

Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach

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Abstract

This work examines whether stepwise discriminant function analysis of a suite of craniodental variables enables feeding behaviour and habitat preferences to be identified in fossil ungulates. There are several morphological features of the ungulate skull, mandible and dentition that are well correlated with dietary adaptations, and thus can be used for estimating the feeding ecology of extinct taxa. However, most studies have followed an univariate approach for characterizing the relationship between diet and craniodental structure in extant ungulates (but see Pérez-Barberia & Gordon, 2001), even though such a relationship has been revealed to be complex because of functional, phylogenetic and biomechanical constraints. In this paper a multivariate perspective is followed, developing quadratic discriminant functions for pairwise comparisons of dietary/habitat groups in modern species. Given that the stepwise method for selecting the morphological variables to be included in the algorithms was used, alternative discriminant functions are provided. Results obtained show that these algorithms reclassify correctly the species according to their feeding and habitat ecology, and thus may be useful for obtaining reliable palaeoautecological inferences (i.e. those related to the life style of extinct species, such as feeding ecology and habitat preferences) when applied to extinct ungulate taxa.

Key words: Ungulata, craniodental morphology, dietary adaptations, ecomorphology, discriminant analysis

INTRODUCTION

The relationship between ungulate diet and craniodental morphology has been studied intensively in the past few decades (Gordon & Illius, 1988; Solounias & Dawson-Saunders, 1988; Solounias, Teaford & Walker, 1988; Solounias & Moelleken, 1993; Janis, 1995; Solounias, Moelleken & Plavcan, 1995; MacFadden, 2000; Pérez-Barberia & Gordon, 2001; Williams & Kay, 2001), in an attempt to discriminate between grazers, mixed feeders, and browsers. These feeding categories are related to the proportion of grass ingested: in this article grazers are defined as species in which grass represents >75% of diet, browsers include ungulates consuming <25% of grass, and those species taking between 25% and 75% of grass are considered as mixed-feeders. Many of these studies have shown that reliable palaeoautecological inferences on feeding preferences of extinct ungulates can be obtained through comparative analysis of their

craniodental architecture, using ecomorphological comparisons with living species of known diet. For example, the hypsodonty index or relative tooth crown height (*HI*, estimated dividing unworn molar tooth height by molar width) has been shown to be a useful indicator of feeding behaviour in herbivores, with ungulates that feed upon abrasive grasses with high silicophytolith contents having higher hypsodonty values than leaf-eating browsers (Janis, 1988; Solounias & Dawson-Saunders, 1988). Table 1 lists other important craniodental features that are also indicative of feeding habits in ungulates.

Although the hypsodonty index is probably the best single variable for predicting diet in both extant and extinct ungulates (see also Pérez-Barberia & Gordon, 2001), molar crown height does not always seem to be a good indicator of feeding habits. For example, most grazing and mixed-feeding ungulates have hypsodont teeth, but the hippo *Hippopotamus amphibius* has brachydont (i.e. short-crowned) teeth (*HI* < 1.4), and the rock hyrax *Procapra capensis* has a hypsodonty index of only 1.69. However, both hippos and hyraxes have relatively low metabolic rates, and consume less

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Table 1. Craniodental features which allow discrimination between leaf-eating, dicot feeders and grazers. Sources: Fortelius (1985), Gordon & Ilius (1988), Janis (1988, 1990a, 1995), Solounias & Dawson-Saunders (1988), Solounias, Teaford *et al.* (1988), Solounias & Moelleken (1993), Spencer (1995, 1997), MacFadden & Shockey (1997), MacFadden (2000), Palmqvist *et al.* (2002), Pérez-Barbería & Gordon (2001), Williams & Kay (2001)

Craniodental feature	Grass-eating grazers	Leaf-eating browsers
Skull length relative to body size	Large	Short
Braincase angle	Narrow	Wide
Height of the glenoid fossa above the occlusal plane	High	Low
Length of the paracondylar process	Long	Short
Anterior extension of the zygomatic arch	Well developed	Poorly developed
Masseteric prominence above M ¹	Present	Absent
Position of the orbit	Starts above M ³ or further back	Starts above M ²
Shape of the incisor arcade	Straight	Curved
Muzzle morphology	Broad	Narrow
Relative width of premaxillae (premaxillary width/palatal width at molars)	High	Short
Mandible size (mandibular corpus depth and width)	Large	Small
Mandibular diastema (length between incisors and premolars)	Long	Short
Size of incisors	I ₁ and I ₃ of similar size	I ₁ larger than I ₃
Hypsodonty index (unworn M ₃ height/M ₃ width)	High	Low
Relative length of the premolar tooth row (premolar row length/molar row length)	High (perissodactyls) Low (artiodactyls)	Low (perissodactyls) High (artiodactyls)

