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Singular patterns of skull shape and brain size change in the domestication of South American camelids

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3 **American camelids**
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21
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Abstract

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Patterns of selection in South American camelids (Lamini) and their unique demographic history establish the llama and alpaca as remarkable cases of domestication among large herd animals. Skull shape is implicated in many changes reported between wild and domestic taxa. We apply 3D geometric morphometric methods to describe skull shape, form and size differences among the four Lamini species, and between wild and domestic individuals. In doing so, we test if domesticated Lamini exhibit changes similar to those in other domesticated groups, not only in the skull, but also in brain and body size. In contrast to other domesticated artiodactyls, very little change has occurred in domestic alpacas and llamas compared to their wild counterparts. Nonetheless, their differences are statistically significant and include a flatter cranium, inclined palate and increased airorhynchy in the domestics. Selection pressures that contrast with those on other herd animals, as well as recent population bottlenecks have likely influenced the morphological patterns we note in Lamini. High-resolution 3D morphospace allows skull size, shape and form to discriminate all four species, with form providing the greatest separation. These results help differentiate the Lamini morphologically, which in nature are distinguished mainly by body size, and provide an additional tool to archaeologists for distinction of wild and domestic remains. Most of our shape analyses suggest a marginally closer relationship between the alpaca and vicuña, over the guanaco, supporting the genetic relationships for this group. The expected brain size change between wild and domestic populations is lower than previously thought, with a 15.4% reduction in llama, and 6.8% reduction in alpaca. This is the lowest brain reduction value reported thus far among domesticated Artiodactyla.

INTRODUCTION

63
64 Llamas and alpacas are the largest animals to have been domesticated in the Americas
65 (Mengoni-Goñalons and Yacobaccio 2006). These iconic South American ungulates have
66 been integral to the culture and economy of Andean communities for millenia (Cardozo 1975;
67 Wheeler 1995a; Goepfert 2010; Wheeler 2012). At present, it is generally accepted that
68 llamas (*Lama glama*) and alpacas (*Vicugna pacos*) are the domesticated descendants of the
69 guanaco (*Lama guanicoe*) and vicuña (*Vicugna vicugna*), respectively (Kadwell et al. 2001;
70 Wheeler et al. 2006; Wheeler 2012). Altogether, these four species are the only living
71 members of the Lamini clade (Kadwell et al. 2001; Wheeler et al. 2006; Casey et al. 2018;
72 Marin et al. 2018).

73
74 Throughout most of the 20th century researchers argued for various permutations of
75 ancestry among the four Lamini species. The varied permutations were due primarily to the
76 considerable morphological similarity (Menegaz et al. 1989; Davis and Gasco 2019). The
77 species are distinguishable by body size and vary from largest to smallest: guanaco, llama,
78 alpaca, and vicuña (Wheeler 1995a; Vigne et al. 2005). Archaeologists base their
79 identifications mainly on postcranial size differences and three incisor characters: root
80 presence, shape, and growth pattern (Wheeler 1995a). Their similarity is further evidenced by
81 phylogenetic analyses that find a single dental character distinguishes the two wild species
82 (guanaco vs. vicuña) from each other (Scherer 2012). Features separating wild and domestic
83 species are less clear. A common pattern in domestication is a reduction in overall size, at
84 least initially (Arbuckle 2005; Zeder 2012). This general pattern led to the false assumption
85 for many decades that the alpaca was a domestic descendant of the guanaco (rather than the
86 vicuña) (Herre and Thiede 1965; Kruska 1980, 1982; Stanley et al. 1994). However, incisor
87 morphology reveals potential hybridization of the alpaca because it has dental features similar
88 to those of both wild species (Wheeler 1995a). Recent genetic work has confirmed

89 hybridization in the alpaca (Stanley et al. 1994; Kadwell et al. 2001). Although different
90 genetic markers provide conflicting signals, these studies conclude a strong “likelihood” of
91 vicuña-alpaca descent (Kadwell et al. 2001; Marin et al. 2018; Casey et al. 2018). Admixture
92 is observed in both domestic species, but hybridization is confirmed between the alpaca and
93 guanaco (Kadwell et al. 2001). Unsurprisingly, identifying morphological features that
94 distinguish wild versus domestic Lamini is challenging. To resolve this issue, we analyze
95 morphological attributes in wild and domestic species and identify skull differences between
96 all four Lamini. We also assess skeletal expression of genetic hybridization in the alpaca.

97
98 Domestication of llamas and alpacas benefits humans: as a source of food, hide, fiber
99 and as beasts of burden (Wheeler 1995a; Mengoni-Goñalons and Yacobaccio 2006). Selection
100 began approximately 9-6 KA and had a significant effect on the group’s current genetic and
101 morphological diversity (Wheeler 1995a; Stanley et al. 1994). Understanding the specifics of
102 these historical interactions is key to interpreting the differences we observe today. During the
103 first half of the Holocene, humans preyed on wild guanacos and vicuñas, selecting first
104 through generalized hunting and then specialized hunting until eventual herd control by
105 approximately 6 KA (Tschudi 1885; Custred 1979; Wheeler 1995a). By 5-3.8 KA, herd
106 management similar to modern day breeding practices was established. This last phase is
107 evidenced through faunal composition at archaeological sites throughout the Puna region of
108 Peru, as well as mortality rates and differences in incisor morphology (Mengoni-Goñalons
109 and Yacobaccio 2006; Yacobaccio and Vilá 2012). Since then, at least two major population
110 bottlenecks reduced the genetic diversity of the group. Around 3.3 KA human population
111 expansion caused guanaco and vicuña numbers to fall from 20,000 to approximately 1000
112 (Casey et al. 2018). This event was detected through genomic studies of wild populations, but
113 we speculate it may have occurred in the domestic populations as well. It is well documented
114 that 500 years ago, the European invasion of South America affected both human and Lamini

115 populations (Tschudi 1885; Wheeler 1995a, 1995b; Casey et al. 2018). During this time,
116 Lamini numbers were reduced by an estimated 90% and human Andean populations by 80%
117 (Tschudi 1885; Wheeler 1995a). Pre-conquest domestic populations, which appear to have
118 been more diverse than today, were lost together with the breeding practices that created them
119 (Wheeler 1995a, 2012). The resultant genetic effects as well as modern breeding protocols
120 must be considered when interpreting changes related to domestication in this group.

