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A cranial morphometric study of deer (Mammalia, Cervidae) from Argentina using three-dimensional landmarks

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This study examines morphological variation in the crania ($n = 70$) of eight cervid species from Argentina. Forty 3-dimensional landmarks were acquired on each adult cervid cranium. The data were analysed using Morphologika software. The co-ordinates were registered and scaled to remove size differences by Procrustes analysis, and then principal components analysis was applied to examine shape variation. Shape variation associated with each principal component can be visualised in the program. The first principal component correlates strongly with the centroid size of the crania and also with the body mass and height of each species. The larger species were distinguished by relatively longer snouts and relatively smaller brains. The smaller *Mazama* and *Pudu* species cluster closely on the first as well as the other principal components. Among the larger species, the two *Hippocamelus* species, which live at higher altitudes, were clearly distinguished from the lowland species, *Ozotoceros bezoarticus* and *Blastocerus dichotomus,* on the basis of cranial flexion and the orientation of the occipital region. Finally *O. bezoarticus* and *B. dichotomus* were compared directly and small differences were noted in the orbital region. The shape data was used to produce a distance matrix and a phenogram, which we relate to some of currently accepted phylogenetic relationships of this group of cervids.

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Introduction

Deer (Mammalia, Cervidae) entered South America from North America through the Panamanian bridge, around 2.5 million years before present (mybp) (Stehli and Webb 1985). Once in South America they underwent a rapid adaptive radiation in the Pleistocene (2.5–0.01 mybp) to fill some niches that are occupied by bovids in other continents (Redford and Eisenberg 1992). Recent revisions of the South American cervids or Odocoileinae propose around 15 species (Anderson 1997, Duarte and Merino 1997), making this the most diversified group of ungulates in the Neotropical region. Some authors recognise three main genera, *Mazama*, *Pudu* and *Odocoileus* (Ximenez *et al*. 1972, Bianchini and Delupi 1978) or 4 genera with *Hippocamelus* (Delupi and Bianchini 1995). Wilson and Reeder (1993) split *Odocoileus* into 4 genera (*Odocoileus*, *Blastocerus, Ozotoceros*, and *Hippocamelus*). In Argentina, there are eight species that, following the more recent systematic arrangement, are distributed in the genera *Blastocerus*, *Ozotoceros*, *Hippocamelus*, *Mazama*, and *Pudu* (Galliari *et al*. 1996).

The phylogeny of the group is controversial. Groves and Grubb (1987) proposed a single monophyletic tribe Odocoileini for the last five genera plus *Odocoileus* and *Rangifer*. Hershkovitz (1982) regarded *Pudu* as the most primitive within the group. Based on karyotypic characters, Neitzel (1987) suggested that *Ozotoceros* and *Blastocerus* formed a clade together with *Odocoileus.* However, it seems that the derived characters are also shared by *Pudu* and partially by *Mazama*. The shape of the antler gives support to Hershkovitz's (1982) idea that *Odocoileus* is not immediately related to the genera *Ozotoceros*, *Blastocerus* and *Hippocamelus*. More recently, Webb (2000) split the South American cervids into two tribes: Rangiferini, including the circumboreal *Rangifer* and the South American *Hippocamelus* and *Pudu*, and Odocoileini, including *Odocoileus, Blastocerus, Ozotoceros* and *Mazama*.

South American cervids are adapted to a wide range of habitats, from densely forested to open environments. These adaptations include morphological, physiological and behavioural traits that maximize efficient natural resource utilization (Putman 1988)**.** In the following paragraphs, we describe the distribution and ecology of each of the cervid species analysed occurring in Argentina.

Blastocerus dichotomus (Illiger, 1815) – Marsh deer. The marsh deer is the largest South American cervid. Males have an average body mass of 130, while females are 100 kg, reaching a height of 1.3 m at the shoulder (Duarte 1996). In Argentina it is distributed in the north and east provinces. It lives in lowlands bordering rivers, always near marsh regions or wet savannahs with high pasture. Morphological adaptations to their environment include the presence of an interdigital membrane as well as long limbs, which make them able to walk fast through their flooded environment.

Ozotoceros bezoarticus (Linnaeus, 1758) – Pampas deer. The Pampas deer is a medium-size cervid, with body mass of around 30 kg, and 65 cm height at the shoulder. It is distributed from the north of Argentina through the centre and east to Northern Patagonia (Cabrera and Yepes 1961). It is characteristically found in grasslands, bearing few trees, never in closed habitats like dense forests.

Hippocamelus antisensis (d'Orbigny, 1834) – North Andean deer. The North Andean deer is the smaller species of the genus, with a body mass of 60 to 75 kg, and 80 cm height at the shoulder. It is distributed in the Andes, from Ecuador, Peru, Bolivia and northern Chile and a very restricted area in northern Argentina. It inhabits rocky areas in the Andean mountains and highland fields between 2500 and 4500 meters in elevation (Redford and Eisenberg 1992).

Hippocamelus bisulcus (Molina, 1782) – South Andean deer. The South Andean deer is a robust cervid, with males being larger than females. Body mass of up to 95 kg and the height at the shoulder reaches 80 to 100 cm. It is distributed in southern Andes from Argentina and Chile, from 37° latitude to the Straits of Magellan. It is found mostly at or just below the tree line (Redford and Eisenberg 1992).

Pudu puda (Molina, 1782) – southern pudu. The southern pudu is the smallest cervid, with a body mass of 7 to 12 kg and a height at the shoulder of 30–44 cm. In Argentina it is found in Patagonia along the foothills of the Andes (Hershkovitz 1982).

Mazama gouazoupira (G. Fischer, 1814) – grey brocket. The grey brocket is a small cervid with an average body mass of 18 kg and rarely exceeds 20 kg. The average height is 50 cm at the shoulder. It is the most common species of deer found in South America, occupying many kinds of environments. In Argentina they are widespread in the north, central and east provinces. It feeds on hard, dry fruit in the dry season and soft, fleshy fruit during the wet season and also eats leaves, buds, flowers, twigs, and roots.

