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Postnatal ontogenetic scaling of pampas deer (*Ozotoceros bezoarticus celer*: Cervidae) cranial morphology

Abstract: The pampas deer *Ozotoceros bezoarticus* is a medium-sized, elegant, and lightly built cervid that was once a characteristic inhabitant of open grasslands across a wide geographical distribution in South America. In Argentina, the subspecies *Ozotoceros bezoarticus celer* is the most southern and abundant populations and relatively well represented in osteological collections permitting a morphometric study of cranial ontogeny. We measured 17 cranial variables on an ontogenetic series in order to evaluate the multivariate allometry of neurocranial and splanchnocranial components through developmental stages. The cranial ontogenetic pattern in *O. b. celer* exhibits a conservative plan in which both sexes share most of the allometric trends except in three variables related to the rostrum. Isometry was detected in 9 out of 17 variables, whereas four grows with negative allometry, and only nasal length showed positive allometry. As for most mammals, those variables related to the neurocranial components and sensorial capsules exhibit negative allometry. The growth of the rostrum indicates that both sexes have longer face than younger. However, the lack of allometry in most of the variables seems to be supporting the idea of a younger with the general appearance of an adult but smaller size.

Keywords: Cervidae; early development; multivariate allometry; skull; South America.

Introduction

Cervidae account for the larger diversity of South American extant ungulates with five genera and eight species recognized in Argentina (Merino 2006). The pampas deer *Ozotoceros bezoarticus* (Linnaeus, 1758) was once a characteristic inhabitant of open grasslands across a wide geographical distribution, from 5° to 41°S including regions of Brazil, Bolivia, Paraguay, Argentina, and the whole Uruguay (Jackson 1987, Jackson and Giulietti 1988, Pautasso et al. 2002, Merino 2006, González et al. 2010, Merino and Vieira Rossi 2010). Only few small isolated populations remain at present, and the pampas deer is considered by the UICN as near threatened in South America (González and Merino 2008). Four separated populations of two subspecies are present in Argentina: *Ozotoceros bezoarticus leucogaster* Goldfuss, 1817, in the provinces of Santa Fe and Corrientes (Parera and Moreno 2000, Pautasso et al. 2002), and *Ozotoceros bezoarticus celer* Cabrera, 1943, in the provinces of San Luis and Buenos Aires (Dellafiore et al. 2003, Pérez Carusi et al. 2009). The southern and more abundant population of *O. b. celer* is relatively well represented in osteological collections and pertinent for morphological studies.

The pampas deer is a medium-sized (30–40 kg), elegant, and lightly built cervid (Jackson 1987). As most cervids, it presents sexual dimorphism, with males having three pointed small antlers (~30 cm) and females lacking antlers and showing instead a white twisted shape tuft on the frontal zone (Cabrera 1943, Cosse Larghero 2002). The offspring weigh 1.5–2 kg at birth, and at the age of 7 months, they show almost complete adult aspect, except for the smaller body size (Fräderich 1981, Gimenez-Dixon 1991). The pampas deers have broad feeding strategies throughout their distribution in relation to phytogeographical variation (Merino 2003) and, consequently, are described as having an opportunistic foraging strategy typical of intermediate or mixed feeders (Cosse et al. 2009). Different populations of the subspecies studied here, *Ozotoceros bezoarticus celer*, presents slightly different feeding behaviors, as those from San Luis Province

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feed primarily on new green growth grass (Jackson and Giulietti 1988, but see Merino et al. 2009), whereas those from Campos del Tuyú Wildlife Reserve (Buenos Aires Province) were described as mixed grass feeders with preference for grasses (Jackson and Giulietti 1988).

Although some authors carried out cranial morphometric studies on South American cervids including *Ozotoceros bezoarticus* (e.g., Wemmer and Wilson 1987, Delupi and Bianchini 1995, Beade et al. 2000, González et al. 2002), they are focused primarily on taxonomic variations. More recently, Merino et al. (2005) correlated diet and morphology in this species and made preliminary observations on ontogeny. Perhaps the first contribution to the skull ontogeny of ungulates was the Allen (1913) paper on *Ovibos moschatus* (Zimmermann 1780). However, with some exceptions as horses (Radinsky 1984), camels (Al-Sagair and ElMougy 2002), hippos (Weston 2003), and the extinct South American toxodontids (order Notoungulata) (Cassini et al. 2012), little is known about the ontogenetic development of ungulate cranium and its relationships with the transition to a herbivorous feeding style in an allometric framework. To date, some studies on ontogeny in ungulates suggest that the medioanterior regions of the mandible (i.e., diastema and premolar parts of the mandibular corpus) growth is mainly prenatal, whereas the posterior section of the jaw (i.e., molar part of the mandibular corpus and ramus of the mandible) develops in parallel with the transition in main food source from milk to herbal forage (Todd and Wharton 1934, Pond 1977, Herring 1985, Høye and Forchhammer 2006).