food per day than would be expected for an animal of their body size (Novak, 1999). This means that they would not need to have teeth that were so highly-crowned (as the total amount of wear on the teeth would correspondingly be less). In addition, hippos are fresh grass grazers, feeding in or near water habitats on grasses that are less abrasive as a result of being frequently immersed in water, which removes dust and grit. Similarly, Janis (1988) showed that the pronghorn *Antilocapra americana*, which consumes both grass and browse material, has higher molar crowns than some ungulates that eat exclusively abrasive dry grasses (e.g. the sable antelope *Hippotragus niger* and the white rhino *Ceratotherium simum*). Higher molar crowns in the pronghorn could be because this species lives in deserts and open grasslands where dust could be a factor. There is also a phylogenetic effect, since not all exclusive grass-eaters are similar in their degree of hypsodonty (Janis, 1988; Williams & Kay, 2001): for example, the grazing warthog *Phacochoerus aethiopicus* has higher molar crowns than other more omnivorous or browsing suids but lower crowns than grazing bovids of the tribe Alcelaphini.

There are several extinct taxa, such as some camelids and one giraffid, for which the claim has been made that they were grazers with brachydont teeth. Modern llamas are mixed-feeders which take > 50% grass and have hypsodont teeth ($HI \sim 4$; Janis, 1988). A biogeochemical study of stable carbon isotopes from tooth enamel (MacFadden & Shockey, 1997) has revealed that the llamas *Lama angustimaxilla* and *Vicugna provicugna* from middle Pleistocene deposits at Tarija (Bolivia) fed predominantly on C₄ plants (i.e. herbaceous, arid-adapted grasses and warm/dry herbs that follow the C₄-dicarboxylic acid photosynthetic pathway), which is interpreted as indicative of grazing habits. These species

show, however, remarkably low values of hypsodonty ($HI < 1$ in both animals), similar to those of browsing ungulates from that palaeocommunity that fed on C₃ plants (i.e. all trees and temperate grasses, which fix atmospheric CO₂ directly through the reductive pentose phosphate pathway), such as llama *Palaeolama weddelli*, cervid *Hippocamelus* sp., peccary *Tayassu* sp., and tapir *Tapirus tarijensis*. Note, however, that cacti and some other succulent dry habitat plants use the crassulacean acid metabolism (CAM) photosynthetic cycle, which could also show up as a C₄ indicator in the tooth enamel.

The Miocene ruminant *Samotherium boissieri* is supposed to have been the only non-browsing giraffid according to patterns of tooth microwear and premaxillary shape (Solounias, Teaford *et al.*, 1988), which are indicative of an abrasive diet on grasses. However, it possesses low-crowned teeth, similar to those of modern giraffe and okapi. Conversely, it has been suggested that some extinct horses with hypsodont or at least mesodont teeth (e.g. *Astrohippus stockii* and *Dinohippus mexicanus*, $HI = 3.1$ and 2.3 , respectively), of late Hemphillian age (~5 Ma) from Florida were principally mixed-feeders or C₃ browsers according to their tooth microwear data and enamel isotopic signature, respectively (MacFadden & Shockey, 1997; MacFadden, 1998, 2000; MacFadden, Solounias & Cerling, 1999). Similarly, hipparionine horses from the Old World were not exclusively grazers as are modern equids, but rather showed a mosaic of dietary preferences as suggested by comparative analysis of tooth microwear scratches in browsing and grazing perissodactyls (Solounias, Teaford *et al.*, 1988; Hayek *et al.*, 1992).

It must be remembered that the actual diets of these extinct ungulates are unknown. One cannot unequivocally claim, for example, that *Samotherium* was a

brachydont grazer: the best claim that can be made is that there are contradictions in the various craniodental signifiers of diet, rendering the interpretation of the ecology of the animal problematical. With regards to dental microwear, the enamel scratches and pits have been shown to change very rapidly over the life of an individual (Solounias, Fortelius & Freeman, 1994). A mixed feeder might well be interpreted as a grazer, if it died at the end of a season when grass was a predominant portion of its diet. These examples do, however, indicate that the hypsodonty index does not unequivocally predict the feeding ecology of ungulates, and other morphological features of the skull, mandible and dentition should also be taken into account.