121

122 Specific changes in skull shape have been observed repeatedly in domesticated taxa
123 across distantly related clades. Although the concept that domestication results in specific
124 changes across groups has been falsified, there is continued discussion of phenotypes that are
125 correlated with domestication (Larson and Fuller 2014; Sánchez-Villagra et al. 2017; Lord et
126 al. 2020). Many of these phenotypes are related to the skull, including rostral length, shape
127 and dorsoventral orientation. These changes have been observed in dogs, pigs and chickens
128 relative to their wild counterparts (Drake and Klingenberg 2010; Owen et al. 2014; Stange et
129 al. 2018). The cranium becomes flattened in equids and some dogs, but becomes more
130 globular in some chickens (Drake and Klingenberg 2010; Heck et al. 2018; Stange et al.
131 2018). Skull size has been shown to decrease in pigs and cattle (Owen et al. 2014;
132 Veitschegger et al. 2018), while overall skull shape is more disparate across these domestic
133 groups compared to their wild counterparts. None of these trends have been tested explicitly
134 in S.A. camelids, although many studies have compared their biometrics, allometry and brain
135 anatomy (Herre1952; Cardozo 1975; Otte and Venero 1979; Kruska 1980; Menegaz et al.
136 1989). Here, we test if domesticated Lamini exhibit morphological changes similar to those
137 described in other vertebrates using high-resolution 3D geometric morphometrics. This
138 method allows us to describe and quantify differences in skull shape independent of size, and
139 in so doing we are able to confirm a “hybrid” phenotype for the alpaca, thus clarifying its
140 relationship to other Lamini.

141

142 We assess body size, the metric most commonly used to distinguish the four Lamini
143 species, and compare it to skull size and relative brain size. Brain size reduction was one of
144 the most documented trends associated with domestication of mammals during the late 20th
145 century (Kruska 1973, 1988; Ebinger 1974) and in fact, Kruska 1980 reported a 17.6%
146 relative brain reduction in alpacas and llamas. Here, we re-evaluate brain size change in
147 domestic Lamini based on the most recent phylogeny for the group and present new brain
148 reduction values for both domestic species.

149

150

MATERIALS and METHODS

151 We use the nomenclature of Gentry et al. (2004) identifying four Lamini species, although we
152 are aware of the idiosyncratic nature of this decision given hybridization and the known
153 history of the group (Zeller and Göttert 2019). Our dataset consists of 139 adult, extant
154 Lamini skulls: 18 *Lama glama* (domestic), 86 *Lama guanicoe* (wild), 14 *Vicugna pacos*
155 (domestic), and 21 *Vicugna vicugna* (wild). Both sexes were included and adulthood was
156 assumed after complete eruption of M3. Specimens were observed at the following
157 institutions: American Museum of Natural History (AMNH, New York, USA), Museum für
158 Naturkunde (MfN, Berlin, Germany), Museo de la Plata (MLP, La Plata, Argentina), Museo
159 Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, Buenos Aires, Argentina),
160 Centro Nacional Patagónico (CENPAT, Puerto Madryn, Argentina), and Muséum National
161 d'Histoire Naturelle, Paris (MNHN, Paris, France). Craniofacial landmarks (3D: n=62) were
162 digitized for each specimen using a Microscribe digitizer (MLX, Revware, Inc., USA) and
163 Microscribe Utility Software (MUS: v.7.0.1.1). Both left and right sides were digitized.
164 Ventral and dorsal landmarks were fused in the MUS program using three reference
165 landmarks (Landmarks 1, 2, and 36) (Fig. 1, Supplementary Data S2). All data were collected
166 by the first author. Body mass ranges for all species were taken from the literature (Table 1).

167

168 <Figure 1>

169

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Analyses

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Skull shape, size and form.—Data were analyzed using 3D landmark-based geometric morphometric methods (Bookstein 1991; Rohlf and Marcus 1993; Klingenberg et al. 2002; Adams et al. 2004; Mitteroecker and Gunz 2009). All analyses and visualizations were performed in RStudio (RStudio Team, 2020) using the packages geomorph (v. 3.1.3, Adams et al. 2019), Morpho (v. 2.6, Schlager 2017), RRPP (v. 0.6.0, Collyer and Adams 2018, 2019), and ggplot2 (v.3.2.1, Wickham 2016). A Generalized Procrustes Superimposition was used to align and scale the coordinates for each skull (Goodall 1991; Rohlf 1999). The symmetrical component of shape was transformed by Principal Components Analysis (PCA) to identify major axes of variation for all four species.

A multivariate regression of Procrustes coordinates on centroid size (CS) was performed to test the extent to which allometry is responsible for skull shape variation (Supplementary Data S5). We assessed normality of shape (PC scores) and size (CS) data using the qqPlot and autoplot functions in R. Parametric Procrustes Analyses of Variance (ANOVA) and Multivariate Analyses of Variance (MANOVA) were used to test the significance of shape, size, and form (shape + size) differences between species and genera, and between wild and domestic samples. Pairwise distances were calculated using the permudist() function in ‘geomorph’. P-values were corrected for multi-test comparisons with the Benjamini-Hochberg (BH) method (Benjamini and Hochberg 1995) and considered significant at values below 0.05. MANOVAs were performed on subsamples of the first principal component scores following a dimensionality reduction approach (mevoICVP

192 function: Owen et al. 2014). This method decreases the effect of unbalanced samples by using
193 a reduced number of PCs for statistical testing. Procrustes ANOVAs used the full set of PCs.
194 Shape, size and form were also tested for their ability to distinguish groups, particularly wild
195 individuals from domestics. This was done using discriminant analyses paired with leave-one-
196 out cross validation. Here again, we applied a dimensionality reduction (mevotCVP function:
197 Owen et al. 2014) to select the lowest number of principal components that maximized
198 between-group differences (Baylac and Friess 2005). Differences in skull size (log10-
199 transformed centroid size), body size and their ratio were tested with the Kruskal-Wallis test
200 and permudist() function. Results are presented as boxplots. To test for homogeneity in the
201 effect of domestication on cranial shape, we examined whether both domestic species
202 displayed parallel trajectories of change using the trajectory analysis in ‘geomorph’.
203 Differences in shape disparity between wild and domestic groups were measured using all
204 Procrustes coordinates with a morphological disparity function in the ‘geomorph’ package.

205

206 The alpaca was given particular attention because it is known to hybridize. We
207 calculated whether it is morphologically closer to the vicuña (ancestor) or to the guanaco
208 (hybridization source) by measuring shape distances to both wild species using Procrustes
209 (GPA), Euclidean (PCA) and Mahalanobis (CVA) distances.

210

211 *Brain size estimates.*—Brain and body mass data were taken from Herre and Thiede
212 (1965) and Kruska (1980) (Supplementary Data S3-S4). Brain and body mass (Kruska 1980)
213 data for 41 individuals were extracted using *Web plot digitizer* (v. 4.2, Rohatgi 2019). This is
214 a web application that imports images of published graphs with defined axes and units, and
215 extracts the raw data points. To test the extraction, we re-executed Kruska’s original analysis,
216 obtaining the same results as in the publication, confirming the recapture. We also included

217 body mass data from specimens at UZH Zoological Museum. Body masses were available for
218 54 individuals, while only 49 had both body and brain masses (Supplementary Data S3),
219 including 24 guanacos, 9 llamas, 8 vicuñas, and 8 alpacas. Relative brain size differences
220 were calculated using the same allometric method used by Kruska: log₁₀-transformed brain
221 and body masses of 49 individuals were regressed against each other (Kruska 1980, 1988).
222 Separate ANCOVAs, each with an interaction term for genus, species, and wild or domestic
223 status, were applied to test for homogeneity of slopes. If slopes were not significantly
224 different, slope homogeneity was assumed and non-interaction ANCOVAs were recalculated
225 at each group level, yielding “common slopes”. Y-intercept differences were then interpreted
226 as differences in cerebralization, or relative brain size (Jerison 1971; Kruska 1980).