Mazama americana (Erxleben, 1777) – red brocket. The red brocket is the biggest and most robust species of *Mazama*, with an average body mass of 30 kg; it may reach 40 kg, and approximately 65 cm height. It inhabits thick forested areas is widespread from Mexico to northern Argentina, except in the western part of Jujuy and Salta provinces.

Mazama nana (Hensel, 1872) – dwarf red brocket. The dwarf red brocket is a not well known species. It is small, and rarely exceeds 15 kg and 45 cm height. Its distribution is small (Duarte 1996). It inhabits mountain areas covered by dense vegetation. It is found in a much reduced area of the forest of northeast of Argentina.

Some craniometric work on South American cervids has been reported by Cabrera (1941) and Wemmer and Wilson (1987). The most recent contributions deal with *Ozotoceros bezoarticus* from Uruguay (Gonzalez *et al.* 1989, 1992, 2002, Gonzalez 1997) and Argentina (Beade *et al.* 2000), and *Mazama* from Brazil (Rossi 2000). These studies do not attempt to correlate morphology with any ecological or behavioural properties of the species. Previous studies using the same three-dimensional landmark technique on members of *Macropus* in Australia revealed differences in cranial morphology associated with latitude and diet, and also found some phylogenetic factors were influencing cranial shape (Milne and O'Higgins 2002). The present study examines a range of cervid species from Argentina and explores shape variations in their crania, which may be related to species, sex, size and diet. With this in mind, we set up a number of working hypotheses: there are no morphological differences associated with sex; there will be no morphological differences associated with the size of either the crania or the body; and there will be no shape differences associated with latitude, habitat and diet.

Material and methods

Material

Seventy skulls of adult cervids of 8 species were examined (Appendix I). Numbers of specimens for each species are given in Table 1. All specimens are in mammal collections of Argentina: Museo de Ciencias Naturales de la Universidad Nacional de Salta (MCNUNSA), Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and Facultad de Ciencias Naturales e Instituto Miguel Lillo (CML).

Data collection

The data set comprised 40 three-dimensional landmarks (Fig. 1) acquired with a Polhemus 3 Space Isotrak II digitiser (Polhemus Incorporated, 1 Hercules Drive, PO Box 560, Colchester, VT 05446, USA) linked to a PC running a spreadsheet program. To minimise error, the specimens were digitized exclusively by the first author. Tests of the digitising location, where the electromagnetic emitter and receiver are both fixed to a rigid board and that board is moved and rotated in the area where the data were collected, showed that electromagnetic interference from nearby metal objects accounts for variations of only 0.01 mm. The geometric morphometric approach used in this study requires that homologous landmarks are used to represent the shapes of specimens. Accordingly the landmarks in Fig. 1 are mostly at sutural junctions, but some were selected specifically to capture aspects of the dentition and masticatory apparatus.

Morphometric analysis

The morphometric analysis was carried out using the morphologika software (http://www.york.ac.uk/res/fme/resources/software.htm). The three-dimensional co-ordinates were registered and scaled to remove size differences by Procrustes analysis. The centroid sizes for the landmark configurations representing each specimen are retained and used in later examination of size related shape differences. Then principal components were extracted to examine the variation in the shapes. Visualisation of variation in shape represented by the principal components is achieved by 'warping' the mean shape along each PC of interest by adding to the mean co-ordinates the product of the eigenvectors (for the PC of interest) and the score on that PC (Kent 1994). Since the PCA is based on tangent space co-ordinates, a projection of those of the hypothetical specimen into configuration space (the space of the original specimens) is also carried out. These visualisations were further interpreted using Cartesian transformation grids calculated from triplets of thin-plate splines (TPS) (Bookstein 1989, Marcus *et al.* 1996, Dryden and Mardia 1998). The grids derived from TPS indicate how the space surrounding a reference shape might be deformed into that surrounding a target shape

Table 1. Numbers of male and female specimens examined and diet information for each species of cervid from Argentina. Dicot (%) – percentage of dicotyledons in the diet.

Species	Males	Females	Dicot (%)	Reference
Mazama americana	4	6	100	Bodmer 1997
Mazama gouazoupira	7	4	100	Bodmer 1997
Mazama nana	1	4	99	Czernay 1987
Pudu puda	1	1	99	Hershkovitz 1982, Czernay 1987
Hippocamelus bisulcus	8	2	99	Colomes Gonzalez 1978
Hippocamelus antisensis	3	2	82	Galaz Leigh 1998
Blastocerus dichotomus	2	5	69	Beccaceci 1996, Beccaceci and Merino 1994
Ozotoceros bezoarticus	8	12	20	Jackson and Giullietti 1988

