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DOCUMENTING PAST SOUTH AMERICAN CAMELID DIVERSITY AT TELARMACHAY (PUNA OF JUNÍN, PERU) USING FIRST PHALANGES MORPHOMETRICS

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ABSTRACT

To get insights into the elusive process of the domestication of South American Camelids (SAC), we focused on the Central Andean zone and the long sequence from Telarmachay (Puna of Junín, Peru), for which an early process of domestication, dating 5500-5000 BP, has been proposed. We explored the camelid diversity of Telarmachay with a morphometric approach using modern guanaco and vicuña first phalanges. Our results support the previous identification of both wild camelids and indicated hunting practices. They also suggest earlier camelid anthropic control based on the occurrence of intermediate sized specimens. However, Telarmachay camelids require further investigated using a more powerful approach to access reliable proxies of changes in locomotor behaviors.

Keywords: South American Camelids; Telarmachay; phalanges.

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DOCUMENTACIÓN DE LA DIVERSIDAD DE CAMÉLIDOS SUDAMERICANOS ANTIGUOS DE TELARMACHAY CON UN ENFOQUE MORFOMÉTRICO CLÁSICO EN LAS PRIMERAS FALANGES

RESUMEN

Para obtener más información sobre el elusivo proceso de domesticación de los camélidos sudamericanos, centramos nuestro estudio en los Andes Centrales y en la larga secuencia de Telarmachay (Puna de Junín, Perú), donde se ha propuesto un proceso temprano de domesticación hacia 5500-5000 BP. Exploramos la diversidad de los camélidos con un enfoque morfométrico utilizando primeras falanges de guanacos y vicuñas modernas. Nuestros resultados apoyan la identificación previa de los camélidos salvajes y de las prácticas de caza. También sugieren un control antrópico anterior de los camélidos con la aparición de ejemplares de tamaño intermedio. Sin embargo, los camélidos de Telarmachay necesitan ser investigados en más detalle utilizando un enfoque más especializado para acceder a proxies de los cambios en los comportamientos locomotores.

Palabras clave: Camélidos Sudamericanos; Telarmachay; falanges.

DOCUMENTANDO A DIVERSIDADE DE CAMELÍDEOS SUL-AMERICANOS DE TELARMACHAY (PUNA DE JUNÍN, PERÚ) A PARTIR DE UM ENFOQUE MORFOMÉTRICO CLÁSSICO NAS PRIMERAS FALANGES

RESUMO

Para obter informações sobre o elusivo processo de domesticação dos camelídeos sul-americanos, concentrou-se na zona central andina e na longa sequência arqueológica de Telarmachay (Puna de Junín, Peru), onde se propôs um processo de domesticação precoce em torno de 5500-5000 BP. Explorou-se a diversidade camelídea com uma abordagem morfométrica usando a primeira falange dos guanacos e vicunhas modernas. Os resultados apoiam a identificação prévia de camelídeos selvagens sugerida pelas práticas de caça. Eles também sugerem um controle antrópico anterior dos camelídeos com o aparecimento de espécimes de tamanho intermediário. No entanto, os camelídeos Telarmachay precisam ser investigados com uma abordagem poderosa para acessar procuradores de mudanças nos comportamentos locomotores.

Palavras-chave: Camelídeos sul-americanos; Telarmachay; falanges.

