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First record of *Equus neogeus* from Abaucán River (Catamarca, Argentina)

Primer registro de Equus neogeus *en río Abaucán (Catamarca, Argentina)*

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ABSTRACT

The fossil vertebrate record in Catamarca province is widely recognized in the Neogene deposits, but the quaternary mammal records are poorly represented. Here, we describe remains of fossil horses from Pleistocene sediments outcropping in the Abaucán River in the locality of Tinogasta. A comparative study was made with the known record of these groups of mammals in South America, identifying the remains as *Equus neogeus*, which constitutes the first records of this species for the Late Pleistocene of Catamarca (Argentina). These data increase the record of Equidae in South America and provide new evidence about the chronological and geographical distribution. *Equus neogeus* is the largest and slenderest morphotype of the South American horses, and occurs in eastern South America, but does not recorded outside of lowland Argentina, Uruguay, and Brazil. This is the first record in the higher altitude regions. In addition, the lithostratigraphic context was analyzed, allowing paleoecological considerations. The chronostratigraphic context recognize that the carrier levels are referable to the Lujanian Age.

Keywords: Equidae; Paleoecology; late Pleistocene; Catamarca Province; Argentina.

RESUMEN

En el presente trabajo se describen restos de caballos del Pleistoceno procedentes de afloramientos en el río Abaucán de la localidad de Tinogasta (Catamarca). El estudio comparativo se realizó con los registros conocidos de este grupo de mamíferos en América del Sur y se identificó como *Equus neogeus*. Es el primer registro de esta especie en el Pleistoceno tardío de Catamarca (Argentina). Estos datos representan un nuevo registro de Equidae en América del Sur y aportan nuevas evidencias sobre su cronología y distribución geográfica. *Equus neogeus* es el caballo más grande y más grácil de los de América del Sur y se encuentra en su zona más oriental. Hasta ahora no se habían registrado fuera de las tierras bajas de Argentina, Uruguay y Brasil. Este es el primer registro en regiones más altas altitudinalmente. Además, el contexto litoestratigráfico permite obtener consideraciones paleoecológicas. Desde el punto de vista cronoestratigráfico los niveles fosilíferos se refieren a la edad Lujaniense.

Palabras clave: Equidae; Paleoecología; Pleistoceno superior; provincia de Catamarca; Argentina.

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Introduction

The stratigraphic records of Neogene sedimentary basins in northwestern Argentina have traditionally been the source of great amounts of information regarding the structural and tectonic evolution of the Andes (Reynolds *et al*., 2000; Irigoyen *et al*., 2000). These Neogene sequences have made the Catamarca province one of the best-dated terrestrial sequences in South America. This stratigraphic approach combined with geophysical methods has established a tectonic segmentation of the foreland which corresponds with segmentation of the sub-ducted Nazca plate (Jordan & Gardeweg, 1989). For these sedimentary sequences we have one of the extensive and better-known records of Vertebrates fossil from Argentina (Riggs & Patterson, 1939; Cabrera, 1944; Marshall & Patterson, 1981; Esteban & Nasif, 1996, 1999; Bonini, 2014; Esteban *et al*., 2014; Bonini & Brandoni, 2015). On the contrary, the mammal records in Pleistocene sediments are very scarce. The few known records are mainly associated with remains found in archaeological sites referring to the Late Pleistocene. Martínez *et al*. (2004, 2007, 2010) and Martínez (2014) mention the presence of *Hippidion* and one Megatherinae indet. in sediments dated between 13,350 to 12,510 years BP in high archaeological sites in Antofagasta de la Sierra.

Horses are one of the best known of fossil mammal recorded in South America. This group is originated in North America during the Eocene, where a great radiation is evidenced during Neogene (Cantalapiedra *et al*., 2017). The first fossil of horses in South America was founded 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 recent papers of Equidae in South America (Alberdi, 1987; Alberdi & Prado, 1992, 1993, 2004; Prado & Alberdi, 1994, 1996, 2012; Alberdi *et al*., 1989, 2001a, b, 2003; Prado *et al*., 1987, 1998, 2000, 2005, 2013a, b; 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 earliest appears of *Equus* in South America record correspond 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 the knowledge of the *Equus* species in South America (Machado *et al*., 2017). 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.

