–12,405	11,284	V	Bonadonna et al. 1995
GrA-49131	*Smilodon populator*	Salto de Piedra	10,140 ± 60 (AMS)	11,363–11,974	11,673	IV	Prado et al. 2015
GrA-47178	*Equus neogeus*	Salto de Piedra	13,590 ± 60 (AMS)	16,091–16,567	16,318	III	Prado et al. 2015
	L. parchappei	Salto de Piedra	19,930 + 650–600	22,496–25,474	23,955	III	Bonadonna et al. 1995
LP-396	*L. parchappei*	Salto de Piedra	21,040 ± 450	24,154–26,080	25,218	III	Figini et al. 1995
	L. parchappei	Salto de Piedra	21,940 ± 230 (AMS)	25,715–26,684	26,147	III	Bonadonna et al. 1999
	L. parchappei	Avellaneda	27,980 +1500–1350	28,957–34,803	32,047	III	Bonadonna et al. 1999
	L. parchappei	Avellaneda	34,500 ± 100 (AMS)	38,585–39,281	38,908	III	Bonadonna et al. 1999
	L. parchappei	Avellaneda	35,300 + 1300–1100 (AMS)	36,677–42,051	39,681	III	Bonadonna et al. 1999

humerus (FCS-P.91.1), one magnum left (FCS-P.91.5), one scaphoid left (FCS-P.91.4), one lunatum left (FCS-P-91.3), one pyramidal left (FCS-P.91.6), one MCIII left (FCS-P.91.2), one distal epiphysis of tibia right (FCS-P.5), one first phalanx of the central digit (FCS-P.29). Plus, two remains from lower level V of Salto de Piedra that appeared next to a tooth, may correspond to *Hippidion*: one m1-2 left (FCS-P.130) and one proximal epiphysis of MTIII left (FCS-P.8).

Determination of the skull remains was made on a comparative study with other skulls from different South American localities. Morphometric and comparative analysis of the MCIII and 1PHIII was made using a large database already utilized in previous works (Prado & Alberdi 1994; Alberdi & Frassinetti 2000; Alberdi et al. 2003; Alberdi & Prado 2004; Prado et al. 2005; Rincón et al. 2006; Prado & Alberdi 2008; Prado & Alberdi 2012). To classified the new remains we used the discriminate analysis (DA) that allowed us to know the affinity of the new elements with the previously established groups. The DA matrix of skeletal measurements is based on 31 MCIII and 83 1PHIII. 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. The statistical package SPSS 15.0 was used for these analyses.

Taphonomic studies provide evidence on the preservation processes and how they affect the information on the fossil record (Behrensmeyer & Kidwell 1985) and is a primary step in paleoecological and paleoenvironmental research (Andrews 1995; Hart 2012). Taphonomic studies in faunal assemblages are important nowadays due to the possibility of knowing the biostratinomic and diagenetic processes that acted on them (Andrews 1990; Lyman 1994). New methodological tools have been developed as a result of access to more sophisticated technologies (Scanning Electron Microscope, among others) that, together with experimental studies, provide new ways of investigating the integrity of fossil assemblages (Dauphin & Brugal 2013). Recognition of site formation processes that could have disturbed the original assemblages enables the degree of bias in the faunal composition to be corrected, leading to a better understanding of the relationship between the living and fossil environment and a more precise paleoenvironmental interpretation (Weigelt 1927; Efremov 1940; Behrensmeyer 1978; Andrews 1990; Fernández-Jalvo et al. 2010).

In this study, we analyzed the taphonomic of bones horses using the following variables:

Degree of weathering: the six stages defined by Behrensmeyer (1978) for macromammals were evaluated: stage 0 represents remains with no evidence of weathering; stage 1 cracking parallel to fiber structure; stage 2 concentric flaking associated with cracks, with loss of most of the outer bone; stage 3 altered compact bone resulting in fibrous texture; stage 4 coarsely fibrous and rough surface, splinters of bone loose on surface; stage 5 bone falling apart in situ with large splinters lying around indicates an extreme degree of weathering. For micromammals, it was evaluated by the four stages defined by Andrews (1990): stage 0 no modifications; stage 1 slight splitting on bone parallel to fiber structure chipping of teeth and splitting of dentine; stage 2 more expansive splitting on bone and teeth leading to loss of parts of crown; stage 3 deep splitting and some loss of deep segments or flakes and extensive splitting teeth.

Degree of abrasion: This was analyzed according to the three categories proposed by Alcalá (1994): category 0: remains with intact surfaces; category 1: remains with rounded edges, and category 2: remains with polished external surfaces.

Degree and type of breakage: The degree of breakage was evaluated based on whether the remains were complete or incomplete. The types of fracture were evaluated only for long bones, following the classification proposed by Marshall (1989).