INTRODUCTION

South American Camelids (SAC) had great economic and cultural importance for pre-Hispanic societies in the Andes and still do for rural Andean communities (MENGONI GOÑALONS, 2008). DNA evidence has shown the northern guanaco subspecies (*Lama guanicoe cacsilensis* Müller, 1776) to be the ancestor of the llama (*Lama glama* Linnaeus, 1758) and the northern subspecies of vicuña (*Vicugna vicugna mensalis* Molina, 1782) to be the ancestor of the alpaca (*Vicugna pacos* Linnaeus, 1758) (FAN *et al.*, 2020). Zooarchaeologists have currently proposed (CARTAJENA, 2003; CARTAJENA; NÚÑEZ; GROSJEAN, 2007; MENGONI GOÑALONS, 2008; MENGONI GOÑALONS; YACOBACCIO, 2006; MOORE, 2016; WHEELER, 1985) three independent domestication centers within the *puna* ecosystem of high elevation valleys and plateaus above 3500 masl in the Andes (WINTERHALDER; THOMAS, 1978). They are distributed in the Central (central Peru) and South-Central Andes (southern Peru, northern Chile, Bolivia, and northwest Argentina) (MENGONI GOÑALONS, 2008; MENGONI GOÑALONS; YACOBACCIO, 2006). The South-Central Andes has two centers: one in the wet Bolivian *puna* south of Lake Titicaca and another in the dry *puna* of the *Salar de Atacama* region of Chile and Northwestern Argentina (MENGONI GOÑALONS; YACOBACCIO, 2006). Recent research in the South-Central Andes suggests that llama domestication occurred around 4400 BP (CARTAJENA, 2013; CARTAJENA; NÚÑEZ; GROSJEAN, 2007; MENGONI GOÑALONS, 2008; MENGONI GOÑALONS; YACOBACCIO, 2006). A separate process of guanaco domestication may have started as early as 7100 cal BP in Northwestern Argentina (YACOBACCIO, 2021). The third and oldest center of domestication lies in the humid *puna* of the Junín region of the Peruvian Central-Andes. Our current understanding of domestication in this region comes from pioneering archaeozoological studies from the 1970s and 1980s (KENT, 1982; MOORE, 1989; WHEELER PIRES-FERREIRA; PIRES-FERREIRA; KAULICKE, 1976; WING, 1972, 1975). The zooarchaeological study of the Telarmachay faunal materials suggested the early domestication of alpaca and llama around 6000-5000 BP and 5000-3800 BP, respectively (WHEELER, 1985). However, these analyses have never been supported by a quantitative approach. The most recent fieldwork and laboratory analyses dates from the 1970s to the 1990s but terrorist violence in Peru between the 1980s and 2000s ended archaeological fieldwork in these high-altitude areas until quite recently (SALCEDO CAMACHO; MARCOS, 2019).

Our study aims to explore camelid diversity across the stratigraphic layers of Telarmachay, in which both wild camelids were previously identified (WHEELER, 1985), using a quantitative morphometric approach that is accessible to all archaeozoologists. Our study is based on the first phalanx linear measurements proposed by Kent (1982) and the development of a machine learning algorithm (LE NEÜN *et al.*, 2023). We compared phalange measurements from Telarmachay to those of modern northern wild subspecies of SAC *Lama guanicoe cacsilensis* and *Vicugna vicugna mensalis* compiled in LE NEÜN *et al.* (2023).

MATERIAL

Modern samples

Measurements of modern Andean camelids have been compiled from data published starting in the 1970s (CARTAJENA; NÚÑEZ; GROSJEAN, 2007; COSTA; IZETA, 2016; ELKIN, 1996; GASCO; MARSH, 2015; GASCO; MARSH; KENT, 2014; GRANT, 2010; HESSE, 1982; IZETA, 2004; IZETA; OTAOLA; GASCO, 2009;

KAUFMANN; L'HEUREUX, 2009; KENT, 1982; LE NEÜN *et al.*, 2023; L'HEUREUX, 2007, 2008, 2010; LÓPEZ, 2003; MENEGAZ; SALEMME; ORTIZJAUREGUIZAR, 1988; MILLER, 1979; MILLER; BURGER, 1995; MONDINI; MUÑOZ, 2017; MOORE, 1989; WING, 1972; YACOBACCIO, 2010; YACOBACCIO *et al.*, 1997-1998). In this study, we used the first phalanges from three modern adult guanacos (*Lama guanicoe cacsilensis*) and the first phalanges from seven modern adult vicuñas (*Vicugna vicugna mensalis*) originating from Peru, Argentina, and Bolivia (IZETA; OTAOLA; GASCO, 2009; LE NEÜN *et al.*, 2023) (tab.1 and see supplementary data for the raw data).

Table 1. Modern camelid information (see supplementary data 1 for hind phalanges and raw data).

