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Skull ontogeny of the pronghorn *Antilocapra americana* (Antilocapridae) in the comparative context of native North American ungulates

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Abstract

The pronghorn *Antilocapra americana* (Ord 1815) is the single survivor of a largely extinct, isolated pecoran lineage (Antilocapridae) native to North America. We describe postnatal ontogeny of its skull in a comparative framework inclusive of representatives of other typical North American ungulate linages, all of which partially overlap in geographic distribution and share habitat with the pronghorn. To describe allometric growth we took 23 linear cranial measurements in 30 specimens of *Antilocapra* and applied bi- and multi-variate statistics. The skull of *Antilocapra* generally grew with negative rates in width and height dimensions, and with positive rates in length, including an elongation of rostrum, in particular of nasals, and a relative narrowing of the braincase. We compared skull development in Antilocapra with development in Odocoileus virginianus Zimmermann 1780, Cervus canadensis Erxleben 1777 (Cervidae), Ovis canadensis Shaw 1804, and Bison bison Linnaeus 1758 (Bovidae). The multivariate ontogenetic trajectory of *Antilocapra* overlapped greatly with that of *Odocoileus*, and differed from the other species in varying degrees. These results indicated an essentially convergent pattern of skull growth with species showing important functional similarities, such as cervids of comparable size and feeding habits.

Key words: cranial development; artiodactyla; Antilocapra americana; Odocoileus

virginianus; Cervus canadensis; Ovis canadensis; Bison bison

Introduction

Antilocapridae is an artiodactyl family endemic to North America (Kemp 2005 and references therein) and is among the oldest branches of extant pecoran families (Chen et al. 2019). Antilocaprids are abundant in the fossil record; the group was more diverse in the past, with over 20 described genera, most of which disappeared along the Plio-Pleistocene periods (McKenna and Bell 1997; Prothero and Schoch 2002), perhaps as a consequence of other ungulate groups entering the continent including cervids (c. 6 mya; Mattioli 2011) and boyids (c. 2 mya; Prothero and Schoch 2002). At least three genera of antilocaprids survived to the Late Pleistocene (McKenna and Bell 1997). However, the pronghorn antelope, Antilocapra *americana* (Ord 1815), is the sole taxon of the entire antilocaprid lineage to reach the Recent, and it might thus be seen as an evolutionary window into an essentially Tertiary lineage of native North American artiodactyls (Kemp 2005 and references therein). Antilocapra americana inhabits treeless plains, basins, and deserts of central and western North America, from the prairie provinces of southern Canada, southward into the western United States and northern Mexico (Krejci and Dewey 2009; IUCN SSC Antelope Specialist Group 2016). Antilocapra is an herbivore with highly hypsodont dentition (Dow and Wright 1962; Janis and Manning 1998), and it is a dainty feeder, selecting specific parts of plants from a wide variety of species (O'Gara 1978; Byers 2011), primarily on sage, forbs and grasses, but also cacti in some areas (Krejci and Dewey 2009). Body size is 24-70 kg. (Beatty et al. 2008). The pronghorn is the fastest land mammal in the Western Hemisphere, able to run upward of 88-97 km h (55-60 m.p.h.; Beatty et al. 2008). As such, the pronghorn has remarkable adaptations for running; e.g., it has high oxygen transport capacity, far above the value predicted by its average body mass (McKean and Walker 1974; Hildebrand and Hurley ¹Supplementary data are available with the article through the journal Web site

1985; Byers 2011), and countercurrent heat exchange in extensive carotid and orbital retia to avoid brain overheating while running (Carlton and McKean 1977). The pronghorn also presents levels of annual reproductive expenditure that are higher than those of other ungulates, and an unusually long and highly variable gestation period (Byers 2011). Sexual dimorphism in body mass and dimensions is slight just about 10%, likely because of the strong, predator-based selection on running capacity, and because females evolved sex choice criteria that are congruent with running selection (Byers 2011). In skull shape, sexual dimorphism has only been reported in horn size, with males possessing larger horns, with forked horn sheaths ranging from 33 to 50 cm. Females exhibit smaller, unforked horn sheaths (O'Gara 1978; Janis and Manning 1998).

Considering morphological characters, the pronghorn exhibits several states that are either unique, or intermediate between those of other major groups of pecoran ruminants. For example, unlike bovids and cervids, the pronghorn has entirely lost the lateral digits having only the cannon bones (O'Gara 1978); also, similar to tragulids and bovids but unlike cervids, they present a gallbladder (O'Gara 1978; Wilson and Mittermeier 2011). Among characters of the skull and their associated ornaments, pronghorns of both sexes bear supraorbital horns formed by ossicones; i.e., a permanent horn-bearing appendage of the frontal bone as in bovids. However, these appendages are covered by a horny sheath that is branched (chiefly in males) and is shed annually as in cervids (Janis and Manning 1998). Pronghorn has large orbits with postorbital bar; the lacrimal bone is separated from nasal by a vacuity and the lacrimal canal has one orifice inside the rim of the orbit; it has not sagittal crest; and the basicranial axis is bent (O'Gara 1978). In addition, dentition, bodily proportions, habits, trophic characteristics, and physiological adaptations such as those mentioned above, all point