Another example of a cranial feature well-correlated with grazing is the presence of a masseteric prominence (Solounias, Moelleken *et al.*, 1995), since the masseter superficialis muscle leaves a strong prominence above the first upper molar (M^1) in grazers but not in browsers. Similarly, the position of the orbit is correlated with dietary preferences: the orbit is positioned above the second upper molar (M^2) in browsers, but because of the enlarged maxilla of grazers, the orbit tends to move posteriorly in grazing ungulates, starting above the third molar (M^3) or even further back (Radinsky, 1985; MacFadden & Shockey, 1997). The depth and breadth of the mandibular corpus are also diagnostic features: both are larger in grazers because of the presence of high-crowned molars and the need of a greater surface for the insertion of the masseter superficialis. Finally, muzzle shape is a good indicator of the specific adaptations related to the 'cropping mechanism', which includes the shape of the premaxilla and corresponding mandibular symphyseal region as well as the relative proportions of the incisor teeth (Gordon & Ilius, 1988; Janis & Ehrhardt, 1988; Solounias, Teaford *et al.*, 1988; Solounias & Moelleken, 1993; MacFadden & Shockey, 1997). Browsing ungulates usually have narrow muzzles (i.e. low values of premaxillary width) containing a rounded incisor arcade, with the first incisor generally larger than the third, while grazing ungulates have broader muzzles with transversely straight incisor arcades, showing equal or sub-equal sized teeth (but see Pérez-Barberia & Gordon, 2001, who show that significant differences could not be found after controlling for phylogenetic effects).

Although the above are general morphological patterns found among extant ungulates, there are some second-order differences of craniodental morphology related to phylogenetic constraints: for example, horses have relatively more narrow muzzles than grazing ruminants of similar body size (Janis & Ehrhart, 1988; MacFadden & Shockey, 1997), and they also have a relatively deeper angle of the mandible (Janis, 1990a). Furthermore, different ungulate groups have adopted different solutions when faced with the same ecological specializations. For example, grazing species that feed on non-succulent, abrasive grasses require a comparatively greater grinding area of cheek teeth than browsing ungulates consuming leaves and fruits. An obvious way

to achieve this is by enlarging the size of the premolar tooth row, formed by the second, third and fourth lower premolars (P_2 – P_4), which in low-crowned, browsing and mixed-feeding perissodactyls (e.g. tapir, black and one-horned rhinos) is comparatively shorter than the molar tooth row, formed by the first, second and third lower molars (M_1 – M_3). Thus, in these species the mesiodistal length of P_2 – P_4 represents ~75% of the corresponding measurement for M_1 – M_3 , but grazing perissodactyls have lower premolar and molar cheek teeth of nearly the same length, as can be seen in the white rhino, or even have a premolar row that is longer than the molar row, as in horses. However, ruminant artiodactyls show an opposite trend in the size of the premolar tooth row, since grass-eating species show comparatively shorter premolar tooth rows than browsers (premolars ~45% of the molar tooth row, vs ~70%). This indicates that perissodactyls emphasized the development of premolars in the evolution of adaptations for grazing, these teeth being progressively enlarged for increasing the total chewing area. In contrast, the molar teeth were further developed during the evolution of grazing ruminants and camelids, with the elongation of the third molar, and the premolar row was correspondingly reduced (Janis, 1988, 1990a,b; Solounias & Dawson-Saunders, 1988). This difference is probably the result of differences in the way food is orally processed in foregut and hindgut fermenters (Janis & Constable, 1993).

There are also differences in the postcranial morphology of ungulates from different habitats that help to determine niche occupation and resource partitioning. Differences can be seen between species from closed habitats and open, unforested environments, as well as between those that select vegetation at low or high levels above the ground. Such anatomical differences are correlated in part with diet, since the species from closed environments are usually browsers and open-habitat inhabitants are predominantly grazers, although all types of feeders are found in open habitats. These morphological features include the degree of development of neural spines in the thoracic vertebrae (Spencer, 1995), the relative proportions between forelimb and hindlimb bones (e.g. metacarpal and metatarsal length divided by radius and tibia length, respectively; Scott, 1985), and the morphology of the femur (e.g. femoral head shape and cross-sectional functional properties of the diaphysis; Kappelman *et al.*, 1997).

The studies referred to above suggest that the discrimination of feeding habits in ungulates is a rather difficult task, due to functional, historical and biomechanical constraints. Firstly, adaptation to a given trophic niche involves a complex pattern of covariation between many morphological characters of the skull and the mandible (see Table 1). Secondly, different phylogenetic groups, each constrained by their own evolutionary history, have developed convergent adaptations to exploit the same plant resources departing from different ecological and anatomical situations (e.g. grazing perissodactyls and artiodactyls, see above).