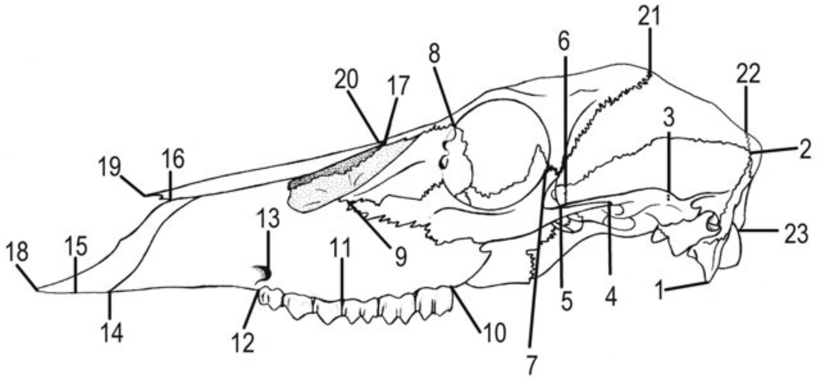

Fig. 1. The landmarks used in this study are shown on a left lateral view of a cervid cranium and their descriptions are given below. Landmarks numbered 1 to 17 are duplicated on the right side as numbers 24 to 40. Definition of landmarks of the cranium: 1 and 24 – Extreme of the paracondylar process, 2 and 25 – Asterion (parieto-occipito-temporal junction), 3 and 26 – Superior root of the zygoma (directly above the glenoid fossa), 4 and 27 – Posterior end of the zygomatico-temporal suture, 5 and 28 – Zygomatico-temporal suture on the upper edge of the zygomatic arch, 6 and 29 – Anterior end of the parieto-temporal suture, 7 and 30 – Fronto-zygomatic suture at the posterior orbital margin, 8 and 31 – Fronto-lachrymal suture at the medial orbital margin, 9 and 32 – Zygomatico-maxillo-lachrymal junction, 10 and 33 – Alveolar margin at the posterior aspect of the last molar, 11 and 34 – Alveolar margin between premolar and molar, 12 and 35 – Alveolar margin at the anterior aspect of the first cheek tooth, 13 and 36 – Infraorbital foramen, 14 and 37 – Maxillary-premaxillary suture at the alveolar margin, 15 and 38 – Widest point of the premaxilla, 16 and 39 – Naso-premaxillary suture at the margin of the nasal aperture, 17 and 40 – Fronto-nasal junction laterally, 18 – Interpremaxillary suture anteriorly, 19 – Tip of the nasal bones in the midline, 20 – Naso-frontal suture in the midline, 21 – Bregma, 22 – Lambda, 23 – Mid-point on the dorsal margin of the foramen magnum.

such that landmarks in the reference map exactly into those of the target. The thin plate spline ensures that this deformation involves minimum bending. It is chosen for this purpose since the grid fits the landmarks exactly and is bent minimally in between. Thin plate splines in three dimensions can be used to examine the shape change represented by each PC. Correlations of the principal components of shape with independent variables such as, for example, centroid size, body weight, and latitude, can be calculated. For more detailed descriptions of the morphologika program and it application to interspecific analyses see O'Higgins and Jones (1998), O'Higgins and Strand Vidarsdottir (1999), O'Higgins (2000 a, b), and Milne and O'Higgins (2002).

Statistical analyses

Permutation tests using the Procrustes registered co-ordinates for each individual were used to check for shape differences between the sexes in each species, and also between the species (Good 2000). Procrustes distances are calculated from the species means of the configurations of the Procrustes registered landmarks in multidimensional "shape space" and give an indication of differences between pairs of species (O'Higgins and Jones 1998).

Tests of correlation were used to examine the relationship of principal components with the diet factor, and latitude where the individuals lived, as well as with weight and height data derived from the literature. For the purposes of this study, the diet of each cervid species is given as the percentage of dicotyledons (dicots) in the diet (see Table 1 and literature cited therein).

Results

Figure 2 shows the first and second principal components plotted for the whole sample of adult cervids. The first principal component accounts for 42% of the variation and the second for 8% (PC3 accounts for only 5% and the remaining PCs account for still smaller fractions of the total variation). Principal component 1 has