In this contribution, we investigate the way in which the cranial configuration of both populations of *Ozotoceros bezoarticus celer* changes from juveniles to adults, applying a multivariate quantitative approach on a well-represented ontogenetic series of skulls of different inferred age stages. This statistical approach is possible thanks to recent efforts to collect dead carcasses in San Luis province and "Campos del Tuyú Wildlife Reserve" yielded to enlarge the number of *O. b. celer* skulls in museum collections of Argentina (Figure 1A–F). Together with the collections made in the late 1960s, an excellent ontogenetic series for the two localities of this endangered species is available. The ontogenetic series studied here allows the evaluation of the morphological changes on functional grounds, during a period of development in which critical changes occur, as interactions between growth of neurocranial and splanchnocranial components through developmental stages causes modifications in the function of

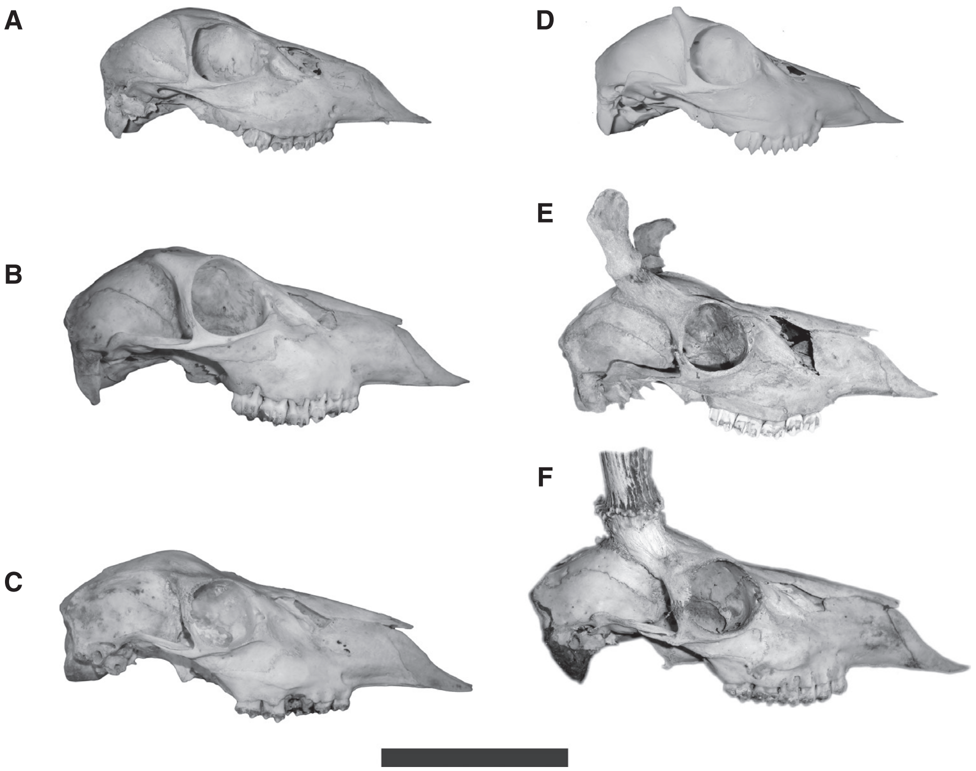

Figure 1 Three ontogenetical states of *Ozotoceros bezoarticus*. (A) Female juvenile MLP 18.VIII.92.4 (TSL=168 mm mirror image); (B) female subadult MLP 31.VIII.98.1 (TSL=197 mm); (C) female adult MLM 388 (TSL=218 mm); (D) male juvenile MLP 23.VIII.96.1 (TSL=150 mm mirror image); (E) male subadult MLM 401 (TSL=188 mm); (F) male adult CDT 096 (TSL=223 mm).

the skull linked to the transition from juvenile to adult diets (Abdala et al. 2001, Giannini et al. 2004, Flores et al. 2006). In addition, we compared the allometric trends of *O. b. celer* with other larger-size ungulates as hippos (Weston 2003) and the fossil toxodontids *Adinotherium* and *Nesodon* (Cassini et al. 2012), in order to evaluate the differences and similarities of the ontogenetic pattern (in allometric terms) of the skull in three nonrelated and morphologically divergent ungulates.

Materials and methods

Study specimens

We analyzed an ontogenetic series of 70 specimens (36 females and 34 males) (Tables 1 and 2) of *Ozotoceros bezoarticus celer* housed at the mammal collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN, Buenos Aires, Argentina), Museo de La Plata (MLP, La Plata, Argentina), and Museo Regional de la Reseva de Vida Silvestre "Campos Tuyú" (CDT, Buenos Aires Province). Two age stages were estimated from dental formulae, dental wear states, and observations of sutural fusion at the basicranium (Morris 1972, Bianchini and Delupi 1993, Anders et al. 2011). They consist in ages classes (AC) related to time intervals following Bianchini and Delupi (1993) and an individual dental age stages (IDAS) following Anders et al. (2011) as infant, juveniles, adults, and late adults. In our sample, 12 specimens (six of each sex) retained deciduous dentition, whereas the other 58 has a complete adult dentition with different stages of wear. The female sample are constituted by only one infant (*sensu* Anders et al. 2011), the smallest specimen of about 3–6 months old of 168 mm in total skull length (MLP 18.VIII.92.4); five juveniles (two with 6–9 months old and the remaining three with 9–12, 12–18, and 18–20 months old each (Table 1); 27 adults (5 between 2 and 3 years, 12 between 3 and 4 years, and 9 between 4 to 6 years old) and three late adults of about 6–8 years old (Table 1). The largest female specimen was a late adult of 218.4 mm in total skull length (MLM-388), with highly and advanced worn adult dentition. The male sample includes two infants (*sensu* Anders et al. 2011) of about 3–6 months old whose smallest specimen has 150 mm in total skull length (MLP 23.VIII.96.1, Table 2); four juvenile (one of 9–12, one of 18–20 and two of 20–24 month old); 27 adults (11 between 2 and 3 years, 7 between 3 and 4 years and 7 between 4 to 6 years old) and only one late adult of about 6–8 years old. The largest male specimen was an adult of 255.2 mm in total skull length (MLM-391), with highly worn adult dentition. We chose the specimens coming from the two aforementioned populations (*O. b. celer* from Buenos Aires and San Luis Provinces) in order to avoid the ecogeographic effects.