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to a striking convergence with evolutionarily derived ruminants originated in other continents. particularly Eurasia, chiefly similar to deer and antelopes (Brown 2006; Beatty et al. 2008). Given the host of mixed character states, the phylogenetic position of Antilocapridae remains essential to understand the evolution of this relictual group; however, this has been contentious in several aspects, hindering the understanding of the evolution of the diverse ungulates phenotypes (Chen et al. 2019). Antilocapridae has been united with Bovidae in Bovoidea, or with Cervidae in Cervoidea (Janis and Manning 1998; Janis and Theodor 2014). Several other studies have recovered Antilocapridae either as the earliest branch of pecoran ruminants (e.g., Beintema et al. 2003; Hassanin et al. 2003), or as a clade with Giraffidae forming together the branch sister to higher ruminants (i.e., Cervidae, Moschidae, Bovidae; Cronin et al. 1996; Marcot 2007; Hassanin et al. 2012; Cernohorska et al. 2013; see Supplementary Fig. S1a¹). Particularly, the latter is the arrangement recovered in the latest phylogeny of Ruminantia (Chen et al. 2019; see Supplementary Fig. S1b¹). At present, Antilocapra co-occurs geographically with representatives of different lineages of native North American ruminants such as cervids of the genera *Odocoileus* (e.g., the whitetailed deer, Odocoileus virginianus Zimmermann 1780) and Cervus (the wapiti, Cervus canadensis Erxleben 1777), and bovids of the genera Bison (i.e., the American bison, Bison bison Linnaeus 1758) and Ovis (e.g., the bighorn sheep, Ovis canadensis Shaw 1804). The aim of this study is to comparatively describe the postnatal skull ontogeny of the pronghorn as representative of a unique North American lineage, in the wider phylogenetic framework of pecoran ruminant ungulates with which Antilocapra shares habitat. Our predictions here is find traces of the uniqueness and antiquity of the antilocaprid lineage, such as divergent skull growth trajectory with respect to any of the representatives of more modern lineages codistributed in the North American continent. Alternatively, skull development in the ¹Supplementary data are available with the article through the journal Web site

pronghorn may reflect functional similarity with modern lineages of pecoran ruminants with similar habits.

Material and methods

Study specimens

We sampled a postnatal ontogenetic series of 30 specimens (ten females, ten males, and ten of unknown sex) of *Antilocapra* housed at the Mammal Collections of American Museum of Natural History (AMNH, New York, USA), Field Museum of Natural History (FMNH, Chicago, USA) and National Museum of Natural History, Smithsonian Institution (USNM, Washington, D.C. USA). The list of specimens used in this study is available in Appendix. Our sample comprised specimens from 117.86 mm to 282.07 mm in condyle-basal length (USNM 120702 and AMNH 142361 respectively), representing a 42% of smallest-to-largest specimen size ratio.

Study of growth and measurements

The allometric association between size and shape in individuals sampled across different age stages can be used to estimate a population's ontogenetic trajectory (Mitteroecker et al. 2013). Sex dimorphism was evaluated using bivariate linear regressions analysis contrasting males and females for each variable (Supplementary Table S1¹). Generally in this species, sexual dimorphism in body mass and linear dimensions is slight (c. 10%), but considering skull characters, there is obvious sexual dimorphism only in the horn, with males possessing larger, forked horn sheaths, and females exhibiting smaller, unforked horn sheaths (O'Gara 1978; Janis and Manning 1998). As most of the variables did not present significant sexual ¹Supplementary data are available with the article through the journal Web site

dimorphism, in our allometric analysis we pooled males, females and specimens of unknown sex of all ages into a single set, and in this sample we measured 23 linear skulls (Fig. 1) including length, breadth, and height of neurocranial and splanchnocranial components that describe overall skull structure and represent proxies of general functional attributes. These cranio-mandibular measurements have great comparative potential as they overlap with those taken in other morphometric studies of mammalian skulls (e.g., Abdala et al. 2001; Giannini et al. 2004, 2010; Cassini et al. 2012, 2015; Flores et al. 2013; Tarnawski et al. 2014*a*,*b*, 2015; Moyano and Giannini 2017; Moyano et al. 2018).

Multivariate analyses

We used a multivariate approach based on the generalized allometry equation (originally proposed by Jolicoeur 1963*a*). In which, size is considered as a latent variable affecting all original variables simultaneously (see Giannini et al. 2004). Relationships of these variables with the latent size are expressed in the first eigenvector of a principal components analysis (PCA). If growth is isometric, the first-eigenvector elements are all the same and the value of these elements is the expected isometric value, calculated as the squared root of 1/p with p equal to the number of variables. For each variable, allometry is the nominal deviation with respect to this hypothetical isometric eigenvector element value, which represents pure size change. We applied jackhrife as in Giannini et al. (2004) to assess the statistical significance of deviations from isometry of our set of variables. This technique generates confidence intervals for each of the empirically derived first-eigenvector elements (see details in Giannini et al. 2010). If the confidence interval (hereafter CI) includes the isometric value (here 0.208 because p = 23), the variable is statistically indistinguishable from isometry; alternatively, if CI excludes the isometric value, the variable is allometric, being positive for observed values "Supplementary data are available with the article through the journal Web site

exceeding the isometric value, or negative allometry for values below the isometric value. The multivariate statistical analysis (PCA + jackknife resampling; Giannini et al. 2010) was programmed in an R script (R Development Core Team 2015) available from the corresponding author and it was used together with the XLConnect package 0.2-13 (Ksiezopolska 2017).