In this context, the main objective of this work is to present the results obtained from the study carried out on fossils of horses deposited in the collection of the Anthropology Direction of the Catamarca province. A comparative analysis will be carried out with specimens from other locations in South America. In this way, the new records and biogeographic data presented in this research allow us to contribute about the distribution of equids in the mountain range.

Stratigraphic and chronological context

Fossils equids described in this contribution came from a lens of towing materials belonging to the sedimentary basin of the Abaucán River in the town of Tinogasta, Catamarca. This basin is located into the geological province denominated Northwestern Pampean Ranges. The regional tectonics is conditioned for inverse type faulting due to the action of compressive forces (Pinotti *et al*., 2010). Intermountain sectors are mainly covered by sandy, limolitic and tuffaceous tertiary sediments, represented by some scattered outcrops together with quaternary sediments. Pleistocene outcrops are represented by alluvial sediments and conglomerates which constitutes the low sectors.

The regional stratigraphy sequence is composed of Creston and Vinchina Formations at the base and recent and sub-recent piedmontane deposits to the top. Creston Formation is represented by normal stratified sequences of red-brown sub-rounded conglomerates and sandstones with limestones and gypsum nodules. Red-brown limestones with laminar stratification and fines and compact interbedded sandstones. This unit was interpreted as a whole as fluvial deposits (Fauque & Caminos, 2006). Creston Formation lacks

fossils and was correlated with several units assigning it without distinction to Mesozoic and Cenozoic (Fauque & Caminos, 2006). Vinchina Formation consists of a powerful succession of red banks composed by sandstones, claystones, conglomerates and very scarce tuff (Turner, 1964). Posteriorly, Ramos (1970) separated this unit in two members. Lower member represented by fines to medium red-brown sandstones with cross and ripples stratification of the fluvial origin. The upper member is characterized by the presence of red light to yellowish volcanic sediments of absent in the lower. Since point of view of the tectosedimentary and paleoenvironmental evolution, Tripaldi *et al*. (2001) suggest that it sediments were deposited in an Andean foreland basin developed in the Miocene, between Northwestern Pampean Ranges and Precordillera. Respect to the age of Vinchina Formation, Bonaparte (1965) assigned this unit to late Miocene-early Pliocene from the find ichnofossils, whereas Ciccioli *et al*. (2014) propose that the bulk of the Vinchina Formation is Miocene in age, they do not preclude a longer time span for the sedimentation of the whole unit. Quaternary sequences are represented by recent and sub-recent piedmontane deposits. These units are characterized by unconsolidated paraconglomerates (matrix-supported), with sandy matrix and sabulite lenses with lime-clay matrix deposited over of piedmontanes.

The place of the finding is completely altered by anthropic activity, since it is located two blocks from the central square of the city of Tinogasta (28 ° 3’ S / 67 ° 34’ W; 1214 MASL; fig. 1). The site reflects the lithology of the area, composed of ancient piedmontane deposits with conglomerates and unconsolidated sandstones of the Upper Pleistocene. The profile presented in Figure 2 illustrates the sedimentary succession exposed on sequences outcropping along the Abaucán River. The neotectonic processes affect the deposition of these sediments. Fauqué & Caminos (2006) consider that the subdevelopment