Finally, there are also biomechanical constraints related to biomaterials and development: several extinct mammals from South America such as notoungulates (e.g. *Toxodon*) and some xenarthrans (e.g. ground sloths and glyptodonts) had hypselodont (i.e. ever-growing) teeth. Further, in xenarthrans the teeth lacked enamel, being composed of osteodentine, a biomaterial which has different structural properties.

The main objective of this article is to identify, with the help of multivariate statistics, those complex patterns in the craniodental structure of modern ungulates that correlate well with each dietary type. These correlations would then enable the determination of the diet of extinct taxa. Additionally, the discriminant functions also help to more precisely characterize the craniodental patterns related to feeding adaptations such as browsing or grazing, because a mathematical representation of these patterns can be obtained if the corresponding algorithm is set to define the location of the centroid of each group in the discriminant function.

Most researchers have focused on evaluating the morphological differences between feeding types in ungulates using univariate and bivariate approaches, such as *t*-tests for differences of means and regressions of metric characters on body mass (e.g. Janis, 1988, 1990a,b), although there have been some attempts at developing a multidimensional approach (e.g. Janis, 1995; Spencer, 1995, 1997; Pérez-Barberia & Gordon, 2001).

Janis (1995) showed that it is often possible to discriminate between grazers, mixed-feeders and browsers using only three morphological ratios, the hypsodonty index, the muzzle/palatal width ratio, and the relative length of the lower premolar tooth row. However, a discriminant analysis with variables previously selected from their predictive power in univariate or bivariate analyses (e.g. the hypsodonty index) does not take full advantage of the possibilities of this methodology for obtaining the most successful combination of variables for discriminating among the feeding groups compared (see below). In addition, although ratios of characters have a long tradition in vertebrate palaeontology (e.g. Simpson's ratio diagrams), their use in morphometric studies is strongly discouraged by many authors (see review and references in Palmqvist, Arribas *et al.*, 1999), because ratios are seldom normally distributed and tend to produce outliers. Additionally, as generally used, ratios contain only two characters, and thus afford a poor appreciation of shape differences; that is, to compound two characters into a ratio implies that there is only one contrast of form to be studied, and that this unique contrast is well assessed in terms of two characters of equal weights, but opposite in sign (Reyment, Blackith & Campbell, 1984). Finally, ratios may not be constant for organisms of the same species unless they are also of the same size, due to the effects of allometric growth. However, it is worth mentioning that the hypsodonty ratio used by Janis (1988) was size adjusted, since all molar dimensions scale isometrically and are well-correlated with body

mass, showing similar slopes in the least-squares regression lines (Janis, 1990b). Thus, these ratios are very different from most other ratios used in comparative morphological studies, such as intermembranal limb lengths.

We use here the statistical technique of discriminant analysis but following a different approach from that of Janis (1995), since each morphological variable is considered *a priori* as potentially useful for discriminating between the ungulate groups compared. In this way, the best combination of variables in the data set of ungulate species and craniodental measurements is selected for each discriminant function using a stepwise procedure.

MATERIAL AND METHODS

We used discriminant analysis for the following reason. In many instances 2 groups of samples (e.g. 2 clusters of species) may be characterized by a set of morphological measurements that are clearly different, as in the theoretical case depicted in Fig. 1, but their overall differences are not achieved by any single measurement (i.e. the range of values for each group in any morphological variable shows a considerable overlap with that of the other group and each measurement does not allow discrimination on its own). Instead, the discrimination between both groups usually implies a given relationship among the variables. If the differences involve only 2 variables, as in the situation shown in Fig. 1, a single ratio often makes it possible to discriminate between the groups compared. However, the morphological differences between 2 or more groups usually rely on the relationship among a larger set of measurements. In such cases each group may be characterized by a rather complex morphological pattern, which corresponds to a region of the theoretical morphospace defined by the variables that can not be easily represented over a bi-dimensional surface. Discriminant analysis helps to identify these patterns, since it provides mathematical algorithms (i.e. the discriminant functions) that are those linear combination of variables which better distinguish the differences between the multivariate means or centroids of the groups compared in the multidimensional shape space (Reyment *et al.*, 1984; Davis, 1986).

Discriminant analysis has usually been applied following the direct method, which implies that all the variables considered in the study enter in the discriminant function. However, some of the variables can be irrelevant for the patterns that characterize the groups compared, and their inclusion in the discriminant function may then obscure the interpretation of the results obtained. Moreover, discriminant analysis also increases the probability of obtaining a discrimination based on the particular features of the samples compared, instead of those general properties that characterize each group; this is specially true if the sample size is not large enough and the groups are not heterogeneous in composition.