227

228 <Table 1>

229

230

RESULTS

231 *Skull shape and disparity.*—The PCA of symmetrical shape components yielded a
232 morphospace of 94 non-null dimensions, with 60% of the total variance on the first seven
233 principal components (PCs). The regression of shape on size indicated that overall, allometry
234 explained only 8.2% of skull shape variation ($F_{1,136} = 12.227$, $P = 0.001$) (Supplementary
235 Data S5). Differences in skull shape between species were tested with a MANOVA with
236 reduced dimensions, and a Procrustes ANOVA with the full set of shape scores. Both tests
237 confirm significant shape differences between all species (MANOVA: $F_{3, 134} = 8.28$, $P <$
238 0.0001), Procrustes ANOVA: $F_{3, 134} = 11.316$, $P = 0.001$). Because allometric trends appear
239 non-homogenous, allometry was not removed from the remaining shape analyses. All four
240 species overlap in a plot of PC1 vs. PC2 (Fig. 2). PC1 (23.58 % of total variance) appears
241 correlated with phylogeny, with guanacos and llamas located toward the positive end of the
242 axis, while alpacas and vicuñas are on the negative end. Thus, both llamas and guanacos had

243 proportionally 1) dorsoventrally flatter skulls, 2) narrower inter-zygomatic breadth, 3)
244 marginally longer rostra, and 4) more posteriorly-positioned orbits when compared to alpacas
245 and vicuñas (Fig. 2). In contrast, alpacas and vicuñas displayed a deeper dorsoventral
246 dimension between the palato-basiscranial floor and the skull roof (Fig. 2). The orbits of
247 alpacas and vicuñas are not only more anterior in the skull, but also more anteriorly-oriented.
248 Llamas and guanacos were most similar in overall shape, and notably, the alpaca overlapped
249 with all three other species. PC2 (8.92% of total variance) was more correlated with
250 domestication because it tended to separate the wild groups (guanacos and vicuñas) on the
251 positive end and the domestic groups (llamas and alpacas) on the negative end of the axis.
252 Along PC2, domestics showed proportionally 1) flatter and lower cranial vaults, 2) a lower
253 basicranial floor and 3) markedly higher airorhynch (Nussbaumer 1982) (Fig.2).

254

255 <Figure 2>

256

257 Overall, the crania of domesticates had a more uniform dorsoventral dimension than
258 their wild species: lower at mid- and anterior-cranium and higher at its posterior end. A
259 striking difference existed in the orientation of the rostrum: wild individuals had a relatively
260 downward pointing snout while the domesticates' rostrum was raised and more horizontal in
261 lateral view. This increased airorhynch was effected by an upward-sloping palate, beginning
262 at P4 and rising continuously toward the anterior premaxillae. However, shape differences
263 between wild and domestic samples depended on genus (Procrustes ANOVA: $F_{1, 134} = 3.23$, P
264 $= 0.001$). The trajectory analysis confirmed the amount of change (path distances) was the
265 same ($P = 0.185$) for both domesticates, but they changed in non-parallel directions
266 (trajectory angles) ($P = 0.005$). A pairwise test of shape distances indicated llama and
267 guanaco were morphologically closer than alpaca and vicuña (Table 2).

268

269 <Table 2>

270

271 Disparity in skull shape was homogenous between wilds and domestics ($P = 0.103$).

272 Of the two domestics, the alpaca had a nearly significant difference in disparity between it

273 and its wild counterpart ($P = 0.052$). However, after correction for multiple test comparisons,

274 all disparity comparisons were non-significant (Table 3).

275

276 <Table 3>

277 *Discrimination: skull shape.*—Discriminant analyses of shape correctly identified

278 species with a mean leave-one-out cross validation of 76.8 % (Table 4). Wild and domestic

279 specimens were different (MANOVA: $F_{2, 135} = 27.29$, $P = 0.0001$; Procrustes ANOVA: $F_{1, 136}$

280 $= 6.97$, $P = 0.001$) with a cross validation of 80.5%. In analyses of only the genus *Lama*,

281 guanaco and llama differed significantly (MANOVA: $F_{2, 102} = 16.2$, $P < 0.0001$); Procrustes

282 ANOVA: $F_{1, 102} = 5.08$, $P = 0.001$), with a cross validation of 81.4%. In the genus *Vicugna*,

283 both species also differ significantly (MANOVA: $F_{2, 32} = 27.27$, $P < 0.0001$; Procrustes

284 ANOVA: $F_{1, 32} = 4.13$, $P = 0.001$), with a cross validation of 81.5% (Table 4). The CVA plot,

285 whose first two axes explained 76.1% and 16.3% of total variance respectively, presented the

286 main shape differences between species (Fig. 3). Along the first axis (CV1), wild species were

287 clearly differentiated while domestic species overlapped. CV2 separated the alpaca from the

288 vicuña, but showed great overlap between llama and guanaco.

289

290 <Figure 3>

291

292 <Table 4>

293

294 *Discrimination: skull size.*—The four species differed in their skull size ($X^2_3 = 73.12$,
 295 $P < 0.0001$) with a leave-one out cross validation of 69.8% (Table 4). Both *Lama* species were
 296 larger than both *Vicugna*; *V. vicugna* was the smallest (Fig. 4D). Pairwise comparisons
 297 indicate size was significantly different in all comparisons except between llama and guanaco
 298 (Table 5). Differences in size between the wild and domestic species depended on genus ($P =$
 299 0.001). The domestic llama had a smaller skull than its wild counterpart (guanaco), while the
 300 domestic alpaca had a larger skull than the vicuña. When analyzing the genera separately,
 301 mean leave-one out cross validation accuracy was 61.4% between llama and guanaco, and
 302 88.9% between alpaca and vicuña (Table 4).

303
 304 *Discrimination: skull form.*—The four species differed in their skull form (size +
 305 shape) (MANOVA: $F_{15, 396} = 17.95$, $P < 0.0001$; Procrustes ANOVA: $F_{3-134} = 81.3$, $P < 0.001$),
 306 with a cross validation of 79.5% (Table 4). Form distinguished wild and domestic species
 307 with a cross validation of 80.5%. In separate generic analyses, llama and guanaco had a cross
 308 validation of 78.9%, and alpaca and vicuña 78.5% (Table 4). Pairwise comparisons indicated
 309 that form was significantly different in all comparisons, except between the llama and
 310 guanaco (Table 5). MANOVAs and Procrustes ANOVAs also indicated differences.
 311 Domestic species: MANOVA: $F_{5, 26} = 7.41$, $P < 0.0001$; Procrustes ANOVA: $F_{1, 30} = 18.724$,
 312 $P = 0.001$). Wild species: MANOVA: $F_{5, 100} = 175.91$, $p < 0.0001$; Procrustes ANOVA: $F_{1, 104}$
 313 $= 227.36$, $P = 0.001$).

