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1 **Can first phalanx multivariate morphometrics help document past taxonomic diversity in**
2 **South American camelids?**

3
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25 Keywords: South American camelids, taxonomy, size, morphometrics

26

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28 **Abstract:**

29

30 South American Camelids (SAC) were of great economic and cultural importance for pre-
31 Hispanic societies in the Andes and still are important for rural Andean communities. However,
32 understanding their specific role and function over time is hampered by the lack of reliable
33 taxonomic identification of their archaeological remains. Although this problem has been
34 acknowledged since the 1970s, the identification of SAC from archaeological contexts still
35 mostly relies on the first phalanx multivariate morphometrics developed by Kent in 1982. The
36 goal of this study is to further explore the taxonomic potential of this method using a machine
37 learning approach including new measurements of phalanges from modern Peruvian, Bolivian
38 and Argentine SAC with additional measurements taken from the literature. Results have shown
39 that fore phalanges reliably distinguish the wild guanaco and vicuña, but the distinction between
40 the domestic forms and their wild relatives still remains tentative despite the new statistics. This

41 is largely due to limited domestic SAC comparative material, especially for the alpaca, but also
42 underlines the presence of an intermediate size morphogroup among the domestic SAC.
43 Morphometric variations recorded for the pre-Hispanic SAC are greater than those of current
44 SAC, preventing reliable identification of the archaeological specimens. These results
45 emphasize the need to improve the current SAC measurements data base and develop new
46 multiproxy approaches in the study of pre-Hispanic camelid diversity directly from the
47 archaeological material.

48

49

50 **Introduction**

51 South American Camelids (SAC) were of great economic and cultural importance for pre-
52 Hispanic societies in the Andes, providing everyday commodities (meat, fiber, leather, raw
53 materials for tool making, dung for fuel etc.) and playing an important role in the religion
54 (Bonavia, 2008; Flores Ochoa *et al.*, 1994). SAC domestication eventually led to the appearance
55 of pack animals, permitting the emergence of complex pre-Hispanic American societies
56 (Bonavia, 2008; Capriles and Tripevich, 2016). Extant SAC include two domestic species, the
57 alpaca (*Vicugna pacos* Linnaeus, 1758) and the llama (*Lama glama* Linnaeus, 1758),
58 respectively descended from the two wild species, vicuña (*Vicugna vicugna* Molina, 1782) and
59 guanaco (*Lama guanicoe* Müller, 1776) (Kadwell *et al.*, 2001; Fan *et al.*, 2020). According to
60 genetic studies, the wild SAC presently include two subspecies of guanaco, *Lama guanicoe*
61 *cacsilensis* in the north (8°-20°S) and *Lama guanicoe guanicoe* in the south (21°- 55°50'S)
62 (Gonzalez *et al.*, 2006; Marín *et al.*, 2006; Wheeler, 2012), and two of vicuña, *Vicugna vicugna*
63 *mensalis* in the north (9°30'-18°S) and *Vicugna vicugna vicugna* in the south (18-29°S)
64 (Kadwell *et al.*, 2001; Marin *et al.*, 2006; Wheeler, 2012).

65 According to archaeozoological data, the current consensus considers several
66 independent domestication events for llama and alpaca. One in the Central Peruvian highlands
67 around 6000 and 5500 BP (Wheeler, 1985) and two others one in the South-Central Andes
68 including the Salar de Atacama and Argentine *Puna* and a second in the vicinity of Lake
69 Titicaca at 4400-2000 BP (Mengoni Goñalons and Yacobaccio, 2006; Moore, 2016).

70 A recent genetic study analyzed samples from the entire geographic range of both wild
71 species, and samples of Chilean llamas and alpacas (Fan *et al.*, 2020), concluded that llama and
72 alpaca are domesticated from the Northern subspecies of guanaco (*L. g. cacsilensis*) and vicuña
73 (*V. v. mensalis*) respectively, and have undergone extensive hybridization since the European
74 conquest. In 2021, paleogenetics and classic morphometry of current and archaeological SAC

75 from Northern Chile (Diaz-Maroto *et al.*, 2021) point to llama domestication from an extinct
76 ancient guanaco population confirming both the existence of multiple centers of domestication
77 and, together with evidence of extensive hybridization between the domestic forms (Fan *et al.*
78 2020), raises serious questions concerning the reliability of using morphometrics from living
79 animals to identify SAC species from archaeological deposits.

80 Both descriptive and quantitative approaches have been used for taxonomic
81 identification of SAC from South American archaeological sites. Descriptive studies relied on
82 discrete dental (Altamirano, 1987; Wheeler, 1982) and appendicular bone characters (Adaro
83 and Benavente, 1990). Quantitative studies have been performed on the skull (Balcarcel *et al.*,
84 2021; Otte and Venero, 1979; Puig, 1988) and on fibers (Reigadas, 2001; Wheeler *et al.*, 1995;
85 Wheeler, 1996). In 1972, the first comparative morphometric study of the SAC in which she
86 concluded that guanacos and llamas grouped together as large camelids, in contrast to a second
87 group containing the small vicuña and alpaca (Wing, 1972). Since these two groups included
88 both the wild ancestor and its domestic form, it was clearly impossible to distinguish which
89 species was represented. Subsequently, because species identification was not possible, Andean
90 archaeozoologists followed the large/small classification (Miller, 1979; Miller and Burger,
91 1995; Moore, 1989). In 1982, Kent showed that phalanges provided the greatest resolution for
92 identifying the four species of camelids using a multivariate morphometric approach with
93 predictive statistics (Kent, 1982). First phalange morphometrics were then applied throughout
94 the Andes, mainly in regions where all four species may not have been present (Cartajena *et al.*,
95 2007; Costa and Izeta, 2016; Elkin, 1996; Gasco *et al.*, 2014; Gasco and Marsh, 2015; Grant,
96 2010; Hesse, 1982; Izeta, 2004; Izeta *et al.*, 2009; Kaufmann and L'Heureux, 2009; L'Heureux,
97 2010, 2007, 2008; López 2003; Menegaz *et al.*, 1988; Mondini and Muñoz, 2017; Yacobaccio
98 *et al.*, 1998; Yacobaccio, 2010).