Comparative analyses

We integrated the results obtained from the developmental series of *Antilocapra* with postnatal ontogenetic series that covered all stages of age, of other four native North American ungulate species. These species were *Bison bison* (represented by 23 specimens), *Cervus canadensis* (25 specimens), *Odocoileus virginianus* (33 specimens) and *Ovis canadensis* (30 specimens). All these species co-occur geographically with *Antilocapra*. For all species, we analyzed sexual dimorphism, contrasting males versus females and using the total set of variables. Then, we selected those species with more than one third of the variables tested (i.e. eight or more) with significant changes in the slope and intercept (interpreted as sexual dimorphism). Although this limit is arbitrary, we consider that specimens of species with few sexually dimorphic variables can be pooled together in a single sample for statistical analysis. The list of specimens with sex data is available in Appendix and the number of specimens disclosed per species, sex and age is available in Supplementary Table S2¹.

A covariance matrix was generated on the 23 log-transformed linear variables of all specimens (known and unknown sex) of every species and subjected to Principal Component Analysis to generate a morphofunctional developmental space to project specimens of all ages of the five species examined. This Principal Component Analysis was performed using the ¹Supplementary data are available with the article through the journal Web site

program InfoStat (Di Rienzo et al. 2017). We compared the ontogenetic trajectories of different species using the angle between pairs of species obtained with the R command: angle = acos(sum(a*b)/ (sqrt(sum(a*a))*sqrt(sum(b*b)))), (see Moyano et al. 2018). Here, *a* is the first eigenvector of *Antilocapra americana*, and b is the first eigenvector of any other of our four chosen species (*Bison bison, Cervus canadensis, Odocoileus virginianus* and *Ovis canadensis*), as appropriate. To test the significance of directional difference between vectors under the null hypothesis that the angle value is smaller than obtained by chance, we performed a permutation test.

In addition, we used bivariate linear regressions to obtain ontogenetic trajectories for each variable of the North American Ungulates studied here. Each variable was transformed (log 10; Weston 2003) and corrected by size using the geometric mean (GM), as size variable. GM corresponds to the Nth root of the product of N measurements (number of morphometric variables). In this common size-shape space, size is a proxy of developmental time (see Reilly et al. 1997; Abdala et al. 2001; Piras et al. 2011; Sheets and Zeldith 2013; Tarnawsky et al. 2015). Linear allometric changes were calculated with respect to overall size (the GM) using the log transformation of the power growth function: $y = b0.x^{b1}$, where y is the focus variable, log(b0) is the y-intercept, x is the size proxy (GM), b1 is the slope of the line or coefficient of allometry, and e is the error term (see Alexander 1985). We used the standardized major axis (SMA) model of regression. All species, with or without sexual dimorphism were treated as in *Antilocapra*, i.e., we pooled together all specimens and used them in bivariate analyses for each of the variables, but in this case contrasting Antilocapra with each of the selected species. Additionally, for those species with observed sexual dimorphism (i.e., those with eight or more dimorphic variables), a second round of comparisons was performed, separating variables according to the presence or not of sexual ¹Supplementary data are available with the article through the journal Web site

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dimorphism. Those variables with sexual dimorphism were contrasted with *Antilocapra* in two ways: 1. versus all males of the dimorphic species, and 2. versus all females of that species. Finally, those variables with no sexual dimorphism were contrasted as in those species with no dimorphism, i.e. pooling together all sexed and unsexed specimens (Supplementary Tables S1¹, S3¹ and S4¹). In practice, sexual dimorphism did not modified substantially our inter-specific comparisons and we used the pooled set per species in multivariate inter-specific analyses.

The paired comparison of growth trajectories between any two species can show three patterns of developmental changes in which ontogenetic trajectories may differ, in direction (slope), position (y-intercept), and in length (Weston 2003; Tarnawski et al. 2014a,b; Moyano et al. 2018). These patterns are: 1. directional change: trajectories differ in slope and/or intercept (i.e., direction and/or position), indicative of difference in postnatal growth rate; 2. lateral shift: trajectories share the same slope but differ in the intercept (i.e., parallel trajectories with different intercept), indicative of difference in onset of growth; 3. ontogenetic scaling or length shift: trajectories overlap (share slope and intercept) but differ in offset of growth. Then we tested for common coefficients between the species for each variable following Weston et al. (2003). First, we analyzed if slopes were shared by a species pair (e.g., Antilocapra vs. Odocoileus) using a likelihood ratio test to find common SMAslope. When two species shared the slope, the next step was to compare the significance of the intercept using the Wald statistic. Finally, when both slope and intercept were shared, the hypothesis of ontogenetic displacement along the common axis of variation was tested to find truncation or extension of one growth trajectory with respect to the other. We used the Wald statistic to test the hypothesis that there might be an ontogenetic shift along the axis (Warton

et al. 2006). All coefficients, statistical parameter estimations, and tests were performed using smatr 3.4-3 and plyr 1.8.4 packages in R (Warton et al. 2012; Wickham 2016).

Results

Skull growth in Antilocapra

The allometric analysis indicated that twelve out of 23 variables were negatively allometric (52%, CBL, PAB, MZB, MZHr, MZHc, ORL, BZB, BMB, BCB, OCH, MCDr and CPH), nine were positively allometric (39%, UPL, LPD, MZL, PAL, NLS, NLM, LPL, LPDm and MCDc), and two were isometric (9%, CSL and CPW; Fig. 2; Table 1). Variables associated with length of different parts of the cranium and mandible of *Antilocapra* showed greater growth rates than those variables related to breadth and height of cranial structures (Figs. 1 and 2; Table 1). The upper tooth row and diastema (UPL, LPD) grew with positive allometry; as expected, this pattern was also reflected in the mandible (LPL, LPDm; Figs. 1 and 2). The length of nasals (NLS, NLM) showed the most positive allometric trend of all cranial variables (Figs. 1 and 2; Table 1), resulting in proportionally longer nasal bones in adults. The muzzle grew less in width dimensions, showing negative allometry in its caudal region (PAB) and more so in the rostral region (MZB; Figs. 1 and 2; Table 1). The variables of the braincase region and zygomatic arch showed negative growth trends (BZB, BCB, BMB, and OCH; Figs. 1 and 2; Table 1).