314
 315 <Table 5>

316
 317 *Allometry.*—Skull allometry differed between species and genera (Procrustes
 318 ANOVA: $F_{1, 34} = 4.0075$, $p = 0.001$; $F_{3, 130} = 2.2106$, $P = 0.001$, respectively), and between
 319 domestic and wild samples (Procrustes ANOVA: $F_{1, 134} = 27.294$, $P = 0.001$). In separate

320 analyses of genera, allometry differed significantly between llama and guanaco (Procrustes
321 ANOVA: $F_{1, 100} = 1.93$, $P = 0.023$), and between alpaca and vicuña (Procrustes ANOVA: $F_{1, 30}$
322 $= 2.03$, $P = 0.008$).

323

324 *The alpaca.*—Both Procrustes and Euclidean distances indicated greater skull shape
325 similarity between the alpaca and vicuña (Procrustes= 0.047, Euclidean= 0.037), over the
326 guanaco (Procrustes= 0.061, Euclidean= 0.052). Mahalanobis distances provided a
327 contrasting result, suggesting a closer relationship between the alpaca and guanaco (4.35,
328 versus 5.01 with vicuña).

329

330 *Brain and body mass.*—The four species differed in their brain ($X^2_3 = 29.33$, $P <$
331 0.0001) and body ($X^2_3 = 15.82$, $P = 0.001$) masses. The llama had a significantly smaller
332 absolute brain size than the guanaco while the alpaca and vicuña did not differ (Table 6, Fig.
333 4A). Body mass differed significantly between genera but not within them, so differences
334 between each wild and domestic pair were not significant. Brain to body size ratio was
335 highest in the guanaco, making it the only species whose brain to body ratio differed
336 significantly from the rest (Fig. 4C).

337

338 <Figure 4>

339

340 <Table 6>

341

342 *Brain reduction.*—We used log₁₀-transformed brain and body masses, as per Kruska
343 (1980) in order to compare our results with his, and to test the effect of including the vicuña in
344 the analysis. Although sample sizes were small, brain-body mass allometry differed between

345 wild and domestic individuals (ANCOVA: $F_{3, 43} = 35.03$, $P = 0.02$). The two genera had the
346 same brain-body allometry ($F_{3, 43} = 24.75$, $P = 0.48$). Thus, we calculated generic
347 cerebralization differences with a non-interaction ANCOVA, yielding a common allometric
348 slope. Based on y-intercept differences, *Vicugna* had a 16.24% smaller brain than *Lama*.
349 Next, we tested for brain reduction correlated with domestication *within* each genus.
350 Allometric differences between alpaca and vicuña were not significant ($F_{3, 10} = 5.74$, $P =$
351 0.259) and their common allometric slope was 0.493. Cerebralization calculations indicate the
352 alpaca brain was 6.8% smaller than that of the vicuña. Guanaco and llama also showed a
353 common brain-body allometry ($F_{1, 29} = 2.44$, $P = 0.12$) with a common slope of 0.203.
354 Cerebralization calculations showed a 15.4% reduction in relative brain mass for the domestic
355 llama. Executing the analysis with the cubed root of mass, results were consistent with those
356 above: brain-body mass allometry differed between wild and domestic samples (ANCOVA:
357 $F_{3, 43} = 35.06$, $P = 0.02$). Cerebralization was 15.4% lower in llama than in guanaco, and 6.8%
358 lower in alpaca than in vicuña.

359

360

DISCUSSION

361 *Skull changes.*—Overall, skull shape is highly conserved among living Lamini. Much of the
362 variation observed is more strongly correlated with taxonomy than with domestication.
363 Although size accounts for only 8% of the total variation, the main axis of shape space still
364 separates the larger genus (*Lama*) from the smaller (*Vicugna*). We note that the two larger
365 *Lama* species have slightly longer rostra. This is a subtle difference between the genera, but is
366 consistent with the hypotheses of craniofacial evolutionary allometry (CREA), which states
367 that larger species have relatively longer faces in comparison to closely related taxa (Cardini
368 and Polly 2013; Tamagini et al. 2017). These rostral differences are not correlated with
369 domestication, only with taxonomy. Procrustes distances indicate the guanaco and llama are

370 the most similar, followed by the vicuña and alpaca (Table 2). The main difference between
371 the two genera is in the dorsoventral dimension of the skull—with both wild and domestic
372 *Vicugna* possessing a deeper, rounder cranium. These skull shape differences concur with
373 brain shape differences described by Herre and Thiede (1965): wild and domestic *Vicugna*
374 have a rounder brain in both lateral and posterior views compared to the genus *Lama*, which
375 has a more rectangular-shaped brain. A more thorough comparison of this group's brain
376 anatomy, particularly that of optic and olfactory regions, would further these interpretations.
377 The genera also differ in that *Vicugna* have more anteriorly positioned orbits, and wider
378 zygomatic arches compared to *Lama*. Forward-facing orbits likely provide vicuñas and
379 alpacas greater depth perception, which may be beneficial at the higher elevations they inhabit
380 (Kohler and Moya-Sola 2004). Wider zygomatic regions could be related to habitat and
381 dietary differences in that *Vicugna* have traditionally occupied higher elevations than *Lama*,
382 where drier and tougher food sources may select for larger masticatory muscles (Wheeler
383 1995; Bruner et al. 2004). There is also an enlargement of the splanchnocranial region for
384 *Vicugna*. In primates, this is correlated with increased vocalization, but we are unaware of the
385 existence or variation of vocalizations in Lamini. These differences may be developmental
386 artifacts, resulting from skull changes that are not necessarily selected for individually.

387

388 Unlike other domesticated herd animals, few skull shape differences distinguish llama
389 and alpaca from their wild relatives. For example, in horses and pigs 3D morphometric
390 comparisons show clear separation between wild and domestic species (Owen et al. 2014;
391 Heck et al. 2018). However, the changes observed in our study affect the same skull regions
392 as in other domestics, and are statistically significant differences despite their small
393 magnitude. Both domestic species have dorsoventrally flatter crania, a finding previously
394 noted by Otte and Venero (1979) when comparing the alpaca and vicuña. Unlike most other

395 domesticated mammals, we do not observe a shortening of the face in domestic Lamini
396 (Wilkins 2014). However, the most striking difference in both domesticates is an increase in
397 airorhynchy, caused by an inclined palate and simultaneous lowering of the basicranial floor.
398 This creates a more acute angle between the palate and basicranium, and places the anterior
399 rostrum on a higher horizontal plane relative to the basicranium. Various aspects of cranial
400 anatomy have been correlated with diet in herbivores, but airorhynchy is not one of them
401 (Lazagabaster et al. 2016; Codron et al. 2019). However, if the palatal angle is correlated with
402 amount of food intake, we postulate that airorhynchy may be as well. A grazing strategy
403 focused on dry, ligneous grasses has remained stable throughout the last 12,000 years for all
404 South American camelids (Wheeler 1995a). If breeding has affected food availability as we
405 would expect, then greater intake capability would be advantageous when selecting for larger
406 mass. Such a correlation would require analysis of the lower jaw and its articulation with the
407 cranium: only with this kind of study could we begin to test this hypothesis. Airorhynchy has
408 been correlated with flattening of the skull, in both primate and canid studies (Bruner et al.
409 2004; Drake and Klingenberg 2010). This is a proposed result of modularity of the face and
410 neurocranium (Drake 2011; Asahara 2013). A study on primates suggested an additional link
411 between this modularity and reduced cerebralization (Bruner et al. 2004). Although our
412 domestic camelid sample displays all three changes simultaneously: flattening of the skull,
413 airorhynchy and reduced encephalization, we can only speculate on the functional or
414 developmental implications. However, a covariance of cranial and rostral changes is certainly
415 observed in our sample and suggests modularity of these features.