Degree of bioerosion: This was assessed based on the presence of modifications caused by two kinds of bio erosive trace fossils were recognized. One of them is due to root growth on the bone element sediment interface and the second kind of trace fossil is due to soil fungal and/or bacterial activity the mechanical action of other organisms (Lyman 1994; Behrensmeyer et al. 1989; Mikuláš 1999; Montalvo 2002; Montalvo 2004; Tomassini & Montalvo 2013).

The presence of manganese deposition is related to an environmental condition characterized by wet, mildly alkaline and oxidizing, as well as the involvement of bacteria (Courty et al. 1989; López-González et al. 2006; Fernández-Jalvo & Andrews 2016). The calcium carbonate encrustations are mainly due to the precipitation of these salts on the surface of the bones by water filtration (Lyman 1994).

The other taphonomic variables recorded are trampling and flakering (Andrews 1990; Behrensmeyer
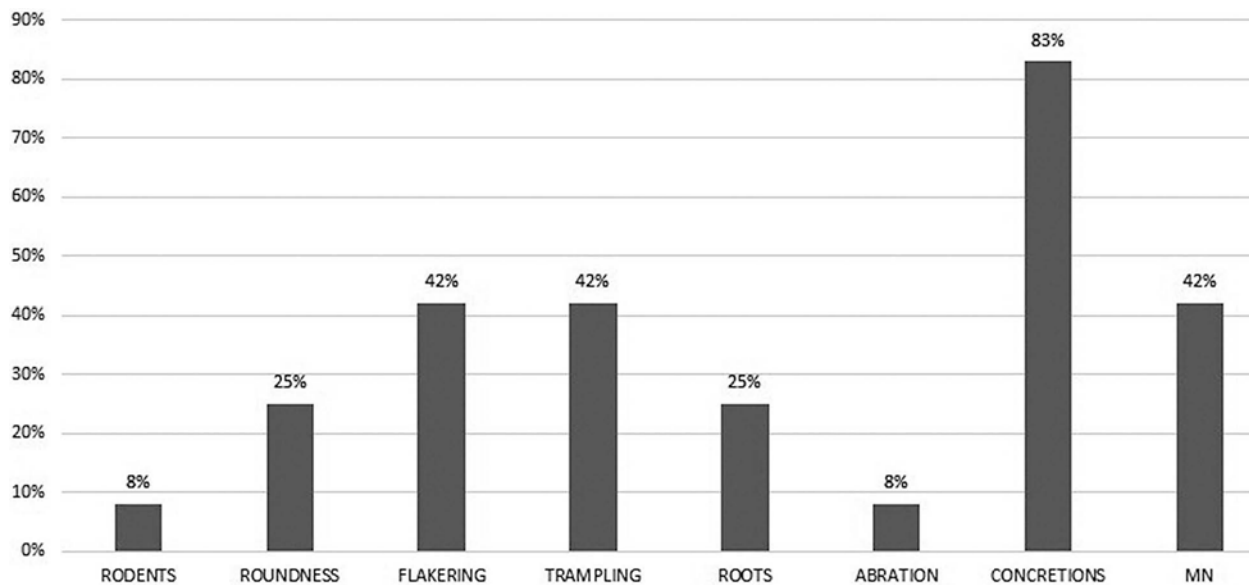
Fig. 4. Taphonomic variables identified on horse bones from Tapalqué creek.

1978; DENYS et al. 1996; DENYS et al. 1997), these variables are related to soil movements or fossil diagenesis agents like water transport or eolian modifications (VOORHIES 1969; DODSON 1973; KORTH 1979)

Abbreviations: P/M, upper premolars and molars; p/m, lower premolars and molars; MTIII and MCIII, third metacarpal or metacarpal of the central digit; 1PHIII, first phalanx of the central digit; Col.num., Collection number; DA, discriminant analysis; L trans, transversal length; L a-p, antero-posterior length; H, height; G, thickness; AP, proximal articulation; AD, distal articulation.

6. Taphonomy

We analyzed thirteen horse bone elements and the only complete long bone, a metacarpal. The rest of the skeletal parts are fractured; they correspond to long bones and cranial bones, with dry fractures with irregular edges.

According to the variables considered, evidences of flaking and trampling are the most numerous (42%). The manganese stains are present (42%) and cover the entire bone surface. The calcium carbonate is present in 83% of the sample. Another variable considered is roundness (25%) which, principally, may be the result of water action on the bone surface. The percentage of abrasion registered is 8% (Fig. 4) which is low but it is still important since within the scale proposed by ALCALÁ (1994) they

generally fall within the scale 1 and 2, which indicate that certain elements have been subject to significant abrasion, probably due to water transport. The abrasion can be associated with 25% of registered rounded elements, especially in the acute edges of the epiphyses that are smoothed, which correspond to small-sized elements such as tarsal bones, teeth or phalanges. Concerning bioerosion produced by other organisms, 25% have root marks, and 8% indicate the activity of rodents.