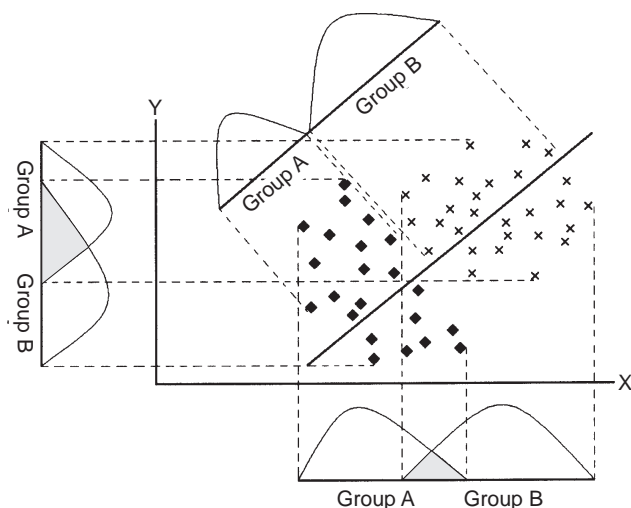


Fig. 1. Scatter-plot of projections of the values measured for two metric variables (X, Y) in two hypothetical groups of species (diamonds and crosses) with different feeding behaviour (e.g. browsers and grazers). Although each axis shows a considerable overlap between both trophic groups, it is possible to discriminate between them using a new, oblique axis (i.e. the discriminant function) defined as a linear combination of variables X and Y : $DF = \lambda_1 X + \lambda_2 Y$.

In contrast, the stepwise method allows the establishment of a criterion for selection of those variables that will be included in the discriminant function (e.g. the Mahalanobis distance between the group centroids or the value of the Wilks' lambda coefficient; see Davis, 1986). Following this methodology, the first variable included in the function is the 1 that has the largest acceptable value for the selection criterion; once this variable has entered, the value of the criterion is re-evaluated for all variables not in the function, and the variable with the largest acceptable criterion value is entered next. After each new inclusion, all the variables already included in the function are re-evaluated using a removal criterion, for example, a threshold Mahalanobis distance. Variables not meeting the criterion are removed from the function. Variable selection terminates when no more variables meet entry or removal criteria.

This methodology offers an interesting possibility for selecting the final set of variables that will compose the discriminant function: if a series of successive analyses are performed, increasing the value of the selection criterion each time, different algorithms are then obtained involving a progressively smaller but more significant number of variables. Each of these algorithms can be evaluated taking into account the percentage of correct reclassifications obtained using the discriminant function with the groups compared, and the total number of variables that it includes. In this way, the algorithms most efficient for discriminating between groups (i.e. those that provide a higher percentage of correct reclassifications) and involving a smaller set of variables (thus easier to interpret and measure in

new samples) or those variables more easily available in the samples in which the algorithms will be applied (e.g. in fossil specimens) can be selected.

Feeding types

Canonical discriminant analysis was based on 115 species of ungulates, including representatives of all living genera. These species were classified into the following habitat/dietary categories and subcategories:

(1) Omnivores (Omn): species whose food is mainly composed of non-fibrous vegetal matter, mushrooms and animal tissues ($N = 5$ species).

(2) Herbivores: species feeding exclusively on vegetal matter ($N = 110$).

(a) Species from open habitats ($N = 58$):

General grazers (GGr), feeding mainly on grasses; this category includes those species in which $> 75\%$ grass is consumed throughout the year ($N = 21$).

Fresh-grass grazers (FGr), feeding predominantly on fresh-grass in near-water environments, which represents $> 75\%$ of the diet ($N = 7$).

Mixed-feeders from open habitats (OMf), including those species in which plant resources comprise both grass and leaves, with grass consumption between 25% and 75% of the diet ($N = 30$).

(b) Species from closed habitats ($N = 52$):

Browsers (Br), those species whose food is mainly composed by leaves, with grass representing $< 25\%$ of the diet ($N = 24$). This trophic category is further subdivided into: *general browsers* (GBr), feeding at any level above the ground ($N = 19$); *high-level browsers* (HBr), feeding from trees and bushes at high levels above the ground ($N = 5$).

Frugivores (Frg), whose food is mainly composed by fruits ($> 50\%$ of the diet) and other non-fibrous soft matters ($N = 8$).

Mixed feeders from closed habitats (CMf), including those species in which grass consumption throughout the year ranges from 25% to 75% ($N = 20$).

