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2	Article Sub- Title		
3	Article Copyright - Year	Springer Science+Business Media, LLC, part of Springer Nature 2020 (This will be the copyright line in the final PDF)	
4	Journal Name	Journal of Mammalian Evolution	
5		Family Name	Cassini
6		Particle	
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8		Suffix	
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28	Address	Buenos Aires, Argentina
29	e-mail	
30	Received	
31	Schedule	Revised
32		Accepted
33	Abstract	<p>South American cervids have a relatively recent evolutionary history in the Neotropics. Present taxonomical richness includes six genera and 17 species grouped in at least two clades, Blastocerina and Odocoileina. With few exceptions, functional morphology or ecomorphological approaches have not been rigorously applied to the masticatory apparatus of Neotropical deer. In order to understand the relationship between craniomandibular integration and feeding behavior, we used geometric morphometric methods (3D landmarks) to quantify the strength and significance of the correlation between morphology and feeding behavior. Two blocks Partial Least Squares analyses, angular comparison, regression analysis, and independent contrast were performed to explore the patterns of covariation between cranial and mandibular shape and size, and between them and continuous dietary characters. The main variation in shape is related to a gradient from a brachycephalic cranium with a robust mandible in small deer to a dolicocephalic cranium with a gracile mandible in large deer. These shape changes seem to be modeled by a complex interplay of allometric trends and biomechanically significant features related to the proportions of dietary monocotyledon, fruit, or dicotyledonous plant material. We find remarkable convergences in the brocket deer ecomorphotype in the two clades of Neotropical cervids, as well as similar craniomandibular traits between marsh and pampas deer with African mixed feeder bovinds related to monocotyledon consumption. These findings lead us to share Radinsky's interest on convergences in the masticatory apparatus of herbivorous mammals.</p>
34	Keywords separated by ' - '	Skull integration, jaw biomechanics - Brocket ecomorphotype - Herbivorous morphofunctional convergences - 3D landmarks - Radinsky
35	Foot note information	The online version of this article (https://doi.org/10.1007/s10914-020-09499-5) contains supplementary material, which is available to authorized users.

Electronic supplementary material

ESM 1
(PDF 514 kb)

ESM 2
(PDF 7074 kb)

ESM 3
(PDF 2820 kb)

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ORIGINAL PAPER

4

An Ecomorphological Approach to Craniomandibular Integration in Neotropical Deer

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Q1 7

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10

Abstract

11

12 South American cervids have a relatively recent evolutionary history in the Neotropics. Present taxonomical richness
 13 includes six genera and 17 species grouped in at least two clades, Blastocerina and Odocoileina. With few excep-
 14 tions, functional morphology or ecomorphological approaches have not been rigorously applied to the masticatory
 15 apparatus of Neotropical deer. In order to understand the relationship between craniomandibular integration and
 16 feeding behavior, we used geometric morphometric methods (3D landmarks) to quantify the strength and significance
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 22 complex interplay of allometric trends and biomechanically significant features related to the proportions of dietary
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 24 ecomorphotype in the two clades of Neotropical cervids, as well as similar craniomandibular traits between marsh
 25 and pampas deer with African mixed feeder bovinds related to monocotyledon consumption. These findings lead us to
 26 share Radinsky's interest on convergences in the masticatory apparatus of herbivorous mammals.

27 **Keywords** Skull integration · jaw biomechanics · Brocket ecomorphotype · Herbivorous morphofunctional convergences · 3D
 28 landmarks · Radinsky

29

Introduction

30

31 Fifty years ago, the considerable parallelism in the early evolu-
 32 tion of Perissodactyla drew Radinsky's (1969) attention. His
 33 interest in functional and adaptive explanations for the evolu-
 34 tionary changes was evident during the course of his profes-
 35 sional career (Kay 2019). Radinsky (1985) was interested in
 36 how morphological variation correlates with phylogenetic re-
 37 lationships and ecology, and studied the biomechanics of the
 38 ungulate jaw apparatus. In chapter 17 of the posthumously
 39 published "The Evolution of Vertebrate Design", Radinsky
 40 (1987) expressed intrigue in the convergences of the masticatory
 41 and locomotor apparatus of distant lineages of herbivorous
 42 mammals.

43 Today, terrestrial artiodactyls constitute the morphological-
 44 ly and taxonomically richest and most diverse clade of extant
 45 ungulates (Janis 2007). In South America they have become
 46 the most diverse small to large herbivores, represented mainly

Electronic supplementary material The online version of this article
 (<https://doi.org/10.1007/s10914-020-09499-5>) contains supplementary
 material, which is available to authorized users.

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Q3

47 by cervids (Cassini et al. 2016). The phylogenetic analyses of
 48 Duarte et al. (2008) highlighted convergent evolution for
 49 brocket deer morphology in Neotropical deer. This seems to
 50 occur at least once in both Blastocerina and Odocoileina sensu
 51 Heckeberg et al. (2016). Here, we honor Leonard Radinsky’s
 52 work by studying these morphological convergences in an
 53 ecomorphological approach, using geometric morphometric
 54 methods to evaluate the morphological integration between
 55 the cranium and mandible of Neotropical deer.

56 **Neotropical Deer**

57 The evolutionary history of cervids in South America is rela-
 58 tively recent; they arrived approximately 1.8 Ma in the early
 59 Pleistocene and survive to Recent times (Cassini et al. 2016).
 60 According to current hypotheses Neotropical deer are united
 61 in Capreolinae (with *Alces*, *Capreolus*, *Hydropotes*, and
 62 *Rangifer*) and are represented by six genera: *Blastocerus*
 63 (marsh deer), *Hippocamelus* (huemuls), *Mazama* (brockets),
 64 *Odocoileus* (white tailed deer), *Ozotoceros* (pampas deer), and
 65 *Pudu* (pudus) with 17 species recognized (Duarte and
 66 González 2010). Recent phylogenetic studies highlighted the
 67 paraphyly of *Hippocamelus* and *Pudu*, and the polyphyly of
 68 *Mazama* (see Gutiérrez et al. 2017 and references therein).
 69 With the exception of *Pudu mephistophiles*, Neotropical deer
 70 are included in Blastocerina (sensu Heckeberg et al. 2016),
 71 including *B. dichotomus*, *H. antisensis*, *H. bisulcus*,
 72 *M. chunyi*, *M. gouazoubira*, *M. nemorivaga*, *Ozotoceros*
 73 *bezoarticus*, and *Pudu puda*, and Odocoileina (sensu
 74 Heckeberg et al. 2016), including *M. americana*, *M. bororo*,
 75 *M. bricenii*, *M. nana*, *M. pandora*, *M. temama*, *M. rufina*, and
 76 *Odocoileus virginianus*. As is evident, recent deer richness is
 77 dominated by species of *Mazama*, the brockets, which are
 78 characterized by spike-like antlers.

79 Neotropical deer occupy a variety of environments, from
 80 lowland plains to high mountains, each with open or closed
 81 and dry or wet regions (Merino and Rossi 2010). In many
 82 cases the geographic distribution of two or more species over-
 83 laps, although they do not necessarily use the same habitat or
 84 occupy the same ecological niche. Duarte and González
 85 (2010) compiled and reunited the scarce and scattered litera-
 86 ture on Neotropical deer, providing a great body of knowledge
 87 suitable for ecomorphological studies. However, most
 88 craniomandibular morphometric studies on Neotropical deer
 89 are aimed at identifying taxonomic or ontogenetic variations
 90 (Delupi and Bianchini 1995; González et al. 2002; Cassini
 91 et al. 2015; Gonzalez et al. 2018), and Merino et al. (2005)
 92 is the only published form-function study. Moreover,
 93 ecomorphological studies that have investigated the associa-
 94 tions between feeding behavior and craniomandibular mor-
 95 phology include deer within a broad ungulate sample (e.g.,
 96 Janis 1995; Mendoza and Palmqvist 2008; Cassini 2013;
 97 Fraser and Rybczynski 2014). With few exceptions, such

works are aimed at recovering taxon-free ecomorphological 98
 patterns from extant ungulates to predict feeding behavior 99
 in extinct ones (i.e., the application of Radinsky’s 1987 form- 100
 function correlation paradigm). In these studies, some authors 101
 found that the mandible better reflects diet than does the cra- 102
 nium (see Vizcaíno et al. 2016). However, these structures (or 103
 morphological units) are linked not only by their anatomical 104
 interactions, but also by developmental and functional de- 105
 mands (Cuvier’s correlation of parts principle; Vizcaíno and 106
 Bargo 2019). This covariation of traits is known as morpho- 107
 logical integration, and geometric morphometric methods are 108
 particularly useful for quantifying the strength of association 109
 between morphological traits, as well as with ecological ones 110
 (Klingenberg 2009; Olsen 2017). 111