Study of growth and measurements

Allometry of growth explicitly considers timing of changes throughout the life of an individual (Kunz and Robson 1995, Prestrud and Nilssen 1995, Maunz and German 1996, Stern and Kunz 1998). By contrast, allometry of size compares changes against overall size along a growth series, and the time frame is implicitly incorporated but not specified. Allometry of size may, in turn, be interspecific with the purpose of studying functional changes from an evolutionary perspective within a lineage (Davis 1962, Radinsky 1984, Silva 1998, Hayssen and Kunz 1996), or intraspecific with an aim similar to studying the allometry of growth (Nelson and Shump 1978), that is, to describe relative modifications in structures as the animal grows (Klingenberg and Zimmermann 1992, Klingenberg 1996). For the allometric analysis, we used 17 cranial variables (Figure 2) including length, width, and height of several neurocranial and splanchnocranial components describing functional compromises.

The multivariate approach is based on the generalization of the allometry equation proposed by Jolicoeur (1963). In multivariate allometry, size is considered as a latent variable affecting all original variables simultaneously, and the allometric relationships of all variables with the latent variable are expressed in the first eigenvector of a principal component analysis (extracted from a variance-covariance matrix of log-transformed variables). Under isometry, all variables respond in the same way to growth, and the elements of the isometric unit eigenvector are equal to an expected value calculated as $1/p^{0.5}$, where p equals the number of variables (17 in our study). The value of the eigenvector of the first principal component represents the observed multivariate coefficient of allometry of the corresponding variable. Comparison of each of the empirical elements of the first-unit eigenvector with the isometric eigenvector allows us to detect negative (<0.2425) and positive (>0.2425) departures from isometry in each variable. Statistical departures from isometry were estimated applying Jackknife (Quenouille 1956, Manly 1997). The aim of this technique is to generate confidence intervals for the empirically obtained eigenvector elements. Thus, pseudosamples are generated such that a new first unit eigenvector is calculated from a matrix with

Table 1 List of female crania examined with teeth replacement and wear states.

Catalog number	UPL	TSL	GM	dP2	P2	dP3	P3	dP4	P4	M1	M2	M3	AC	IDAS
MLP 18.VIII.92.4	54.21	167.96	56.21	Worn	–	Worn	–	Worn	–	Erupted	1/2 Erupting		1.5	1
MLM 387	63.69	187.92	61.60	Highly worn	–	Advanced worn	–	Advanced Worn	–	Early worn	Early worn	Very early erupting	1.6	2
CDT 109	55.99	188.02	60.37	Fully worn	–	Advanced worn	–	Worn	–	Erupted	Almost fully erupting	Opening alveoli	1.6	2
MLM 395	63.08	185.12	61.84	Advanced worn	–	Advanced worn	–	Advanced worn	–	Early worn	Erupted	Very early erupting	1.7	2
MLP 18.VIII.92.11	60.86	175.2	57.66	–	Opening alveoli	–	Opening alveoli	Fully worn	Opening alveoli	Worn	Early worn	Almost fully erupting	2.1	2
MLP 18.VIII.92.10	64.25	190.68	62.66	Advanced worn	–	Advanced worn	–	Advanced worn	–	Worn	Early worn	3/4 Erupting	2.2	2
MLM 399	67.25	192.08	61.18	–	Early Worn	–	Early Worn	–	Early worn	Worn	Early worn	Erupted	3	3
MLP 23.VIII.96.6	63.05	193.43	64.13	–	Worn	–	Worn	–	–	Worn	Worn	Early worn	3	3
MLM 402	68.40	203.28	63.69	–	Worn	–	Worn	–	Worn	Worn	Worn	Early worn	3	3
CDT 27	59.97	209.97	67.13	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	3	3
CDT w/n	64.83	210.03	66.75	–	Worn	–	Worn	–	Worn	Worn	Worn	Early worn	3	3
CDT 112	67.19	211.19	67.16	–	Early worn	–	Early worn	–	Early worn	Worn	Early worn	Early worn	3	3
CDT 20	59.90	187.33	63.70	–	Advanced worn	–	Advanced Worn	–	Advanced Worn	Advanced Worn	Advanced worn	Worn	4.1	3
MLP 1338	63.78	191.13	63.38	–	Early worn	–	Worn	–	Worn	Advanced worn	Worn	Worn	4.1	3
MLP 1339	65.97	193.34	64.82	–	Early worn	–	Worn	–	Worn	Advanced worn	Worn	Worn	4.1	3
MLP 31.VIII.98.1	62.82	197.02	65.96	–	Advanced worn	–	Advanced worn	–	Worn	Advanced worn	Worn	Worn	4.1	3
MLP 23.VIII.96.4	64.62	198.96	66.54	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
MLP 18.VIII.92.14	59.68	200.02	64.77	–	Early worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT 11	60.46	201.37	64.88	–	Worn	–	Worn	–	Worn	Advanced worn	Worn	Worn	4.1	3
CDT 67	63.39	202.7	65.61	–	Erupted	–	Early worn	–	Erupted	Early worn	Early worn	Erupted	4.1	3
MLP 1632 TYPE	62.66	204.65	64.57	–	Worn	–	Worn	–	Worn	Advanced worn	Worn	Worn	4.1	3
CDT w/n	63.19	210.11	68.59	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT 5	62.58	212.32	66.71	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT 87	64.05	217.88	71.14	–	Worn	–	Worn	–	Worn	Worn	Worn	Eorn	4.1	3
MLM 386	64.91	187.69	61.89	–	Advanced worn	–	Advanced worn	–	Advanced worn	Highly worn	Advanced worn	Advanced worn	4.2	3
MLM 406	72.07	190.93	62.52	–	Worn	–	Worn	–	Worn	Advanced worn	Advanced worn	Worn	4.2	3
MLP 5.VI.97.2	61.05	190.98	62.25	–	Worn	–	Worn	–	Worn	Advanced worn	Advanced worn	Worn	4.2	3
MLP 5.VI.97.4	59.57	193.02	64.66	–	Missing	–	Missing	–	Advanced worn	Highly worn	Advanced worn	Advanced worn	4.2	3
MLP 6.VIII.98.1	57.72	194.78	64.42	–	Worn	–	Worn	–	Worn	Advanced worn	Advanced worn	Worn	4.2	3
MLM 393	69.60	196.31	64.55	–	Worn	–	Worn	–	Worn	Advanced worn	Advanced worn	Worn	4.2	3
CDT PR 3	67.01	197.95	66.16	–	Open alveoli	–	Worn	–	Worn	Advanced worn	Advanced worn	Worn	4.2	3
MLM 404	62.66	201.52	64.94	–	Worn	–	Worn	–	Advanced worn	Advanced worn	Advanced worn	Worn	4.2	3
CDT 70	62.01	202.32	67.16	–	Advanced Worn	–	Advanced worn	–	Advanced worn	Advanced worn	Advanced worn	Advanced worn	4.2	3
MLM 410	64.09	197.11	64.09	–	Highly worn	–	Highly worn	–	Highly worn	Fully worn	Highly worn	Highly worn	4.3	4
MLP 5.VI.97.3	57.70	202.37	65.16	–	Advanced worn	–	Advanced worn	–	highly worn	Fully worn	Highly worn	Highly worn	4.3	4
MLM 388	62.22	218.4	69.28	–	Highly worn	–	Advanced worn	–	Advanced worn	Highly worn	Advanced worn	Advanced worn	4.3	4