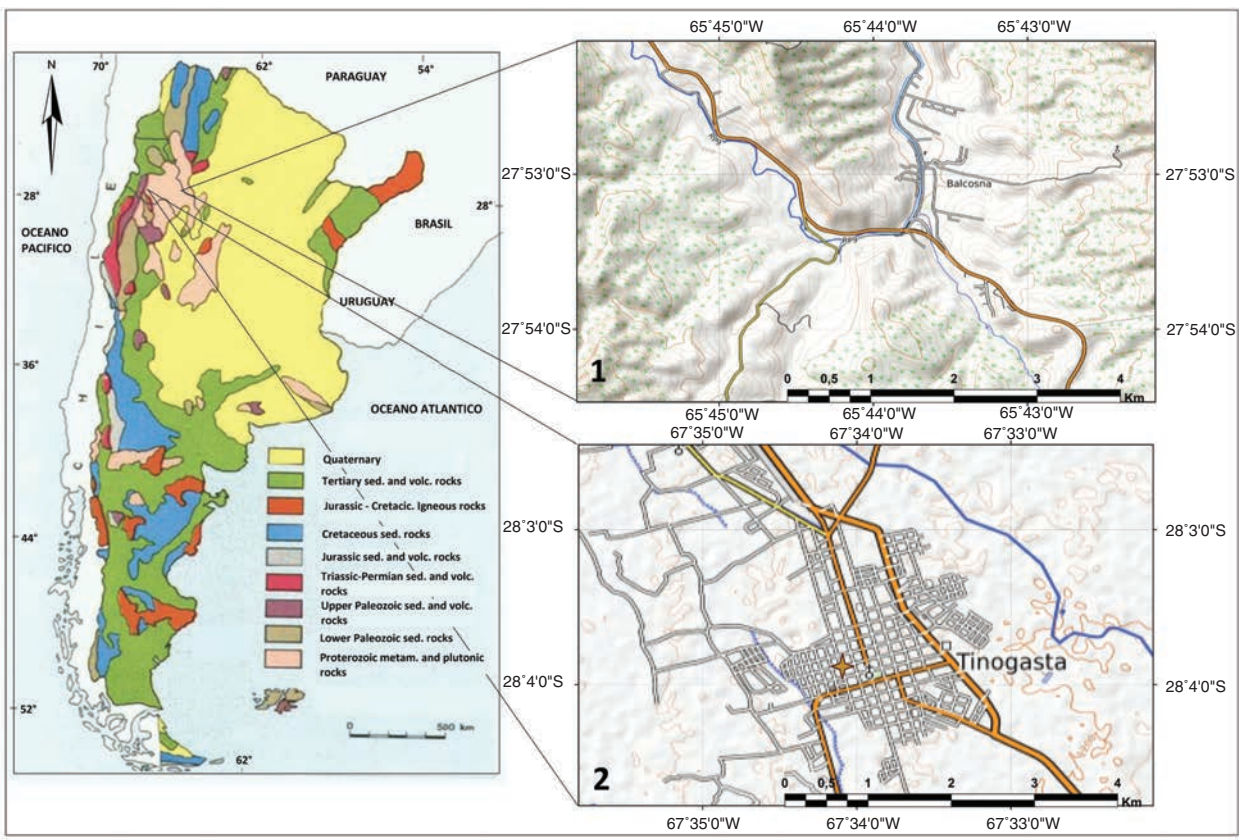

Fig. 1.—Location map of the fossiliferous localities. 1: to the right above, the central sector of the Balcosna-San Ignacio basin; 2: right below, sketch of the city of Tinogasta.