Neotropical deer constitute an ideal group for testing hypo- 112
 theses assessing craniomandibular integration and feeding 113
 behavior. They have a recent evolutionary history and had 114
 achieved their greatest diversity by the late Pleistocene 115
 (Lujanian South American Land Mammal Age), after which 116
 all genera with large antlers (e.g., *Antifer*, *Morenelaphus*), 117
 except *Blastocerus*, became extinct and the brocket 118
 ecomorphotype became dominant (Cassini et al. 2016). If 119
 feeding behavior is a primary driver of craniomandibular 120
 shape diversification in Neotropical deer, then diet should ex- 121
 plain most of the covariation in cranial and mandibular shape. 122

Material and Methods 123

Specimens 124

We studied a sample of 194 crania and mandibles of both 125
 sexes of adult specimens representing 11 of the 17 126
 Neotropical cervid species (Table 1). Sample size reflects 127
 specimen availability and completeness. *Mazama chunyi*, *M.* 128
bricenii, *M. pandora*, *M. temama*, and *M. rufina* are lacking. 129
 Their biology and ecology are poorly documented (Merino 130
 and Rossi 2010), precluding ecomorphological analyses. 131
 Even so, the morphological and ecological diversity among 132
 Odocoileini is well represented. In addition, three Nearctic 133
 deer, *Alces americanus* (one female), *Odocoileus virginianus* 134
 (one female and five males), and *Rangifer tarandus* (three 135
 unsexed adults) were included in order to conduct the phylo- 136
 genetic signal analyses. Materials are housed in the mammal- 137
 ogy collections of the following institutions: American 138
 Museum of Natural History (AMNH, New York, USA); 139
 Administración de Parques Nacionales de la Delegación 140
 Regional Patagonia (APN-DRP, Bariloche, Argentina); 141
 Museo Regional de la Reserva de Vida Silvestre “Campos 142
 Tuyú” (CDT, Buenos Aires, Argentina); Colección Félix de 143
 Azara, “Fundación Felix de Azara” (CFA, Buenos Aires, 144
 Argentina); Colección Mamíferos Lillo, “Instituto Miguel 145
 Lillo” (CML, Tucumán, Argentina); Museo Argentino de 146

t1.1 **Table 1** Neotropical deer sexed sample and diet composition for each species

t1.2 Species	<i>n</i> (F/M)	body mass (kg) F/M	Diet	Fruit	Bryophyte and Pteridophyte	Gymnosperm	Dicot	Monocot
t1.3 <i>Blastocerus dichotomus</i> (marsh deer)	13 / 9	100/130	M.	0	0.031	0	0.423	0.546
t1.4 <i>Hippocamelus antisensis</i> (taruca)	1 / 1	55/60	B	0	0.058	0.031	0.723	0.188
t1.5 <i>Hippocamelus bisulcus</i> (huemul)	2 / 7	69.3/75.2	B	0.004	0.005	0.002	0.937	0.052
t1.6 <i>Mazama americana</i> (red brocket)	10 / 15	30	F	0.658	0	0	0.198	0.143
t1.7 <i>Mazama bororo</i> (small red brocket)	2 F	25	B	0.489	0	0	0.511	0
t1.8 <i>Mazama gouazoubira</i> (brown brocket)	13 / 20	16.4	B	0.106	0.025	0.0001	0.834	0.036
t1.9 <i>Mazama nana</i> (dwarf red brocket)	1 / 6	10	B	0.010	0	0	0.990	0
t1.10 <i>Mazama nemorivaga</i> (Amazonian gray brocket)	11 / 8	14	F	0.696	0	0	0.193	0.111
t1.11 <i>Ozotoceros bezoarticus</i> (pampas deer)	43 / 24	35/40	M	0.001	0	0	0.434	0.565
t1.12 <i>Pudu mephistophiles</i> (northern pudu)	2 / 1	5.8	B	0.250	0	0	0.75	0
t1.13 <i>Pudu puda</i> (southern pudu)	3 / 2	9.54	B	0.041	0	0.02	0.911	0.028

Notes: *N* number of specimens belonging to females (F) and males (M). Body mass (kg) following appendix 2 in Cassini et al. (2012), Mattioli (2011) and Duarte and Gonzalez (2010). When sexual dimorphism exists both values are expressed with F (female) and M (male). Diet categories follow Mendoza and Palmqvist (2008): browser (B), frugivore (F) and mixed feeder (M). Dietary composition expressed as proportion of each food item was obtained following Olsen (2017) (see M&M section and Supplementary information 1)

147 Ciencias Naturales “Bernardino Rivadavia” (MACN, Buenos
 148 Aires, Argentina); Museo de La Plata (MLP, La Plata,
 149 Argentina); Museo Provincial de Ciencias Naturales
 150 “Florentino Ameghino” (MFA-ZV, Santa Fe, Argentina);
 151 Museo de Zoología de la Universidad de São Paulo
 152 (MUZSP, São Paulo, Brazil); Nucleo de Pesquisa e
 153 Conservação de Cervídeos (NUPECCE, Jaboticabal, Brazil);
 154 and Yale Peabody Museum (YPM, New Haven, USA).

155 **Landmark Data**

156 The 3D landmark coordinates were acquired by GHC with a
 157 Microscribe G2L digitizer (Immersion Corporation, San José,
 158 CA, USA). The 84 landmarks are listed in Online Resources
 159 1–2, and shown in Fig. 1. They comprise type I (anatomic), II
 160 (mathematic), and III (semilandmarks). Both sides and the
 161 midline of the cranium were included. Semilandmarks were
 162 placed over the horny pad scar (L9–11) and anterior margin
 163 (L15–16) of the premaxilla; on the ventral (L25–27) and dorsal
 164 (L38–41) margin of the zygomatic arch; and on the dorsal
 165 (L31–32) and ventral (L35–36) margin of the orbital rim (Fig.
 166 1a; Online Resource 1).

167 In the mandible 33 landmarks were digitized.
 168 Semilandmarks were placed along the dorsal aspect of the
 169 diastema (L7–8); anterior (L13–15) and posterior (L17–18)
 170 margin of the coronoid; posterior margin of the mandibular
 171 angle (masseteric scar L24–25); and the ventral margin of the
 172 alveolar region (L27–31; Fig. 1b and Online Resource 2).
 173 During digitization sessions additional semilandmarks were
 174 taken to characterize the curves, and they were reduced in
 175 number and equispaced using “resample” software of

NYCEP (Reddy et al. 2007). On the first day of digitization
 sessions on each collection, one specimen of each sex was
 digitized five times in order to assess measurement error.

Dietary Information

Information on the feeding ecology of Neotropical deer
 species was obtained from the published literature and
 theses available online, including 16 quantitative studies
 based on microhistological fecal and gut analyses, six
 quantitative studies based on direct observations, and
 six qualitative descriptions (Online Resource 3).
 Following Olsen (2017), we transformed diet composi-
 tion for each deer species as relative percentages, so
 that frequencies would sum to 1. In order to make the
 categories comparable across studies, we aggregated the
 botanical classes into five categories: fruits (including
 fungi when present), bryophytes and pteridophytes,
 gymnosperms, dicotyledons (dicots), and monocotyle-
 dons (monocots). For each deer species, we averaged
 the proportions within each diet category across differ-
 ent habitats or seasonal values in all studies (Table 1).
 The use of proportions violates assumption in linear
 models (Warton and Hui 2011). For this reason, these
 five continuous dietary characters were logit-transformed
 prior to the analysis using the function “logit” from the
 R package car 2.1–6 (Fox and Weisberg 2011) with an
 adjustment factor of 0.1 to avoid values of zero or one.
 This protocol allows inclusion of dietary information,
 even when it is scarce and no consistent experiments
 were developed for all species (Olsen 2017).