Growth of the mandible in *Antilocapra* was isometric in overall length (CSL), thus matching skull length (CBL) with the same pattern. Lower toothrow length (LPL) showed the greatest positive growth rate of all mandible variables (Figs. 1 and 2). Height of the mandibular body, measured in two points, exhibited a negative growth rate rostrally (MCDr), and positive ¹Supplementary data are available with the article through the journal Web site

growth rate caudally (MCDc; Figs. 1 and 2). The coronoid process showed a negative allometric trend in height (CPH) and an isometric trend in width (CPW; Figs. 1 and 2; Table 1).

Comparison of Antilocapra with other NA ungulates

The intraspecific sexual dimorphism analysis showed that males and females differed in less variables in *Antilocapra* (only 5, 4 in slope, 1 in intercept), as compared with other species, with 7 variables in *Bison* (2 in slope, 5 in intercept), 7 variables in *Ovis* (4 in slope, 3 in intercept), twelve variables in *Cervus* (8 in slope, 4 in intercept) and 13 in *Odocoileus* (8 in slope, 5 in intercept; see Supplementary Table S1¹). Species showing sexual dimorphism in one third or more of the tested variables were *Cervus* and *Odocoileus* (see Supplementary Table S1¹). This is obviously related to the increasing degree of sexual dimorphism of these species, with female cervids lacking head ornaments.

Multivariate growth trajectories.—The PCA of ontogenetic trajectories of all five species showed that the first component (PC1) explained much of the morphofunctional variation in our data (87.4%; Fig. 3, Supplementary Table S5¹), and that all the variables were positively correlated with the PC1.

The distribution of the ontogenetic series in the developmental morphospace showed the expected continuous gradient of specimens from young to old adults along PC1 in all species (Fig. 3). Younger specimens of all species located towards the negative side of PC1, and adults toward the positive end of PC1. *Antilocapra, Odocoileus* and *Ovis* showed the same offset of growth, while *Cervus* and especially *Bison* considerably differed from other species. PC2 structured the specimens in layers with largely overlapping trajectories of *Antilocapra* ¹Supplementary data are available with the article through the journal Web site

and *Odocoileus*, slightly separated from the trajectory of *Ovis* and *Cervus*, and more clearly distinguished from *Bison*. This variation was related with increasing basicranial width (BCB, widest in the *Bison* series) toward the positive side of PC2, as opposed to variation toward the negative side of PC2, associated with variables: length of both upper and lower toothrows (UPL, LPL), diastema (LPD, LPDm), and coronoid process (CPW, CPH).

Antilocapra, *Odocoileus*, and *Ovis* showed ontogenetic series with similar trajectories and relatively small angles of divergence—smallest between *Antilocapra* and *Odocoileus* at 5.59° (p=0.025). Angles were intermediate between *Antilocapra* and *Cervus* (9.48°; p<0.001) and between *Antilocapra* and *Ovis* (10.42°; p=0.002); finally, *Antilocapra* showed the greatest angular difference with *Bison* (15.29°; p<0.001). These angles represent divergences between ontogenetic trajectories of two species as projected onto the developmental morphospace.

Bivariate comparisons.— *Antilocapra* showed, as expected, the greatest differences in trajectories with *Bison*: 16 variables exhibited statistically different slope and seven remaining variables yielded different intercept (Supplementary Table S6¹).

In the remaining bivariate pairwise comparisons, *Antilocapra* vs. *Cervus* exhibited eight variables with directional change (CBL, UPL, LPD, MZL, PAL, BZB, CSL and MCDr), 14 with lateral shift (PAB, MZB, MZHr, MZHc, NLS, NLM, ORL, BMB, BCB, OCH, LPL, LPDm, MCDc and CPW), and only 1 with ontogenetic scaling (CPH). Similarly, *Antilocapra* vs. *Ovis* showed seven variables with directional change (UPL, LPD, MZL, MZHc, BMB, LPL and LPDm), 12 with lateral shift (CBL, PAL, MZHr, NLS, ORL, BZB, BCB, CSL, MCDr, MCDc, CPH and CPW), and two with ontogenetic scaling (MZB and OCH). *Antilocapra* was remarkably similar to *Odocoileus*, showing only three variables with directional change (NLM, LPL and MCDr), 11 with lateral shift (CBL, PAL, PAL, PAB, ¹Supplementary data are available with the article through the journal Web site

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MZHr, MZHc, NLS, BZB, OCH, MCDc and CPW; Supplementary Table S6¹), and none with ontogenetic scaling. In the variables with directional change, slope was greater in *Antilocapra* for length of nasals (NLM) and lower toothrow (LPL), and greater in *Odocoileus* in height of anterior mandibular body (MCDr).