99 Since the 1980's, a new statistical theory of shape was developed (Adams *et al.*, 2004)
100 also named geometric morphometrics (Bookstein, 1978), which is now routinely applied in
101 zooarchaeology (Cucchi *et al.*, 2015) and has proven highly reliable for distinguishing the
102 diversity of wild and domestic forms of suines (Cucchi *et al.*, 2011, 2016; Evin *et al.*, 2015)
103 equines (Cucchi *et al.*, 2017), bovines (Cucchi *et al.*, 2019) and caprines (Jeanjean *et al.*, 2022).
104 Geometric morphometrics have been applied to SAC first and second phalanges as well as
105 scapulae (L'Heureux and Hernández, 2017; 2019; Hernández *et al.*, 2021) but only to
106 distinguish llama from guanaco. Subsequently, other studies have explored the impact of
107 domestication on the skulls of the four-modern species (Balcarcel *et al.*, 2021; Wilson *et al.*,
108 2021) but these results have not yet been applied in archaeozoological studies. To date, no

109 studies have been conducted which attempt to identify archaeological remains from contexts
110 where all four SAC species may have been present.

111 Here we explore whether the multivariate morphometric approach to first phalange
112 measurements proposed by Kent can be accurate enough to document SAC taxonomic diversity
113 in archaeological contexts where all wild and domestic forms may be present. This approach
114 has the advantage of (1) being accessible to all zooarchaeologists, including those who do not
115 have expertise in Geometric morphometrics, and (2) relies on a large dataset of samples
116 recorded beginning in the 1970's. For this study we have collated published measurements with
117 data that we have collected from different institutions. Since first phalanges are often found
118 isolated in archaeological deposits, we first assessed the accuracy of these measurements in
119 discriminating hind and fore first phalanges. We then tested the interspecific taxonomic
120 resolution of first phalanges, taking into account their anatomical position (hind or fore).
121 Finally, we compared current and pre-Hispanic archaeological phalanges from Peru, Bolivia
122 and Argentina to assess the reliability of contemporary SAC comparative materials for
123 identifying SAC species in the pre-Hispanic period. Unfortunately Chilean populations are not
124 represented in our samples, as analysis using the five Kent measurements have not been
125 published for sites in this area. Hopefully this information will be available for future analyses.

126

127 **Material and methods**

128 *Modern samples*

129 The modern dataset includes measurements we collected and measurements taken at the
130 comparative anatomy collection of the Muséum national d'Histoire naturelle (MNHN), France,
131 the Museo de Historia Natural de San Rafael, Argentina, the collections of the Cátedra de
132 Anatomía Comparada, Universidad Nacional de Salta, Argentina (Mengoni Goñalons and Elkin
133 2021) and the Instituto de Arqueología, Universidad de Buenos Aires, Argentina
134 (supplementary data 1). We measured first fore and hind phalanges from 19 modern adult
135 camelids of all four species from the Central and Southern-Central Andes as well as the MNHN
136 zoological garden (captive specimens) France (tab. 1). We also measured 2 fore and 2 hind first
137 phalanges from one *Lama guanicoe cacsilensis* specimen; one fore phalange from one captive
138 alpaca specimen and 35 fore and hind phalanges of 32 *Lama glama* from 4 different herds
139 (*Cieneguillas*, *Angela*, *Rio Salado* and *Demetria*) in the Argentine *puna* (supplementary data
140 1). The “Cieneguillas_1” and “Cieneguillas_3” llamas were used for transporting goods and
141 fiber production, respectively, while, “Cieneguillas_2” was used for both purposes.
142 Additionally, 72 fore and 64 hind phalange measurements from 38 individuals, including all

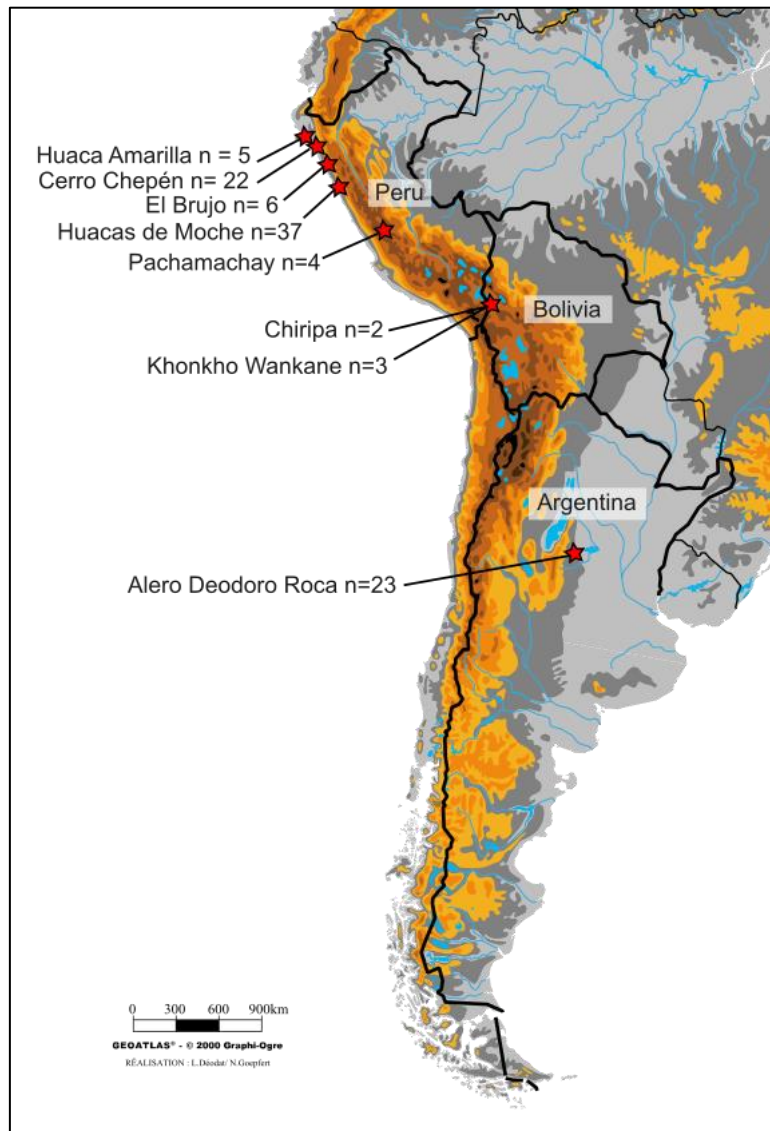
143 four species from the Central and South-Central Andes, have been taken from the literature
 144 (Izeta *et al.* 2009; Gasco and Marsh, 2015, Mondini and Muñoz, 2017; Costa and Barri, 2018)
 145 (tab. 1). Finally, because the skeletal collection is no longer available for study, we used the
 146 mean of first phalange measurements of modern Peruvian domestic SAC published by Kent
 147 (1982) which included 8 *Lama glama* and 26 *Vicugna pacos*. Additional modern Peruvian
 148 skeleton specimens are very rare or non-existent. The raw data and details are available in
 149 supplementary data 1 and 2.