In general, the bone assemblages found along the Tapalqué creek are very well preserved, perhaps due to rapid burial and little exposure to the weather. The highest percentage of weathered elements corresponds to stage 1 (sensu BEHRENSMEYER 1978), characterized mainly by cracking parallel to fiber structure, and in some cases articular surfaces with mosaic cracking. Another feature observed is exfoliation on the surface, which may be caused by abrasion. Only 9% of the material with weathering reaches stage 2, which presents a greater amount and depth in the longitudinal fractures and a marked exfoliation on the surface of the bones. The precipitation of calcium carbonate salts in some cases it is difficult to remove and the bone surface is covered by these concretions (Fig. 4), in some cases the calcium carbonate covers partially the bone surface, while in other bones, principally small ones like phalanges or autopodial, it covers almost entirely the bone surface. The fluvial transport can bury or move the bones; this
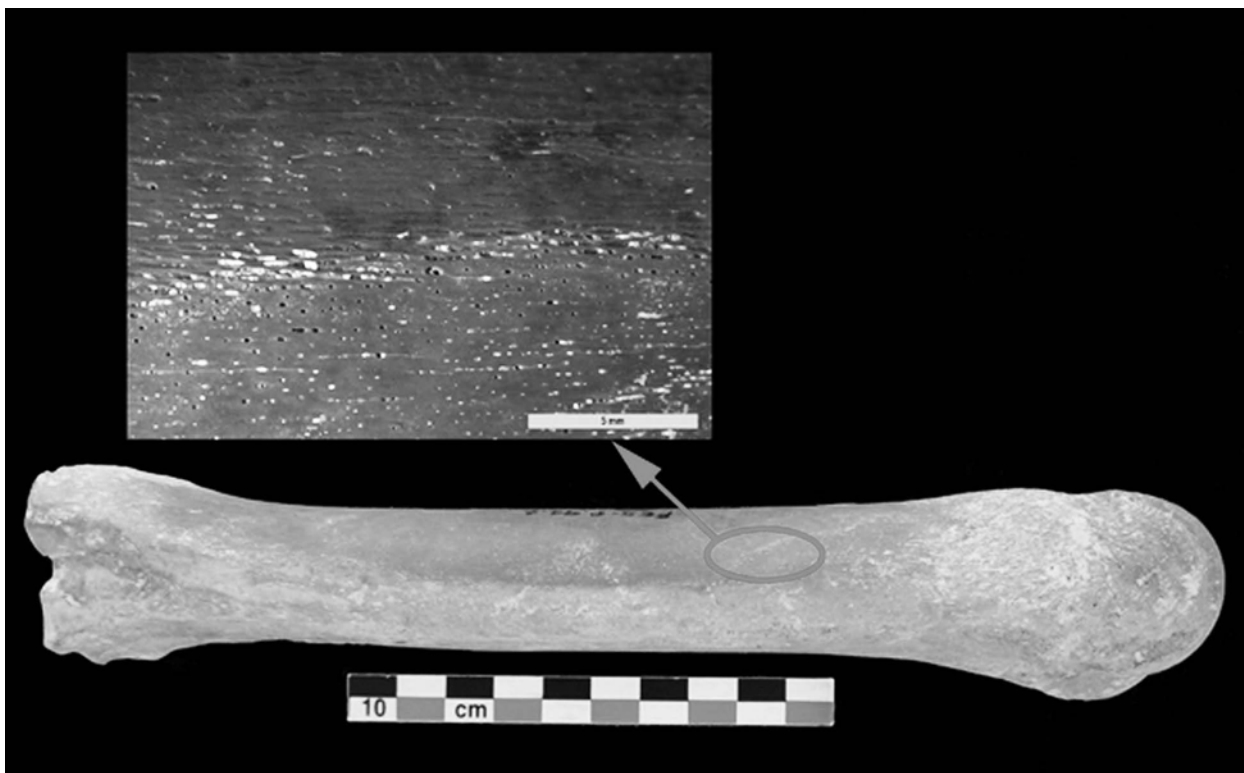
Fig. 5. Horse metatarsal wherein some areas of the diaphysis appear polished, on left superior picture the area detailed appears the difference between the surfaces, in one can it see the normal surface above and the surface polished below. Other taphonomic characteristics that can be observed on the metatarsal are the calcite incrustations, not only on the surface, but also inside the bone tissue.

action can be reflected by the broken bones, especially when the sediments are coarse. Some bones have their surfaces, partially or entirely, polished (25 %; Fig. 5).

The faunal assemblage has undergone intensive fossil diagenetic modifications, especially those that have favored a drag of certain skeletal parts; however, the small distal parts have not managed to be damaged, unlike the long bones, which generally have taphonomic fractures and alterations produced by trampling, and polishing probably by the action of water.