416

417 Unlike other domesticated taxa, including dogs, horses, pigs, cattle, chicken and
418 pigeons (Drake and Klingenberg 2010; Owen et al. 2014; Evin et al. 2017; Young et al. 2017;
419 Heck et al. 2018; Stange et al. 2018; Veitschegger et al. 2018), llamas and alpacas do not

420 express greater skull shape disparity than their wild counterparts, nor are there significant
421 differences between any species pairing. Therefore, we disagree with Otte and Venero (1979),
422 who only compared *Vicugna*, and reported “much greater” morphological disparity in the
423 alpaca. However, larger sampling, particularly of alpacas and vicuñas, is needed to draw more
424 general conclusions.

425

426 The subtlety of differences correlated with domestication in South American camelids
427 may reflect 1) selection pressures on llamas and alpacas, and 2) the short time since the
428 genetic upheaval of the 15th century. Llamas and alpacas have not experienced strong
429 selection similar to that applied to other commercially herded mammals, from which meat and
430 dairy products are obtained. Their primary use is the production of fine quality fiber (Wheeler
431 1995b). This was true both before and since the Spanish Conquest (Wheeler 1995a, 1995b).
432 Domesticated sheep have been similarly selected for their fiber, although they have a much
433 wider geographic distribution, body size range, and breed variation (Ekarius 2008).
434 Comprehensive 3D cranio-morphometric analyses have not yet been performed in sheep
435 (Baranowski 2017; Gündemir et al. 2020). Comparisons with sheep breeds, which are selected
436 mainly for fiber, as well as other domestic taxa primarily used for their integument, could
437 further inform interpretation of our results. Of course, disentangling selection pressures
438 across groups would be very difficult. The timespan of domestication is not intrinsically a
439 limiting factor in determining amount of change (Trut 1999; Geiger and Sánchez-Villagra
440 2018). However, the conservation of skull shape between wild and domestic Lamini may be,
441 at least in part, influenced by genetic bottlenecks around 3300 and 500 years ago and the
442 relatively short period since then for population recovery and domestication.

443

444 We found that alpacas and llamas express different directions and magnitudes of skull
445 size change. As expected, the llama skull becomes significantly smaller in size compared to
446 the guanaco. This type of reduction has also been reported for domestic pigs (Owen et al.
447 2014), and may be true for domestic cattle (van Vuure 2005). Skull size is correlated with
448 body size (Jerison 1971, 1975; Finarelli 2011) and thus it is noteworthy that the domestic
449 alpacas have a larger skull, larger body mass but no increase in brain size compared to the
450 vicuña. We expected a more uniform decrease in size, as found in most domestic taxa. This
451 unusual combination of traits may result from demographic and selective history as well as
452 hybridization in the alpaca. Also, there maybe functional or ontogenetic effects that have not
453 been tested. Comparisons of computer tomography or magnetic resonance imaging of skulls
454 of all four species could clarify why the alpaca brain is so similar in size to the vicuña's, while
455 its skull is larger. Perhaps there is greater pneumatization or meningeal thickness in the alpaca
456 skull.

457

458 *Discrimination of groups.*—Skull shape can be used to discriminate all four species
459 with an accuracy of about 77%. However, they are most successfully differentiated by skull
460 form (shape + size). Skull size alone is much less successful at distinguishing species.
461 Unsurprisingly, llama and guanaco are best distinguished by their shape (~81%) because they
462 are so similar in size. In contrast, the alpaca and vicuña are best distinguished by skull size
463 (~89%). Wild and domestic species are equally differentiated by both shape and form
464 (80.5%). We conclude that although Lamini skulls are morphologically very similar, they are
465 distinct enough to be classified with high accuracy. Complete crania are rarely found in the
466 archaeological record, and 3D geometric morphometrics is a powerful tool for discrimination
467 of wild and domestic camelid remains. It would be worthwhile to assess the discriminatory
468 power of subsets of skull landmarks for fragmentary remains (Owen et al. 2014).

469

470 *Alpaca*.—Two of three distance tests indicate a marginally closer relationship
471 between the alpaca and vicuña over the guanaco. However, the Mahalanobis distance, which
472 places the alpaca closer to the guanaco, may be more relevant here. It measures inter-group
473 differences in relation to within-group differences, giving greater weight to differences in
474 directions where within group variance is less (Foote 1993). However, in discriminatory
475 analyses, the most frequent misidentification of the alpaca is for a vicuña. These mixed results
476 parallel those of Kadwell et al. (2001) that show contradicting signals from different genetic
477 markers. Larger samples would be needed for more robust results. Given the unique
478 combination of skull size and shape differences, as well as its increased body size, we
479 conclude that the alpaca phenotype certainly reflects its hybrid history.

480

481 *Overall size*.—Llamas and alpacas have a larger body mass than their wild ancestors.
482 This is unlike most other domesticated mammals, and is especially rare among the
483 Artiodactyla (Tchernov and Horwitz 1991). Domesticated goats, sheep and pigs are generally
484 smaller than their wild ancestors. There are of course the exceptionally large breeds in all
485 these species (Ekarius 2008). This reduction has been linked to a decrease in aggressive
486 behavior, sexual selection patterns, and changes in life history; all correlated with
487 domestication (Clutton-Brock 1999; Vigne et al. 2005; Zeder et al. 2006; Hongo et al. 2009;
488 Wilkins 2014). In non-artiodactyls such as rabbits and guinea pigs, body size can be larger in
489 the domesticated group (Spotorno et al. 2006; Brusini et al. 2018). For alpacas, we postulate
490 that hybridization with the larger guanaco has had a strong effect on their overall size through
491 the cumulative effect of the two parental genomes. In contrast, the much less hybridized llama
492 is more similar in body size to the guanaco (Kadwell et al. 2001). It is possible that selection
493 for fine fiber, a primary goal for herders, is less energetically demanding than products such
494 as meat and milk (Tchernov and Horwitz 1991), and therefore size reduction is offset in these
495 species. However, certain llama populations are bred primarily as pack animals (Tschudi

496 1885). Such selection could reasonably result in larger body mass. It is also reasonable that
497 larger individuals, through larger surface areas, also produce more fiber and thus body mass
498 increases generally in these domesticates. Variation in selection exercised at the population
499 level is not well documented for Lamini; this type of research would be necessary in order to
500 correlate different selection pressures with specific changes in body size. Furthermore, our
501 sample does not control for population differences in llama nor in the guanaco, whose
502 northern and southern populations are known to vary significantly in body mass (Yacobaccio
503 and Vilá 2012).