The muzzle of *Antilocapra* had a greater growth rate in length than the other ungulates except *Odocoileus*, as deduced from the steeper slopes of variable MZL (Supplementary Table $S6^{-1}$). By contrast, the muzzle of all four species grew at the same rate in width as reflected in similar slopes for variable MZB, and partially PAB (rate greater than in *Bison*; Fig. 5b; Supplementary Table S6¹). In addition, a shift was observed in MZB when compared with *Cervus*, which differed in having a significantly higher intercept (but same slope) than Antilocapra. The latter and Odocoileus shared both slope and intercept, and therefore their growth pattern was statistically indistinct (Fig. 5b; Supplementary Table S6¹). Antilocapra shared slope of BMB, BCB and OCH (Supplementary Table $S6^{1}$) with Odocoileus, Cervus and Ovis (except BMB in the latter), indicating a similar growth pattern of the braincase. By contrast, *Bison* exhibited a steeper slope in all three variables as compared with *Antilocapra*, demonstrating the growth toward a more massive braincase in the former. The variables braincase width (BCB) and the zygomatic width (BZB) are negatively allometric in *Antilocapra* and in the other species, but growth rate is slower in braincase width than in zygomatic width. Comparatively, the intercept is lower in both variables in Antilocapra versus the other species, indicating absolutely smaller size of this region along the entire ontogenetic trajectory in this species, except Odocoileus with which Antilocapra shares slope, onset and offset of this entire region, with just a slight difference in intercept. Regarding the mandible, the most important difference across species was observed in the height of the mandibular body (at first and last lower functional postcanine teeth; MCDr, ¹Supplementary data are available with the article through the journal Web site

MCDc). *Antilocapra* showed a slender mandibular body rostrally, with a smaller growth rate than that of *Ovis* and *Cervus* (slope of MCDr Aa < Ov and Cc; Supplementary Table S6¹).

Discussion

Skull growth in Antilocapra

As seen in other ungulates (Moyano and Giannini 2017; Moyano et al. 2018), in Antilocapra, variables associated with length of cranial structures showed greater growth rates than those variables describing skull breadth and height. The skull of *Antilocapra* grew isometrically in length (see CBL in Figs. 1 and 2), thus keeping the same relative proportion in adults as in juveniles, while toward adulthood the muzzle grew to be relatively longer, narrower and lower than the muzzle of juveniles. In the muzzle, the combination of fast growth in length and reduced growth in width, reflected in the adult having a long, narrow rostrum. This shape matches the feeding habits of *Antilocapra*, which has been described as a dainty (or highly selective) browser of a wide variety of plants (O'Gara 1978). A relationship exists between breadth and length of a ruminant's muzzle, which determines the degree of selectivity of plant material intake (Illius and Gordon 1987; Gordon and Illius 1988). The muzzle in grazing ungulates is relatively broader and shorter than high-level browsers; this has been attributed to maintaining a large daily intake in grazers, or to forage selectively in a stand of vegetation in browsers (e.g., Gordon and Illius 1988; Janis and Ehrhardt 1988; Fraser and Theodor 2011; Tennant and MacLeod 2014). In ungulates in general, different species, as well as sexes within species, tend to separate along axes of ecological variation, especially the feeding niche (Illius and Gordon 1987). In Antilocapra, variables associated with the muzzle showed no sexual dimorphism (same slope and intercept) except in the upper and lower postcanine toothrows, with females showing higher growth rates than males (see Supplementary Table ¹Supplementary data are available with the article through the journal Web site

S1¹). The lower growth rate of the toothrows in males suggests some difference in food processing toward the end of development and along adulthood. The choice of high-quality food is considered one of the most important factors influencing the extraordinary reproductive capacity of *Antilocapra* when contrasted with other ungulates (Byers 2011). Thus, longer toothrows in females might be related to a higher processing capability in females, which require extra energy for reproduction, and to the use of less-quality vegetation in males that occupy a slightly more relegated habitat as compared to females (O'Gara 1978). Another variable of strong environmental influence is the orbit dimension; orbits in the newborn are very large, housing large and protruding eyes that allow all-round vision since the animal is born (Beatty et al. 2008). This condition remains with little absolute change as the animal grows, which is reflected in the strong negative allometry of orbit length (ORL). This is a common feature with other ungulates that need a broad peripheral vision to detect potential predators distantly enough to have time to escape (Moyano and Giannini 2017; Moyano et al. 2018).

The negative growth in zygomatic breadth (BZB) and braincase variables (BCB, BMB, and OCH), has been observed in diverse hoofed mammals (e.g., cervids, Cassini et al. 2015; tapirs, Moyano and Giannini 2017; hyraxes, Moyano et al. 2018). This negative trend was also observed in *Antilocapra* and indicate that the skull of the pronghorn experiences a strong relative narrowing of the braincase toward adulthood. The supraorbital position of horns in both sexes (O'Gara 1978) might be related to this ontogenetic pattern, and it certainly is one major difference explaining the developmental contrast with *Bison*, in which ossicones spread laterally in a skull growing strongly in the width dimensions (see Fig. 3). By contrast, breadth of the braincase (BCB) showed the most negative allometry of all cranial variables in *Antilocapra*; in combination with the less-marked negative allometry of bilateral zygomatic ¹Supplementary data are available with the article through the journal Web site

breadth (BZB) a space is created for temporal muscles which enlarges as the animal grows (unbiased BCB = 0.067 and BZB = 0.15; Table 1). Still, this space is modest (Figs. 1 and 2), as is in most hoofed mammals, and slightly larger in males (Supplementary Table S1¹). The mandible growth in *Antilocapra* was heavily influenced by development of dentition. As a result of positive growth pattern for length (LPL) and caudal height (MCDc) and negative for rostral height (MCDr), the mandible of the adult is thin anteriorly and deeper posteriorly, where most of the mastication load is located. Antilocapra americana has a highly hypsodont dentition (hypsodonty index [H.I.] = 4.61; O'Gara 1978; Janis 1988; Janis and Manning 1998), and successively larger cheek teeth emerge in rostro-caudal order (further details in Dow and Wright 1962). The hypsodont molars continue to emerge throughout the life of the animal (Dow and Wright 1962), thus requiring a larger posterior space in the mandible to accommodate the roots of cheekteeth (Janis and Theodor 2014; Cassini et al. 2017; Moyano et al. 2018). The negative allometry observed in the height of the coronoid process (CPH) results in a low process indicating the little influence of temporal muscles in anterior (incisor) mastication, a typical feature of herbivores, which need stronger mastication forces exerted in the molar region that is related to stronger masseter, rather than temporal muscles (Janis 1983; Joeckel 1990).