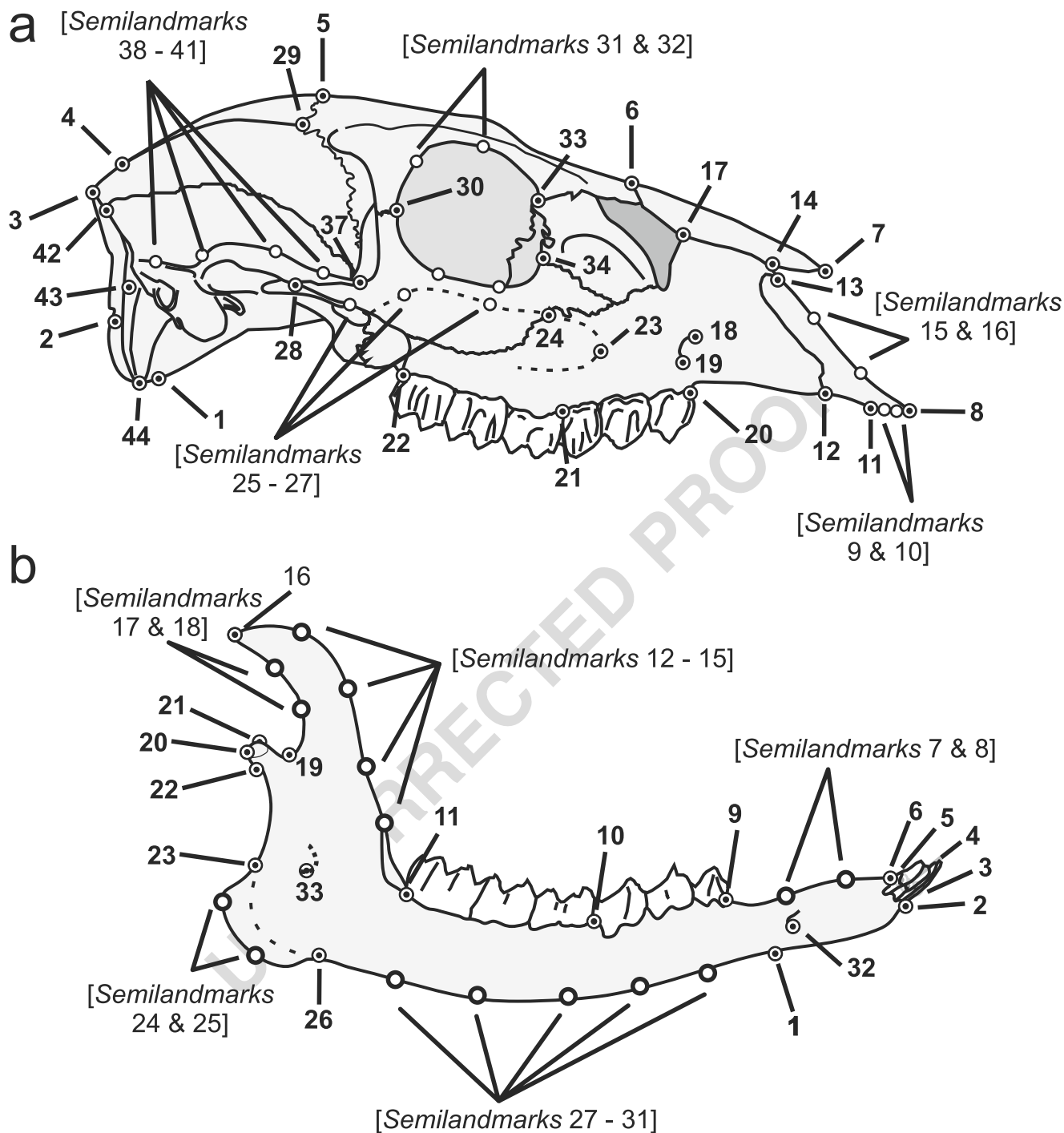


Fig. 1 Landmarks used in this study. **a** cranium and **b** mandible of *Mazama gouazoubira* (brown brocket deer) showing the landmarks on the right side and midline. Definitions listed in Online Resources 1 and 2

205 **Geometric Morphometrics**

206 Spatial variation that does not correspond to shape in the land-
 207 mark configurations were removed using Generalized
 208 Procrustes Analysis applying rotation, translation, reflection,
 209 and scaling transformations (Rohlf 1990). Centroid size was
 210 used as a proxy for size (Dryden and Mardia 1998). To assess

the influence of phylogeny on both craniomandibular shape 211
 and size on the one hand and on continuous dietary characters 212
 on the other hand, two evolutionary scenarios were considered 213
 (Online Resource 4). The first scenario was obtained from the 214
 10KTrees website version 1 (Arnold et al. 2010). The northern 215
 pudu (*Pudu mephistophiles*) was added as a sister group of 216
 Rangiferini + Odocoileini based on the phylogeny of 217

218 Heckeberg et al. (2016). The second scenario was the
 219 Cetartiodactyla tree by Zurano et al. (2019), pruned to consid-
 220 er only the species present in this study. In this scenario, the
 221 northern pudu is the sister group of Blastocercina sensu
 222 Heckeberg et al. (2016). The branch weighted squared-
 223 change parsimony method was used to reconstruct the ances-
 224 tral stages of internal nodes (Maddison 1991), and the phylo-
 225 genetic signal was tested by a permutation test (with squared-
 226 change parsimony) with 10,000 rounds of permutation test.
 227 Independent contrasts of shape and size were stored for sub-
 228 sequent analyses.

229 The Partial Least Squares analysis (PLS) was used to
 230 find correlated pairs of linear combinations between two
 231 block sets that maximize covariation between them
 232 (Klingenberg 2013). The PLS produces vectors of shape
 233 variation and individual scores that accounts for major
 234 covariation between the two blocks, and provides an
 235 estimate of covariation (R^2) based on Pearson's correla-
 236 tion coefficient. Significance of each PLS axis was cal-
 237 culated by 10,000 rounds of permutation test.

238 Evolutionary craniomandibular integration (i.e., cranium
 239 Block-1 and mandible Block-2) was studied using PLS on
 240 both the superimposed coordinates and the independent con-
 241 trasts (Klingenberg and Marugán-Lobón 2013). The extent
 242 and significance of the association between each significant
 243 PLS and log-transformed centroid size was assessed via a
 244 permutation test with 10,000 rounds.

245 Following Merino et al. (2005), two ecomorphological
 246 patterns of covariation were evaluated in: (1) Neotropical
 247 deer as a whole and (2) small and large Neotropical deer.
 248 A cut-off point between 30 and 35 kg was applied for
 249 distinguishing the small species without sexual size di-
 250 morphism from large species with reported size dimor-
 251 phism. The correlation between cranial shape and diet,
 252 and between mandibular shape and diet, were assessed
 253 via two-block PLS. Cranial or mandibular shape (i.e.,
 254 landmark configurations) and continuous diet characters
 255 (i.e., the logit-transformed diet proportions matrix) were
 256 defined as Block-1 and Block-2, respectively.

257 All morphometric analyses produce vectors in shape
 258 space (Drake and Klingenberg 2008). Angular compar-
 259 isons of vector directions were performed to evaluate the
 260 similarity in shape changes between them. The angles
 261 between these vectors were compared under the null
 262 hypothesis of orthogonality. When these angles are close
 263 to zero the shape change vectors are similar and conse-
 264 quently explain a similar shape change (Klingenberg
 265 and Marugán-Lobón 2013).

266 All morphometric analyses were performed in MorphoJ
 267 1.07a software (Klingenberg 2011). The visualization and
 268 graphics were made using the Morpho 2.6 R-package
 269 (Schlager 2017; Core Team 2018), which allows visualizing
 270 shape changes using color patterns.