UPL, upper postcanine tooth row length; TSL, total skull length; GM, geometric mean of 17 measurements. Units in millimeters; AC, age classes following Bianchini and Delupi (1993); IDAS, individual dental age stages following Anders et al. (2011).

Table 2 List of male crania examined with teeth replacement and wear states.

Catalog number	UPL	TSL	GM	dP2	P2	dP3	P3	dP4	P4	M1	M2	M3	RAC	IDAS
MLP 23.VIII.96.1	43.10	150.04	51.13	Erupted	–	Worn	–	Early worn	–	3/4 Erupting	Opening alveoli		1.5	1
CDT 88	43.82	158.83	51.86	Erupted	–	Early worn	–	Early worn	–	Almost fully erupting	Opening alveoli		1.5	1
MLP 1.XII.00.1	53.78	181.72	57.83	Advanced worn	–	Highly worn	–	Advanced worn	–	Early worn	Almost fully erupting	Opening alveoli	1.7	2
MLP 18.VIII.92.8	64.13	184.28	60.11	Early worn	–	Worn	–	Worn	–	Early worn	Almost fully erupting	1/2 Erupting	2.2	2
MLP 18.VIII.92.9	65.00	191.03	63.72	Highly worn	–	Highly worn	Very early erupting	Highly worn	Opening alveoli	Worn	Early worn	Almost fully erupting	2.3	2
CDT w/n	66.63	200.91	63.78	Worn	–	Worn	–	Worn	–	Early worn	Early worn	1/2 Erupting	2.3	2
MLP 1340	59.74	177.47	60.44	–	Erupted	–	Worn	–	Worn	Advanced worn	Worn	Early worn	3	3
MLM 401	66.59	188.42	61.96	Fallen	Open alveoli	–	Early worn	–	Worn	Worn	Worn	Early worn	3	3
MLM 390	63.02	192.39	64.20	–	Opening alveoli	–	Early worn	–	Early worn	Worn	Early worn	Erupted	3	3
MLP 18.VIII.92.2	67.16	198.91	65.61	–	Erupted	–	Erupted	–	Erupted	Worn	Early worn	Erupted	3	3
CDT 101	69.35	199.13	65.05	–	Early worn	–	Early worn	–	Early worn	Worn	Worn	Early worn	3	3
MLP 1.XII.00.2	63.17	205.01	67.19	–	Worn	–	Worn	–	Worn	Worn	Worn	Early worn	3	3
MLP 1631 TYPE	63.23	205.23	67.55	–	Early worn	–	Worn	–	Worn	Worn	Worn	Early worn	3	3
CDT 79	65.67	211.55	67.15	–	Erupted	–	Erupted	–	Erupted	Early worn	Early worn	Erupted	3	3
CDT GC 7	60.54	218.73	69.50	–	Worn	–	Worn	–	Worn	Worn	Worn	Early worn	3	3
CDT 86	65.72	218.87	71.20	–	Worn	–	Worn	–	Early worn	Early worn	Early worn	Early worn	3	3
MLP 14.VI.00.2	63.10	219.95	70.71	–	Worn	–	Worn	–	Worn	Worn	Worn	Early worn	3	3
MLP 30.XII.02.92	64.80	206.99	67.74	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT 26	66.39	210.25	66.24	–	worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
MLM 396	68.64	211.06	68.93	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT 84	65.36	211.77	67.52	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT 113	63.94	212.51	68.26	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT w/n	64.06	213.37	68.11	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
CDT 30	67.26	219.46	70.78	–	Worn	–	Worn	–	Worn	Worn	Worn	Worn	4.1	3
MLM 394	62.84	197.88	65.89	–	Worn	–	Worn	–	Worn	Advanced worn	Advanced worn	Worn	4.2	3
MLM 408	65.42	200.01	67.74	–	Worn	–	Worn	–	Worn	Advanced worn	Advanced worn	Advanced worn	4.2	3
MLM 389	68.43	200.42	66.97	–	Highly worn	–	Advanced worn	–	Advanced worn	Highly worn	Advanced worn	Advanced worn	4.2	3
MLM 409	59.35	201.06	65.52	–	Worn	–	Worn	–	Advanced worn	Advanced worn	Advanced worn	Worn	4.2	3
CDT 38	62.80	217.83	71.75	–	Advanced worn	–	Advanced worn	–	Advanced worn	Advanced worn	Advanced worn	Advanced worn	4.2	3
CDT 98	63.33	218.02	68.95	–	Advanced worn	–	Advanced worn	–	Advanced worn	Advanced worn	Advanced worn	Advanced worn	4.2	3
CDT 77	64.42	218.77	71.76	–	Advanced worn	–	Advanced worn	–	Advanced worn	Highly worn	Advanced worn	Advanced worn	4.2	3
CDT 96	65.03	223.27	70.68	–	Worn	–	Worn	–	Advanced worn	Advanced worn	Advanced worn	Worn	4.2	3
MLM 391	65.88	224.7	72.03	–	Highly worn	–	Highly worn	–	Highly worn	Highly worn	Advanced worn	Advanced worn	4.2	3
MLM 392	64.62	200.92	68.26	–	Highly worn	–	Highly worn	–	Highly worn	Highly worn	Highly worn	Highly worn	4.3	4