	Argentina	Bolivia	Patagonia	Peru	Origen unknown
Guanaco (<i>Lama guanicoe</i>)					
Fore	5	-	3	1	5
northern form (<i>L.g. cacsilensis</i>)	2	-	-	1	-
southern form (<i>L.g. guanicoe</i>)	11	-	3	-	-
subspecies unknown	2	-	-	-	5
Hind	5	-	3	1	6
northern form (<i>L.g. cacsilensis</i>)	2	-	-	1	-
southern form (<i>L.g. guanicoe</i>)	1	-	3	-	-
subspecies unknown	2	-	-	-	6
Fore or Hind	-	-	-	1	-
northern form (<i>L.g. cacsilensis</i>)	-	-	-	1	-
Llama (<i>Lama glama</i>)					
Fore	17	6	-	-	3
Hind	17	4	-	-	5
Fore or Hind	7	-	-	-	-
Vicuña (<i>Vicugna vicugna</i>)					
Fore	3	1	-	5	2
northern form (<i>V.v. mensalis</i>)	1	1	-	5	-
southern form (<i>V.v. vicugna</i>)	1	-	-	-	-
subspecies unknown	1	-	-	-	2
Hind	2	1	-	4	2
northern form (<i>V.v. mensalis</i>)	-	1	-	4	-
southern form (<i>V.v. vicugna</i>)	1	-	-	-	-
subspecies unknown	1	-	-	-	2
Alpaca (<i>Vicugna pacos</i>)					
Fore	2	-	-	-	4
Hind	2	-	-	-	3

150
 151 tab. 1: Modern samples by origin and anatomical element. Individuals from Kent (1982) (n=8
 152 *Lama glama* and n= 26 *Vicugna pacos*) are not included in this table because the raw
 153 measurements for each phalanx are no longer available.

154
 155 *Selection and origin of archeological specimens*

156 In this study, we took phalanx measurements and also collated published data from eight
157 archaeological sites located across regions where different domestication events occurred
158 (fig.1). For Peruvian archaeological contexts, the measurements come from one cave site
159 located in the *puna* of Junín at 4250 masl, three Moche culture sites (AD 100–800) and one
160 Lambayeque-Sicán culture site (AD 800–1350) located on the northern coast (fig.1). Four
161 phalanges from the high elevation cave site of Pachamachay date to phase 5 (1500 BC) (Kent,
162 1982), while phalanges from the Moche culture come from domestic and funerary contexts at
163 the Huacas de Moche complex (n = 37; Vásquez and Tham, 2009; Vásquez *et al.*, 2020), Cerro
164 Chepén (n = 22; Vásquez and Tham 2009) and El Brujo complex graves (n = 6 fore; Goepfert,
165 2011). The Lambayeque-Sicán culture phalanges come from the Huaca Amarilla (n = 5 fore)
166 in the Sechura Desert (Goepfert *et al.*, 2018). The Bolivian archaeological camelids come from
167 domestic contexts dated AD 300 to 450 at Khonkho Wankane (n = 3), a ceremonial center
168 located on southern shore of Lake Titicaca at 3835 masl (Gasco and Marsh, 2015). Other
169 samples (n = 2) come from phase 4 of the Formative Period Chiripa complex also located on
170 the southern shore of Lake Titicaca (Browman 1980) and dated to 100 BC (Kent, 1982). Finally,
171 the Argentinian camelids come from at Alero Deodoro Roca (n = 23), a rockshelter located
172 1000 masl in the mountainous region of the *Sierras Pampeanas Australes* of the Gran Chaco
173 dated between 4500-1900 BP (Costa and Izeta, 2016). The raw data and archaeological details
174 are available in supplementary data 1 and 2.



175

176

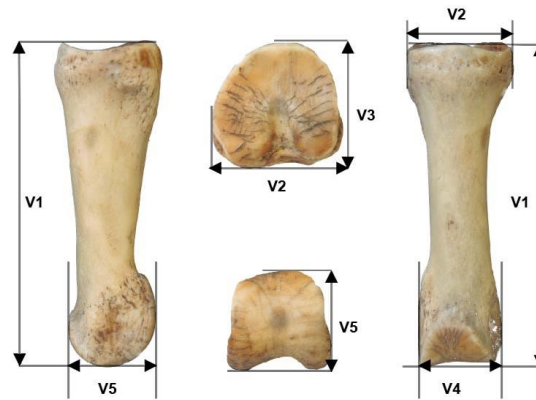
177 Figure 1. Localization of archaeological sites associated with the number of phalange
 178 measurements used in the present study. One phalange equal to one individual (map modified
 179 from Dufour and Goepfert 2020).