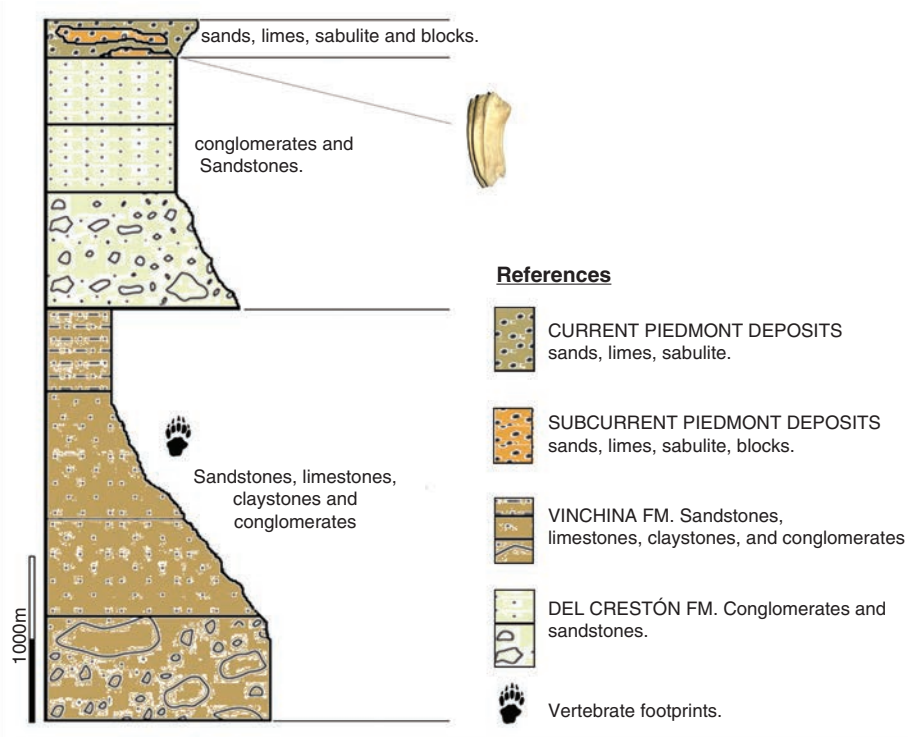

Fig. 2.—Profile representing the sedimentary succession exposed on sequences outcropping along of the Abaucán River (Catamarca).

piedmontane deposits of the basin are composed of little consolidated elastic sediments composed by paraconglomerates (matrix-supported) of sub-rounded to poorly selected sub-rounded edges, which often include large blocks. The matrix is sandy, with some sort of order that indicates a tractive transport. Gravel lenses are interspersed with a finer matrix, silt-clayey, which indicates the presence of dense flows of the debris flow type. In some cases, a thick stratification is observed with a primary inclination towards the center of the basin.

Material and method

The studied fossil remains are deposited in the collection of the Anthropology Direction of the Catamarca province, and correspond to the following specimens: DPA-Pv-01 (06) a: distal fragment of left scapula; DPA-Pv-01 (06) b: proximal fragment of left scapula (fig. 3); DPA-Pv-01 (2 to 6): P2-M1 upper right series and DPA-Pv-01 (1): isolated canine (fig. 4).

For determination of the remains we used morphological characters of the upper molars (P3-4 and M1). However, for morphometric and comparative analysis, we used the remains from other 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). Because we only have upper teeth we have used their dimensions on the surface and at 1 cm from it base (length and width) and length of the protocone in surface, to elaborate a multivariate analysis. We used a matrix with 22 P3-P4 and 64 M1 for made the discriminant analysis (DA). The *Equus* species have been identified in previous paper (Prado & Alberdi, 1994; Alberdi *et al*., 2003; Alberdi & Prado, 2004; Prado *et al*., 2005; among other) using Principal Component Analysis (PCA) and DA was used to establish a rule for differentiating among these groups (fig. 5). The nomenclature and measurements are based on the recommendations and rules elaborated by the "*Hipparion* Conference" (Eisenmann *et al*., 1988). All dimensions are expressed in millimeters. We have used South American Land Mammal Ages (SALMA) proposed by Pascual *et al*. (1996) to establish the chronological positions of the horse