Data Availability

All data generated during our analyses in the current study are
 available from the corresponding author on reasonable
 request.

Results

Evolutionary Integration

The analyses showed no significant phylogenetic signal in
 cranial and mandibular shape (Procrustes coordinates) or size
 (i.e., log-transformed centroid size). The exception was the
 cranial shape evaluated on the phylogenetic hypothesis of
 Zurano et al. (2019) (Table 2). Similar results were found for
 continuous dietary characters for both phylogenetic hypothe-
 ses (Table 2).

The PLS analysis on the Capreolinae species (PLSca) showed that the first two pairs of PLS explains about 91% of covariation (Table 3). The shape change vectors associated with the first pair were very similar to those of analysis on the independent contrasts obtained on the Zurano et al. (2019) phylogeny (PLSicz; Online Resources 5, 6). The angular comparison showed an angle between vectors of 12.139° for cranium (Block-1) and 13.831° for mandible (Block-2), both p -values <0.00001 . In addition, scores of the first pair of axes (PLSca1) of the two blocks correlated significantly and positively with cranium and mandible log-transformed centroid size ($R^2 = 0.75$ and $R^2 = 0.56$ respectively for Block-1 and Block-2, both p value <0.0001 ; see Table 3).

The PLSca1 vectors were visualized as surface plus thin plate spline (TPS) gridline deformations (Fig. 2). The shape changes associated with Block-1 ranged from a short but broad cranium (negative values) to a long and slender cranium (positive values, Fig. 2a). Consequently, small forms were characterized by the muzzle tip placed above the occlusal plane, short but high rostrum, broad palate, similar premolar and molar row lengths, anteriorly displaced large orbits, a laterally expanded zygomatic arch delimiting a large temporal fossa, and a posteriorly displaced occiput and foramen magnum (negative end, Fig. 2.a). By contrast, large forms were characterized by the muzzle tip placed below the occlusal plane, long and low rostrum, narrow palate, premolar row shorter than molar row, posteriorly displaced small orbits, medially compressed zygomatic arch delimiting a small temporal fossa, and an anteriorly displaced occiput and foramen magnum (positive end, Fig. 2.a). These shape changes correlated to a range of shapes in Block-2 from a mandible with an acute angle between the alveolar region and the ascending ramus on the negative end to an obtuse angle on the positive end. In correspondence with cranial shape changes, small forms were characterized by a mandible with robust symphysis with

t2.1 **Table 2** Phylogenetical signal tests for shape, size and ecological data sets

t2.2		Cranial shape	Cranial log(CS)	Mandible shape	Mandible log(CS)	Fruit	Bryo-Pterid	Gymno	Dicot	Monocot
t2.3	Scenario 1									
t2.4	Tree length	0.0563	1.133	0.0272	1.389	7.573	0.167	0.0531	11.285	4.852
t2.5	<i>p</i> value	0.2308	0.4436	0.6206	0.4370	0.1844	0.6265	0.3548	0.9678	0.2281
t2.6	Scenario 2									
t2.7	Tree length	0.0512	1.0011	0.0229	1.231	9.227	0.158	0.0567	10.0871	5.7919
t2.8	<i>p</i> value	0.0262*	0.1355	0.0506	0.1279	0.2722	0.3508	0.4273	0.7152	0.3924

Notes; Scenario 1: 10ktree consensus; scenario 2: Zurano et al. (2019); log(CS) – log-transformed centroid size; Bryo-Pterid - bryophytes; Gymno – gymnosperms; diet continuous character test performed on logit transformed values; tree length based on weighted squared-change parsimony; *p* values after 10,000 rounds of permutation; value marked by asterisk (*) significant at 0.05 level

319 incisor alveoli placed above the occlusal plane, short diaste- 332
 320 ma, curved and high alveolar region, more developed 333
 321 coronoid process, posteriorly directed masseteric fossa, and 334
 322 comparatively lower position of the condyle (Fig. 2-b). 335
 323 Conversely, large forms were characterized by a mandible 336
 324 with gracile symphysis with incisor alveoli placed below the 337
 325 occlusal plane, long diastema, straight and low alveolar re- 338
 326 gion, less developed coronoid process, anteriorly directed 339
 327 masseteric fossa and comparatively higher position of the con- 340
 328 dyle (Fig. 2-b; Online Resource 5). 341
 329 The PLSca1 scores showed a high correlation between 342
 330 blocks ($r = 0.85$, $p < 0.00001$ after 10,000 rounds of permuta- 343
 331 tion tests). The pudus and brockets (i.e., small deer) are in the 344
 double negative quadrant, showing a right point cloud with a
 common pattern of covariation mainly associated with a
 brachycephalic cranium with robust mandible (Fig. 2c).
 Conversely, the large deer including the Neotropical pampas
 deer, marsh deer, and huemuls, and the Nearctic caribou,
 white-tailed deer, and moose clustered in a small region on
 the double positive quadrant, slightly displaced to positive
 values of Block-1 showing a pattern of covariation mainly
 associated with a dolicocephalic cranium with gracile mandi-
 bles (Fig. 2c). The dimensions displayed a clear distinction
 between the small and large species, suggesting a slightly
 different pattern of covariation between these two groups re-
 gardless of sex or their phylogenetic relationships.

t3.1 **Table 3** Partial Least Squares analysis for each data sets

t3.2	Data set	Pair of axes	Singular value	S.v. <i>p</i> value	% Total covar.	Correlation	Corr. <i>p</i> value
t3.3	Capreolinae	PLSca1	0.001009	<0.0001	90.610	0.85502	<0.0001
t3.4	Cr and Md	PLSca2	0.00022315	<0.0001	4.432	0.72998	<0.0001
t3.5	independent	PLSicz1	0.0003408	0.0005	82.111	0.92062	0.0002
t3.6	contrast Cr and Md	PLSicz2	0.0001411	0.0023	14.067	0.90137	0.0021
t3.7	Neotropical deer	PLScd1	0.04409008	<0.0001	93.993	0.84457	<0.0001
t3.8	Cr shape and diet	PLScd2	0.01110595	<0.0001	5.964	0.65176	<0.0001
t3.9	Neotropical deer	PLSmd1	0.01934187	<0.0001	76.520	0.63990	<0.0001
t3.10	Md shape and diet	PLSmd2	0.01068946	<0.0001	23.372	0.57772	<0.0001
t3.11	Small deer	PLScsd1	0.03067931	<0.0001	99.763	0.71940	<0.0001
t3.12	Small deer	PLSsmd1	0.02731151	<0.0001	99.695	0.63227	<0.0001
t3.13	Large deer	PLSlcd1	0.01363645	<0.0001	98.224	0.84822	<0.0001
t3.14	Large deer	PLSlmd1	0.01220972	<0.0001	98.957	0.73461	<0.0001

Notes; PLS: Partial Least Squares; S.v. *p* value: permutation test on Singular values; % Total covar.: Total covariance percent; Correlation: Pearson correlation coefficients between PLS scores of Block 1 and Block 2; Corr. *p* value: permutation test on correlation values from the PLS scores; Cr: cranium; Md: mandible; PLS subindices: (ca) the whole Capreolinae sample, (icz) independent contrast from Zurano et al. (2009) phylogeny, (cd) cranial shape and diet, (md) mandibular shape and diet, (scd) cranial shape and diet in small neotropical deer, (smd), mandibular shape and diet in small neotropical deer, (lcd) cranial shape and diet in large neotropical deer and (lmd) mandibular shape and diet in large neotropical deer