The distal epiphysis of humerus (FCS-P.91.1) belongs to a juvenile individual; this is reflected in the distal portion that show evidence of unfused bone; it can be described as depression on the bone surface similar to a cut mark, but deeper on the limit of the unconsolidated surface and the humerus diaphysis. This element must be analyzed and compared because there could be evidence of a wound with an infectious process with the consequences of not finishing the ossification process in that portion (Fig. 6).

7. Systematic paleontology

In 1950, the French paleontologist ROBERT HOFFSTETTER created the subgenus *Amerhippus* to include all species of the genus *Equus* from South America. The author justified this subgenus by a single character: the absence of infundibulum along the surface of the lower incisors and, therefore, the loss of enamel on the chewing surface. In a later work on the revision of mammals from Ecuador, HOFFSTETTER (1952) indicated that the ulna is stronger in the South American horses than in other *Equus*. In the literature, the recognition of the subgenus *Amerhippus* is controversial. Recently, PRADO & ALBERDI (2017) questioned the use of the subgenus *Amerhippus*. ORLANDO et al. (2008) conducted DNA-based phylogenetic analyses revealing that all Pleistocene South American species of *Equus* were members of the caballine horse lineage, not a distinct subgenus as first suggested by HOFFSTETTER (1950). Therefore, the validity of the subgenus *Amerhippus* is questionable and is not employed herein.
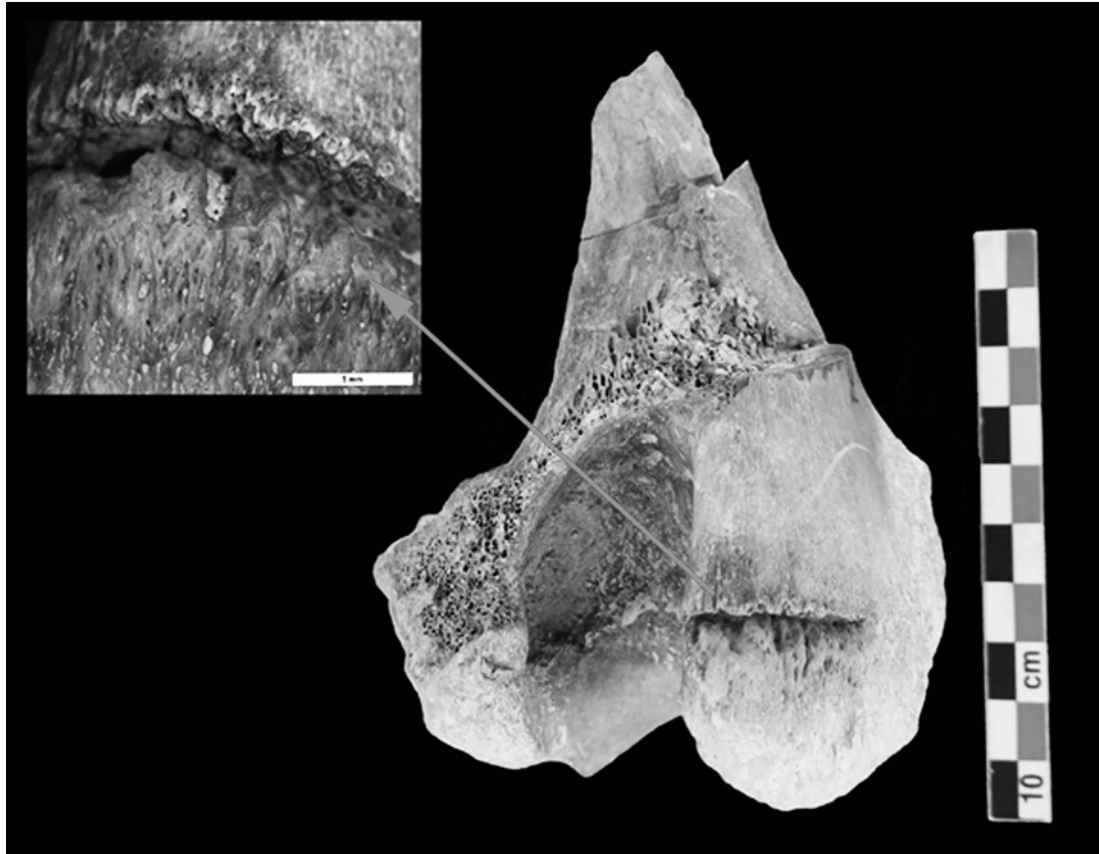
Fig. 6. Distal part of a humerus with a scare of a wound on the condyles. This element belongs to a juvenile individual. The detailed picture (top left) shows the characteristics of the wound and part of not solder with the rest of the bone. Probably this wound suffered an infectious process.