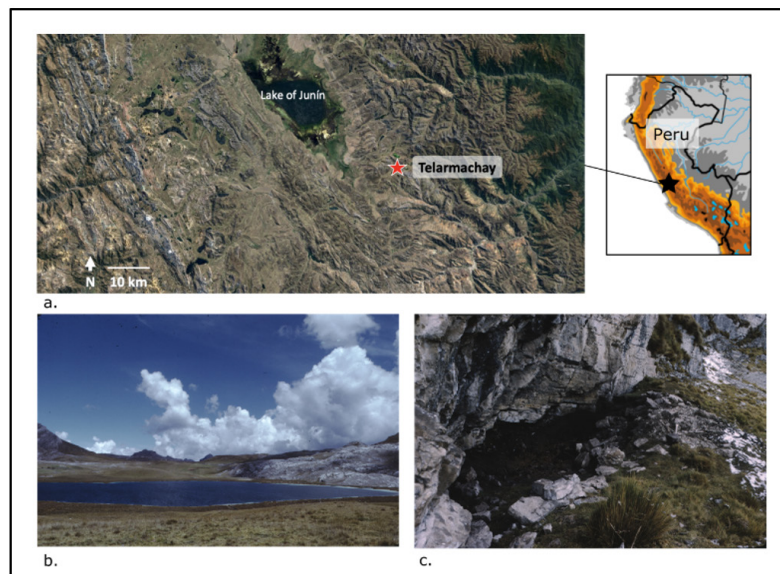
Reference	Id	Species	First phalanx location	Country and locality of specimen origin
Le Neün <i>et al.</i> , 2023	1957_1304	<i>V. v. mensalis</i>	fore	Peru, Checayani
Le Neün <i>et al.</i> , 2023	1957_1305	<i>V. v. mensalis</i>	fore	Peru, Checayani
Izeta; Otaola; Gasco, 2009	G149-7	<i>L.g.cacsilensis</i>	fore	Argentina, Catamarca
Izeta; Otaola; Gasco, 2009	G1100-1	<i>L.g.cacsilensis</i>	fore	Argentina, Salta
Izeta; Otaola; Gasco, 2009	V999-14	<i>V. v. mensalis</i>	fore	Peru, Huanuco
Izeta; Otaola; Gasco, 2009	V999-5	<i>V. v. mensalis</i>	fore	Peru, Huanuco
Izeta; Otaola; Gasco, 2009	V999-9	<i>V. v. mensalis</i>	fore	Peru, Huanuco
Izeta; Otaola; Gasco, 2009	V500	<i>V. v. mensalis</i>	fore	Argentina, Jujuy
Izeta; Otaola; Gasco, 2009	va4	<i>V. v. mensalis</i>	fore	Bolivia, Oruro
Le Neün <i>et al.</i> , 2023	GUA_02_jane	<i>L.g.cacsilensis</i>	fore	Peru, Reserva Nacional San Fernando

Source: Author's elaboration for this study.

Archeological samples

The Telarmachay rock shelter lies at 11° 11' S latitude and 75° 52' W longitude in the *puna* of Junín at an altitude of 4420 m above sea level (Fig.1). It is a shallow triangular indentation between 2.5 and 3 m in depth and 8 m in length at the base of a limestone cliff that dominates a large glacial depression containing the small Parpacocha glacial lake (LAVALLÉE, 1990; LAVALLÉE; JULIEN; WHEELER, 1985). The excavation of this site, directed by Danièle Lavallée and Michèle Julien between 1975 and 1980 (LAVALLÉE, 1990; LAVALLÉE; JULIEN; WHEELER, 1985), uncovered an exceptional bone assemblage of over 400,000 well-preserved remains (WHEELER, 1985).

The archaeological dataset is composed of first phalanges from the five archaeological layers of Telarmachay that have been dated between 9000 and 2000 BP from charcoal remains according to the chronostratigraphy established by Lavallée, Julien, and Wheeler (1985) and Lavallée and Julien (1980): two phalanges came from layer VII (9000-7200BP), 17 from layer VI (7200-6800BP), 39 from layer V (6800-5000BP), 6 from layer IV (5000-3800 BP), and 17 from layer III (3800-2800 BP) (see supplementary data for information and raw data).