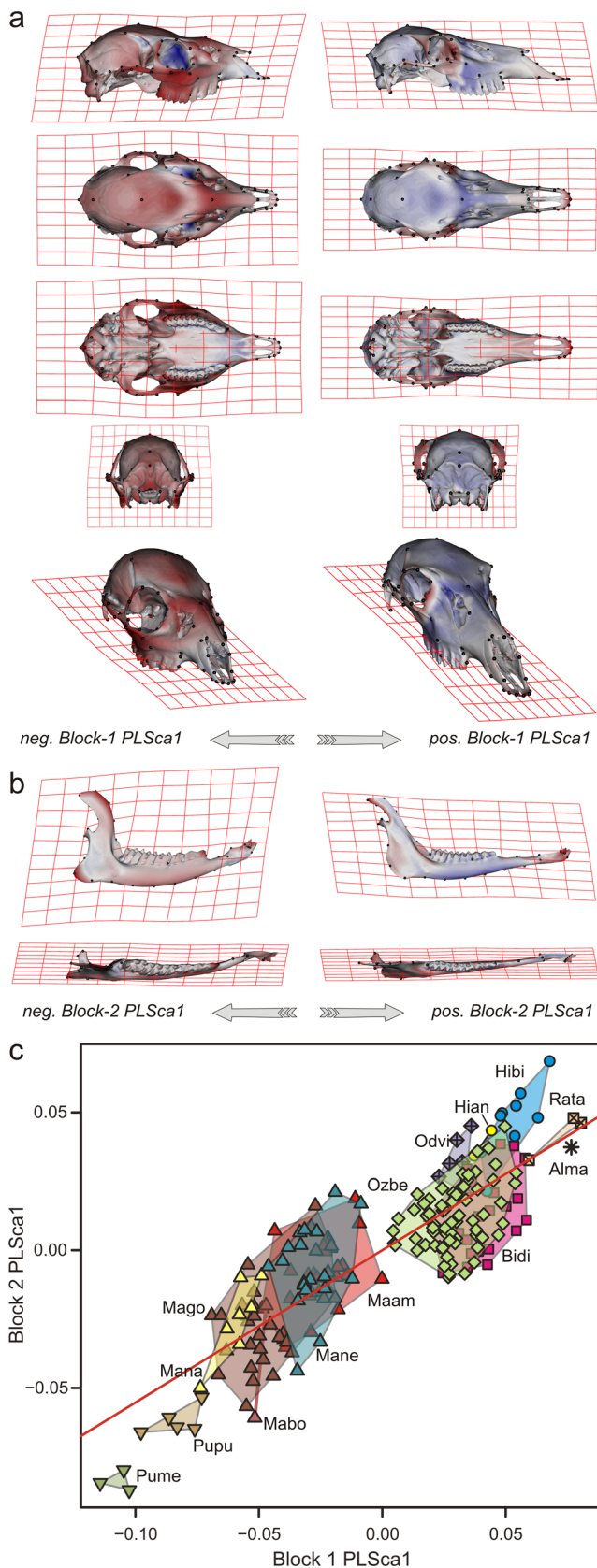


Fig. 2 PLSca of Capreolinae specimens. **a** thin plate spline gridlines and meshes of cranium shape (Block-1) of negative and positive most first pair of PLS; **b** thin plate spline gridlines and meshes of mandibular shape (Block-2) of negative and positive most first pair of PLS; **c** taxa distribution on the morphospace depicted by the two first PLS dimensions. Reference: *Alces americanus* (asterisk - Alma); *Blastocercus dichotomus* (squares - Bidi); *Hippocamelus* spp. (circles - Hian, *H. antisensis* and Hibi, *H. bisulcus*); *Mazama* spp. (triangles - Maam, *M. americana*; Mabo, *M. bororo*; Mago, *M. gouazoubira*; Mana, *M. nana*; Mane, *M. nemorivaga*); *Odocoileus virginianus* (crossed rhombus - Odvi); *Ozotoceros bezoarticus* (rhombus - Ozbe); *Pudu* spp. (inverted triangles - Pume, *P. mephistophiles*; Pupu, *P. puda*); and *Rangifer tarandus* (crossed squares - Rata)

Ecomorphology of Neotropical Deer

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The PLS analysis on both cranium and mandible of Neotropical deer showed a significant relationship between shape and diet. The PLS analysis on the cranial and mandibular shape indicated that the first pair of PLS explains about 94% and 76% of covariation, respectively (PLScd1 and PLSmd1, Table 3). In both analyses the shape change vectors associated with the first block (i.e., cranium and mandible; Online Resource 7) were similar to the respective Block-1 and Block-2 of the Capreolinae PLSca1 (angle between vectors: 17.22° for cranium and 19.591° for mandible; both $p < 0.00001$). The Block-2 PLS coefficients of the five diet categories for each analysis were quite similar. In both, the monocot items showed similar high negative values (ca. -0.77) and the fruit items very similar high positive value (ca. 0.59 for cranium and ca. 0.57 for mandible). While the PLScd1 scores showed a very high and significant correlation between Block-1 and Block-2 ($r = 0.845$, $p < 0.00001$; Table 3), the scores of first pair of PLS for mandible and diet (PLSmd1) showed lower but significant correlation ($r = 0.6399$; $p < 0.00001$; Table 3). The morphospace of both analyses are strongly similar and lack any sexually dimorphic pattern (Online Resource 7). Among the large Neotropical deer, the mixed feeders *Ozotoceros bezoarticus* and *Blastocercus dichotomus* fall into the double negative quadrant, and the browser *Hippocamelus* spp. on negative values of Block-1 and near the zero and positive values of Block-2 scores (Online Resource 7). The small deer, the browser *Pudu* spp. and *Mazama* spp., including browsers and frugivores, are in the double positive quadrant.

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Ecomorphological Integration in Small Deer

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The PLS analysis on both the cranium and mandible of small deer showed a significant relationship between shape and diet. Both PLS analyses showed that the first pair of PLS explains about 100% of covariation (PLSscd1 and PLSsmd1, respectively; Table 3). The shape changes associated with the PLSscd1 vector of Block-1 (Fig. 3a) ranged from a short

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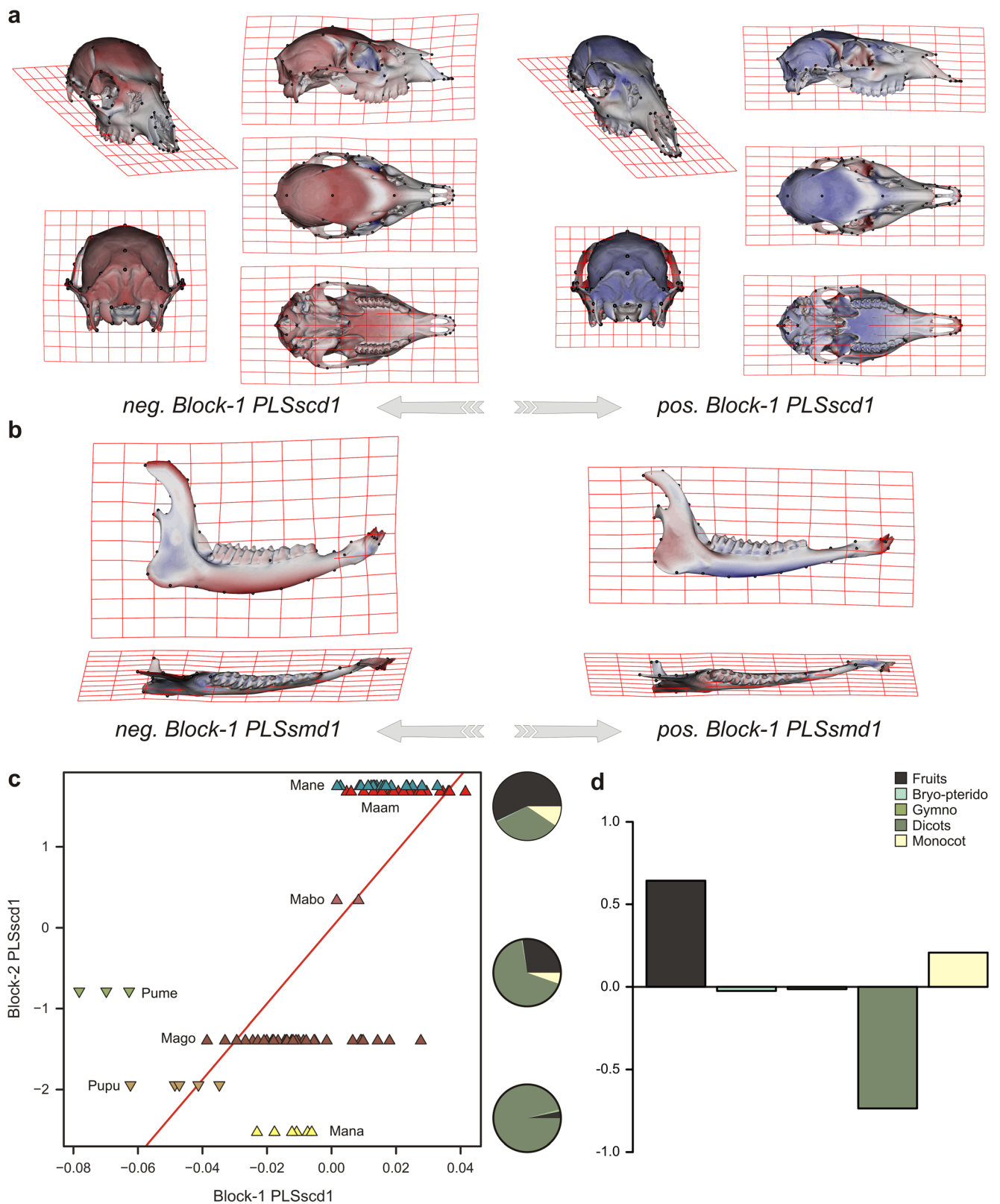