180

181 *Linear measurements*

182 Five linear measurements (Variables 1 to 5) on both fore and hind first phalanges (fig.2; see
 183 supplementary data 2 for measurement details and Gasco *et al.*, 2014) were taken following
 184 Duerst (1926), Kent (1982) and Von den Driesch (1976). Measurements were collected to the
 185 nearest 0.01 mm with a Mitutoyo Absolute (IP 67) digital caliper. Each linear measurement was
 186 taken three times on three different days to obtain a mean value reducing measurement error.
 187 In case of a complete skeleton or limbs, an average value was calculated for the four fore or

188 hind phalanges. To make comparison possible, we considered published data obtained in similar
189 conditions (or reproduced them when all the raw data were available).
190



191
192 Figure 2: Illustration of the five linear measurements from both fore and hind first phalanges of
193 a *Lama glama*.

194
195 *Statistical analysis*

196 Kent (1982) used size and discrete criteria to separate fore from hind phalanges in
197 archaeological collections. Here, we used the five variables measured on the modern specimens
198 to test differences between hind and fore phalanges, while taking into account the differences
199 among the four taxa of SAC using a factorial Multivariate Analysis of Variance (MANOVA).
200 We then assessed the accuracy of the anatomic and taxonomic classifications of phalanges using
201 the five variables using a machine learning approach based on the k-Nearest Neighbors
202 algorithm (k-NN; Ripley, 1996). This approach allowed us to classify an individual within a
203 group based on its similarity to the group using k nearest data points. We used $k = 1$ for the
204 anatomical position and $k = 3$ for the taxonomic status because of the exploration of four
205 different species. For 11 archaeological specimens, the anatomical position was known because
206 the skeletons were found articulated during excavation and their anatomical position was tested
207 (See supplementary data 2). Afterwards, depending on the classification rate results, the k-NN
208 method was applied to archaeological phalanges in order to predict their anatomic and
209 taxonomic status.

210 The univariate size of the phalanx was computed as the geometric mean of the five
211 variables per specimen following L'Heureux (2008) and L'Heureux and Fernández (2015). The
212 size variation among modern and archaeological samples was displayed with a box plot and

213 their differences assessed with an analysis of variance (ANOVA). The sample size of the Huacas
214 de Moche and Alero Deodoro Roca sites ($n > 10$ individuals) allowed a clustering approach using
215 finite Gaussian mixture models to explore the structure of phalange size variation and to identify
216 the occurrence of several size groups within the archaeological samples.

217 To visualize and synthesize the patterns of differentiation among the modern and
218 archaeological samples we used a Principal component analysis (PCA) and a dendrogram
219 computed with the neighbor-joining algorithm performed on euclidean distances. Both PCA
220 and the neighbor joining tree were performed on a mean of the 5 variables for each modern and
221 archaeological sample.

222 All analyses were performed with R software version 1.2.5033 (R Core Team (2019))
223 and the statistical packages R Core Team (2019), class (Venables and Ripley, 2002), MASS
224 (Venables and Ripley, 2002), mclust (Scrucca *et al.*, 2016) and ape (Paradis and Schliep, 2019)
225 with the graphical display ggplot2 (Wickham, 2016).

226

227 **Results**

228

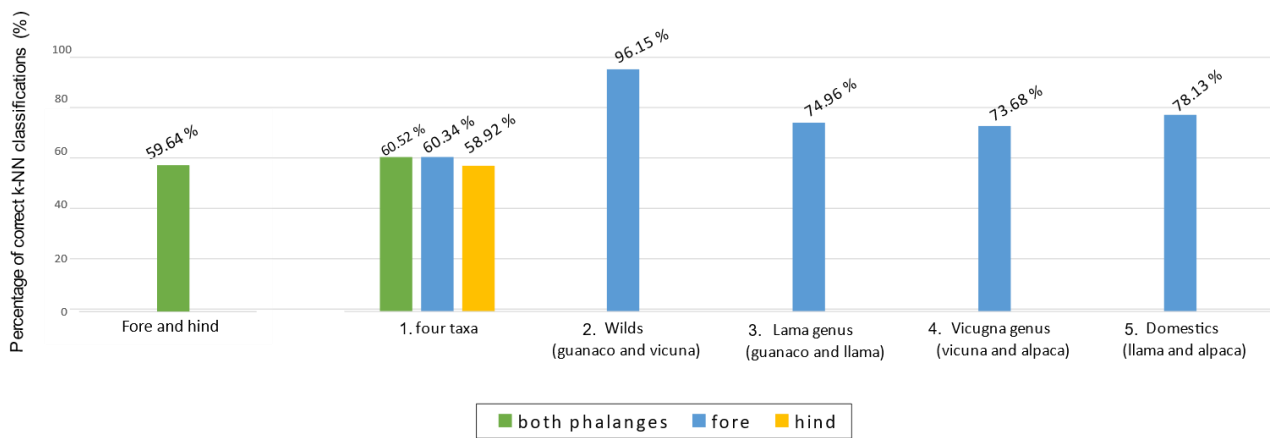
229 1. *Anatomic and taxonomic resolution in first phalange morphometrics*

230

231 We found significant differences between modern fore and hind phalanges ($p < 0.0001$) and
232 SAC taxa ($p < 0.0001$), but no interaction between anatomic (hind and fore) and taxonomic
233 groups (species) in the data set ($p = 0.17$), suggesting that anatomical differentiation between
234 hind and fore is shared among the four species of SAC and does not interfere with their
235 taxonomic differentiation. The k-NN results on modern fore and hind phalanges find a correct
236 anatomical attribution with 59,64 % accuracy (Fig. 3 and see supplementary data 2 for
237 anatomical test predictions on the 11 archaeological phalanges).