Figure 1. Location and illustration of the Telarmachay rock shelter,

a. location of the site in the *Puna* of Junín (map modified from Google Earth), b. general view of the Telarmachay environment (TE_1978_9 © Danièle Lavallée, Telarmachay project/NumArchAm, (ArchAm - CNRS & Université Paris 1 Panthéon-Sorbonne), and c. view of the rock shelter entrance (TE_1975_15© Danièle Lavallée, Telarmachay project/NumArchAm, (ArchAm - CNRS & Université Paris 1 Panthéon-Sorbonne).

Source: Author's elaboration for this study.

METHOD

Linear measurements

In total, five linear measurements (Variables 1 to 5) on both fore and hind first phalanges (GASCO; MARSH; KENT, 2014; LE NEÜN *et al.* 2023) were taken following Duerst (1926), Kent (1982), and von den Driesch (1976). Modern camelid measurements were collected to the nearest 0.01 mm with a Mitutoyo Absolute (IP 67) digital caliper, whereas Telarmachay camelid measurements were acquired from three-dimensional (3D) surfaces in a PLY format. Telarmachay camelid phalanges were previously scanned using a computed tomography (CT) scanner with a spatial resolution between 100 and 500 μm at the SI Bio-Imaging Research (SIBIR) of the Smithsonian Institution Natural History Museum and segmented using Avizo v8.0 software segmentation tools. Linear measurements were collected using the IDAV Landmark v3.0 software dimension caliper tool (WILEY *et al.*, 2005). Each linear measurement was recorded three times on three different days to obtain a mean value to reduce measurement errors. In the case of complete skeletons or limbs, an average value was calculated for the four fore or hind phalanges of each individual. To validate comparisons, published data obtained under similar conditions (or replicated them when all the raw data were available) were considered.

Statistical analysis

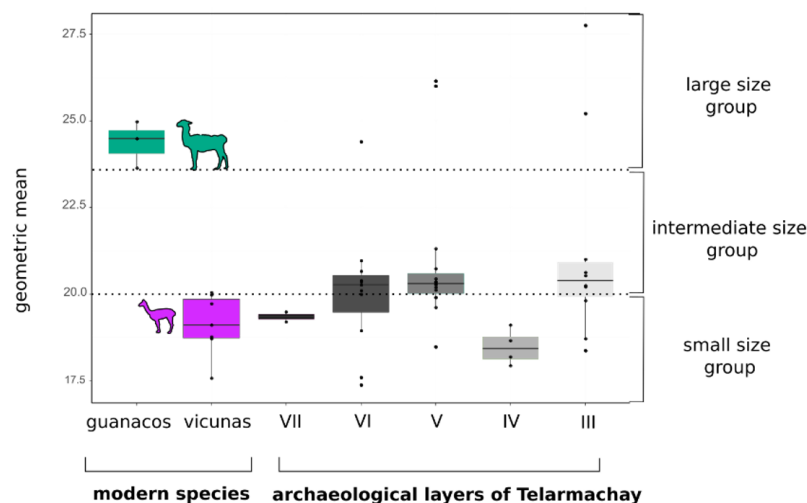
The approach of LE NEÜN *et al.* (2023) was used to identify the anatomical status of the isolated phalanges from Telarmachay. The five variables proposed by Kent (1982) were measured on both fore and hind first phalanges on modern specimens and a machine learning approach based on the k-nearest neighbors algorithm (RIPLEY, 1996) was applied to evaluate for anatomical status. Results enabled classification of individual