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Subfamily Equinae Gray, 1821
Tribe Equini Gray, 1821
Subtribe Pliohippina Prado & Alberdi, 1996
Genus *Equus* Linnaeus, 1758
Equus neogeus Lund, 1840
Fig. 7

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, Aguas do Araxa (Paula Couto 1979), and Cota dos Ossos (Alberdi et al. 2003) in Brazil; and Arapey Grande creek and So-pas Creek in the Sopas Formation, Uruguay (Ubilla et al. 2004); 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: A large skull (Fig. 7) that lacks the symphysis and the dorsal part including the left orbit and the paraoccipital processes (FCS-P.10.1.1).

Description: The skull is not complete, lacks the symphysis and the anterior dentition. The two complete dental rows are preserved, P2-M3 right and left, in a state of medium wear, no presence of P1. The dentition presents the premolars greater than the molars. The premolars with wide styles and molars with fine ones. The enamel wrinkles reduced, with triangular protocone except in P2, which is more oval, with a slight lingual cleft and a marked caballin fold in the premolars while in the molars are being lost. The hypoconus is
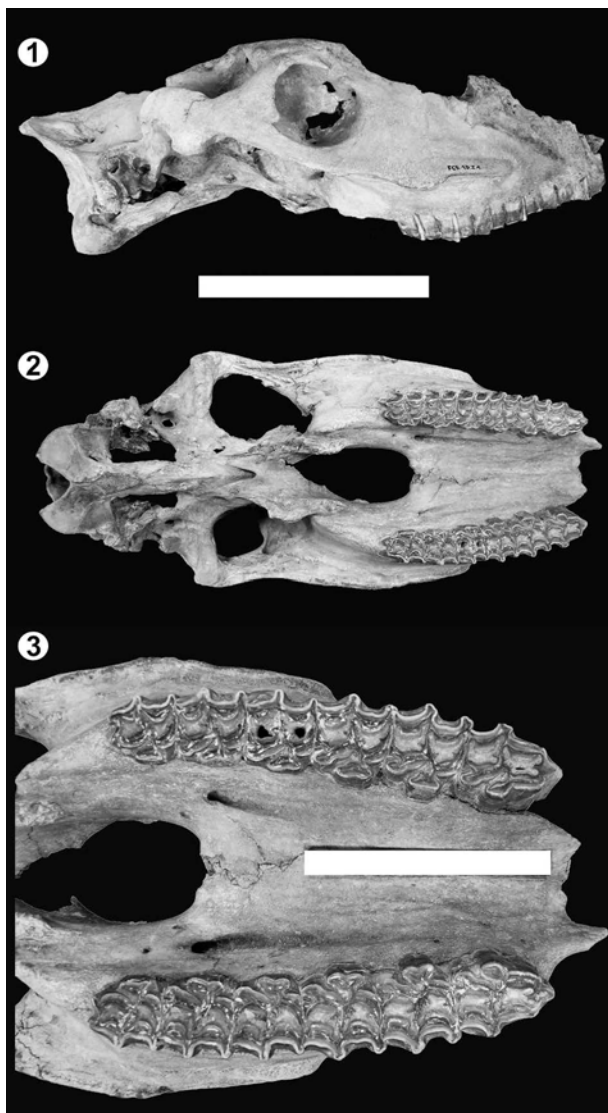
men magnum (basion) and the foramen ethmoidal 176 mm, frontal breadth >190 mm, bizygomatic breadth 199 mm, occipital breadth 69.4 mm, occipital height 72 mm, posterior ocular line 222 mm, exterior height of the meatus auditive externus 13 mm, anterior-posterior orbital diameter 62 mm, orbital diameter perpendicular to the former 55 mm, height of back of the foramen infra-orbital above the alveolar border 67 mm.

Genus *Hippidion* Owen, 1869
Hippidion devillei (Gervais, 1855)
Fig. 9

Synonyms: See Prado & Alberdi (2017).

Holotype: The material figured by Gervais (1855, pl. 7, figs. 11, 12 (the left P2M3 row fragment and right astragalus). Institut de Paléontologie IPMNHN, Paris (France).

Type locality: Uquía, Jujuy, Argentina.

Geographic distribution: Esquina Blanca in Uquía and Barro Negro in Jujuy, San Luis, Uspallata in Mendoza (Cerdeño et al. 2008) and several localities of the Buenos Aires province (Argentina). In Santana and Toca dos Ossos in the Bahia State and in the Lagoa Santa area in Mina Gerais State in Brazil (Alberdi et al. 2003). Tarija and Ulloma in Bolivia, and Tirapata in Perú.

Stratigraphic distribution: Late Pliocene to Pleistocene, Uquian to Lujanian SALMA.

Studied material: Distal epiphysis of humerus (FCS-P.91.1); left magnum (FCS-P.91.5); left scaphoid (FCS-P.91.4); left lunatum (FCS-P-91.3); left pyramidal (FCS-P.91.6); left MCIII (FCS-P.91.2), distal epiphysis of right tibia (FCS-P.5) and first phalanx of the central digit (FCS-P.29).