238 When both fore and hind phalanges are analyzed together using the k-NN algorithm, correct
239 species classification of the four taxa is 60.52%, when using just the hind phalanges it is 58.92%
240 and when using the fore phalanges, it is 60.34% (Fig. 3). These results suggest that fore
241 phalanges yield better taxonomic resolution. When fore phalanges are used we obtain more
242 robust percentages of correct classification and especially for the classification when only both
243 wild taxa are analyzed (96.15%) (Fig. 3). Nonetheless, the taxonomic signal for accurate
244 identification of isolated SAC phalanges is weak and could lead to a high probability of
245 misidentification when the four species are analyzed together.

246



248

249 Figure 3: Percentage of correct k-NN classifications assessing the discrimination accuracy of
 250 modern SAC first phalanges between fore and hind first phalanges and between different
 251 taxonomic units: (1) all four taxa, (2) wild taxa only, (3) *Lama* genus only, (4) *Vicugna* genus
 252 only and (5) domestic taxa only.

253

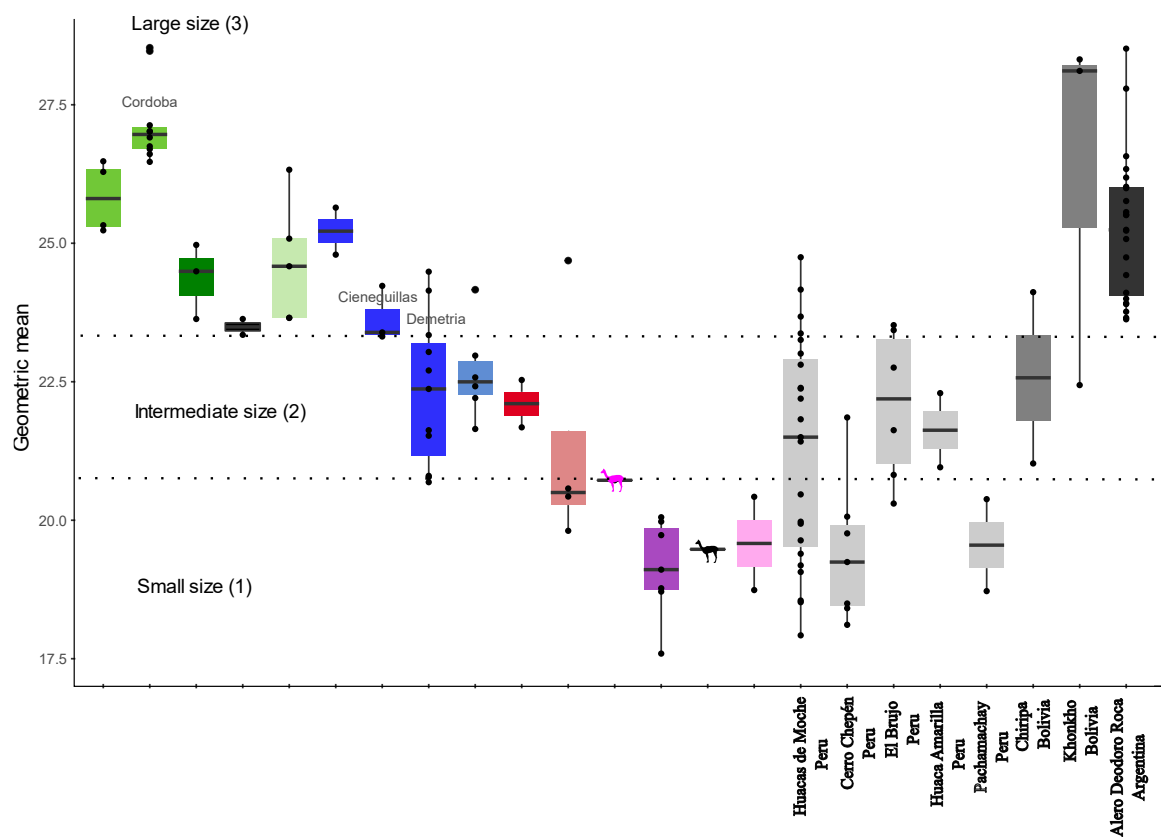
254

255 2. Morphometric variation in modern and archaeological SAC fore phalanges

256

257 We found non-overlapping size differences in wild taxa, i.e. between the small vicuña
 258 and the large guanaco, but a size continuum for the domestic taxa (Fig. 4). This continuum can
 259 be divided into: a small size group comprised of alpacas of unknown origin, an intermediate
 260 sized group which includes alpacas from Argentina and llamas from Bolivia and Argentina and
 261 a large size group which includes llamas from Argentina (Fig.4).

262



263
 264 Figure 4: Box plot displaying size variation in modern (color gradient (see Fig.2) and
 265 archaeological (grey gradient) fore phalanges of South American camelids using the geometric
 266 mean of five linear measurements.