UPL, upper postcanine tooth row length; TSL, total skull length; GM, geometric mean of 17 measurements. Units in millimeters; AC, age classes following Bianchini and Delupi (1993); IDAS, individual dental age stages following Anders et al. (2011).

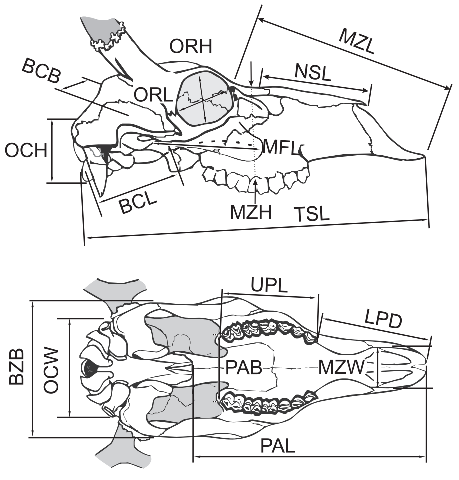

Figure 2 Cranial measurements of the *Ozotoceros bezoarticus* used in this study. BCB, braincase breadth; BZB, bizygomatic breadth; BCL, basicranial length; LPD, diastema length; MFL, masseteric fossa length; MZH, muzzle height; MZL, muzzle length; MZW, muzzle width; NSL, nasal suture length; OCH, occipital height; OCW, occipital width; ORH, orbital height; ORL, orbital length; PAB, palate breadth; PAL, palate length; TSL, total skull length; UPL, upper postcanine tooth row length.

one individual removed at a time. Giannini et al. (2004, 2010) and Flores et al. (2006, 2010) followed Manly (1997) in using trimmed values for the calculation of pseudovalues. Trimming the largest and smallest pseudovalues for each variable significantly decreased the standard deviations. Herein, we report untrimmed as well as trimmed values, opting for the results with either the lower average standard deviation or bias. The multivariate statistical analysis (PCA+Jackknife resampling) was programmed in R (R Development Core Team 2012), and the script is available from the author (Giannini et al. 2010).

Results

The mean difference in the absolute bias favors untrimmed over trimmed analysis in both sexes. The mean of modulus of bias for the untrimmed analysis in females was 0.00962 vs. 0.01365 in the trimmed analysis (i.e., 1.42 times higher). In males, the values were 0.00474 and 0.00496, respectively (1.047 times higher). The cranial ontogenetic pattern in *Ozotoceros bezoarticus celer* exhibits a conservative plan in which both sexes share most of the allometric trends. The untrimmed multivariate analysis detects sexual dimorphism only in 3 out of 17 cranial variables (Table 3): predental length (LPD), palatal length (PAL), and muzzle length (MZL). While in females PAL and MZL were isometric and LPD had positive allometry, in males, only LPD was isometric, whereas PAL and MZL were positively allometric. In the case of the remaining variables for which both sexes shared the same trend, eight were isometric (UPL, MFL, TSL, LBC, OCW, ORH, MZH, MZW, and PAB), four grow with negative allometry (ORL, BZB, OCH, and BCB), and only nasal length (NSL) showed positive allometry. With the exception of BCB, the departure of isometry was always higher for females (Table 3).