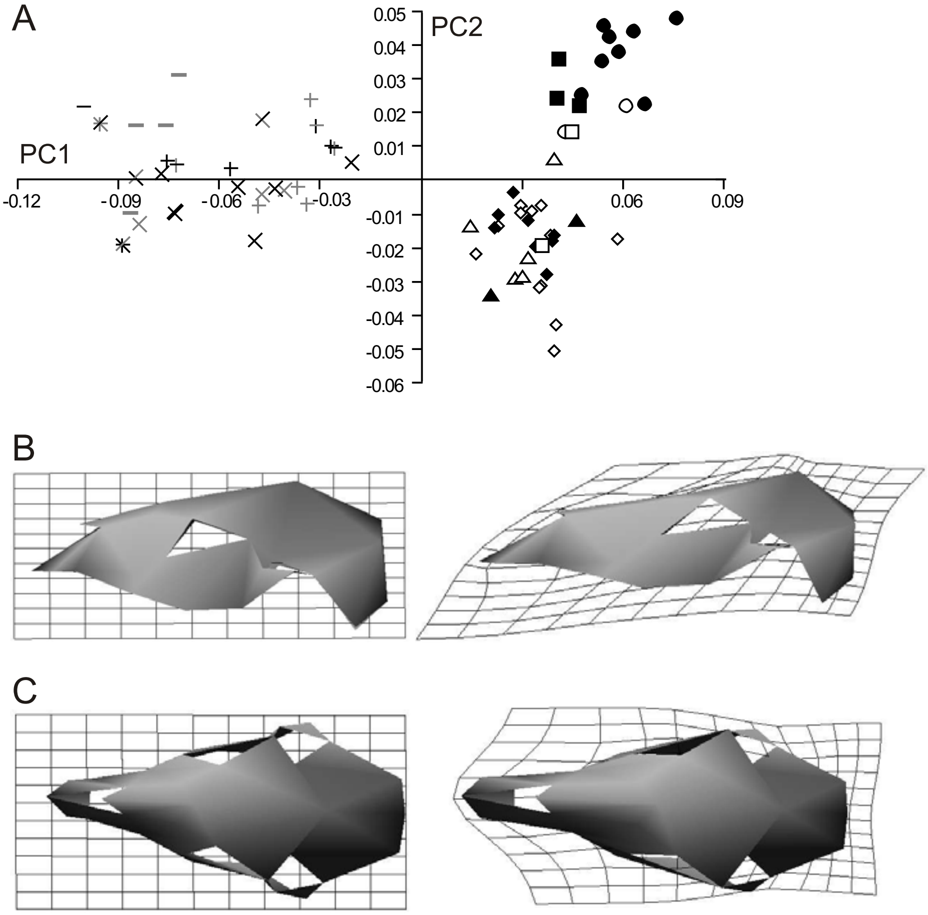

Fig. 2. Sex and species differences in the cervid sample from Argentina. Plot of PC1 against PC2 from the analysis of all 70 adult specimens. Males are indicated by black shapes, females are represented by open figures or paler shading. PC1 represents 42% and PC2 represents 8% of the total variation? ▲ *O. bezoarticus*; ● *B. dichotomus*, ■ *H. bisculus*, □ *H. antisensis*, ✳ *P. puda*, + *M. americana*, × *M. gouazoupira* and – *M. nana*. Also shown are the changes in cranial morphology associated with the first principal component, where a representation of the skull morphology for low (–0.09) and high (0.09) scores along PC1 is provided, both in the lateral (B) and superior (C) views. Parts B and C show the crania with transformation grids illustrating the shape changes from low to high PC scores. These grids are exaggerated by a factor of two to improve visualisation of the changes.

a strong correlation ($r = 0.85$, $p < 0.001$) with the centroid size of the crania. This PC also correlates strongly with both body mass (0.62) and height at the shoulder of the species (0.66). Figure 2 also shows the changes in morphology associated with PC1. Representations of the crania at high (0.09) and low (–0.09) values for PC1 are shown, with transformation grids. The transformation grids on the right indicate how the shape of a small skull (left) would be deformed to produce the shape of a large skull (right). The main shape difference related to PC1 (and also to size) is an increase of the relative length of the snout, mostly due to lengthening of the palate, especially that part of the maxilla in front of the cheek teeth. The nasal bones do not increase in length to the same extent that the palate does, resulting in an increased obliquity of the nasal opening. The braincase is relatively smaller in the larger species. In addition, there seems to be a relative increase in the width of the skull in the region of the orbits, and a decrease in the width of the zygomatic arches.

While the first two principal components clearly reflect morphological differences relating to differences between the species, there does not appear to be any consistent pattern of sexual dimorphism. Sex differences were examined within each species using permutation tests (Good 2000). The only species to show a significant sex difference was *B. dichotomus*, and in that species the significance level of this comparison was marginal ($p = 0.049$). It should be noted that the sample sizes (see Table 1) were such that in *P. puda* tests were not possible, and that in some other species the numbers were small and the sex distribution was uneven, making the tests less meaningful. The sexes were combined for subsequent analyses of the species differences using the same statistic.

The Procrustes distances between the species means were calculated, and the results are given in Table 2 (lower half). Permutation tests were carried out on the Procrustes registered landmarks of each pair of species to determine the significance of the differences between species, and these results are given in the upper half of Table 2. All species comparisons were significant at less than the 0.05

Table 2. Species differences. The upper half of the table gives the significance of the differences between species, and the lower half give the calculated Procrustes distances between their means for species of cervid examined from Argentina.

	B. dichotomus	*H. antisensis*	*H. bisulcus*	*M. americana*	*M. gouazoupira*	*M. nana*	*O. bezoarticus*	*P. puda*
B. dichotomus		0.01	0.001	0.001	0.001	0.001	0.001	0.05
H. antisensis	0.0616		0.01	0.001	0.001	0.01	0.001	0.05
H. bisulcus	0.070877	0.0489		0.001	0.001	0.001	0.001	0.05
M. americana	0.0915	0.0994	0.1098		0.01	0.01	0.001	0.05
M. gouazoupira	0.0996	0.1084	0.1217	0.0402		0.001	0.001	0.01
M. nana	0.1274	0.1345	0.1470	0.059196	0.055303		0.001	0.05
O. bezoarticus	0.0512	0.0562	0.0621	0.086735	0.0956	0.1267		0.01
P. puda	0.1340	0.1480	0.1623	0.075515	0.0697	0.0595	0.1381	

level. Comparisons involving species represented by larger samples were generally highly significant, while those involving the smaller samples were less significant. The smallest Procrustes distances are seen in comparisons within the genera *Mazama* and *Hippocamelus*. Small distances were also noted between the two smallest species (*P. puda* and *M. nana*) and also between *O. bezoarticus* and *B. dichotomus*.

Principal component 2 in Fig. 2 shows very little variation or species separation among *Mazama* and *Pudu* species on the left hand side. On the other hand the