Fig. 3 PLS of cranial and mandibular shape (Block-1) vs. logit continuous dietary characters (Block-2) in small deer specimens. **a** thin plate spline gridlines and meshes of cranium shape (Block-1) of negative and positive most first pair of PLSscd; **b** thin plate spline gridlines and meshes of mandibular shape (Block-1) of negative and positive most first

pair of PLSsmd; **c** taxa distribution on the morphospace depicted by the two first PLS dimensions of cranium analysis (PLSscd), with pie charts depicting dietary composition near extreme and midpoint y-axis values; and **d** pairwise correlation coefficients between diet PLS axis and each dietary category (logit-transformed) for PLSscd. References as in Fig. 2

382 and high cranium with the muzzle tip above the occlusal
 383 plane, orbits placed above the masseter's origin, laterally ex-
 384 panded and dorsally curved zygomatic arch, wide cranial
 385 vault, and posteriorly directed occiput and foramen magnum
 386 (on the negative end) to a short but low cranium with the
 387 muzzle tip below the occlusal plane, orbits placed towards
 388 the third molar, medially compressed and straight zygomatic
 389 arch, narrow cranial vault, and anteriorly directed occiput and
 390 foramen magnum (on the positive end).

391 Shape changes associated with the PLSsmd1 vector of
 392 Block-1 (Fig. 3b) ranged from a mandible with a curved dia-
 393 stema and high alveolar region, ventrally placed distal margin
 394 of angular process, and high and anteriorly directed coronoid
 395 process (on the negative end) to a mandible with a straight
 396 diastema, low alveolar region, dorsally placed angular pro-
 397 cess, and low and posteriorly directed coronoid process (on
 398 the positive end).

399 The Block-2 PLS coefficients of the five diet categories for
 400 each analysis were very similar. In both cranial and mandibu-
 401 lar PLS the dicot items showed similar high negative values
 402 (ca. -0.73) and the fruit items high positive values (ca. 0.64).
 403 While the PLSscd1 scores showed a high and significant cor-
 404 relation between Block-1 and Block-2 ($r = 0.719$,
 405 $p < 0.00001$; Table 3), the PLSsmd1 scores showed lower
 406 but significant correlation ($r = 0.632$; $p < 0.00001$; Table 3).
 407 In both analyses the morphospaces looked quite similar but
 408 in mandible Block-1 PLS axis showed greater dispersion.
 409 There was no sexual dimorphism pattern in the morphospace
 410 depicted by the first PLSscd and PLSsmd dimensions. The
 411 browser pudus and brockets *Mazama gouazoubira* and
 412 *M. nana* are in the double negative quadrant, and the frugiv-
 413 orous brockets *M. nemorivaga* and *M. americana* in the dou-
 414 ble positive quadrant (see Fig. 3c for PLSscd).

415 **Ecomorphological Integration in Large Deer**

416 The PLS analysis of both the cranium and mandible of
 417 large deer showed a significant relationship between
 418 shape and diet. Both PLS analyses showed that the first
 419 pair of PLS explains about 98% covariation (PLSlcd1
 420 and PLSlmd1, respectively, Table 3). The PLSlcd1 vec-
 421 tor of Block-1 shape changes (Fig. 4a) ranged from a
 422 cranium with a flexion between the rostrum and the
 423 orbital region plus cranial vault, muzzle tip above the
 424 occlusal plane, ventral and anteriorly placed large orbits
 425 and infraorbital foramen, robust zygomatic arch, and
 426 posteriorly directed occiput and foramen magnum (on
 427 the negative end) to a cranium with flexion between
 428 the orbitofacial region and the cranial base and vault,
 429 muzzle tip above the occlusal plane, dorsal and posteri-
 430 orly placed orbits and infraorbital foramen, gracile zy-
 431 gomatic arch, and anteriorly oriented occiput and fora-
 432 men magnum (on the positive end).

The shape changes associated with PLSlmd1 vector of
 Block-1 (Fig. 4b) ranged from a mandible with a curved and
 high alveolar region (particularly along the molar region),
 more developed angular process, and anteriorly directed
 coronoid process on the negative end to a mandible with a
 straight diastema and alveolar region, less developed angular
 process, and posteriorly directed coronoid process (on the
 positive end).

The Block-2 PLS coefficients of the five diet categories for
 each analysis showed very similar values. In both the cranial
 and mandibular PLS the monocot items showed similar high
 negative values (ca. -0.72) and the dicot items very high posi-
 tive values (ca. 0.69). While the PLSlcd1 scores show a very
 high and significant correlation between Block-1 and Block-2
 ($r = 0.848$, $p < 0.00001$; Table 3), the PLSlmd1 scores showed
 lower but significant correlation ($r = 0.734$; $p < 0.00001$;
 Table 3). In both analyses, the morphospace depicted by first
 dimensions of these PLS looked quite similar and clustered
 the mixed feeders *Ozotoceros bezoarticus* and *Blastocerus*
dichotomus towards the negative quadrant, while the browsers
Hippocamelus spp. clustered towards positive scores (see Fig.
 4c and d for PLSlcd). No sexual dimorphic pattern was
 detected.

456 **Discussion**

Our study suggests that feeding ecology in Neotropical deer
 has strongly influenced craniomandibular shape and size di-
 versification. There is a remarkable convergence between the
 brockets in their feeding behavior (e.g., high proportion of
 fruit in their diet) and morphology (brachycephalic cranium
 with robust mandible). Conversely, marsh and pampas deer
 share craniomandibular traits (e.g., large attachment areas for
 masseter plus pterygoid muscles) related to monocotyledon
 consumption. It is noteworthy how close the morphology re-
 flects the actual diet instead of the phylogeny, suggesting a
 high correspondence between fundamental and realized niche
 (see Vizcaíno et al. 2016 and references there in). In addition,
 as noted in Merino et al. (2005), sex differences were not
 apparent in any of the analyses performed. Phylogenetic sig-
 nal was not significant in almost all the morphogeometric data
 and continuous diet characters. Similar results were obtained
 using the independent contrast, suggesting a lack of phyloge-
 netic constraints, conversely to what was proposed for shape
 data of other ungulates and mammalian groups (e.g., Cardini
 and Elton 2008; Barčiová 2009; Cassini 2013).