As a basis for comparison with other cervids, we interpreted our results from allometric growth trends of the untrimmed coefficients (Table 3) in order to describe the process of modeling of the skull in *Ozotoceros bezoarticus celer* during ontogeny. The growth of the rostrum was the only area exhibiting sexual dimorphism, with males showing higher rates of growth in the palate and muzzle lengths and females showing higher rate of growth of the predental section of the muzzle. In males, the muzzle and palate become slender because of the positive allometry of the muzzle and palate length, and the isometry of its width. In females, the positive allometry of the predental length implies also an enlargement of the palate during growth, at least on their anterior region. In addition, nasals in both sexes become longer in adults due to their positive allometry. The remaining measurements linked to the rostrum (e.g., UPL, PAB, MZW, MLH) increase its length isometrically, keeping the relative general proportions of the rostrum almost constant. The slender appearance of the adult skull is indicative of the negative allometry of the zygomatic breadth and the smaller volume/development of temporal musculature in this species. However, and in concordance with the importance of the masseteric muscles for mastication, the masseteric fossa grows isometrically. As described above, the neurocranium grows in a complex way, with some variables exhibiting higher rate of growth than expected for sensorial capsules (Emerson and Bramble 1993). For instance, the length of the basicranium, orbital height, and occipital width maintain their proportions according to their pattern of growth, increasing their length isometrically and keeping the relative size of such structures almost constant in those specific dimensions. On the other hand, the occipital height, braincase, and orbital length grow with negative allometry, with young specimens exhibiting proportionally larger braincases and orbit lengths than adults. These differences suggest a complex way of growth of the neurochranium, in which the braincase and orbit change its proportions in adults: orbit becomes higher, and braincase becomes longer in its base and wider in its occipital section.

Table 3 Results by sex of the multivariate analysis of cranial allometry in *Ozotoceros bezoarticus celer*.

Variable	Sex	Untrimmed					Trimmed				
		Unbiased coeff.	Bias	99% CI	Departure	Growth trend	Unbiased coeff.	Bias	99% CI	Departure	Growth trend
BCB	F	0.080	2.106E-03	-0.021–0.181	-0.162	-	0.103	-9.390E-03	0.036–0.171	-0.139	-
	M	0.064	7.430E-04	-0.001–0.13	-0.178	-	0.062	2.121E-03	0.016–0.107	-0.181	-
BZB	F	0.120	2.854E-03	0.046–0.194	-0.122	-	0.127	-7.076E-04	0.069–0.185	-0.115	-
	M	0.148	2.540E-04	0.067–0.23	-0.094	-	0.146	1.712E-03	0.114–0.178	-0.097	-
LBC	F	0.153	1.169E-02	-0.036–0.342	-0.089	iso	0.191	-7.250E-03	0.098–0.284	-0.052	iso
	M	0.202	-3.713E-03	0.145–0.259	-0.040	iso	0.200	-2.807E-03	0.167–0.234	-0.042	-
LPD	F	0.336	-1.151E-02	0.255–0.417	0.093	+	0.348	-1.751E-02	0.279–0.416	0.105	+
	M	0.294	-3.948E-04	0.223–0.365	0.052	iso	0.310	-8.271E-03	0.266–0.354	0.067	+
MFL	F	0.272	-5.720E-03	0.185–0.359	0.029	iso	0.248	6.236E-03	0.187–0.309	0.006	iso
	M	0.199	-4.689E-03	0.154–0.245	-0.043	iso	0.189	2.771E-04	0.158–0.221	-0.053	-
MZH	F	0.214	-4.600E-03	0.081–0.348	-0.028	iso	0.196	4.771E-03	0.121–0.27	-0.047	iso
	M	0.271	-4.075E-03	0.172–0.37	0.028	iso	0.244	9.194E-03	0.182–0.307	0.002	iso
MZL	F	0.330	-1.579E-02	0.222–0.437	0.087	iso	0.284	7.298E-03	0.239–0.328	0.041	iso
	M	0.324	-5.816E-03	0.284–0.364	0.082	+	0.308	2.384E-03	0.292–0.323	0.065	+
MZW	F	0.271	1.469E-03	0.091–0.452	0.029	iso	0.303	-1.432E-02	0.186–0.419	0.060	iso
	M	0.274	5.467E-03	0.173–0.375	0.031	iso	0.269	7.980E-03	0.195–0.343	0.026	iso
NSL	F	0.601	-3.074E-02	0.315–0.887	0.358	+	0.516	1.180E-02	0.362–0.67	0.273	+
	M	0.496	-3.191E-03	0.355–0.636	0.253	+	0.522	-1.616E-02	0.422–0.621	0.279	+
OCH	F	0.039	1.284E-02	-0.147–0.226	-0.203	-	0.113	-2.425E-02	0.049–0.177	-0.129	-
	M	0.080	5.242E-03	0.021–0.139	-0.162	-	0.091	-4.442E-04	0.053–0.13	-0.151	-
OCW	F	0.249	3.841E-03	0.129–0.369	0.006	iso	0.288	-1.584E-02	0.219–0.358	0.046	iso
	M	0.222	6.395E-03	0.153–0.292	-0.020	iso	0.242	-3.677E-03	0.205–0.28	0.000	iso
ORH	F	0.178	1.227E-06	0.094–0.261	-0.065	iso	0.157	1.016E-02	0.105–0.21	-0.085	-
	M	0.146	4.868E-03	0.037–0.254	-0.097	iso	0.184	-1.417E-02	0.143–0.224	-0.059	-
ORL	F	0.067	1.011E-02	-0.082–0.217	-0.175	-	0.141	-2.669E-02	0.088–0.194	-0.102	-
	M	0.109	8.921E-04	0.07–0.149	-0.133	-	0.114	-1.357E-03	0.085–0.143	-0.129	-
PAB	F	0.182	9.197E-03	-0.018–0.383	-0.060	iso	0.248	-2.366E-02	0.148–0.348	0.005	iso
	M	0.151	3.285E-03	0.043–0.26	-0.091	iso	0.165	-3.301E-03	0.114–0.215	-0.078	-
PAL	F	0.289	-1.525E-02	0.166–0.412	0.047	iso	0.240	9.634E-03	0.18–0.299	-0.003	iso
	M	0.291	-2.641E-03	0.251–0.331	0.048	+	0.289	-1.756E-03	0.26–0.318	0.046	+
TSL	F	0.258	-5.774E-03	0.214 –0.301	0.015	iso	0.254	-4.120E-03	0.219–0.29	0.012	iso
	M	0.257	-3.156E-03	0.227–0.287	0.014	iso	0.255	-2.236E-03	0.235–0.275	0.013	iso
UPL	F	0.115	-2.005E-02	-0.105–0.335	-0.128	iso	-0.002	3.855E-02	-0.083–0.078	-0.245	-
	M	0.290	-2.576E-02	0.105–0.475	0.048	iso	0.226	6.530E-03	0.095–0.356	-0.017	iso