Description: The remains of the appendicular skeleton seem to correspond to young individuals; the sutures of their epiphyses are still observed, which suggests that they correspond to the same individual. The distal epiphysis of the humerus is quite robust (measurements in Table 3). The magnum, scaphoid, lunatum, and pyramidal of left talus are very well preserved, (measurements in Table 3). The MCIII is relatively small and slender, it corresponds to a young individual by the sutures of his epiphyses, which are clearly observed and more pronounced in the distal end than in the proximal (this could indicate an increase in its final size). The fingerprint of the fingers sides exceeds in length to the midpoint of the diaphysis. The distal epiphysis of a right tibia is also robust (measurements in Table 3). A very robust 1PHIII is observed, typical of *Hippidion*, with its strong muscular insertions on the posterior side, even with a faint line corresponding to the proximal epiphysis footprint (Table 3). MCIII and 1PHIII have been included them in their respective DA with the groups of *Hippidion* species already studied, in order to observe which of them are best associated. Results of DA indicate that the analyzed specimen of MCIII was identified to the *Hippidion saldiasi* group with a correct previous classification of 94.3 % and 74.3 % by cross-validation, but it is placed among the remains of *H. devillei* (see Fig. 8, top diagram). Possibly this is a con-

Fig. 7. Skull of *Equus neogeus* from the Avellaneda avenue profile. **1** – Lateral view right; **2** – ventral view; **3** – detail of dentition. Scales: Figs. 1 and 2 20 cm; Fig. 3 10 cm.

open with large distal sinus and lingual reduced to a notch except in the M3, where the hypoconus is very retracted with the distal and buccal sinuses marked (measurements of the dentition in Table 2; Fig. 7). The measurements of the skull that can be taken are: palatal length 139 mm, vomer length 122 mm, post-vomer length 127 mm, post-palatal length 240 mm, premolar row length 92.8 mm both the right and the left, molar row length 75.4 mm right and 74.6 mm left, P2-M3 row length 166 mm right and 164 mm left, choana length 72 mm ca, minimal breadth of the choana 35.2 mm and maximal breadth of the choana 43.6 mm, palatal breadth at level of P4-M1 77 mm, length of fossa temporalis maximal right 82 mm and left 87 mm, length between the edge of the fora-
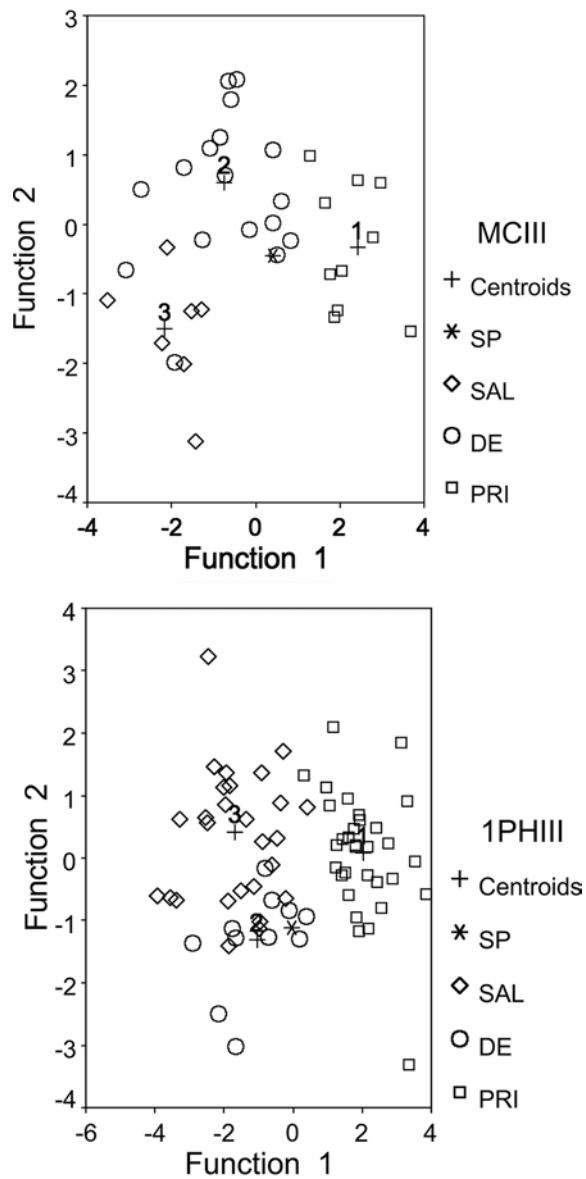
Fig. 8. Discriminant Analysis (DA) of MCIII and 1PHIII of *Hippidion*. Abbreviations: SP, remains from the Salto de Piedra; SAL, *Hippidion saldiasi*; DE, *Hippidion devillei*; PRI, *Hippidion principale*. In the first diagram, the asterisk of the MCIII of Salto de Piedra is located next to the other metacarpals of *Hippidion devillei*.