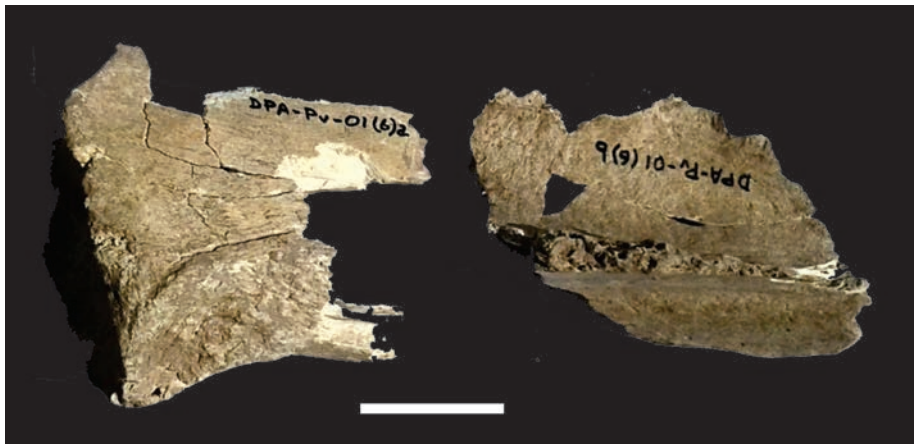

Fig. 3.—DPA-Pv-01 (6). Left scapula in lateral view, where the following bone accidents are observed: a. DPA-Pv-01 (6) a, distal fragment of left scapula; b. DPA-Pv-01 (6) b, proximal fragment of the left scapula. Scale bar 2 cm.

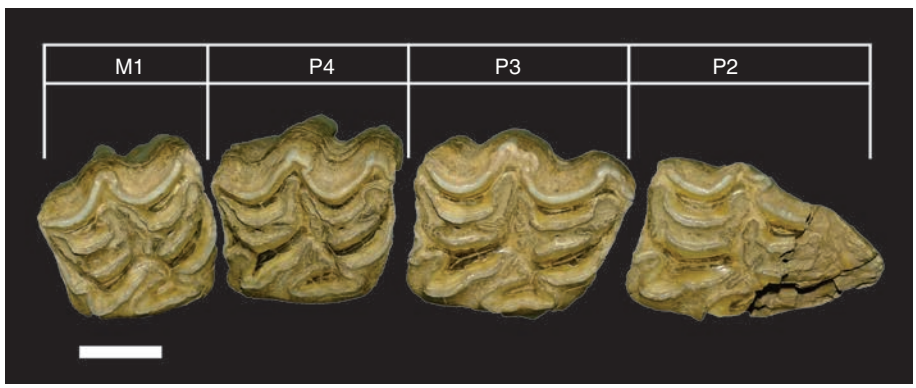

Fig. 4.—Top, occlusal view of the dental series belonging to the upper right side, presenting from right to left, below side view respectively: DPA-Pv-01 (1), the second isolated right upper premolar P2; DPA-Pv-01 (2), third upper right premolar isolated P3; DPA-Pv-01 (3), fourth upper right premolar isolated P4; DPA-Pv-01 (4), isolated first upper right molar M1. Scale bar 2 cm.

records. We do not used the bioestratigraphic scheme proposed by Cione & Tonni (2005) for Argentina, because is not useful to determine relative chronologies and temporal correlations among distant areas of South America. The SALMAs are stratigraphic units not formally recognized by any stratigraphic code of nomenclature but, as an organizing device, they have proven to be very useful in studies on mammalian stratigraphy and evolution (Savage, 1962; Simpson, 1971), and in establishing intracontinental and intercontinental correlations (Pascual *et al*., 1996).

Systematic paleontology

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Subfamily EQUINAE Gray, 1821
Tribe EQUINI Gray, 1821
Subtribe PLIOHIPPINA 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 (Prado & Alberdi, 1994; Alberdi *et al*., 2003; Alberdi & Prado 2004; Prado *et al*., 2005; among other); others from Lagoa Santa (Lund, 1840), Corumba (Cunha, 1981), Sao Raimundo Nonato, Piaui (Guérin, 1991), Chique-Chique and Aguas do Araxa (Paula Couto,