Columns shows jackknife results calculated with untrimmed and trimmed sets of pseudovalues (see Materials and methods). Allometry coefficient is the corresponding element of the first (unit) eigenvector per variable. The expected coefficient is the value under isometry (0.2425 for this study). The unbiased coefficient is the first-order jackknife value. Bias is the difference between the unbiased and observed coefficients. The jackknifed 99% confidence interval (CI) is provided; allometric variables are those whose CIs exclude the expected value under isometry (0.2425). The departure coefficients represent the subtraction of expected value under isometry to the unbiased coefficient. Symbols indicate isometry (iso), positive allometry (+), and negative allometry (-). Abbreviations as in Figure 2.

Discussion and conclusions

The trends of postnatal growth in the pampas deer cranium imply a mostly common pattern between both sexes. Although, sexual differences in size are more pronounced in polygynous deer species (Clutton-Brock et al. 1977), in pampas deer, there is no marked sexual dimorphism in size (Jackson 1987). González et al. (2002) studying the Uruguayan subspecies (*Ozotoceros bezoarticus arerunguaensis* and *Ozotoceros bezoarticus uruguayensis*) find sexual dimorphism only in measures related to skull width. In addition, they conclude that males showed greater intrapopulation variation than females, suggesting that social status has a strong influence on morphological variation. Despite the pattern of multivariate allometry in our results, some variables that share trend but not the coefficients could lead to slightly sexual dimorphism in the adult. For example, several variables with similar trends actually exhibit higher untrimmed values in males (e.g., BZB, LBC, MZH, OCH, ORL, UPL), whereas in other cases, untrimmed values resulted higher in females (MFL, NSL, OCW, ORH, PAB) (Table 3). This suggests that sexual differences in this subspecies mostly consist in the intensity of the morphological variation, but not in average size or shape (except for antlers).

The isometry detected in 9 out 17 variables indicates that such variables grow conservatively at a rate indistinguishable from overall cranial size change. Among them, the total length of the skull was considered a good estimator of overall cranium (and body) size for all living ungulates and in most mammals, in general, because it is not affected by allometric trends (Janis 1990, Emerson and Bramble 1993, Flores et al. 2006, Giannini et al. 2010, Cassini et al. 2012). Indeed, this variable was strongly isometric in both sexes, with notably low values of departure (Table 3). This suggests that the total length of the skull must be a good candidate as independent variable in bivariate analyses. In our sample, the onset (smallest specimen) was at about 3–6 months old (age stage 1.5 *sensu* Bianchini and Delupi 1993) for both sexes. This could explain the lack of allometry in most of the variables, as according to Fräderich (1981), the pampas deer acquire an adult aspect but smaller in body size at 7 months (i.e., young seems to be a scaled version of adult). In fact, many of the variables considered in our study remain isometric, supporting the idea of a younger with the general appearance of an adult but smaller size. The pampas deer are weaned to about 4 months; however, they start to eat vegetal material around the second or third month of life (Dellafiore et al. 2001). So, the transition from milk-based diet to plant consumer begins just 1 month earlier than our onset. Unfortunately, we could not evaluate properly the skull growth pattern of *Ozotoceros bezoarticus celer* during the weaning period, and we found a very conservative postweaning growth pattern with no strong sexual dimorphism in the growth of measurements analyzed.

In the ontogenetic series of both sexes, we detected five measurements exhibiting deviation from isometry. Two of them that are clearly related to the neurocranial components [i.e., breadth of the braincase – BCB and occipital height (OCH)] and one to the sensory capsules [i.e., orbital length (ORL)] have negative allometric trends, which is the mammal common pattern and was also reported in other ungulates (Radinsky 1984, Al-Sagair and ElMougy 2002, Weston 2003, Cassini et al. 2012). Therefore, the braincase grows at a slower pace than the skull in these two dimensions, breadth (BCB) and height (OCH), although in a different magnitudes. In females, the height of the occipital plate exhibits a slower rate of growth (unbiased estimate=0.039; departure -0.2) than the breadth of the braincase (unbiased estimate=0.08; departure -0.16), so that the braincase of adult females becomes proportionally wider compared with young specimens. In males, however, the OCH exhibits a high rate of growth (unbiased estimate=0.08; departure -0.16) than the BCB (unbiased estimate=0.064; departure -0.18), so that the braincase of adult males becomes proportionally higher compared with young specimens. This implies that in the adult males, the nuchal ligaments attached to the external occipital protuberance have an improved leverage than in the young.