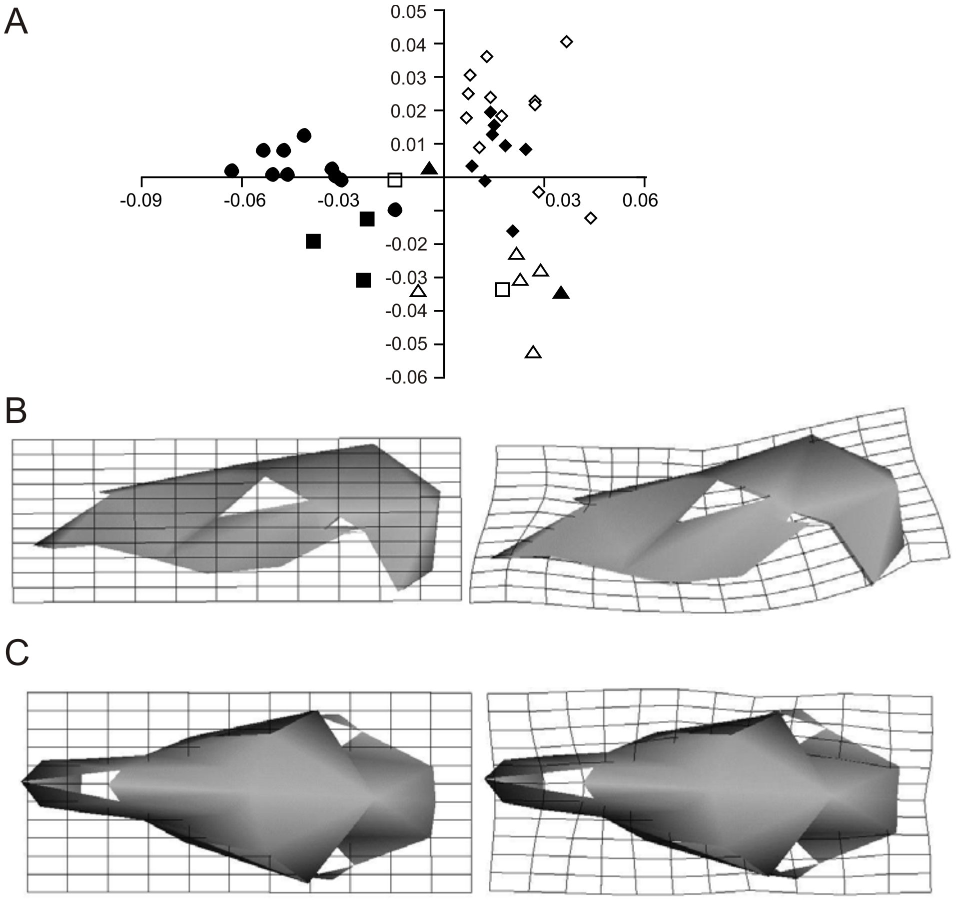

Fig. 3. Differences among the larger species of cervids examined from Argentina. Plot of PC1 against PC2 from the analysis of the 42 specimens from the 4 larger species. PC1 represents 20% and PC2 represents 11% of the total variation. Symbols as in Fig. 2. In parts B and C the changes in cranial morphology associated with PC1 are shown, where a representation of the skull morphology for low (–0.05) and high (0.05) scores along PC1 is provided, both in the lateral (B) and superior (C) views. Parts B and C show the crania with transformation grids illustrating the changes from low to high PC scores. These grids are exaggerated by a factor of 2 to improve visualisation of the shape change.

larger species are arrayed vertically indicating that their differences are related to PC2. The following analysis uses only the 4 larger species to more effectively examine the variation between them.

In Fig. 3, the first two principal components from an analysis that included only the crania of the 4 larger species (*O. bezoarticus, B. dichotomus, H. bisulcus, H. antisensis*) are shown in part A. The first principal component accounts for 20% of the variation, and the second, 11%, (PC3 accounts for only 8% and the remaining PCs account for still smaller fractions of the total variation). Principal component 1 has a strong correlation ($r = -0.77$, $p < 0.001$) with the percentage of dicots in the diet of that species, and it has a weaker but still significant correlation ($r = -0.53$. $p < 0.001$) with the latitude where the specimen lived. The two highland species, *H. antisensis* and *H. bisulcus* lie on the left with low scores for PC1 and the lowland, *B. dichotomus* and *O. bezoarticus* species lie to the right. Parts B and C explore the shape difference indicated by this separation along PC1 in this new analysis. However, it should be noted that the shape change represented by PC1 in this analysis is essentially the same as that represented by PC2 in the previous analysis. On the left hand side of parts B and C, representations of crania with low (–0.05,) values for PC1 are shown with an undeformed grid, while on the right are representations of crania with high (0.05) values for PC1, shown with a transformation grid to illustrate the differences between the two extremes. It would appear that the crania on the right are more upwardly flexed. Anteriorly, the premaxilla is

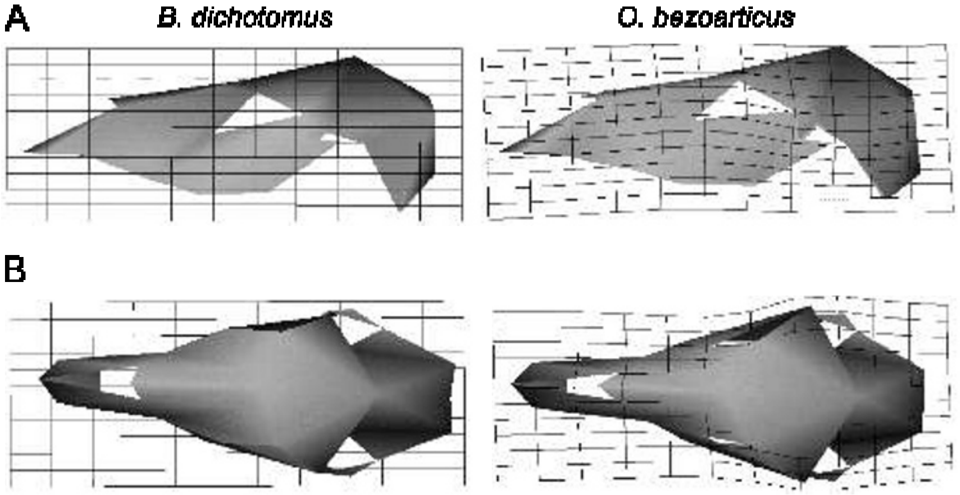

Fig. 4. Analysis using only the *B. dichotomus* and *O. bezoarticus* specimens from Argentina. In this figure *B. dichotomus* is shown on the left and *O. bezoarticus* is on the right. Part A shows a lateral view and part B shows a superior view. The grids show the way *B. dichotomus* would need to be deformed to produce the shape of *O. bezoarticus*. Once again, these grids have been exaggerated by a factor of two.

relatively higher and the posterior parts of the nasal bones are lower. Posteriorly, the parietal bones are higher, but more particularly the occipital bone is flexed upwards and backwards, changing the orientation of the nuchal region.