504

505 *Brain size change.*—Domesticated species reportedly have smaller brains than their
506 wild ancestors (Kruska 1980, 1988). This is a pattern that Lamini share with other
507 domesticates. In the llama and alpaca, Kruska (1980) calculated brain reduction to be 17.6%.
508 However, his study omitted the vicuña, believing the alpaca descended from the guanaco, and
509 that the vicuña was never domesticated (Herre 1952; Kruska 1980). With the inclusion of
510 vicuña, we provide new brain reduction numbers for each domestic species separately. Again,
511 we note that our sample sizes are small, and larger samples would strengthen our conclusions.
512 However, we include the entire Lamini clade in our calculations and recognize the allometric
513 differences between wild and domestic species which necessitates separate generic analyses.
514 *Vicugna* have a 16.4% smaller brain than *Lama*. Relative brain size is reduced by 6.8% in the
515 alpaca, and 15.4% in the llama. These values are lower than those calculated by Kruska
516 (1980). This is also the smallest amount of brain reduction of any domesticated artiodactyl:
517 pig brains reduce by 33.6%, and sheep by 23.9% (Ebinger 1974; Kruska 1988). Jerison (1971)
518 and Hemmer (1990) also noted a smaller brain/body mass ratio in the alpaca compared to the
519 vicuña, although we confirm the difference is not significant.

520

521 The expensive brain hypothesis has been suggested as a potential cause of brain
522 reduction; provision of food and protection from predators removes selection pressures that
523 would require keen senses (Isler and Schaik 2009). It is noteworthy that llama and alpaca
524 express so little brain size change compared to other artiodactyls as well as carnivores (~27-
525 29% brain reduction) (Kruska 1988). For the alpaca, we postulate that its hybridization with
526 much larger species (guanaco and llama) is variably affecting its brain and skull. But, for both
527 llama and alpaca, we speculate that integument might be less energetically demanding than
528 meat or dairy products. Perissodactyls express similar amounts of brain reduction: ~16%
529 (Kruska 1973). There may be phylogenetic inertia behind this commonality, but a multitude
530 of variables could contribute to the similarity. It would be difficult to further explore this
531 comparison, given the extinction and lack of skull material for wild horses (Orlando et al.
532 2013).

533 *Domestication.*—South American camelids are an atypical example of domestication.
534 The intensity of domestication -related change is much less than that recorded in other
535 artiodactyls. Additionally, domestic populations do not display greater disparity than the wild,
536 as in most domesticated taxa. The demographic history of South American camelids is likely
537 to have shaped the evolutionary trajectory of the entire group (Wheeler 1995a; Zohary et al.
538 1998; Larson and Fuller 2014; McHugh et. al. 2017; Casey et al. 2018). Only 3300 years ago
539 the initial phase of their domestication was disturbed by a rapid population reduction (Casey
540 et al. 2018). Even more disruptive, the population bottleneck of the 15th century effected a
541 rather random genetic selection from which stemmed the current members of this clade
542 (Wheeler 1995a). Effects of these events on diversity are partly evidenced by the number of
543 Preconquest llama and alpaca “types” which no longer exist today (Wheeler 1995a; Renieri et
544 al. 2009). They may also explain, in part, the great similarity between wild and domestic
545 Lamini. A better temporal sampling of archaeological specimens would elucidate how the
546 current morphological diversity came to be.

547

548 The post-conquest period was marked by weaker selection protocols and a loss of
549 overall diversity (Wheeler 1995a; Renieri et al. 2009). The degree of hybridization observed
550 in present llama and alpaca may be a direct result of this relaxed selection. The challenge in
551 disentangling different selection pressures and phenotypes is that “breeds” have not yet been
552 formally defined among domestic Lamini (Renieri et al. 2009). Renieri et al. (2009) referred
553 to the complete absence of “razas secundarias” or true races, that would delineate a series of
554 common traits requiring great control, and organized breed associations. Beyond “domestic”
555 llama or alpaca there is simply an “elevated variability of external characteristics” (Renieri et
556 al. 2009). Even the peculiar Suri alpaca, whose pelage is the result of a recent mutation is not
557 considered a true breed (Renieri et al. 2009). It is unclear if present conservation efforts in
558 South America will lead to discreet breed description, preservation of current diversity, or
559 some other outcome. However, the lack of intensive artificial selection, as that exercised on
560 domestics with many breeds, makes South American camelids good proxies for the study of
561 the “early” stages of domestication.

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580 Data Accessibility.

581 Supplementary data files S1-S6 provide all data used in this paper.

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Figure Legends

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Figure 1. Schematic of *Lama guanicoe* skull with 62 landmarks used in this study.

Figure 2. Skull shape variation among the four species as described by PC1 (23.58%) and PC2 (8.92%) of the principal component analysis (PCA). Shape changes described by each axis are shown as two overlaid landmark configurations. Mean shape is in black, shapes at the axis minima and maxima are in magenta. Configurations shown in lateral and dorsal views.

Figure 3. CVA of skull shape differences between the four species, based on 19 PCs. First and second axes of the canonical variate analysis: CV1=76.1%, and CV2=16.3%.

Figure 4. A-C: Brain and body mass comparisons by species, based on log10 transformations of cubed roots of masses. D: Differences in skull size, based on centroid sizes.

913 Table 1. Body mass ranges per species.

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Taxon	Common name	Mass_Kg	Source
<i>Lama glama</i>	llama	130-150	Wheeler 1995
		85-140	Mengoni-Goñalons and Yacobaccio 2006
<i>Lama guanicoe</i>	guanaco	96-130	Wheeler 1995
		85-140	Mengoni-Goñalons and Yacobaccio 2006
<i>Vicugna pacos</i>	alpaca	60	Wheeler 1995
		55-65	Mengoni-Goñalons and Yacobaccio 2006
<i>Vicugna vicugna</i>	vicuña	40-55	Wheeler 1995
		35-50	Mengoni-Goñalons and Yacobaccio 2006

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929 Table 2. Pairwise distances for shape, based on Procrustes coordinates. The upper triangle
 930 shows p-values, while the lower triangle shows distances. Significant p-values, after
 931 correction for multi-test comparisons, are in bold.

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	Llama	Guanaco	Alpaca	Vicuña
Llama		0.0478	0.0097	0.0040
Guanaco	0.0313		0.0003	0.0003
Alpaca	0.0558	0.0606		0.0264
Vicuña	0.0560	0.0584	0.0472	

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947 Table 3. Pairwise comparisons of skull shape disparity. P-values of differences in variance
 948 between species. The Procrustes variance (Pvar.) is provided for each species. *None of the p-
 949 values were significant after correction for multi-test comparisons.

	Llama (Pvar=0.0060)	Guanaco (Pvar=0.0059)	Alpaca (Pvar=0.0103)	Vicuña (Pvar=0.0059)
Llama		0.948	0.058	0.966
Guanaco			0.018*	0.969
Alpaca				0.052

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964 Table 4. Discriminatory accuracy, using leave-one-out cross validation. 90% confidence
 965 intervals (CI).