Fig. 9. Remains of *Hippidion devillei* from the Salto de Piedra profile. **1** – Distal part of humerus in anterior view; **2** – proximal facets of MCIII; **3** – MCIII in anterior view; **4** – MCIII in posterior view; **5** – 1PHIII in anterior view; **6** – 1PHIII in posterior view; **7** – distal articulation of tibia; **8** – upper M1–2 right in occlusal view of *Hippidion principale*. Scales: Figs. 1, 2, 5, 6, and 7: 3 cm; Figs. 3 and 4 10 cm; Fig. 8 3 cm.

Table 2. Measurements of *Equus neogeus* and *Hippidion principale* teeth from the Avellaneda and Salto de Piedra profiles. All dimensions are expressed in millimeters. Abbreviations: Ls, occlusal length; Bs, occlusal breadth; Lb, length of the tooth a 1 cm from the roots; Bb, breadth of the tooth at 1 cm distance from the roots; PrL, occlusal length of the protocone; postfl., occlusal length of the postflexid.

Col.num.	Type of tooth	Species	Locality	Ls	Bs	Height	PrL	Pr shape	Pli caballin	plis fossettes
FCS-10.1.1	P2 right	*Equus neogeus*	Avellaneda street	37.4	25.2	in jaw	7.8	oval short	1	1/4 1/1
FCS-10.1.1	P3 right	*Equus neogeus*	Avellaneda street	28.8	29.0	in jaw	11.0	triangular	1	1/2 1/1
FCS-10.1.1	P4 right	*Equus neogeus*	Avellaneda street	28.9	28.8	in jaw	13	triangular	1	1/5 2/1
FCS-10.1.1	M1 right	*Equus neogeus*	Avellaneda street	24.5	27.0	in jaw	12.4	broken	1	0/4 2/slot
FCS-10.1.1	M2 right	*Equus neogeus*	Avellaneda street	23.5	25 ca	in jaw	13 ca	triangular	slot	0/2 2/1
FCS-10.1.1	M3 right	*Equus neogeus*	Avellaneda street	27.0	23.5	in jaw	12.8	triangular	slot	slot/3 2/0
FCS-10.1.1	P2 left	*Equus neogeus*	Avellaneda street	37.0	26.2	in jaw	9.0	oval short	1	1/5 3/1
FCS-10.1.1	P3 left	*Equus neogeus*	Avellaneda street	26.7	28.4	in jaw	11.0	triangular	1	2/5 2/0
FCS-10.1.1	P4 left	*Equus neogeus*	Avellaneda street	27.0	27.2	in jaw	12.4	triangular	1	1/4 2/0
FCS-10.1.1	M1 left	*Equus neogeus*	Avellaneda street	23.4	27.0	in jaw	11.5	triangular	1	0/4 3/ slot
FCS-10.1.1	M2 left	*Equus neogeus*	Avellaneda street	23.4	25.6	in jaw	11.6	triangular	1	0/5 2/1
FCS-10.1.1	M3 left	*Equus neogeus*	Avellaneda street	29.0	23.2	in jaw	12.0	triangular	0	slot/4 3/1
FCS-P.8	M1-2 right	*Hippidion principale*	Salto de Piedra	30.4	37.0	25.0	9.0	oval round	1	lost
Col.num.	Type of tooth	Species	Locality	Ls	Bs	Lb	Bb	Height	postfl.	double-knot
FCS-P.130	m1-2 left	*Hippidion principale*	Salto de Piedra V level	32.0	17.4	27.1	15.0	66.0	9.0	12.1

sequence of this MCIII corresponding to a young individual The results of the discriminant analysis of 1PHIII indicate that this specimen is grouped within the remains of *Hippidion devillei*, with a correct previous classification of 88.0% of the cases and 78.7% by cross-validation (Fig. 8; Table 4).

Genus *Hippidion* Owen, 1869
Hippidion principale (Lund, 1846)
Fig. 10

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: Pleistocene, Ensenadan and Lujanian SALMA.

Studied material: Right M1-2 (FCS-P.8); left m1-2 (FCS-P.130) and proximal epiphysis of left MTIII (FCS-P.8).

Description: We have a very worn tooth element that could correspond to a right M1-2 (FCS-P.8), where the figures are being lost, the styles almost lost, the fossettes reduced, the rounded protocone and the caballin fold reduced to a minimum notch, the hypocone is fully open, and the distal sinus is lost (Fig. 9.8); the m1-2 left (FCS-P.130, Fig. 10.1) from lower level V of Salto de Piedra is a tooth with morpho-

Fig. 10. Remains from the bottom level of the Salto de Piedra profile (Unit I). **1** – Lower m1–2 left in occlusal view of *Hippidion principale*; **2** – proximal facets of MTIII; **3** – MTIII in anterior view; **4** – MTIII in posterior view. Scales: Figs. 1 and 2 3 cm; Figs. 3 and 4 10 cm.

logical characteristics of *Hippidion*. It was little ware (measurements in Table 2), but already the figures completely formed, the metaconid-metastylid double-knot characteristic for *Hippidion* presents a lot of cement, the enamel in general is quite smooth and the ectoflexid crosses the isthmus without contacting the linguaflexid. No styles are detected at the base of the crown. The fragment of MTIII (FCS-P.8), also from lower level V of Salto de Piedra, is robust, typical of *Hippidion principale* (Fig. 10).