Comparison of ontogenetic trajectories of skull with other ungulates

All the variables were positively correlated with the PC1, indicating that size-related (allometric) variation represents the main structure of the developmental morphospace of North American native ungulates. All species showed ontogenetic trajectories largely overlapping independently of sex, being *Bison* the taxon with the longest trajectory (Fig. 3).

All studied species except *Bison*, shared patterns of growth in variables of the trophic apparatus; i.e., length of both upper and lower toothrows (UPL, LPL), diastema (LPD, LPDm), and coronoid process (CPW, CPH). The ontogenetic trajectory of Antilocapra was significantly similar to that of *Odocoileus*. Between those variables that shared trajectories in bivariate analysis, we remark those related to the growth and shape of the muzzle, where we observed that *Antilocapra* showed more similarity (more variables with equal slopes) with females than males of *Odocoileus* (Supplementary Table S3¹). The sexual dimorphism recovered in *Odocoileus* may be related to the known strong differential ability to obtain their nutrient requirements; males are able to survive on lower quality forage than females (Illius and Gordon 1987). Then, the morphological similarity between Antilocapra and female Odocoileus could reflect a shared ability for a more selective food gathering. Illius and Gordon (1987), observed that females consume high-quality food and this was also observed in Antilocapra (Byers 2011). Morphological differences of the muzzle between males and females of O. virginianus associated with capability of selection for high-quality food gathering are stronger than those observed between sexes of A. americana (see above). *Bison bison* is the largest hoofed mammals of North America and adults are characterized by particularly broad skulls (Forsyth 1999; Moyano 2018). Precisely, braincase breath (BCB) was the most important variable for distinguishing the growth trajectory of *Bison* from that of Antilocapra (see above), differing statistically in slope but also in onset and offset (Fig. 4a; Supplementary Table S 61). That is, postnatal growth of BCB and other variables related with skull and muzzle wide was faster in Bison but also started at a larger size (onset) and ended considerably larger (offset) than in *Antilocapra*, reflecting the opposing morphology of adults (see Fig. 3). These divergent morphologies could be related to their contrasting feeding habits; e.g., the broad muzzle of *Bison*, typical of a generalized grazer and the narrow muzzle of ¹Supplementary data are available with the article through the journal Web site

Antilocapra, specialized in selectivity, but could also relate to their different agonistic behavior, as *Bison* engages more in a ramming kind of combat, contrary to *Antilocapra* which combats' are more of a wrestling kind (Geist 1966). Even though, more specific studies would be necessary to confirm the later hypothesis.

Regarding the mandible, the height of the mandibular body resulted an important variable; the smaller growth rate present in *Antilocapra* resulted in a rostrally slender mandibular body as compared to other species. On the other hand, Antilocapra has molars with a greater hypsodonty index (HI = 4.61) than *Odocoileus* and *Cervus* (HI = 1.23 and 1.96 respectively; Janis 1988), and these species differed in the growth pattern of mandible height at the last lower molar (MCDc) chiefly by lateral shift, with Antilocapra having a greater intercept than the other species (Fig. 5e; Supplementary Table S6¹). Thus, differences observed in the caudal height of the mandible seem to reflect the differences in hypsodonty index across species. Our evolutionary interpretation of these results, one based upon the phylogenetic scheme of Chen et al. (2019), is that either Antilocapra converged with forms of more modern lineages such as browsing cervids (*Odocoileus*) and bovids (*Ovis*), or that the developmental pattern of Antilocapra is ancient and conserved, so development has diverged more in very large bovids such as *Bison*. While a wider sample is needed to address this question quantitatively, we postulate that *Bison* indeed is highly derived, but also *Antilocapra* is a rather unique herbivore in the North American ensemble in that it combines highly derived character states (such as high hypsodonty) typical of grazers, with a retained ability to exploit vegetation in a highly selective fashion, typical of browsers (e.g., Odocoileus).

In conclusion, the analysis of postnatal development of the skull in *Antilocapra americana* revealed patterns of allometry that were directly related with foraging habits of the species as a selective herbivore (O'Gara 1978). As the skull grows, the rostrum elongated and became ¹Supplementary data are available with the article through the journal Web site

narrower in relative terms; the mandible thickened posteriorly to house highly hypsodont molars, while braincase components grew at a slower pace and resulted in a narrow braincase. Our comparisons with Cervus canadensis, Odocoileus virginianus, Ovis canadensis and Bison *bison*, provided the opportunity to demonstrate the different degrees of similarity of Antilocapra americana with those species of sympatric North American artiodactylans that belong to more recent phylogenetic lineages. As expected, development of the *Antilocapra* skull differed more from that of *Bison*; it differed to a lesser degree from the developmental pattern in *Cervus* and *Ovis*, and finally it was strikingly similar to the pattern that we determined for *Odocoileus*. Both, *Odocoileus* and *Antilocapra* developed skulls with long and thin rostra, more so in Antilocapra, as well as narrower neurocrania. The subtle differences that we found between Antilocapra and Odocoileus relate to the greater degree of hypsodonty in the former. We conclude that in terms of skull development and function, Antilocapra is akin to modern forms of browsing cervids of comparable size. This is clearly reflected in the developmental pattern of the skull, and it may have been key in the survival of this particular antilocaprid lineage into the Recent as a selective feeder of the Great Plains.