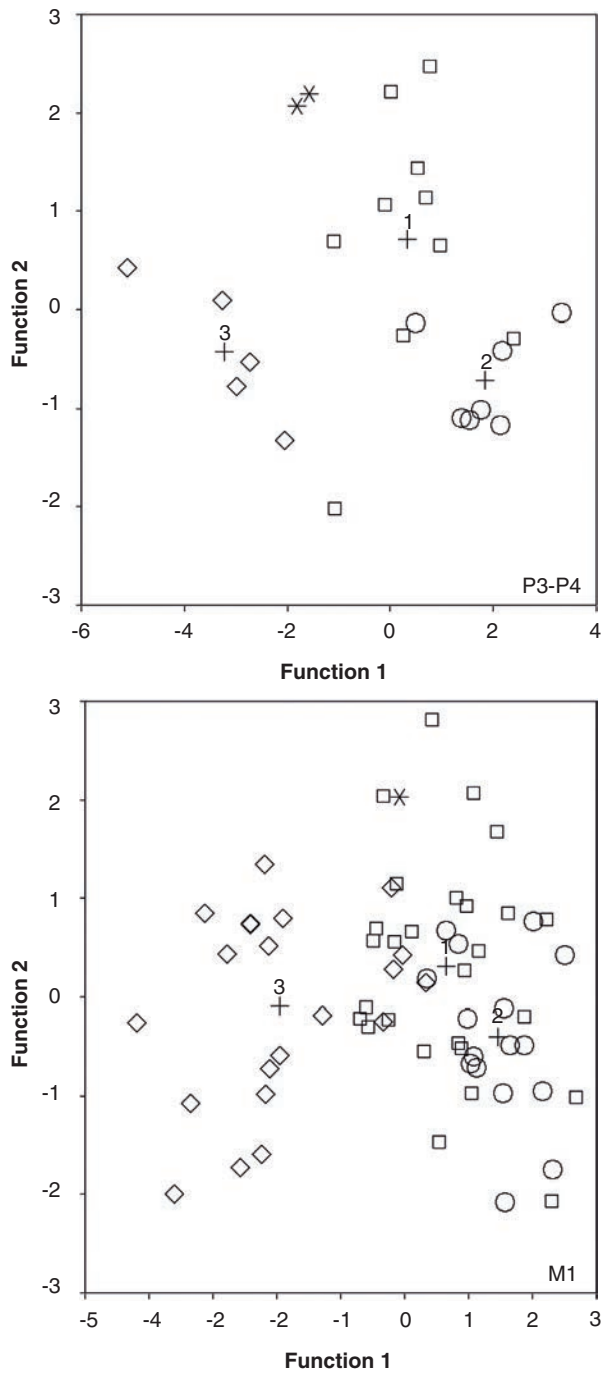

Fig. 5.—Discriminant analysis of the P3-P4 (above) and M1 (below) of different *Equus* species from South America. The specimens from Abaucán River is marked with an asterisk. Symbols: +, Centroids; □, *Equus neogeus*; ○, *Equus insulatus*; ◊, *Equus andium*.

1979), and Cota dos Ossos (Alberdi *et al*., 2003) in Brazil; and Arapey Grande creek and Sopas Creek in the Sopas Formation (Ubilla & Martínez, 2016), Uruguay; Cerro Gordo (Porta, 1960) and Tibitó (Correal Urrego, 1981), Colombia.

Stratigraphic distribution: Late 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 level: Lujanian, South American Land Mammal Age (SALMA).

Diagnosis: *Equus* from South America has a large skull with sharp and marked supraoccipital crest. It is large in relation to the postcranial skeleton. In general, there is a ventral separation of the occipital condyles but sometimes they are joined. It has a peculiar vomer disposition, which reaches the palatal processes of the maxillary anterior to the palatine. Upper cheek teeth contain widely developed fossettes and the enamel line is something wrinkled. The length of upper and lower row is longer than *Equus andium* and *Equus insulatus*. The upper cheek teeth have triangular protocone. The protocone shows the distal part longer than the mesial one, and in some cases there are enamel wrinkles. The mandible is robust and the double-knot in the lower teeth, the metaconid-metastylid, is rounded and angular respectively. The linguaflexid is, in general, shallow and large in U shape. The ectoflexid varies from deep to shallow and sometimes connects with the linguaflexid overall in molars. *Equus neogeus* is largest species of *Equus* in South America and its extremities the most slender.

Description: The recovered fragments of the scapula are poorly preserved. The glenoid cavity is observed without conserving the coracoid process, the adjacent fragment is reconstructed and the scapular spine can be distinguished well. The upper right series, P2 to M1, well preserved and correspond to an adult young individual (with a crown height of 75 mm on average) (table 1). The teeth have a thick layer of cement (2 mm). The length of the dental series from P2 to M1 is 117.6 mm (the series premolar P2-P4 = 92.3), which indicates that they are part of an individual of large size. The morphology of the teeth is typical of *Equus*, with subtriangular protocone, horse fold, the oval hypocone more or less strangled; the styles in the premolar series are wide and in the M1 is narrow (fig. 4).