The feeding categories listed above are those considered relevant in most studies on dietary preferences of ungulates (Janis, 1995; Gagnon & Chew, 2000). However, the boundaries between feeding groups in the percentage of grass consumed used here are somewhat different, since most authors consider browsing species as consuming $< 10\%$ grass and grazers as those in which grass represents $> 90\%$ of the diet, following Hofmann & Stewart (1972). In this paper the boundaries have been established as $< 25\%$ and $> 75\%$, respectively, because we consider that they more accurately reflect resource partitioning among herbivores, according to a recent synthesis on diet information for extant African Bovidae based on an extensive survey of the literature (Gagnon & Chew, 2000; Table 3). Open and closed habitats refer to the degree of tree coverage (closed habitats include forests, closed woodlands and woodlands; bushlands, grasslands and shrublands are clustered in the open habitat category). Such habitat

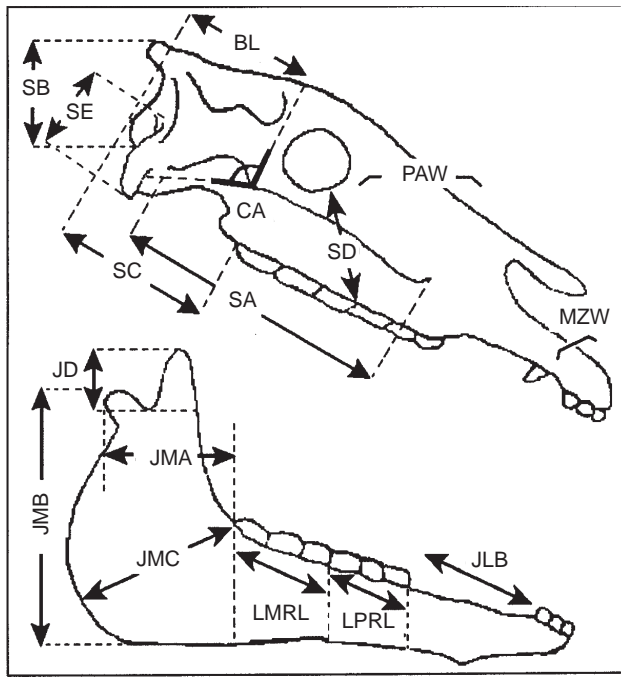


Fig. 2. Craniodental measurements used as variables in this study (adapted from Janis, 1990b).

divisions, as used by Janis (1988), do not correspond strictly to feeding categories, because although most browsing species live in forests and most grazers inhabit unforested regions, there are some exceptions (e.g. *Pelea capreolus*, a browser which dwells mainly in open habitats). However, the majority of the browsing and grazing species are found in closed and open habitats, respectively, and this division can thus be considered broadly as an appropriate approximation for feeding ecology in ungulates.

Craniodental variables and statistical analyses

Twenty-three measurements of the skull, mandible and teeth (Fig. 2, Table 2) were used as variables in the statistical analyses. The squared values of these variables were also used, in order to obtain quadratic discriminant functions. These algorithms allow the relationships between variables to be defined more precisely. For example, a given morphological trait might be positively correlated with body size in small species, but negatively in large ones. The inclusion of both the raw variable in the discriminant function (with a positive coefficient) and also the squared variable (with a negative coefficient) would allow the description of such a non-linear trend.

Canonical discriminant functions were obtained from 2 different data sets. The first was composed of 115 ungulate species and 22 craniodental measurements (see Appendix). This data set included all variables listed in Table 2 except lower molar tooth row length (LMRL), because the information supplied by this measurement

Table 2. Craniodental variables used in this study

Variable	Description
LPRL	Lower premolar tooth row length, measured along the base of the teeth
LM ₃	Third lower molar length, measured at the occlusal surface as the maximum labial excursion of the tooth
HM ₃	Third lower molar height, measured from the base of the crown to the tip of the protoconid
WM ₃	Third lower molar width, measured at the occlusal surface of the tooth, between the outer surfaces of the protoconid and the entoconid
LM ₁₂	Sum of lengths of first and second lower molars, measured at the occlusal surface of each tooth
LMRL	Lower molar tooth row length, measured along the base of the teeth
JLB	Anterior jaw length, measured from the base of the third incisor to the first premolar
JMA	Posterior jaw length, measured as the horizontal distance from the back of the jaw condyle to the posterior border of the third molar
JMB	Depth of mandibular angle, measured from the top of the condyle to the deepest point of the mandibular angle
JMC	Maximum width of the mandibular angle, measured from the junction of the posterior third molar with the jaw to the maximally distant point on the angle of the jaw
JD	Length of the coronoid process, measured as the vertical distance from the top, to the bottom, between the condyle and the tip of the process
SA	Length of the masseteric fossae, measured from the posterior portion of the jaw glenoid to the most anterior extent of the scar for the origin of the masseter muscle
SB	Occipital height, measured from the base of the foramen magnum to the top of the occipital region
SC	Length of the posterior portion of the skull, measured from the occipital condyles to the posterior border of the last molar
SD	Depth of the face under the orbit, measured from the boundary between premolar and molar tooth rows until the nearest point of the orbit
SE	Length of the paraoccipital process, measured from the upper limit of the occipital condyles to the extreme tip of the paraoccipital process
MZW	Muzzle width, measured at the outer junction of the boundary between the maxilla and premaxilla
PAW	Palatal width, measured as the distance between upper second molars at the level of the protocones
BL	Basicranial length, measured from the base of the foramen magnum to the point in the basicranium where a change in angulation occurs between the basicranium and the palate
CA	Basicranial angle, measured as the angle between the basioccipital bone and the palate
IWA	Width of the first lower incisor
IWB	Width of the second lower incisor
TTV	Total molar tooth volume, calculated multiplying the average occlusal surface area estimated for each permanent tooth by its unworn height; the values for each tooth in one side of the lower jaw were summed