phalanges within a group based on their similarity to the group using the nearest k data points. We used $k = 1$ for the anatomical position. We showed, in Le Neün *et al.* (2023), that fore phalanges yielded better taxonomic resolution when only wild taxa were analyzed (96.15%). Nonetheless, the taxonomic signal for accurate identification of isolated SAC phalanges was weak and could lead to a high probability of misidentification when both the wild and domestic species are analyzed together (LE NEÜN *et al.*, 2023). Following the recommendation of Le Neün *et al.* (2023), Telarmachay fore phalanges were selected to explore camelid diversity. The geometric mean of the five variables per specimen were estimated following L'Heureux (2008) and L'Heureux and Fernández (2015). Size variation between modern and archaeological samples was displayed with a boxplot and their differences, tested with analysis of variance (ANOVA) and the pairwise t -tests with a Bonferroni correction. All analyses were performed in the R software version 1.2.5033 (R CORE TEAM 2019) statistical packages (R CORE TEAM 2019), class (VENABLES; RIPLEY, 2002), MASS (VENABLES; RIPLEY, 2002), and ape (PARADIS; SCHLIEP, 2019), and a ggplot2 graphical display (WICKHAM, 2016).

RESULTS

KNN identified 42 fore phalanges out of the 81 phalanges from Telarmachay (supplementary data). Size variations in both the modern and Telarmachay SAC fore phalanges showed non-overlapping differences with both modern wild taxa (Fig.2) and significant differences between modern species and archaeological samples (ANOVA: mean square = 14.54, $F = 3.55$, $p = 0.00584$; Fig.2). We found a small size group that includes individuals from all layers of Telarmachay (VII to III) and encompasses the size range of modern vicuñas; an intermediate-sized group that includes specimens from layer VI, V, and III, which fall between the modern vicuña and modern guanaco size groups; and a large size group which includes modern guanacos, a specimen from Telarmachay layer VI and four specimens larger than modern guanacos from layers V and III (Fig.2). Moreover, we found significant pairwise size differences between guanacos and vicuñas ($p=0.0108$), between guanaco and the camelid groups from layer VI ($p = 0.0482$), and those from layer IV ($p=0.0089$) (tab.3).

Figure 2. Box plot displaying size variation of the fore phalanges in modern guanacos (green), vicuñas (purple), and Telarmachay camelids according to the stratigraphic layers (grey gradient) using the geometric mean of five linear measurements. We found three camelid groups according to size: small, intermediate, and large.



Source: Author's elaboration for this study.

Table 2. Pairwise t-test with Bonferroni correction between both modern wild camelid species and the five archaeological layers of Telarmachay (VII to IV). Significant p-values in bold.

Modern species and archaeological layers of Telarmachay	<i>L. g. cacsilensis</i>	<i>V. v. mensalis</i>	Layer VII	Layer VI	Layer V	Layer IV
<i>V. v. mensalis</i>	0.0108	-	-	-	-	-
Layer VII	0.1976	1.0000	-	-	-	-
Layer VI	0.0482	1.0000	1.0000	-	-	-
Layer V	0.2211	1.0000	1.0000	1.0000	-	-
Layer IV	0.0089	1.0000	1.0000	1.0000	0.7487	-
Layer III	0.5051	0.8252	1.0000	1.0000	1.0000	0.5289

Source: Author's elaboration for this study.

DISCUSSION

Morphologic and demographic data from the first archaeozoological analysis of 137,085 bones from Telarmachay conducted by Wheeler (1985) showed an in-situ change in the relation between camelids and humans during the preceramic occupation dated from 9000 to 5500 BP (LAVALLÉE; JULIEN; WHEELER, 1985). The generalized hunting of deer (*Hippocamelus antisensis*) and wild camelids from 9000 to 7000 BP evolved toward the specialized hunting of vicuñas and guanacos between 7200 and 6000 BP. Wheeler (1985, 1999) posited the appearance of alpaca as the first domestic species during the following period (from 6000 to 5500 BP). She found the appearance of a new type of incisor form specific to alpacas in Layer V and an abrupt increase in the percentage of camelid fetal/neonatal bones (72.99%) in Layer IV. This abrupt increase in the percentage of camelid fetal/neonatal bones suggested that they were kept in captivity (WHEELER, 1985), in which unsanitary overcrowded captive conditions led to epizootic diseases such as enterotoxemia produced by the bacterium *Clostridium perferingens* — which still causes abortions and major mortality among domestic camelids (WHEELER, 1985). The occurrence of epizootic diseases may have been a consequence of the domestication process itself (BAIED; WHEELER, 1993). A potential domestication of the guanaco based on the occurrence of larger size fetal/neonatal individuals and leading to the appearance of llamas in layer IV around 5000 BP is also mentioned. However, this assumption, based on the occurrence of larger size fetal/neonatal individuals, relied on a very small number of individuals and requires further investigation (WHEELER, 1985).