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Figure captions

Figure. 1. Cranial measurements of the pronghorn *Antilocapra americana* (Ord 1815) used in this study. **BCB**, Braincase breadth; **BMB**, Bimeatal breadth; **BZB**, Bizygomatic breadth; **CBL**, Condylo-basal length; **CPH**, Coronoid process height; **CPW**, Coronoid process width; **CSL**, Condylo-symphysis length; **LPD**, Diastema length; **LPDm**, Mandibular diastema length; **LPL**, Lower postcanine tooth row length; **MCDc**, Mandibular corpus depth in last functional tooth; **MCDr**, Mandibular corpus depth in pm1; **MZB**, Muzzle breadth; **MZHc**, Muzzle caudal height; **MZHr**, Muzzle rostral height; **MZL**, Muzzle length; **NLM**, Nasal length maximum; **NLS**, Nasal length on suture; **OCH**, Occipital plate height; **ORL**, Orbital length; **PAB**, Palate breadth; **PAL**, Palate length; **UPL**, Upper postcanine tooth row length.

Figure 2. Distribution of confidence intervals of the pronghorn *Antilocapra americana* (Ord 1815) regarding to the isometric value (0.208). Variable abbreviations as in Fig. 1.

Figure 3. Ontogenetic trajectories of the pronghorn *Antilocapra americana* (Ord 1815), *Cervus canadensis* (Erxleben 1777), *Ovis canadensis* (Shaw 1804), *Odocoileus virginianus* (Zimmermann 1780) and *Bison bison* (Linnaeus 1758) in the morphospace of PCA. Variable abbreviations as in Fig. 1.

Figure 4. Bivariate plots of three skull measurements (**a**, BCB; **b**, BMB; **c**, OCH) against geometric mean of the pronghorn *Antilocapra americana* (Ord 1815) *vs*. the American bison *Bison bison* (Linnaeus 1758). Variable abbreviations as in Fig. 1.

Figure 5. Bivariate plots of five skull measurements (**a**, CBL; **b**, MZB; **c**, BZB; **d**, BCB; **e**, MCDc) against geometric mean of the pronghorn *Antilocapra americana* (Ord 1815) *vs*. the wapiti *Cervus canadensis* (Erxleben 1777), the bighorn sheep *Ovis canadensis* (Shaw 1804) and the white-tailed deer *Odocoileus virginianus* (Zimmermann 1780). Variable abbreviations as in Fig. 1.



Figure. 1. Cranial measurements of the pronghorn *Antilocapra americana* (Ord 1815) used in this study.
 BCB, Braincase breadth; BMB, Bimeatal breadth; BZB, Bizygomatic breadth; CBL, Condylo-basal length; CPH, Coronoid process height; CPW, Coronoid process width; CSL, Condylo-symphysis length; LPD, Diastema length; LPDm, Mandibular diastema length; LPL, Lower postcanine tooth row length; MCDc, Mandibular corpus depth in last functional tooth; MCDr, Mandibular corpus depth in pm1; MZB, Muzzle breadth; MZHc, Muzzle caudal height; MZHr, Muzzle rostral height; MZL, Muzzle length; NLM, Nasal length maximum; NLS, Nasal length on suture; OCH, Occipital plate height; ORL, Orbital length; PAB, Palate breadth; PAL, Palate length; UPL, Upper postcanine tooth row length.

107x255mm (300 x 300 DPI)



Figure 2. Distribution of confidence intervals of the pronghorn *Antilocapra americana* (Ord 1815) regarding to the isometric value (0.208). Variable abbreviations as in Fig. 1.

86x109mm (300 x 300 DPI)



Figure 3. Ontogenetic trajectories of the pronghorn *Antilocapra americana* (Ord 1815), *Cervus Canadensis* (Erxleben 1777), *Ovis canadensis* (Shaw 1804), *Odocoileus virginianus* (Zimmermann 1780) and *Bison bison* (Linnaeus 1758) in the morphospace of PCA. Variable abbreviations as in Fig. 1.

178x101mm (300 x 300 DPI)



Figure 4. Bivariate plots of three skull measurements (a, BCB; b, BMB; c, OCH) against geometric mean of the pronghorn *Antilocapra americana* (Ord 1815) vs. the American bison *Bison bison* (Linnaeus 1758). Variable abbreviations as in Fig. 1.

86x215mm (300 x 300 DPI)



Figure 5. Bivariate plots of five skull measurements (a, CBL; b, MZB; c, BZB; d, BCB; e, MCDc) against geometric mean of the pronghorn *Antilocapra americana* (Ord 1815) vs. the wapiti *Cervus Canadensis* (Erxleben 1777), the bighorn sheep *Ovis canadensis* (Shaw 1804) and the white-tailed deer *Odocoileus virginianus* (Zimmermann 1780). Variable abbreviations as in Fig. 1.

163x245mm (300 x 300 DPI)

Table 1. Results of the multivariate analysis of cranial allometry in *Antilocapra americana*(Ord 1815).