The dimensions and characters of the teeth are detailed in Table 1. The plis pre- and post fossettes

Table 1.—Table of measurements in millimeters of *Equus neogeus* from Tinogasta, Catamarca, following the nomenclature and recommendations of the "*Hipparion* Conference" (Eisenmann *et al*., 1988). Ls: mesio-distal length of the surface; Bs: bucco-lingual breadth on the surface; Lb: mesio-distal length at 1 cm from base; Bb: buco-lingual breadth at 1 cm from base; H: tooth height; LPr: mesio-distal length of protocone in surface; FPr: Protocone shape; PlsFos: folds of the pits: APre: previous prefossette; DPre: distal prefossette; APost: previous postfossette; DPost: Distal postfossette.

Collection number	tooth	Ls	Bs	Lb	Bb	H	LPr	PrS	Apre	Dpre	Apost	Dpost
DPA-Pv-01	P2 right	35.48	25.23	32.58	21.96	53.66				3	2	
DPA-Pv-01	P3 right	29.87	28.85	25.12	24.76	67.45	12.0	Tri	4	6	2	1
DPA-Pv-01	P4 right	28.35	29.02	24.12	26.66	77.0	12.0	Tri	2	4	3	1
DPA-Pv-01	M1 right	25.13	27.25	22.41	23.25	63.99	11.0	Tri	1	3	1	1

are present in all the specimens, more marked in the P3, which shows greater folding, indicating that there was no advanced wear, since the intensity of these loops decreases with wear, coming to disappear. The shape of the protocone is subtriangular, characteristic of caballin equids (fig. 4). The hypocone shape is oval-elongated and more or less open depending to the degree of wear. The hypoconal groove well marked depending on the degree of wear and more pronounced than the hypoconal constriction on premolars. M1 is very open and hypoconal groove is practically lost and hypoconal constriction in a notch. The pli caballine is well marked in premolars and reduced in M1.

Results

DA of the three species of *Equus* provided a correct identification especially from the P3-4 and M1-2 samples (Prado & Alberdi, 2017). The teeth of Abaucán River are placed with *Equus neogeus* clearly separated from the other species of *Equus*. Results of DA indicate that among the analyzed P3 and P4 were correctly identified in origin 86.4% of cases, and with cross validation in 77.3% of cases; while M1 tooth in 73.4% of cases and 64.1% of cases, respectively (fig. 5). The morphology and the size of the teeth (P3, P4 and M1) of Abaucán River are very close to *Equus neogeus*. In the case of DA, these teeth are grouped together with the known remains of *Equus neogeu*s (fig. 5).

Discussion

The molecular dating suggests that *Hippidion* split from *Equus* at 5.6–6.5 Ma (Orlando *et al*., 2009; Der Sarkissian *et al*., 2015), suggesting an early divergence in North America prior to the colonization of South America, after the formation of the Panamanian Isthmus 2.8 Ma and the Great American Biotic Interchange (GABI, O'Dea *et al*., 2017). The paleontological evidence of the dispersion of horses into South America shows different patterns. According to Alberdi & Prado (2004), *Hippidion devillei* was the first species of the Equini recorded in South America. It is found in land-mammal bearing sediments of the Uquian SALMA (Middle to Late Pliocene), in northern Argentina (Prado *et al*., 1998). *Hippidion principale* was recorded for the first time in sediments of the Ensenadan SALMA (Early Pleistocene) in Bolivia. *Hippidion saldiasi* was recorded in sediments of the Lujanian SALMA (Late Pleistocene) in Patagonia (Alberdi & Prado, 2004). In the case of *Equus*, two species (*Equus andium*, and *Equus insulatus*) were recorded in western South America, while *Equus neogeus*, was recorded in eastern South America. This distribution could be correlated with the two inter-American savannah corridors through South America: the high Andean route and the low eastern route (Prado & Alberdi, 2016).