8. Conclusions

The morphological features of the dental and the appendicular skeleton of the remains from Tapalqué

creek are diagnostic and permitted the identification of three species: *Equus neogeus*, *Hippidion devillei*, and *Hippidion principale*.

The morphological features of the skull and their dentition clearly correspond to the species *Equus neogeus*. This is the largest and most slender horse in South America (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. The MCIII and 1PHIII analyzed by multivariate analysis (DA of the MCIII and 1PHIII) situate these remainders with the remains previously classified as *Hippidion devillei*. In the case of the phalanx, we see that the percentages are smaller than in the case of MCIII, which is normal due to the fact that it is difficult to separate the anterior ones from the posterior ones in isolate phalanges and, in general, our database of phalanges is not separated in anterior and posterior ones. In most of the phalanx, horses are maintaining differences between them and we see a higher degree of overlap (Fig. 8). The rests of the carpus bones possibly correspond to *Hippidion devillei* as well, but this is less clear because there are very scarce remains (Table 3). The M1-2 right from Salto de Piedra is strongly worn, where the morphological characters of *Hippidion principale* are lost. In the case of left m1-2 from the lower level V at Salto de Piedra profile, this tooth exhibits morphological characteristics of *Hippidion*. The molar is a little worn, but already the figures are completely formed, its morphology and size suggest a large (adult) *Hippidion principale*. Also, the MTIII from the same level, cannot be compared in DA analysis because it is not complete; however, its measurements of the proximal epiphysis are closer to remains of *Hippidion principale*.

Comparative taphonomic analysis indicated that the faunal assemblages coming from the two different fossiliferous levels recognized in the Tapalqué creek stratigraphic sequence as fluvial deposits, are composed of remains affected by diverse taphonomic (processes) that are common in alluvial environments. *Hippidion principale* is recorded only in the lower level of the sequence (Depositional Unit I, fluvial deposits). *Equus neogeus* and *Hippidion devillei* are recorded in the middle level of the sequence (Depositional Unit II to IV, fluvial deposits).

Table 3. Measurements of *Hippidion devillei* and *Hipparion principale* bones from both levels of the Salto de Piedra profile. Numbers following EISENMANN et al. (1988). All dimensions are expressed in millimeters. Abbreviation: SI, slender index.

Collect number	Bone	Locality	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	SI
FCS-P.91.2	MCIII left	Salto de Piedra	*Hippidion devillei*	205.5	196.4	34.2	25.6	49	32	39	9.5	9.2	51	50	38.1	30	31.5	11	16.6
FCS-P.29	1PHIII	Salto de Piedra	*Hippidion devillei*	68.5	61.2	38.2	54	35	43.4	42.2	27	35							
FCS-P.120	AP MTIII left	Salto de Piedra V principale level	*Hippidion principale*					55	43	49.5	14	9.4							
FCS-P.91.1	AD tibia rigth	Salto de Piedra	*Hippidion devillei*							75	51								
FCS-P.5	AD humerus left	Salto de Piedra	*Hippidion devillei*							77	82	52.4	36.8	42					

Collect number	Bone	Locality	Species	L trans	L a-p	H	G	AP L trans	AP L a-p	AD L trans	AD L a-p
FCS-P.91.5	magnum left	Salto de Piedra	*Hippidion devillei*				20	42	37	41.8	32.2
FCS-P.91.4	scaphoid left	Salto de Piedra	*Hippidion devillei*	38.4	26.5	28.5	26.5	38	23	33.8	27.4
FCS-P.91.3	lunatum left	Salto de Piedra	*Hippidion devillei*				26	36	23.6	30	29.6
FCS-P.91.6	pyramidal left	Salto de Piedra	*Hippidion devillei*	35	24.6	17					

Table 4. Percentage of correct classification of Discriminant Analysis (DA) of *Hippidion* from the Salto de Piedra profile.

	Original	*Hippidion principale*	*Hippidion devillei*	*Hippidion saldiasi*	Total
McIII *Hippidion*	*H. principale*	90%	10%	0	10
	H. devillei	0	95%	5%	20
	H. saldiasi	0	0	100%	5
	Rio Salado	0%	0	100%	1
First phalanx *Hippidion*	*H. principale*	100%	0	0	32
	H. devillei	0	91.7%	8.3%	12
	H. saldiasi	3.2%	22.6%	74.2%	31
	Rio Salado	0%	100%	0	1

Acknowledgements

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