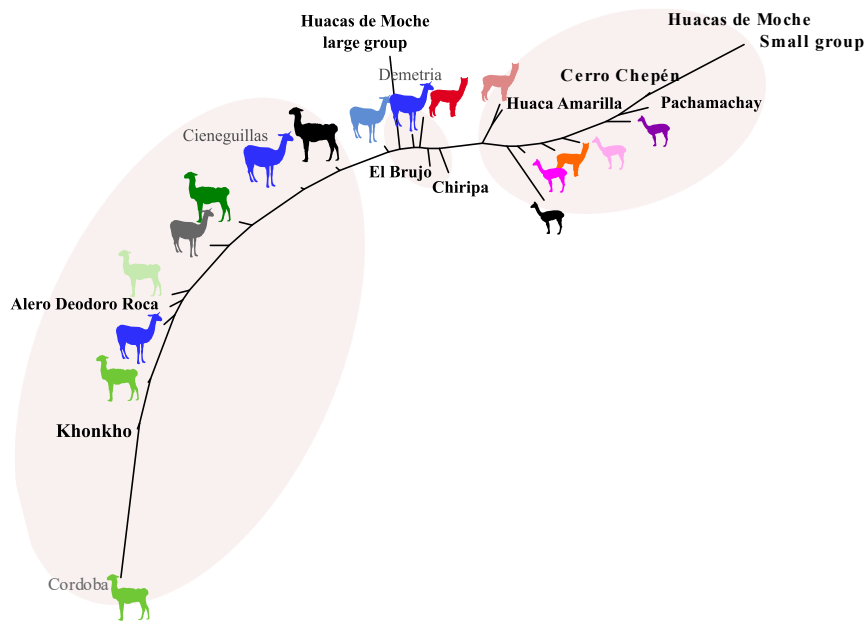
267
 268 Eigenvector output from PCA performed on the five measurements shows that, on PC1
 269 representing 96.00% of the total variance, the great length of the first phalanx (V1) explains
 270 half of the variation (50.57%), while the four other measurements contribute between 15.34%
 271 and 10.23%. When looking at the pattern of similarity and dissimilarity in modern SAC with
 272 the NJ algorithm (Fig. 5) the guanaco and vicuña are at two extremes of the variation range
 273 while the domestic taxa vary along these two extremes and split in three morphogroups: (1) the
 274 vicuña/alpaca group which includes the alpacas from Peru and the MNHN zoological garden,
 275 (2) the intermediate group which includes both llamas from Bolivia and Argentina and a single

276 alpaca from Argentina, and (3) the guanaco/llama group which includes llamas from Argentina
277 and Peru.

278 A north-south cline of size can be observed among the wild SAC (Fig. 4 and 5) with the
279 largest subspecies (*Lama guanicoe guanicoe* and *Vicugna vicugna vicugna*) in the South and
280 the smallest (*L. guanicoe cacsilencis* and *V. vicugna mensalis*) in the North. Fore phalanges of
281 archaeological SAC spread across this gradient in three morphogroups: a small, an intermediate
282 and a large (Fig. 4 and 5). The finite Gaussian mixture model identifies only the large
283 guanaco/llama size group at Alero Deodoro Roca (Fig.4) but identifies two groups at Huaca de
284 Moche even if all three size groups are present, including small vicuña/alpaca size, intermediate
285 alpaca and llama size and large guanaco/llama size animals (Fig.4). At Cerro Chépen and
286 Pachamachay the fore phalanges fall within the small vicuña/alpaca morphogroupe, except for
287 one from Cerro Chépen which falls within the intermediate size morphogroup. The El Brujo,
288 Huaca Amarilla and Chiripa fore phalanges fall within the intermediate llama/alpaca size group,
289 while the Khonkho and Alero Deodoro Roca specimens are within the large guanaco/llama
290 group (Fig. 4).

291 We find significant size differences among modern and archaeological SAC fore
292 phalanges (ANOVA: mean square = 36.90, $F = 10.4$, $p = 2e-16$; Fig.4). When looking at the
293 similarity and dissimilarity relationships among modern and archaeological means (Fig 5), we
294 observe that the Huaca de Moche small size group, Cerro Chépen and Pachamachay fore
295 phalanges are distantly related to the Northern form of vicuña. Among the more intermediate
296 archaeological fore phalanx morphotypes, those from Huaca Amarilla are more closely related
297 to the Alpaca/Vicuña morphogroup while the Huacas de Moche large group, Chiripa and El
298 Brujo are closer to the Argentinian alpaca and small llama morphogroup. Finally, Khonkho and
299 Alero Deodoro Roca are more closely related to the large Southern guanaco and Argentinian
300 and Peruvian llama morphogroup with Alero Deodoro Roca being closer to large llama and
301 captive guanaco while Khonkho is more closely related to the large Southern Guanaco.

302



Guanacos	Llamas	Alpacas	Vicunas
northern form	Peru	Peru	northern form
southern form	Bolivia	Argentina	southern form
northwestern Argentina	Argentina	captivity	northwestern Argentina
captivity			captivity

303

304 Figure 5: Dendrogram displaying the relationship of morphometric similarities and
 305 dissimilarities in fore first phalanges among modern and archaeological SAC using a neighbor
 306 joining algorithm on Euclidian distance between mean group measurements.

Discussion

Current SAC diversity

k-NN classifications found greater taxonomic resolution in fore phalanges indicating that when possible, fore phalanges should be preferred for the investigation of past SAC diversity (Izeta *et al.*, 2009). The approach supports significant differences between wild SAC already observed by Wing (1972) and as well as previous observations of a north-south cline size gradient between subspecies of the same genus (Wheeler, 1995; Yacobaccio, 2006; Izeta *et al.*, 2009; Yacobaccio *et al.*, 1998; Mengoni Goñalons and Yacobaccio, 2006; Izeta, 2004; Mengoni Goñalons, 2008; Gasco, 2014). This geographical size range can be linked to Bergmann's rule (Bergmann, 1848) as currently suggested for modern guanacos, where individuals from colder environments in the South are larger (González *et al.*, 2006; L'Heureux, 2008). Nevertheless, we have to be cautious since only one specimen of each wild taxon from the northwestern Argentine is found in our samples. Moreover, regarding domestic taxa, we observed a great size variation between llama populations which overlap with the intermediate and large size groups. We observed that non-native specimens in Argentina are taller than other Argentinian llama populations from Cieneguillas and Demetria, and those from Bolivia. It is the same for alpaca populations where Argentinian alpacas are taller than captive specimens. We also found large intra-population variation among the captive guanaco, vicuña and alpaca populations. These results support the importance of developing standard osteometric approaches at the regional scale for taxonomic discrimination (Mengoni Goñalons and Elkin, 2021) and raise the question of the interaction between the native origin and size for wild and domestic captive specimens as well.