477 **Evolutionary Integration**

Size emerges as one important factor modeling slightly differ-
 ent patterns of covariation in small and large Neotropical deer.
 Results were similar between the PLS analysis of the entire

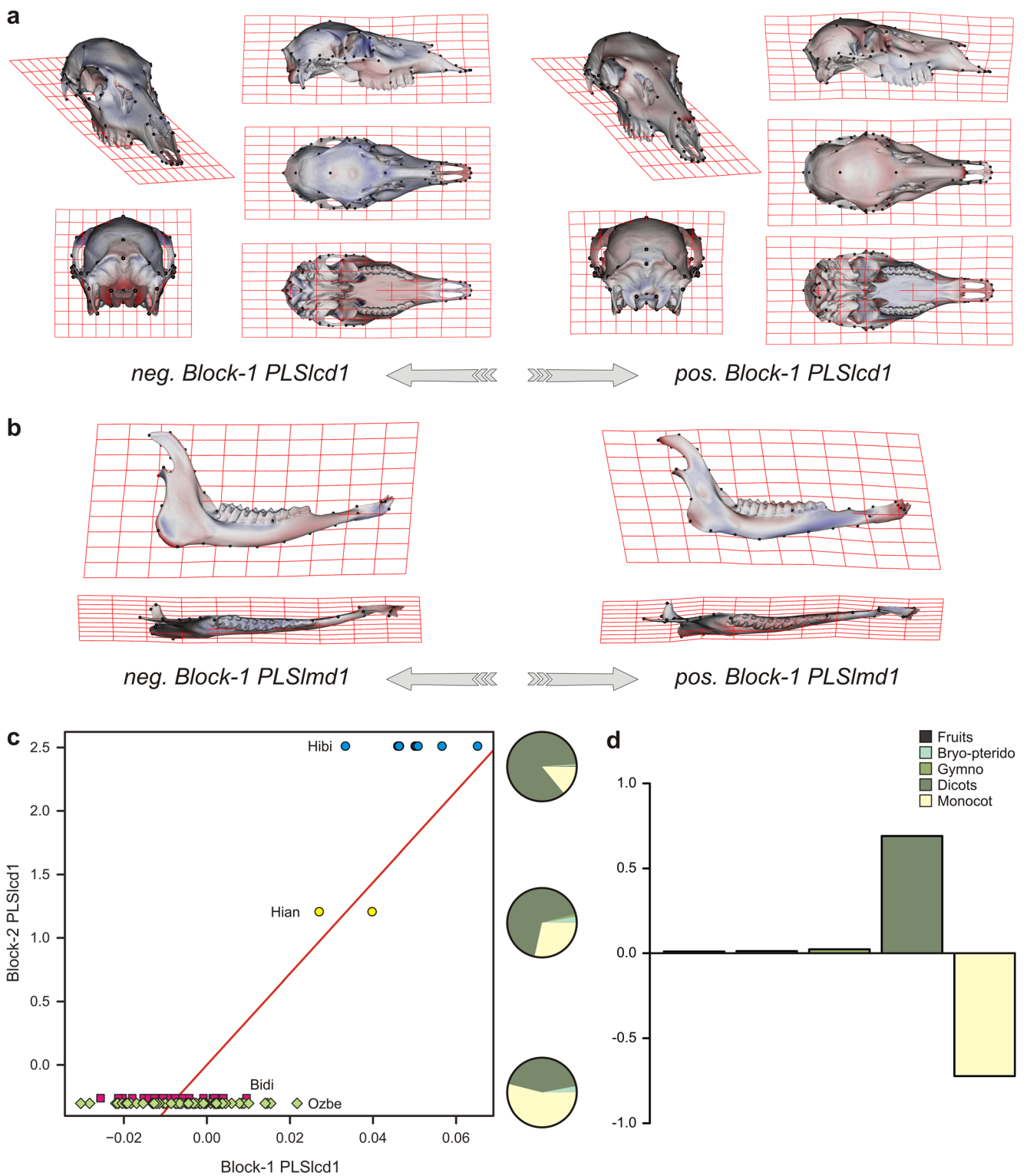


Fig. 4 PLS of cranial and mandibular shape (Block-1) vs. Logit continuous dietary characters (Block-2) in large deer specimens. **a** thin plate spline gridlines and meshes of cranium shape (Block-1) of negative and positive most first pair of PLS1cd; **b** thin plate spline gridlines and meshes of mandibular shape (Block-1) of negative and positive most first

pair of PLS1md; **c** taxa distribution on the morphospace depicted by the two first PLS dimensions of cranium analysis (PLS1cd), with pie charts depicting dietary composition near extreme and midpoint y-axis values; and **d** pairwise correlation coefficients between diet PLS axis and each dietary category (logit-transformed) for PLS1cd. References as in Fig. 2

481 Capreolinae sample and independent contrast of both phylo-
482 genetic hypotheses (i.e., PLSca and PLSic; Online Resource

6). In the morphospace depicted by the first dimensions of
these PLS (Fig. 2), it clearly emerges that the morphological

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485 covariation pattern shared by Capreolinae ranges from a
 486 brachycephalic cranium with robust mandible to a
 487 dolicocephalic cranium with a gracile mandible (Fig. 2a-b;
 488 Online Resource 5). The log-transformed centroid size ex-
 489 plains 75% and 56% of cranial and mandibular variation, re-
 490 spectively (see Results), suggesting that craniomandibular in-
 491 tegration could be explained by allometric scaling (note that
 492 our sample includes the pudu and moose, the smallest and
 493 largest extant cervids). In accordance with Cassini (2013),
 494 many ungulate lineages shared common allometric shape
 495 changes in both cranium (e.g., small forms were characterized
 496 by a narrow muzzle, short rostrum and large temporal fossa
 497 versus a wide muzzle, long rostrum and small temporal fossa,
 498 i.e., brachycephalic vs. dolicocephalic) and mandible (small
 499 forms are characterized by an acute angle between the alveolar
 500 region and the ascending ramus, whereas larger forms are
 501 characterized by an obtuse angle, i.e., robust vs. gracile). A
 502 similar allometric pattern was reported as appearing
 503 convergently in many other mammal groups (e.g. antelopes,
 504 bats, mongooses, and squirrels, see Cardini and Polly 2013).
 505 In addition, Janis and Theodor (2014) indicated that within
 506 Ruminantia there are many highly homoplastic morphological
 507 features related to functional similarities but not to phylogeny,
 508 and Neotropical deer are not an exception. Recent molecular
 509 phylogenetic hypotheses (Heckeberg et al. 2016; Zurano et al.
 510 2019) confirmed the evolutionary scenario of Duarte et al.
 511 (2008), in which brachycephalic morphology (e.g., brockets)
 512 evolved at least twice. Therefore, allometry would be an in-
 513 influential factor shaping the evolutionary craniomandibular in-
 514 tegration in deer.

515 **Ecomorphology of Neotropical Deer**

516 In addition to the craniomandibular covariation pattern ex-
 517 plained by allometric scaling, the Neotropical deer species
 518 analyzed here show shape changes that were found to be re-
 519 lated to diet composition. Surprisingly, as is shown by angular
 520 comparison, the shape changes were similar to the evolution-
 521 ary integration analyses (compare Fig. 2 with online Resources
 522 6 and 7 shape changes). The covariation between shape vari-
 523 ation and diet was higher for the cranium (94%) than for the
 524 mandible (76%; Table 3; Online Resource 7). This contradicts
 525 the accepted hypothesis that the mandible better reflects mas-
 526 ticatory function than the cranium (Janis 1995; Vizcaíno et al.
 527 2016, and references therein).