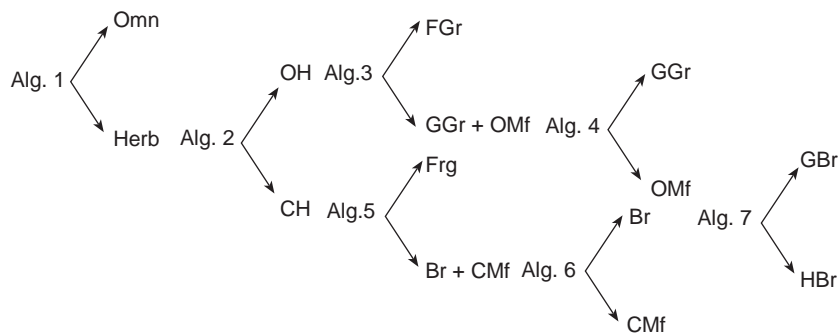


Fig. 3. Sequence of discrimination for characterizing feeding behaviour in ungulates. Feeding/habitat types: Br, browsers; CH, closed habitat; FGr, fresh-grass grazers; Frg, frugivores; GBr, general level browsers; GGr, general grazers; HBr, high-level browsers; Herb, herbivores; CMf, mixed-feeders from closed habitats; OMf, mixed-feeders from open habitats; OH, open habitat; Omn, omnivores.

is contained in the sum of 2 variables, first and second lower molars length (LM_{12}) and third molar length (LM_3). The second set was a matrix with 134 species and 16 craniodental measurements. This included all the variables used in the first data set except those measured at the first and second lower incisors (IWA and IWB, respectively), at the third lower molar (i.e. LM_3 , HM_3 , and WM_3), and the total molar tooth volume (TTV), as these variables were not available for 19 of the ungulate species. LMRL was used as a new variable in this data set and LM_{12} was discarded, given that it is contained within LMRL. The squared values of craniodental measurements were also used as variables in the discriminant analyses based on both data sets. Discriminant functions were obtained using the stepwise method based on maximizing the Mahalanobis distance between the groups compared. Figure 3 shows the sequence of comparison of paired dietary/habitat groups followed to characterize craniodental patterns related to feeding behaviour in ungulates. The data set used in this study was collected during the last decades by CMJ and has been published in part in previous studies (e.g. Janis, 1988).

RESULTS AND DISCUSSION

Quadratic discriminant functions for each pair of groups compared are provided in Table 3, which also includes the following values: the eigenvalue, the canonical correlation, the Wilks' lambda statistic, the χ^2 -value of each function with the statistical level of significance, the values for the centroids of both groups in the discriminant function, and the Mahalanobis distance between the centroids.

The eigenvalue is the ratio of the between-groups to within-groups sums of squares; thus, large eigenvalues are associated with good functions. For the two-groups case, the Wilks' lambda is the ratio of the within-groups sum of squares to the total sum of squares; a lambda of 1 occurs when group means are equal, and values close to 0 indicate that within-groups variability is small

compared to total variability (i.e. when most of the total variability is attributable to differences between the group centroids). Thus, the Wilks' statistic measures the proportion of the total variance in the discriminant scores not explained by differences between groups. Similarly, the canonical correlation is a measure of the degree of association between the discriminant scores obtained by the species and those of the means for the groups compared. The statistical level of significance for the Wilks' lambda is checked transforming it to a variable that has approximately a χ^2 -distribution. It is important to note that even though Wilks' lambda may be statistically significant, it provides little information about the effectiveness of the discriminant function in classification, since small differences may be statistically significant but still may not permit good discrimination among the groups. Thus, this value must be assessed by comparing the percentage of correct reclassifications obtained with the expected misclassification rate (i.e. that expected by chance alone, 50% in the two-groups case).