New exploration of the Telarmachay camelids in this study shows important changes in SAC morphological diversity during the occupation of Telarmachay and enables us to test some of Wheeler's hypotheses regarding human-camelid interactions in the pre-Hispanic *puna*.

First, it shows the occurrence of small vicuña camelids throughout the whole chronology. Second, large camelids were present starting in layers VI, V, and III. Layers VII and IV had no such large camelids but this absence remains inconclusive because of the small size of these two samples. Nonetheless, small and large camelids could suggest a continuity in the exploitation of both forms throughout the occupation.

Third, we found an increase in camelid diversity starting in level VI, with the appearance of intermediate-size forms that fall between vicuña- and guanaco-size groups. This change predates the appearance of alpacas suggested by Wheeler (layer V) and could reflect an earlier date for the initiation of the domestication process of vicuña

toward alpaca or result from crossbreeding between the two wild species. We also found intermediate-size archaeological specimens on the northern Peruvian coast from the Moche (Huacas de Moche and El Brujo sites) and Chimú (Huaca Amarilla site) periods (LE NEÜN *et al.*, 2023). It has been postulated that hybridization between llamas and alpacas was restricted to the post-conquest period and was a consequence of the upheavals induced in the socioeconomic practices of native populations (WHEELER; RUSSEL; REDDEN, 1995). Nonetheless, recent publications have documented crossbreeding prior to the Spanish conquest during the Early Formative at Tulán (3400-2300 BP) in Chile (DÍAZ-MAROTO *et al.*, 2021), the Late Formative at Cerro Narrío in Ecuador, and the pre-Incan Bolivian site of Iwawi (DÍAZ-LAMEIRO *et al.*, 2022). The question of hybridization is important, but methodological limitations of the current classic morphometric approach prevent further investigation as it forbids the distinction between vicuña and alpaca for small camelids or between guanaco or llama for large camelids (LE NEÜN *et al.*, 2023). Geometric morphometric methods have shown the possibility of quantifying the processes of intraspecific morphological changes linked to human selection pressures for wild boars (*Sus scrofa*) in Europe (CUCCHI *et al.*, 2011, 2016, 2017; EVIN *et al.*, 2015) and more recently to changes linked to anthropogenic modifications of the behavior of the animal (HARBERS *et al.*, 2020a, 2020b; NEAUX *et al.*, 2021a, 2021b). Although informative, the use of criteria such as size is insufficient to illustrate its domestication process. A multidisciplinary approach such as that developed for the study of horse domestication in the Eurasian steppe (the Botai culture of northern Kazakhstan) (OLSEN, 2006) could solve our current issues and evaluate more deeply the first stages of the captivity of camelids and their domestication.

CONCLUSION

Morphometric approaches based on linear measurements of first fore phalanges confirms that the exploitation of wild camelid species (vicuña and guanaco) persisted throughout the entire Telarmachay occupational sequence. We also observed an increase in diversity of morphotypes starting in layer VI. Despite the low numbers of specimens analyzed so far, our data support the key role of Telarmachay in the trajectory of the SAC domestication process. Further investigation of the role of anthropic control is needed to overcome the methodological limitations of identifying morphofunctional variation. A new methodology should be developed and applied to a larger sample through the whole chronology of Telarmachay to document the evolution of in-situ interactions between humans and camelids.

AUTHORS' CONTRIBUTIONS

Thomas Cucchi, Elise Dufour, and Nicolas Goepfert designed this research; with Manon Le Neün who conducted this study during her PhD; M.L.N. collected CT and the measurements data and carried out morphometric analyses; M.L.N. and T.C. set the statistical protocol; M.L.N., E.D., T.C., N.G., and J.W. interpreted data; M.L.N. and E.D. drafted the manuscript with scientific and editorial input from T.C., N.G., and J.W.

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