528 In both the cranium and mandible, axes of correlation were
 529 consistent with differences at the level of the primary plant-
 530 food preference (i.e., monocot vs. fruit). However, both shape
 531 changes are quite similar to the craniomandibular integration
 532 in the PLS of Capreolinae (angular between vectors of $\sim 17^\circ$
 533 for cranium and 19° for mandible). Both covariation
 534 morphospaces reveal that the small and large Neotropical deer
 535 have slightly different covariation patterns (Online Resource

7). The most conspicuous features correlated with more than
 536 50% of monocots in diet were: a long rostrum, braincase
 537 flexed on the facial axis, narrow palate, depth of the facial
 538 region below the orbit, small temporal fossa (in the cranium);
 539 and a long diastema, short premolar row, deep masseteric fos-
 540 sa and high articular process with a short and posteriorly ori-
 541 ented coronoid process (in the mandible). As also noted by
 542 Greaves (2012), this morphology emphasizes the
 543 anteroposterior resultant force of jaw musculature, rendering
 544 it more horizontal (because the masseter and pterygoid are
 545 large; Radinsky 1985), with a shorter component of temporal
 546 muscle in the stroke phase in comparison with pterygoid-
 547 masseteric component. In agreement with Merino et al.
 548 (2005), these traits are shared mainly by pampas deer and
 549 marsh deer, which are also very selective on the plant parts
 550 they consume (see Duarte and González 2010). According to
 551 Janis (2007), cervids never became specialized grazers (i.e.,
 552 $>90\%$ of monocot) or developed highly hypsodont teeth as bo-
 553 vids. However, the above mentioned features were demon-
 554 strated to be related to grass consumption in grazing and
 555 mixed feeding African bovids (Spencer 1995; Janis 2000;
 556 Clauss et al. 2008). Thus, this pattern suggests that grass con-
 557 sumption is correlated to distinctive skull features, even if
 558 grass is not the dominant item in the diet.
 559

560 Traits condensed in the opposite extreme of the
 561 morphospace, i.e., short and high rostrum, anteriorly directed
 562 orbits, wide zygomatic arch, and mandible with short diaste-
 563 ma and right angle between the alveolar region and the angu-
 564 lar process, among others, are shared by the red-brocket and
 565 the Amazonian grey-brocket deer, and correlates with a high
 566 percentage of fruit in the diet (i.e., $>60\%$; See
 567 Online Resource 7). While most ungulates have an
 568 anteriorly-directed jaw musculature resultant (Greaves
 569 1991), these traits seems to favor a more posteriorly directed
 570 vector, rendering it more vertical, because of the great devel-
 571 opment of the temporal fossa and muscle (Greaves 2012).
 572 This arrangement brings the third molar closer to the
 573 craniomandibular joint and emphasizes the component of the
 574 temporal muscle during the stroke phase (Greaves 2012). In
 575 addition, a lower condyle leads to reduced muscle stretch,
 576 which can enable a wider gape (Herring and Herring 1974).
 577 This scheme seems be coherent with a high percentage (both
 578 regular and seasonal) of fruit in the diet (Table 1).

579 **Ecomorphological Integration in Small Deer**

580 Size emerges as one important factor that modeled patterns of
 581 covariation within small deer. The correlation of shape variation
 582 and diet was extremely high in both the cranium and mandible
 583 (ca. 100%, respectively; Fig. 3; Table 3). They follow the gen-
 584 eral allometric pattern described above for the entire
 585 Capreolinae sample but within a general brachycephalic-
 586 robust mandible morphotype (compare Figs. 2 and 3 shape

587 changes). Surprisingly, within the small deer the shape change
 588 gradient was inverted, as the *Pudu* spp. consume more dicots
 589 (browser) than *Mazama nemorivaga* and *M. americana*, which
 590 consume more fruits. The covariation morphospaces reveal in-
 591 consistencies in shape and diet correlation that might be ex-
 592 plained by the scarcity and low-grade information on diet. For
 593 example, *Mazama nana* is similar to *M. bororo* in size, habitat
 594 use, and Block-1 (shape) scores, and it would thus be expected
 595 to have similar fruit content (45%, Table 3), rather than the
 596 higher percentage of dicots noted here. Some authors consider
 597 that further studies are required to provide a better understand-
 598 ing of the ecology of these species (see Duarte and González
 599 2010). Indeed, Radinsky claimed on the needs of including
 600 direct field or lab observations of behavior or responses to en-
 601 vironmental factors in adaptation research programs (see
 602 Vizcaíno and Bargo 2019).

603 **Ecomorphological Integration in Large Deer**

604 The observed correlation between cranial and mandibular
 605 shape and diet within the large deer appears to be explained
 606 not by allometric scaling, but rather by the monocot-dicot
 607 gradient. The correlation of shape variation and diet was
 608 slightly higher in the mandible than cranium (ca. 100% and
 609 98%, respectively; Fig. 4; Table 3). In both, axes of correla-
 610 tions are consistent with differences at the level of the primary
 611 plant-food preference (i.e., dicots), as in the entire Capreolinae
 612 sample. There seems to be a gradient in diet composition from
 613 *Hippocamelus bisulcus*, feeding primarily on dicots (>90%),
 614 to the mixed feeders *Ozotoceros* and *Blastocerus*, consuming
 615 lower proportions of dicots (ca. 40%; Table 3). Monocot con-
 616 sumption greater than 50% is associated with flexion between
 617 the rostrum and orbital region, a posteriorly oriented occiput,
 618 and a robust zygomatic arch (Fig. 4:a) in the cranium, and a
 619 high curved alveolar region, expanded angular process, and
 620 masseteric fossa providing more attached surface area for
 621 masseter and pterygoid muscles in the mandible.
 622 Conversely, a high dietary consumption of dicots is associated
 623 with flexion between the orbit and basicranium, an anteriorly
 624 oriented occiput and gracile zygoma (Fig. 4:b), and a slender
 625 mandible with a straight diastema, an alveolar region forming
 626 an obtuse angle with the ascending ramus, and a small mas-
 627 seteric fossa. This gradient of shape variation associated with
 628 monocot to dicot dominated diets (Fig. 4c-d) is consistent with
 629 the convergent functional complex related to habitat/diet and
 630 tooth dimensions described by Cassini (2013) and Fraser and
 631 Theodor (2011) for extant and extinct ungulates.

632 **Conclusions**

633 The covariation between craniomandibular features and feed-
 634 ing behavior, investigated with continuous dietary characters

and modern geometric morphometry techniques, reveals mor- 635
 phological convergences within small and large Neotropical 636
 deer that are explained by a complex interplay of allometric 637
 trends and biomechanically significant features. Notable is the 638
 high correspondence between morphology and feeding behav- 639
 ior in Neotropical cervids, which emerges apparently from 640
 the novel approach of considering diet as a continuous char- 641
 acter rather than as discrete categories. The association of 642
 craniomandibular traits with diets high in monocot, fruit, or 643
 dicot plant material underscores the importance of relative 644
 toughness of food items as an ecological factor shaping skull 645
 variation. Radinsky (1987) highlighted remarkable conver- 646
 gences between distant lineages of herbivorous mammals; 647
 here we postulate some between Neotropical cervids with 648
 African bovids. Although cervids never reached the same de- 649
 gree of dietary specialization as bovids, growing evidence 650
 from several research fields will contribute to understanding 651
 the adaptive role of craniomandibular shape in the recent evo- 652
 lutionary history of deer in the Neotropics. 653

Acknowledgments We thank N. Simmons (AMNH), H. Pastore and E. 654
 Ramilo (APN-DRP), M. Beade (CDT), S. Bogan (CFA), R. Barquez 655
 (CML), Pablo Teta (MACN), D. Verzi and I. Olivares (MLP), A. 656
 Pautaso (MFA), M. De Vivo (MUZSP), J.M. Barbanti Duarte 657
 (NUPECCE), and K. Zyskowski (YPM) for access to mammalogy col- 658
 lections; the organizers of the XXXI Jornadas Argentinas de 659
 Mastozoología, La Rioja, Argentina, A. Chemisquy and F. Prevosti for 660
 allowing us organizing the symposium: “El paradigma de correlación 661
 forma-función en mastozoología: un tributo a Leonard Radinsky 662
 (1937–1985)”; S. Vizcaíno and R. Fariña for having introduced us to 663
 Radinsky’s delightful text as students; S. Bargo, N. Milne, N. Muñoz, 664
 and M. Merino for fruitful discussions on form-function, geometric mor- 665
 phometrics, and deer that inspired this manuscript; G. De Iuliis and the 666
 reviewers whose comments greatly enhanced this manuscript. This is a 667
 contribution to the projects Universidad Nacional de Luján CDDCB 650/ 668
 14; Agencia Nacional Promoción Científica y Tecnológica PICT-2015- 669
 2389. 670

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- Q2. Please check if the affiliations are presented correctly.
- Q3. (Country / City) has been provided to affiliation 3, please check if it is correct.
- Q4. Ref. "Radinsky's (1969)" is cited in the body but its bibliographic information is missing. Kindly provide its bibliographic information in the list.

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