	Skull size (CS)	Skull shape	Skull form (shape + size)
All four species	69.8% (CI= 60.7-76.8%)	76.8% (CI: 67.8-83.9%)	79.5% (CI= 73.2-85.7)
Wild vs. domestic	60.0% (CI: 45.2-65.6%)	80.5% (CI: 73.4-85.9%)	80.5% (CI= 75.0-75.9%)
Llama vs. guanaco	61.4% (CI= 47.2-72.2%)	81.4% (CI= 74.8-88.9%)	78.9% (CI: 72.1-86.1%)
Alpaca vs. vicuña	88.9% (CI= 85.7-92.9%)	81.5% (CI= 75.0-88.9%)	78.5% (CI: 72.1-86.1%)

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977 Table 5. Pairwise differences in skull size (CS), and form (shape + size). The upper triangle
 978 shows p-values, while the lower triangle shows distances. Significant p-values, after
 979 correction for multi-test comparisons, are in bold.

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<i>Size (CS)</i>	Llama	Guanaco	Alpaca	Vicuña
Llama		0.319	0.0022	0.0001
Guanaco	17.31		0.0001	0.0001
Alpaca	73.64	90.95		0.0024
Vicuña	141.07	158.38	67.43	
<i>Form</i>				
Llama		0.189	0.0013	0.0002
Guanaco	0.04		0.0002	0.0002
Alpaca	0.12	0.15		0.0013
Vicuña	0.24	0.26	0.12	

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1001 Table 6. Pairwise differences for body and brain mass. The upper triangle shows p-values,
 1002 while the lower triangle shows distances. Significant p-values, after correction for multi-test
 1003 comparisons, are in bold.

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<i>(Body mass)</i>	Llama	Guanaco	Alpaca	Vicuña
Llama		0.345	0.011	0.000
Guanaco	0.02		0.034	0.000
Alpaca	0.06	0.04		0.158
Vicuña	0.09	0.07	0.03	
 <i>(Brain mass)</i>	 Llama	 Guanaco	 Alpaca	 Vicuña
Llama		0.040	0.084	0.106
Guanaco	0.02		0.000	0.000
Alpaca	0.02	0.04		0.969
Vicuña	0.02	0.04	0.00	
 <i>(Brain-body ratio)</i>	 Llama	 Guanaco	 Alpaca	 Vicuña
Llama		0.000	0.755	0.755
Guanaco	0.11		0.000	0.009
Alpaca	0.01	0.12		0.706
Vicuña	0.02	0.09	0.03	

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1015 Supplementary Data Files:

1016 Supplementary Data S1: List of specimens

1017 Supplementary Data S2: Landmark list

1018 Supplementary Data S3: Kruska data and PIM specimens

1019 Supplementary Data S4: Kruska data WebPlotDigitizer

1020 Supplementary Data S5: Centroid size regression table

1021 Supplementary Data S6: Camelid 3D data

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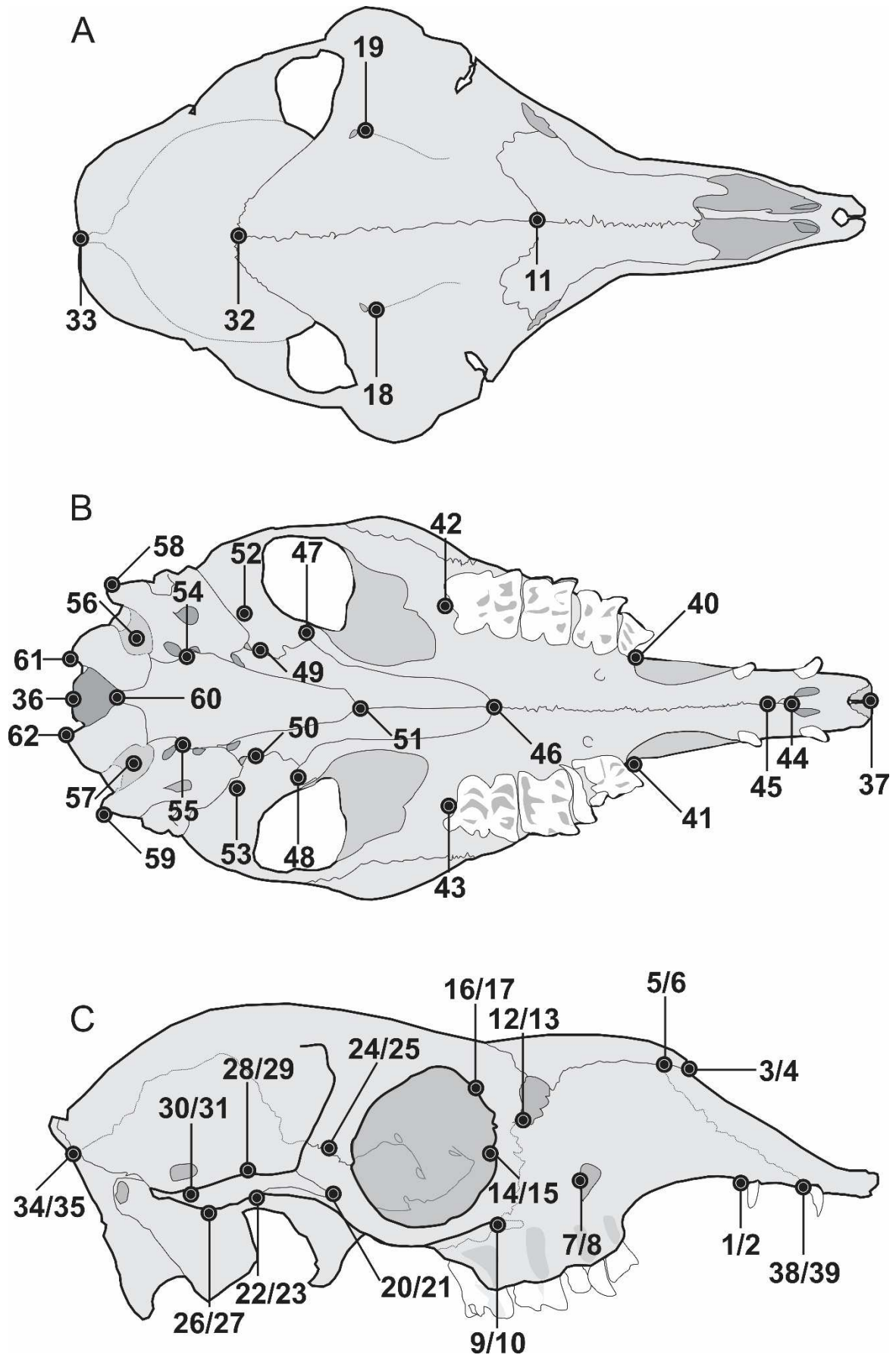
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Figures

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Figure 1.