Besides the straightforward discrimination of wild SAC, our study confirms that the distinction between wild and domestic forms of the same genus and between alpacas and llamas is far more challenging for archaeological sites and time periods where the four taxa may be present. Despite improved data sets and new statistical approaches it still not possible to reliably separate phalanges of the four SAC species. One of the main reasons is the limited sample size, especially for alpacas and *L.g. cacsilensis*, preventing full documentation of their morphometric variation (Kent, 1982). Combining Kent and the present dataset would greatly improve the overall description of modern SAC diversity in general and the representation of llamas and alpacas from Peru in particular. However, only mean measurement data produced by Kent

341 (1982) are available while the raw data are lost for future osteological studies. But regardless
342 of the size of the modern dataset, SAC diversity has drastically decreased since the Spanish
343 conquest, as evidenced by the present study and by pre-conquest alpaca and llama varieties at
344 the site of El Yaral (Wheeler *et al.*, 1995). This loss of diversity has been driven by a genetic
345 bottleneck (Fan *et al.*, 2020) produced by the massive extermination of domestic herds during
346 the Spanish conquest, estimated to be as much as 90% (Wheeler *et al.*, 1995; Flores Ochoa,
347 1982).

348

349 Comparison of modern and archaeological SAC diversity

350

351 Pre-Hispanic events might have also contributed to the loss of diversity in SAC. A study
352 conducted on the mitochondrial genomes of the four modern SAC and archaeological camelids
353 from Northern Chile (sites of Tulán 54 and 58, 3500-2400 BP) reveals reduced vicuña genetic
354 variation during the Early Formative Period and suggests a domestication model based on an
355 ancient guanaco population which is currently extinct (Díaz-Maroto *et al.*, 2020). Moreover,
356 cross-species hybridization and its consequences before and after the Spanish conquest add
357 complexity to the species identification. The existence of hybrid specimens between the
358 domestic species and possibly between wild and domestic SAC could explain the occurrence
359 of the intermediate morphogroup of llama/alpaca size. Crossbreeding between domestic and
360 wild species produces fertile offspring and recently captive rearing of "*pacovicuña*", a hybrid
361 between the vicuña and the alpaca has been undertaken, supposedly to improve alpaca fiber
362 quality (Wheeler, 2012). Crossbreeding between wild and domestic species are also mentioned
363 in written sources from 1555 (see Murra 1978), describing the annual release and return to the
364 wild of llamas as offerings to the gods. Such crossbreeding occurring in the wild happened more
365 recently. In 1940, a population of guanacos and llama hybrids is described as living in the wild
366 in the Province of Córdoba in Argentina (Wheeler, 2012). Mitochondrial and nuclear DNA
367 reveal extensive post Spanish conquest hybridization for 40% of current llamas and for 80% of
368 current alpacas (Kadwell *et al.*, 2001) and may exceed 90% in alpacas, threatening the
369 conservation the original alpaca genome (Wheeler, 2012). More recent phylogenomic studies
370 have found admixture in 36% in alpacas and 5% for llamas (Fan *et al.*, 2020).

371 The loss of diversity and the homogenization of phenotypes due to hybridization since
372 the conquest that induced the phenotypic gap between modern and archaeological SAC strongly
373 suggest that distinguishing the later using current SAC collections is probably vain.

374 However, a range of morphological diversity in pre-Hispanic SAC has been observed here,
375 including smaller Northern archaeological specimens (Peru) compared to larger Southern ones
376 (Argentina) or the occurrence of vicuña-sized camelids on the Peruvian coast (1). Domestic
377 SAC have been reported from the Early Horizon on at sites on the north coast of Peru (Szapak
378 *et al.* 2016), but are now totally absent from the region, suggesting that current geographic
379 distribution cannot be used directly to predict their presence or absence in Andean ecozones
380 during the past. Consequently, we can consider that the vicuña size morphogroup is either now
381 extinct or has not been covered by our modern comparative material, as reported in several
382 studies from different periods and locations in the Andes (Wheeler *et al.*, 1995; Casey *et al.*,
383 2018; Fan *et al.*, 2020; Díaz-Maroto *et al.*, 2021). Nevertheless, the presence of vicuñas on the
384 Northern Peruvian coast is questionable since their habitat is currently restricted to the higher
385 altitudes of the Andes (Franklin, 1983) and it is virtually impossible that it could find suitable
386 habitats on the coast. It is also unlikely that large numbers of complete hunted vicuña corpses
387 were brought to the lowlands. If vicuña meat was consumed, *charqui* (dry meat) might have
388 been the preferred way to bring it from the highlands. The only previous evidence of a vicuña-
389 like species at lower altitude corresponds to the extinct *Lama vicugna gracilis* found in late
390 Pleistocene and early Holocene deposits in the Patagonia and Eastern Pampean region of
391 Argentina and Uruguay, Argentine and Chilean Patagonia and even on the Northern coast of
392 Chile in Calama (Cajal *et al.*, 2010). The latest genetic studies with aDNA (Mitochondrial
393 DNA) assign this species to vicuña (*Vicuna vicuna*) (Weinstock *et al.* 2009), but another aDNA
394 study (Metcalf *et al.* 2016) assigned it to a species distinct from the vicuña. While these two
395 studies used older archaeological material and correspond to different geographical areas, they
396 also highlight the loss of a vicuña like taxon living at lower latitudes. The two size groups
397 identified at Huacas de Moche suggest that both llamas and alpacas were present. This is
398 congruent with isotopic studies indicating that some of the individuals for which phalanges
399 have been measured were raised in the lowlands (Vásquez *et al.*, 2020), as was previously
400 suggested by (Dufour *et al.*, 2014) and at El Brujo (Santana-Sagredo, 2020), although the SAC
401 remains were not assigned to a specific species. The permanent domestic herds in the lowlands,
402 therefore, were likely composed of both domestic species, despite previous reluctance to accept
403 the presence of alpacas outside the highlands (Topic *et al.*, 1987). The most likely hypothesis
404 would be the presence of a vicuña size domestic taxon. The specific functions of each domestic
405 species need to be further explored taking into account the diversity of political, domestic,
406 ceremonial and funeral contexts that could have driven the choices of the Mochica and the
407 Lambayeque-Sicán.