According to MacFadden (2013), the dispersal of *Equus* into South America represents an important event in the historical biogeography of Pleistocene mammals on that continent (MacFadden, 2013). So far as the biochronology is known, most of these occurrences are Late Pleistocene, with one significant exception from the Tarija basin of Bolivia were recorded *Equus insulatus* (occur between 0.99 to 0.76 Ma).

In Argentina dispersal of *Equus* occurred during the Late Pleistocene, and it defines the base of the Lujanian SALMA (*sensu* Pascual *et al*., 1996). The record of *Equus* diminished from North to South,

particularly during the Latest Pleistocene. Unlike *Hippidion* that registers in high latitudes, *Equus* does not present records in Patagonia. The southernmost record is in the El Polvorín limestone Quarry in Calera Avellaneda (Olavarría, Buenos Aires province), at approximately 37º South Latitude (Prado *et al*., 2013b). The unequivocal presence of *Equus* at Tarija starting at 0.99 Ma calls into question the use of this genus as an index fossil for the Lujanian SALMA.

Nevertheless, if *Equus* is restricted to the Pampean species *Equus neogeus*, then the use of this latter taxon still can be used as an index fossil for the Lujanian Stage within the Pampean region. It is clear that, the Lujanian Stage or Biozone of *Equus neogeus* defined by Cione & Tonni (1999, 2005) does not correspond to the Lujanian SALMA of Pascual *et al*. (1965, 1996). Recently, Toledo (2014, 2017) questioned this biozone because recorded *Equus neogeus* in deposit dated around 150 and 200 ky BP from northwest Buenos Aires province. Most Lujanian vertebrates of the Buenos Aires province were found in flood plain sediments of the Guerrero Member of the Luján Formation. This unit was deposited during the interval between ca. 21 and 11 ka BP (Tonni *et al*., 2003), during which several climatic events took part (LGM, Younger Dryas, among others; see Tonni *et al*., 2003 and literature therein) that were reflected in the faunal distribution. Before this article, *Equus neogeus* was not registered in the higher altitude regions, which facilitated its use as fossil index in the plains of the pampas. This new data questions its biostratigraphic use outside said region. In Argentina have allowed discussions on the correlation of type sections in the Pampean area with other regions (*e.g.* Tauber, 2005; Reguero & Candela, 2011). It is necessary to carry out new studies in areas outside the Pampean region to contrast this scheme.

MacFadden (2013) suggest that *Equus neogeus* may have originated independently from a North American sister species within the caballine clade, thus suggesting a second dispersal of *Equus* during GABI 4 at 0.125 Ma. The first corresponded to other species through the Andes corridor. *Equus neogeus* is the largest and most slender morphotype of the South American horses, and occurs in eastern South America, but does not occur outside of lowland Argentina, Uruguay, and Brazil. This species preferred savannas and consequently would have been better adapted to open and arid landscapes (Prado & Alberdi, 1994). However, if one considers the place of the deposit, zone of valleys of height (1214 MASL) and cold climates, it should not be ruled out the possibility that this species also adapted to valleys of height with xerophytic vegetation. Luna & Cruz (2014) proposed similar adaptation for record of horses in northeast of the Córdoba province (Argentina).

The *Equus* species has experienced a massive range collapse since the latest Pleistocene. The archaeological record from Argentina suggests that the timing of horses extinction was controlled by a complex interaction between climate changes that precipitated vegetation change, combined with growing human impacts (Villavicencio *et al*., 2016). Prado *et al*. (2011, 2015) propose that a combination of factors such as diet, habitat preferences, bodymass and physiology would have played an important role in horse extinctions.

Final remarks

The morphological features of the dental remains of *Equus* from Tinogasta are characteristic of *Equus neogeus*. When compared these data with data know from other locations in South America (the series premolar and multivariate analysis) the teeth studied here are grouped with large forms such as *Equus neogeus*. These data increase the record of Equidae in South America and provide new evidence about their chronological and geographical distribution.

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