Principal component 2 (Fig. 3) mainly separates the *B. dichotomus* and *O. bezoarticus*, and so a further analysis was conducted, only including those two species. In that two-species analysis PC1 completely separated the two species and *t*-tests on PC1 show that the difference between these two species is highly significant ($p < 0.0001$). Figure 4 provides representations of *O. bezoarticus* (right) and *B. dichotomus* (left) crania, in both the lateral (A) and superior (B) views. The transformation grids show how a shape representing *B. dichotomus* could be deformed to produce the shape of *O. bezoarticus*. The main differences seem to be in the orbits where *O. bezoarticus* has eyes, which appear to be directed more anteriorly than *B. dichotomus*. The region of the frontal bone between the eyes is wider in *B. dichotomus*, and this is particularly true for the anterior part, while the posterior orbital margin is relatively further lateral in *O. bezoarticus*.

Figure 5 shows a phenogram based on the data in Table 2. This phenogram is produced through the clustering subroutine of the NTSYS-pc (v. 1.8) program using UPGMA option for Euclidean distances (Rohlf 1994). The resulting phenogram shows two tight groups, one formed by the three *Mazama* species (*M. americana, M. gouazoupira, M. nana*) closely clustered with *Pudu puda*, and the other group consisting of the larger species, which are subdivided into *Hippocamelus* (*H. bisulcus* and *H. antisensis*) on one side and the *O. bezoarticus* and *B. dichotomus* pair on the other. This phenogram preserves well the original data matrix, with a product-moment correlation between the cophenetic value matrix and the Procrustes distance matrix amounting $r = 0.88$ (normalised Mantel statistic).

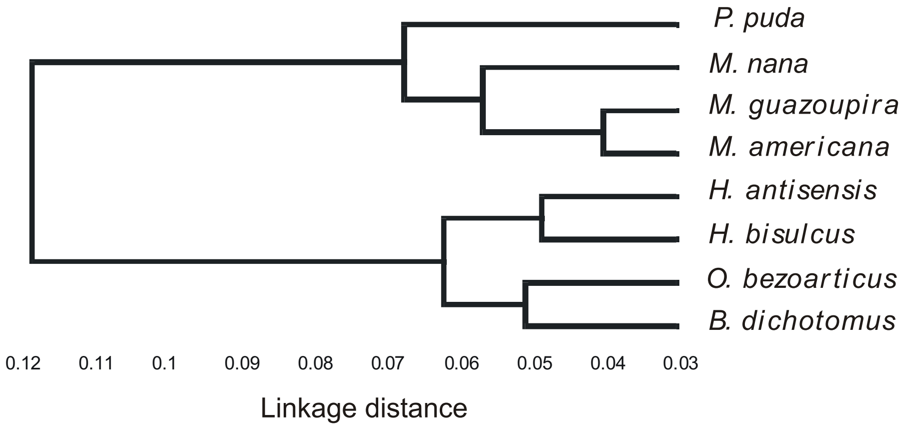

Fig. 5. Phenogram of cervid species examined from Argentina based on the distance matrix in Table 2.

Discussion

Sample size and sex

Due to the paucity of cervid crania in museum collections, it was not possible to have statistically adequate sample sizes for this study. This is especially true for the analysis of sexual dimorphism. Cervid crania show obvious sexual dimorphism where males are much larger and bear antlers. In spite of the small sample sizes, it is quite remarkable that the permutation tests did not show a consistent pattern of sex differences. The same statistic was used to test for species differences and many of those tests were based on equally small sample sizes; however they showed a constant pattern of significant differences. Sex differences were not apparent on any principal component, and this is true even for PC1, which is strongly correlated with size. Thus, although there are size differences between the sexes, these differences are not reflected in differences in their cranial shape. It is interesting that this technique does not detect the sexual dimorphism, which is otherwise so apparent in this group. Clearly the landmarks were not chosen to demonstrate the antler, but it is also clear that shape dimorphism is not evident in other parts of the cranium. It would appear that the sexual dimorphism is purely a difference in scaling. Gonzalez (1997) and Gonzalez *et al*. (2002) found sexual differences in the crania of *Ozotoceros bezoarticus*. They found significant differences in the measurements that reflect skull width and in the upper dental row. These differences were evident when only specimens of *O. bezoarticus* were examined in a separate analysis, but the differences were not statistically significant ($p = 0.08$).

Size, behaviour and diet

Principal component one is strongly correlated with size and clearly reflects allometry. It is difficult to untangle purely allometric differences in this shape variable from those that may reflect function that is related to size differences.

One of the remarkable differences among small and large cervids in our sample is the relatively smaller size of the braincase in the latter. This could be related to encephalisation and behaviour. Wemmer and Wilson (1987), demonstrated that the encephalisation index in cervids is in a parabolic distribution related to body size; the smallest species show the lowest indices, the largest species show moderate values, and the medium-size species have the highest values. Relatively large brains are also correlated with strongly male-biased sexual dimorphism. These authors proposed that this description fits with species occupying a major adaptive zone consisting of seasonally group-forming species, with polygynous mating systems, and probably greater dependence on visual communication patterns than have small solitary forest cervids.

Hence, the largest South American deer, which fall within the medium-size sample of Wemmer and Wilson (1987), with its relatively small braincase, does not seem to fit the expected pattern. This could be related to the fact that these animals are mainly solitary or that they only form much smaller groups (Merkt 1987, Tomas *et al.* 1997, Merino *et al.* 1997, Smith-Flueck 2000) than their northern hemisphere relatives.

The shape changes shown in the transformation grids of Fig. 2 may also have some influence on functional aspects. The relatively decreased width of the zygomatic arches, and space beneath them in the larger species reflects reduced attachments for the main masticatory muscles, temporalis and masseter, which could imply relatively weak input forces in the masticatory system. Also, the relative elongation of the snout in the larger species moves the cropping mechanism (constituted by the lower incisors and the horny pad of the premaxilla) further forward from the cheek teeth, making cropping relatively weak but fast. This, in addition to a narrow muzzle, possibly enhances the capacity for selective feeding, a condition well known for mixed feeding bovids (Spencer 1995). Even the larger South American cervids are not considered as typical grass feeders, as defined by Spencer (1995) for the African bovids. Beccaceci (1996) observed that *B. dichotomus* is a selective feeder, eating only parts of plants. Diaz and Smith-Flueck (2000) have shown that *Hippocamelus bisulcus* is also a concentrate-selector that feeds on small morsels of nutritious plants, and it seems likely that *H. antisensis* also feeds in this way (Galaz Leigh 1998). Although *O. bezoarticus* feeds mainly on grasses, Jackson and Giulietti (1988) state that it depends on green forage all year, plucking small and nutritious morsels from live plants of certain species. A long face would also serve to protect the eyes by distancing them from grasses (Janis 1995), an explanation that may apply in the case of *O. bezoarticus*.