Var	Untrimmed					Trimmed	Trimmed				
	Unbiased coeff.	Bias	95% C.I.	Departure	Growth trend	Unbiased coeff.	Bias	95% C.I.	Departure	Growth trend	
Craniu	n										
CBL	0.201	-1.36E-03	0.191-0.211	-0.007	iso	0.198	1.01E-04	0.19-0.207	-0.01	-	
UPL	0.234	5.40E-03	0.177-0.292	0.026	iso	0.263	-9.25E-03	0.22-0.307	0.055	+	
LPD	0.237	-1.96E-03	0.22-0.254	0.029	+	0.234	-4.21E-04	0.22-0.248	0.026	+	
MZL	0.255	-1.63E-03	0.242-0.269	0.047	+	0.252	-1.48E-04	0.243-0.262	0.044	+	
PAL	0.255	-1.09E-03	0.215-0.235	0.016	+	0.224	-8.02E-04	0.217-0.232	0.016	+	
PAB	0.187	-1.96E-03	0.164-0.21	-0.022	iso	0.179	1.76E-03	0.161-0.197	-0.029	-	
MZB	0.167	-2.94E-03	0.128-0.206	-0.042	-	0.141	9.68E-03	0.121-0.162	-0.067	-	
MZHr	0.163	-1.26E-03	0.146-0.18	-0.045	-	0.16	1.35E-04	0.147-0.174	-0.048	-	
MZHc	0.136	4.94E-04	0.102-0.171	-0.072	-	0.142	-2.23E-03	0.123-0.161	-0.067	-	
NLS	0.311	-1.55E-03	0.297-0.325	0.103	+	0.312	-1.76E-03	0.3-0.324	0.103	+	
NLM	0.309	-2.34E-03	0.289-0.329	0.1	+	0.302	1.08E-03	0.288-0.317	0.094	+	
ORL	0.094	-9.24E-04	0.082-0.107	-0.114	-	0.091	7.73E-04	0.081-0.101	-0.118	-	
BZB	0.152	-1.24E-03	0.14-0.164	-0.056	-	0.15	-4.05E-04	0.141-0.16	-0.058	-	
BMB	0.161	-1.40E-03	0.145-0.178	-0.047	-	0.16	-5.81E-04	0.146-0.173	-0.049	-	
BCB	0.067	-3.36E-04	0.05-0.084	-0.142	-	0.067	-1.72E-04	0.052-0.081	-0.142	-	
OCH	0.101	-2.48E-03	0.072-0.13	-0.108	-	0.09	3.10E-03	0.067-0.112	-0.119	-	
Mandib	ole										
CSL	0.205	-1.06E-03	0.197-0.214	-0.003	iso	0.204	-2.39E-04	0.198-0.21	-0.005	iso	
LPL	0.314	3.63E-03	0.26-0.368	0.105	+	0.341	-1.00E-02	0.303-0.379	0.133	+	
LPDm	0.255	-1.14E-03	0.233-0.278	0.047	+	0.248	2.33E-03	0.232-0.264	0.04	+	
MCDr	0.14	1.93E-03	0.107-0.172	-0.069	-	0.154	-5.04E-03	0.132-0.175	-0.055	-	
MCDc	0.223	3.10E-03	0.186-0.26	0.015	iso	0.239	-4.81E-03	0.209-0.269	0.03	+	
СРН	0.206	-1.92E-03	0.175-0.236	-0.003	iso	0.188	6.85E-03	0.17-0.206	-0.021	-	
CPW	0.226	-1.93E-03	0.193-0.26	0.018	iso	0.22	1.33E-03	0.195-0.245	0.011	iso	

Results from untrimmed (full set of jackknife pseudovalues used) and trimmed analyses (with the *m* smallest pseudovalues removed in the calculations, with m = 1). Variable abbreviations as in Fig. 1. Unbiased coefficient, is the value generated by first-order jackknife resampling; Bias, is the difference between the unbiased and observed coefficients. 95% C.I, the jackknifed 95% confidence interval (CI) is provided; allometric variables are those whose CIs exclude the expected value under isometry (0.208). Departure, represent the subtraction of expected value under isometry to the unbiased coefficient; Growth trend, is the allometric trend of each variable. iso, isometry; –, negative allometry; +, positive allometry. Var, variable.

Appendix A

List of specimens used in this work. Females in bold, males in italic and all other specimens without determined sex.

Antilocapra americana: AMNH: 16139, 19350, 5036, 6349, 77849, 120947, 11147, 142361, 11095, 11107, 11106; USNM: A11574, 013305, 271897, 271896, 181372, 014876, 014873, A22386, 265227, A31278, 011093, 272849, A03460, 271841, A22658, 120702, 120705, 120703, 120704; Bison bison: USNM: 154200, 176397, 270282, 399313, 123302, 15696, 31218, 251148, 174625, 174624, 201047, 201050, 201051, 233522, 154570, 61760, 63364, 261114, 122676, 120568, 120580, 123424, 121008; Cervus canadensis: USNM: 86418, 261744, 105970, **179086**, **168704**, **209708**, A3849, **265053**, **265058**, 265059, **265025**, *265051*, *213407*, **265054**, **265060**, **265062**, *265063*, **265055**, **265067**, *265022*, **265021**; Odocoileus virginianus: FMNH: 172399, 154736, 154737, 167204, 167203, 153836, 154735, 44829, 105775, 196110, 105766, 105767, 105768, 105746, 105747; USNM: 83291, 236958, 282315, 141940, 124665, 141919, 143868, 141915, 1909, 125666, A980, 238130, 250482, 180797, 180796, 238133, 241189, 269752; Ovis canadensis: AMNH: 31299, 17953, 31301, 17956, 17954; FMNH: 10955, 10946, 10947, 10945, 10950, 10948, 10952, 10951, 14811, 14809, 203140; USNM: 203139, 180273, 170680, 203134, 181253, 170679, 117665, 146520, 147513, 147510, 86423, 86422, 81911, 14010.