Although the length of the orbit scales negatively, its height grows isometrically, so in adults, the eye socket is proportionally higher than in juveniles. In other groups of mammals as marsupials (e.g., Abdala et al. 2001, Flores et al. 2003, 2006), carnivorans (e.g., Giannini et al. 2010, Segura and Prevosti 2012), equids (Radinsky 1984), and primates (e.g., Flores and Casinos 2011), the orbit is strongly negatively allometric in its different dimensions, which is consistent with the mode of growth of sensorial capsules in mammals (Emerson and Bramble 1993). However, the unexpected isometry of the orbit seems to be a common growth pattern when evaluating postweaning ontogenetic series, as was also detected in both large mammals as in some native South American fossil ungulates (Notoungulata, Toxodontidae) (Cassini et al. 2012) as well as in small mammals as some specific groups of marsupials [such as *Echymipera* (Flores et al. 2013); *Caluromys* (Flores et al. 2010); *Dormiciops* (Giannini et al. 2004)]. Additional isometric neurocranial variables detected in *Ozotoceros bezoarticus* (such as basicranial length, occipital width, and orbital height) (Table 3) demonstrate the complex mode of growth of the sensorial capsules, in which the general proportions of the orbit and braincase of young change dramatically when final size is reached. Braincase measurements showed to be good predictors of the endocranial volume (Finarelli 2006 and references therein). In addition, Finarelli (2011) postulated that cervids as well as camelids, tayassuids, and giraffids seem to have a relative high degree of encephalization. In fact, in the pampas deer, the brain mass (0.121 kg; Wemmer and Wilson 1987, Pérez-Barbería and Gordon 2005) is about 3% of the body mass. While this relationship seems to be around the mean of Odocoileini, it is higher than the Cervini mean of ~2.2% (see Appendix 1, Pérez-Barbería and Gordon 2005). However, if the isometric or not strongly negative allometric growth of neurocranial variables is related to a high degree of encephalization in pampas deer (and possibly in the Odocoileini) remains to be tested.

The allometric relationships of the different variables of the rostrum as the positive allometry of the nasal length (NSL), and the sexually dimorphic trends of the rostral length (MZL), predental length (LPD), and palatal length (PAL), indicate that both male and female adult pampas deer exhibit proportionally longer face than younger. This morphological pattern of growth was also reported for other ungulate groups like hippos (Weston 2003), horses (Radinsky 1984), camels (Al-Sagair and ElMougy 2002), and nesodontines (Cassini et al. 2012). However, the elongated palate and rostrum observed in both sexes of *Ozotoceros bezoarticus celer* reaches its final size by different ways, considering the allometry detected in its diverse measurements. For instance, although males exhibit a rostrum and palate with positive allometry, females also show a higher allometric trend for predental length (Table 3). Such difference in the growth of the anterior portion of the palate favoring females is adjusted by the higher coefficients of the posterior section favoring males, as demonstrated by the allometric coefficients of the upper postcanine tooth row length in both trimmed and untrimmed approaches (Table 3). Although we detected a differential rate of growth in two regions of the palate in later age stages (see Table 3), the complex growth of the mandible during prenatal and earlier age stages of postnatal periods in ungulates (Todd and Wharton 1934, Pond 1977, Herring 1985, Høye and Forchhammer 2006) suggest a similar complex growth on its upper counterparts also during earlier periods of growth.

The few previous quantitative analyses allometry carried out in ungulates (e.g., Cassini et al. 2012 for the fossils *Adinotherium* and *Nesodon*; Weston 2003 for Hippos) allow a discrete comparison of trends in those common measurements (Table 4), detecting relatively strong differences in the rate of growth of species analyzed. For instance, there is no shared trend among the three groups (cervid, toxodonts, and hippopotamids), at least in those variables where the allometry is known. Although, there are a few variables shared by pampas deer and toxodontis or hippos, it seems to be that the allometric patterns of growth in ungulates would be strongly divergent in this morphologically diverse group.

Table 4 Comparisons with the allometric trends of nesodontines *Adinotherium* and *Nesodon* (Cassini et al. 2012) and hippopotamids *Hippopotamus* and *Hexaprotodon* (Weston 2003).

Variable	***Ozotoceros bezoarticus***		***Hippopotamus***	***Hexaprotodon***	***Adinotherium***	***Nesodon***
	Female	**Male**				
BCB	-	-			iso	-
BZB	-	-	iso	iso	+	-
LBC	iso	iso	-	-		
LPD	+	iso				
MFL	iso	iso			iso	iso
MZH	iso	iso			iso	+
MZL	iso	+			+	+
MZW	iso	iso	+	+	iso	iso
NSL	+	+			+	+
OCH	-	-	-	-	iso	iso
OCW	iso	iso	-	-		
ORH	iso	iso			iso	iso
ORL	-	-			iso	-
PAB	iso	iso			+	iso
PAL	iso	+			+	+
TSL	iso	iso	iso	iso		
UPL	iso	iso			+	iso

Symbols indicate isometry (iso), positive allometry (+), and negative allometry (-). Abbreviations as in Figure 2.

In summary, the medium-sized cervid pampas deer follows the overall allometric trend of a dolichocephalic-like ungulate (i.e., proportionally longer faces and smaller braincases) with increased size. Individuals reach an adult-like shape at early development stages, and then, the main morphological change may occur during weaning or in parallel with the transition in main food source from milk to herbal forage, just before our onset explaining the isometry detected in most variables. For example, male pampas deer has a precocious development of frontal pedicle of antlers, before the replacement of lower deciduous incisors and canine (1.5-age stage) (Figure 1D) in relation to *Odocoileus* species, in which this process begins after these teeth were replaced (see Bianchini and Delupi 1993). On the other hand, the lack of strong sexual dimorphism and the putative influence of male social status in morphological variation would explain a common growth pattern in both sexes. Our examination of its ontogeny may provide a comparative frame for the postweaning ontogeny in all neotropical deer, which has different morphological patterns and ecological demands. Particularly, differences in growth pattern that may be found in smaller and bigger species (e.g., *Mazama* spp. and *Blastocerus dichotomus*, respectively) considered in a phylogenetic context will help to elucidate the evolutionary history of the South American deers.

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