On the other hand, *Mazama* and *Pudu* species have proportionally larger braincases and shorter snouts. This indicates an improvement of the ratio between the input forces generated by temporalis and masseter, and the output forces exerted by the teeth on the food. Hence, the bite forces would be relatively stronger in this species. As it was mentioned above *Mazama* species are able to feed on hard, dry fruit in the dry season and on twigs and roots during the wet season (Stallings 1984). Moreover, at least in some parts of their distribution (Amazonia, Brazil) the proportion of fruits can be over 80% of the diet (Bodmer 1997).

This difference has been recognised and tested for other herbivores such as African bovids. In a recent contribution, Gagnon and Chew (2000) established that "a significant positive correlation exists between body mass and proportion of monocots in the diet and significant negative correlations exist between body mass and proportions of dicots and fruits". These correlations were explained in two different ways (see Gagnon and Chew 2000). One explanation was in terms of metabolic requirements: the smaller animals have relatively higher energetic demands and diets of higher quality foods (young leaves and fruits) than the larger animals (stem, mature leaves and grasses), because the latter are able to retain food in their alimentary canal for longer periods.

Previous work (Underwood 1983, Van Soest 1996) has suggested that mechanical constraints possibly play a role in feeding preferences in bovids, because larger animals have a mouth that is too large to select small foods. This explanation in particular does not fit with the cervid patterns observed in our works. As we noted earlier, even the larger South American cervids are able to select small plants or parts of plants and that their structural features are related to that feeding behaviour. However, we should point out that the body size of the largest South American cervids is much smaller than body size of the largest African bovids.

Diet and habitat among the larger species

Principal component 1 in the analysis including only the larger species had a strong correlation with the percentage of dicots in the diet. The species with the highest scores (*O. bezoarticus* and *B. dichotomus*) have the lowest proportions of dicots in their diet, *H. antisensis* has a higher proportion of dicots in its diet and lower scores on this PC, while *H. bisulcus* which consumes dicots almost exclusively has the lowest scores. Individuals with high scores on PC1 had less flexed crania, shorter nasal bones and a more posteriorly-facing nuchal region (Fig. 3). Interpretation of the functional meaning of these differences is difficult because this PC also had a correlation with latitude and, although specific data was not available for elevation, this PC separates the mountain dwelling *Hippocamelus* species from the lowland *O. bezoarticus* and *B. dichotomus*. The high elevation *Hippocamelus* species have more flexed crania than *O. bezoarticus* and *B. dichotomus*, where the snout and the occipital region are relatively higher. The difference in the occipital region would be expected to alter the way the head is carried on the neck, or alternatively may suggest a different orientation of the neck where the neck is more horizontal in the lowland species. This proposed difference in neck posture is supported by observations (MLM) of *O. bezoarticus* and *H. bisulcus*. Further, the downward flexion of the snout may be an adaptation for better vision of the ground immediately in front of the animal on mountain slopes. Not only is the snout relatively higher in lowland species, but the nasal bones are also relatively shorter. These features may make the nasal cavity a little shorter in the lowland species that could be expected to be breathing warmer, more humid air.

Differences between *B. dichotomus* and *O. bezoarticus*

In the analysis that includes only the larger species, PC1 separates *B. dichotomus* from *O. bezoarticus* (Fig. 4). *B. dichotomus* has orbits that appear to be directed more laterally while in *O. bezoarticus* the proximal part of the snout is narrower and the posterior orbital margin is relatively wider. As a result, the eyes of *O. bezoarticus* seem to face more anteriorly. In addition, the relative positions of the upper and lower orbital margins are different in the two species so that the eyes of *B. dichotomus* face more inferiorly. It appears that in *B. dichotomus*, vision of the ground would be less restricted than that of *O. bezoarticus*, which could be an adaptation to its flooded environment.

Shape and Phylogeny

The phenogram derived from the Procrustes distance data is not a phylogenetic tree, but provides information that can be discussed in a phylogenetic framework (Chapman 1990). It substantially agrees with the phylogenetic analysis of Groves and Grubb (1987) of the cervids in South America, but is not in line with the recent analysis of Webb (2000). If the analysis of Groves and Grubb (1987) is correct then the phenogram is reflecting the phylogenetic heritage of these cervids. However, if the analysis of Webb (2000) is correct then the pattern of shape variation found in this study is more related to function and shows evidence of convergence in their evolution.

The close association in the phenogram of *P. puda* and *Mazama* species would be consistent with the hypothesis set forth by Groves and Grubb (1987) that the spike-antler is a derived character for this group. Indeed, Haltenorth (1963) had included *Pudu* within *Mazama*. Although this suggests great similarity between both forms, Groves and Grubb (1987) have kept them as separate genera.

However, Webb (2000) proposed a different phylogenetic arrangement, in which *Pudu* and *Mazama* belong to different clades. *Mazama* and *Pudu* share a relative increase in the width of the skull in the region of the orbits/zygomatic arch in comparison with the larger species. This could be related to size scaling or it could give us some preliminary idea of the evolutionary processes undergone by the South American cervids. We mentioned above the idea of Groves and Grubb (1987) that the spike-antlers of *Mazama* and *Pudu* are derived from the forked antlers of the remaining Odocoileinae. Development and growth, and more specifically neoteny, would probably be involved in the process.