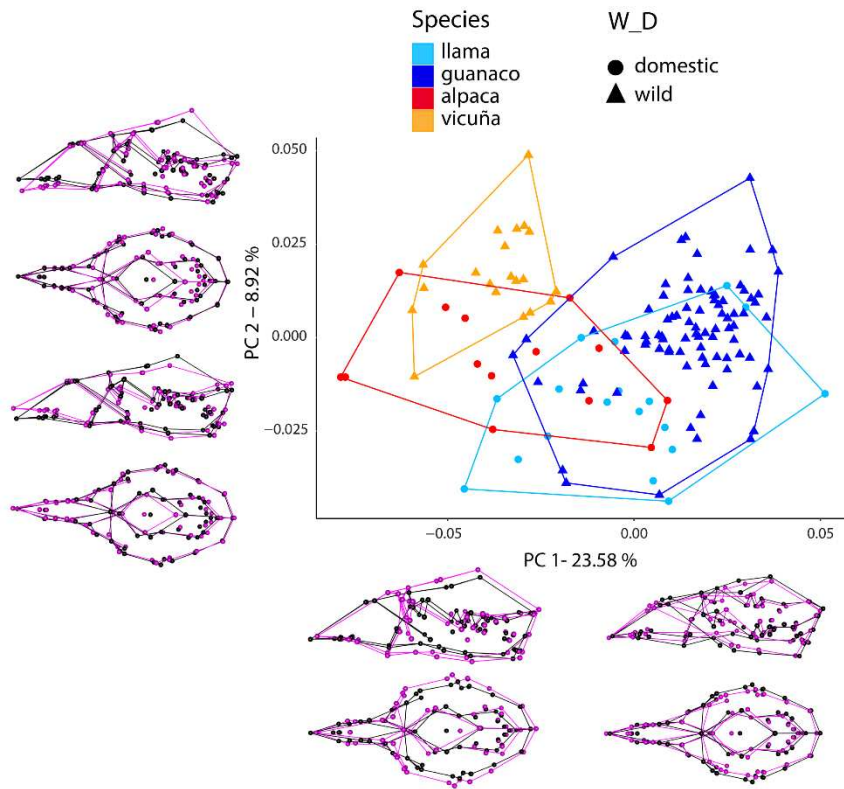


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Figure 2

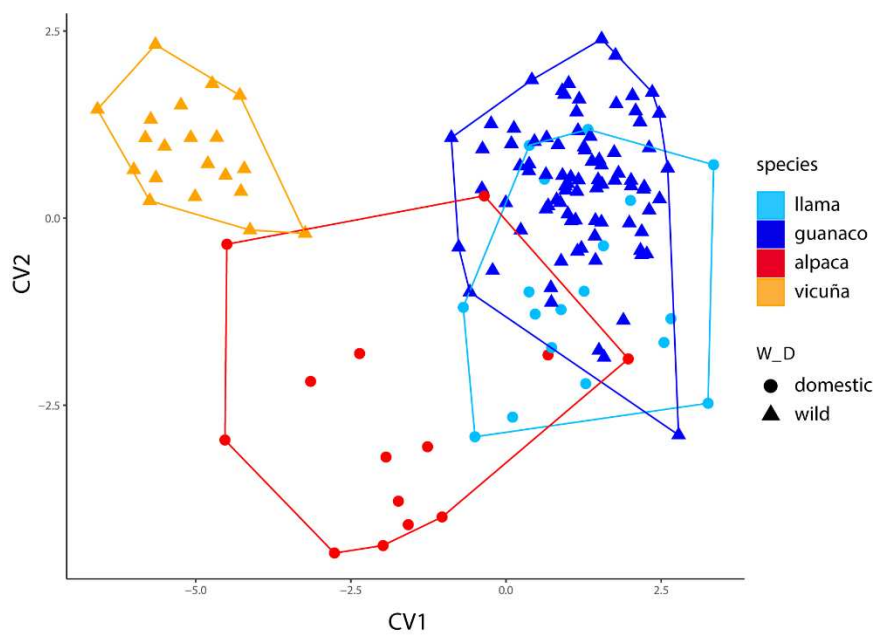


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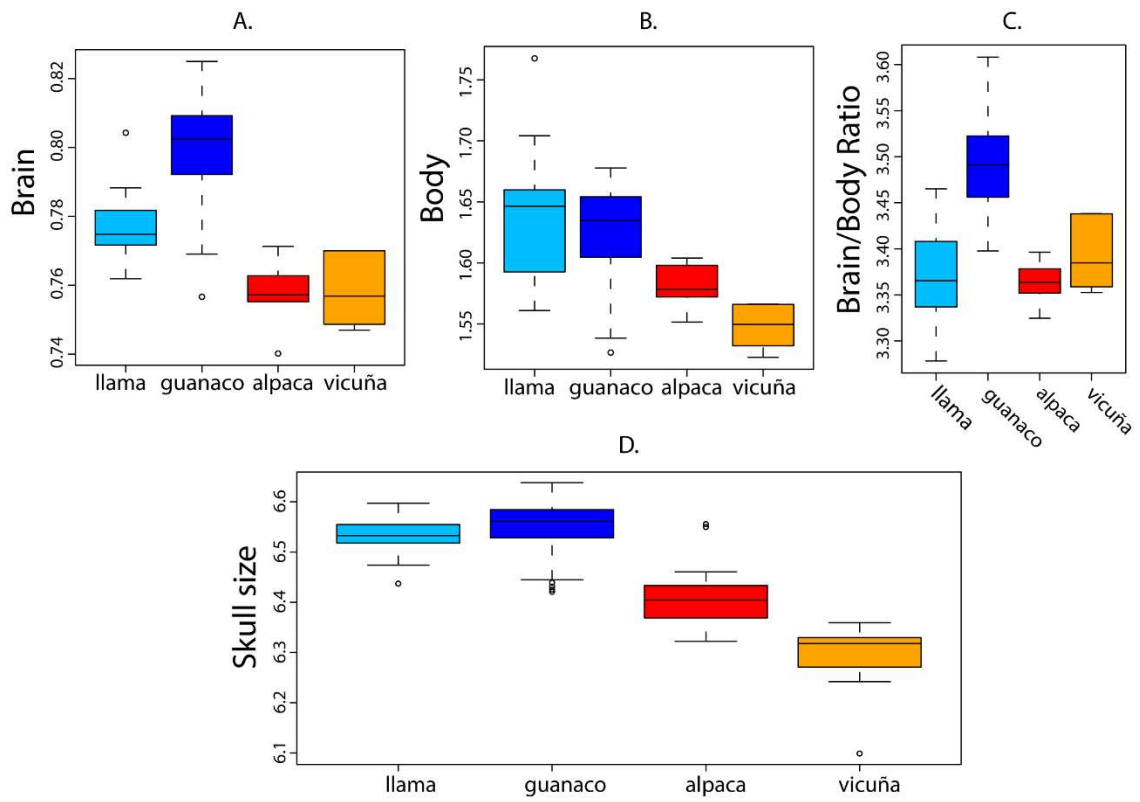
Figure 3



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Figure 4



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