408 Furthermore, the occurrence of intermediate sized SAC (2) in Huacas de Moche, El Brujo,
409 Huaca Amarilla, Chiripa, Khonkho and Alero Deodoro de Roca falling in the range of
410 intermediate modern llama/alpaca size could suggest the occurrence of hybrids. Evidence of
411 crossbreeding practices predating the Spanish conquest have recently been reported for three
412 Early Formative specimens from Tulán, Chile (3400-2300 BP) (Díaz-Maroto *et al.*, 2021). The
413 occurrence of intermediate size animals is very important especially for the north coast of Peru
414 where no local comparative anatomical material is available because no SAC are found in the
415 area today. The identification of Mochica SAC from the Huacas de Moche site specimens is
416 very challenging. Alpaca and llama phalanges were identified in previous reports (Vásquez and
417 Tham, 2009; Vásquez *et al.*, 2020). But according to our results it is impossible to determine
418 the taxa of the Huacas de Moche intermediate group to species level, because it totally overlaps
419 the two modern domestic species morphometrics. Consequently, as previously stated, the
420 question of hybridization should be investigated as a possible cause for the intermediate size
421 archaeological specimens from various origins and predating the Spanish conquest.

422 Finally, the large guanaco/llama group (3) includes both guanacos and llamas from
423 Argentina and llamas from Peru, as well as llamas from the archaeological sites of Khonkho in
424 Bolivia and Alero Deodoro de Roca in Argentina. The largest phalanges in our sample came
425 from llamas at the sites of Khonkho and Alero Deodoro de Roca, surpassing the large Argentine
426 guanacos from Córdoba in size. The phalanges from Khonkho were previously identified as
427 castrated male llamas (Gasco and Marsh, 2015). Early castration produces exceptionally large
428 animals, and these taller, stronger and more docile camelids are often selected for caravan use
429 above individuals breed for meat or wool (Browman, 1990; Tomka 1992; Nielsen, 2000; Gasco
430 and Marsh, 2015). In our sample, the larger modern llama from Cieneguillas, (Cieneguillas 1)
431 was used for the transport of goods. The presence of camelids from Huacas de Moche and El
432 Brujo in the large guanaco/llama group should be further investigated because they are larger
433 than the mean values of modern Peruvian llamas included in our sample. Previous analysis of
434 the Alero Deodora Roca materials showed the presence of three different size groups of
435 guanacos (Costa and Izeta ,2016), while our results show that the Alero Deodora Roca samples
436 overlap in size with the large Southern guanaco subspecies (including the Córdoba guanacos)
437 and the large Argentine llamas, but we detected the presence of only one taxa with the finite
438 Gaussian mixture model. These results raise the possibility that llamas may also have been
439 present with the introduction of llamas in the region during the late Holocene (3000-3600 BP).
440 Although llamas are not found in the region today (Diaz *et al.*, 1987; Rosacher, 1992, 2004;
441 Geisa, 2012) ethnohistorical descriptions, rock art and pottery representations (Costa and Izeta

442 2016) support their previous existence. The possible presence of castrated males requires
443 further research, especially for Argentine archaeological sites because of the very large size of
444 the wild modern guanaco population of Córdoba (Costa and Barri, 2018). The effect of
445 castration on body size of camelids should also be further analyzed in the future.

446

447 **Conclusion**

448 The analysis of first phalanx linear measurements using machine learning algorithm
449 provides very accurate identification of wild SAC taxa, but has proven inefficient for accurately
450 separating wild from domestic forms. For this reason, it may therefore be prudent to keep
451 species specific distinction at the level of large versus small forms (*Lama* vs. *Vicugna*) when all
452 four SAC species are potentially present in an archaeological deposit. Nonetheless, the
453 approach does provide taxa specific identification for samples from sites or levels dated prior
454 to the beginning of domestication and from sites or levels dated after domestication where only
455 one wild ancestor was present. Moreover, in comparison to the classical gradients previously
456 defined by Kent (1982) and Gasco and Marsh (2015), our approach includes an additional taxa
457 gradient classification. Here we have defined three morphogroups of SAC size (small,
458 intermediate and large) using modern and archaeological SAC data from across their present
459 and past distributions. At this scale, we think that a general gradient definition is more
460 appropriate to identify SAC archaeological remains.

461 Although our study remains a work in progress requiring the addition of new data from
462 contemporary SAC reference collections, it remains an inexpensive method available to all
463 zooarchaeologists for documenting past SAC diversity. It is important to continue to improve
464 this kind of classical zooarchaeology analysis, conducting studies with available open access
465 data and reference tools for determination of present and past SAC diversities.

466 Nevertheless, it should be noted that our comparative approach has limitations since we
467 could not always obtain data on the native origin and life history of the modern specimens.
468 There is an urgent need to improve SAC reference collections to include specimens of known
469 origin and with life history data from across their entire range. This would be particularly
470 important to permit the study of camelid diversity in regions such, as those in Chile, which are
471 particularly lacking in this study. Since we have shown that only the identification of the wild
472 taxa is reliable, we also recommend using 3D geometric morphometrics to the highest
473 organismal resolution possible, in association with paleogenomic and isotopic proxies, to
474 examine the domestication process across the several millennia of intensification between SAC
475 and human societies (Vigne *et al.*, 2005).

476

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485

486 **Declaration of Competing Interest**

487 The authors declare no financial or conflict of interests.

488

489 **Appendix A Supplementary material**

490

491 Supplementary Component 1. Modern and archaeological camelids raw measurements.

492 Supplementary Component 2. Modern and archaeological camelids complementary
493 information.

494

495

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