Our results indicate that *O. bezoarticus* and *B. dichotomus* are very similar and the phenogram also closely links them. In spite of their different size, these genera have very similar values for PC1 (see Fig. 2) and only small differences in the orbital region can be observed. The similarity is in accordance with the phylogenetic hypothesis, based on antler shape (Groves and Grubb 1987) and karyotipic evidence (Neitzel 1987) of both genera forming a clade. Several authors (Delupi and Bianchini 1995) have proposed that *Ozotoceros* and *Blastocerus* together with *Hippocamelus* and the Panamerican *Odocoileus*, should be considered a single genus namely *Hippocamelus*. This does not correspond with the phylogenetic and taxonomic hypothesis of Webb (2000) indicating that *Ozotoceros* and *Blastocerus* form a clade together with *Odocoileus*, with *Blastocerus* being more closely related to *Odocoileus*.

Conclusions

Our study has demonstrated that this thechnique of shape analysis can be used to explore the relationships between size, form and function. The main findings of this study are as follows: (1) In spite of the obvious sexual dimorphism in cervids (males are larger and possess antlers), there do not appear to be any significant shape differences in the crania associated with sex; (2) There are clearly some shape differences associated with the size of cervid crania in this study. However, it is difficult to discriminate purely allometric differences in this shape variable from those that may reflect function that is related to size differences; (3) When only the larger species were examined, a strong correlation could be found between PC1 and diet, however this PC also correlates with latitude and separates the highland from the lowland species; (4) While otherwise remarkably similar in cranial shape, *O. bezoarticus* and *B. dichotomus* can be distinguished on the basis of small differences in the shape of the orbital region. We speculate that these may be related to differences in habitat; (5) The interpretation of the relationship among shape and diet was difficult and detailed functional, biomechanical and ecomorphological studies are needed. However, some morphological differences seem to be related to differences in feeding habits. The larger species have relatively lesser-developed origins for the main masticatory muscles and the cropping mechanism is located forward, improving cropping ability for selective grass feeding; and (6) The phenogram derived from the Procrustes distance data agrees more closely with the phylogenetic analysis of Grove and Grubb (1987) rather than that of Webb (2000); whether this represents support for the former or evidence of convergence is yet to be seen.

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Appendix I. List of deer skulls examined from Argentina including species identification, collection numbers, sex and geographic precedence.

Ozotoceros bezoarticus: MLP18.VIII.92.14. female Bahía Samborombón, Buenos Aires; MACN 49–240 female Misiones; MLP5.VI.97.2 female Bahía Samborombon; MLP18.VIII.92.5 female Bahía Samborombón, Buenos Aires; MLP5.VI.97.3 female Bahía Samborombón, Buenos Aires; MLP1632 female Bahía Samborombón, Buenos Aires; MLP23.VIII.96.4 female Bahía Samborombón, Buenos Aires; MLP1339 female Pigue, Buenos Aires; MLP23.VIII.96.6 female Bahía Samborombón, Buenos Aires; MLP6.VIII.98.1 female Bahía Samborombón, Buenos Aires; MLP31.VIII.98.1 female Bahia Samborombón, Buenos Aires; MLP5.VI.97.4 female Bahía Samborombón, Buenos Aires; MLP18.VIII.92.2 male Bahía Samborombón, Buenos Aires; MLP1340 male Pigue, Buenos Aires; MLP1631 male female Bahía Samborombón, Buenos Aires; MLP1341 male Santiago del Estero; MLP18.VIII.92.9 male Bahía Samborombón, Buenos Aires; CMLM028 male Bahía Samborombón, Buenos Aires; MLP1149 male Buenos Aires; MACN 49–183 male Bahía Samborombón Gral. Lavalle, Buenos Aires.

Blastoceros dichotomus: MLP 1066 female Corrientes; MLP1723 female Brazo Largo, Buenos Aires; MACN 35–24 female Isla Martin Garcia Buenos Aires; MACN 31–231 female Corrientes; MACN 51.72 female Ituzaingo Corrientes; MACN13–2 male Chaco; MLP22.II.99.1 male Otamendi Buenos Aires.

Pudu puda: MACN 47.219 male Zoo Buenos Aires; MACN 17810 female Rio Negro.

Hippocamelus bisulcus: MLP1143 female Patagonia; MLP1366 female Patagonia; MLP1359 female SantaCruz; MLP1364 male Patagonia; MLP1350 male Patagonia; MLP1352 male Patagonia; MLP1346 male Patagonia; MLP1145 male Patagonia; MACN 216 male Chubut; MACN 44–28 male Patagonia; MACN218 male Chubut.

Hippocamelus antisensis: MCNUNSA 3583 female Salta; MACN 53–60 female Catamarca; MACN 53–62 male Catamarca; MACN20–69 male NO. Argentina; MCNUNSA OI male Salta.

Mazama americana: MACN 49.321 female Misiones; MACN 49.356 female Misiones; MACN 48.289 female Misiones; MACN 49.411 female Misiones; MACN 51.119 female Misiones; MACN 51.139 male Misiones; MACN 51.129 male Misiones; MACN 49.380 male Misiones; MACN 47.210 male Misiones; MACN 49.313 female Misiones.

Mazama gouazoupira: CML 01 male Chicligasta, Tucuman; CML 04088 female Salta; CML00023 female Chicligasta, Tucumán; MACN 32.137 female Jujuy; MACN 53.65 female Catamarca; MACN 36.181 male Salta; MACN 47.205 male Salta; MACN 39.431 male Chaco; MCNUNSA 003984 male Salta; CML 00339 male Tucumán; CML 05770 male Pozo de los Novillos Ocampo, La Rioja.

Mazama nana: MACN 50.32 male Misiones; MACN 51.128 Misiones; MACN 51–36 female Misiones; MACN 51.111 female Misiones; MACN 51.126 female Misiones.