Quadratic discriminant functions portrayed in Table 3 include the unstandardized discriminant function coefficients, which are the multipliers of the variables when they are expressed in the original units of measurement. The interpretation of the coefficients, in terms of the contribution of each variable to the discrimination process, is always difficult to assess. This is because the variables are usually correlated, so the value of the coefficient for a particular variable depends on the other variables included in the function. However, it is tempting to interpret the magnitudes of the unstandardized coefficients as indicators of the relative importance of variables when they do not differ in the units in which they are measured, as is the case here. In other situations, the standardized coefficients must be evaluated. Finally, the signs of the coefficients inform about the relationship among the variables within the discriminant function (i.e. those variables with a positive sign are positively correlated among them, and negatively with those of negative sign).

Table 3. Two-groups quadratic discriminant functions between ungulate feeding/habitat groups. Alg, algorithm; Eigen, eigenvalue; r , canonical correlation; λ , Wilks' lambda; χ^2 , test for Wilk's lambda (all functions are statistically significant at $P < 0.00001$); R , group centroids (R_A , R_B) and limit between groups (R_O); D^2 , Mahalanobis distance between group centroids. $P < 0.00001$

Group compared	n	Alg	Discriminant function	Eigen	r	λ	χ^2	D^2	R
Herbivores ^(A) vs omnivores ^(B)	$n_A = 110$ $n_B = 5$	1.1	$2.121LPRL - 5.059PAW + 0.533SB + 1.331SD - 0.238SA + 0.711LM_3$ $+ 2.703WM_3 - 0.141LPRL^2 + 0.266PAW^2 - 0.047SD^2 - 0.087SE^2 + 1.436$	5.166	0.915	0.162	195.55	11.04	$R_A = -0.48$ $R_B = 10.57$ $R_O = 5.01$
	$n_A = 64$ $n_B = 65$	2.1	$1.207JMB - 0.400LPRL - 0.506JLB - 0.171JMA - 0.813JMC$ $- 1.038MZW - 2.233PAW - 0.924SB + 0.548SD + 1.656JD + 0.716LMRL$ $+ 0.592SC - 0.574CA - 0.0345LPRL^2 + 0.011JLB^2 - 0.022JMB^2$ $+ 0.022JMC^2 + 0.046MZW^2 + 0.187PAW^2 + 0.029SB^2 - 0.008SD^2$ $- 0.001SE^2 - 0.140JD^2 - 0.054LMRL^2 + 0.008SA^2 - 0.014SC^2$ $+ 0.002CA^2 + 48.513$	3.873	0.892	0.205	179.74	3.90	$R_A = 1.97$ $R_B = -1.94$ $R_O = 0.02$
Grazers and mixed- feeders from open habitats ^(A) vs browsers and mixed- feeders from closed habitats ^(B)	$n_A = 58$ $n_B = 52$	2.2	$1.000JMB - 0.267LPRL - 1.074JLB - 3.375PAW - 0.805SB + 0.219BL$ $+ 0.778SD + 3.237JD + 0.174SC - 0.264CA + 0.130HM_3 - 4.931WM_3$ $+ 0.027TTV - 0.034LPRL^2 + 0.034JLB^2 - 0.031JMA^2 - 0.027JMB^2$ $+ 0.220PAW^2 + 0.026SB^2 - 0.258JD^2 + 0.001CA^2 - 0.411IWA^2 + 1.741WM_3^2$ $+ 24.841$	4.650	0.907	0.177	167.11	4.28	$R_A = 2.02$ $R_B = -2.26$ $R_O = -0.12$
		2.3	$0.995HM_3 - 0.506LPRL - 1.234$	1.365	0.760	0.423	92.08	2.32	$R_A = 1.10$ $R_B = -1.22$ $R_O = -0.06$
Fresh-grass grazers ^(A) vs general grazers and mixed feeders from open habitats ^(B)	$n_A = 7$ $n_B = 51$	3.1	$0.874SC - 0.670JLB - 0.677PAW - 2.821SB - 1.309BL - 0.488SA$ $+ 13.447IWB + 1.502LM_3 + 1.526LM_{12} + 0.118SB^2 + 0.0405BL^2 + 0.029JD^2$ $- 4.723IWB^2 + 9.184$	2.327	0.836	0.301	59.50	4.61	$R_A = 0.56$ $R_B = -4.05$ $R_O = -1.75$
General grazers ^(A) vs mixed feeders from open habitats ^(B)	$n_A = 21$ $n_B = 30$	4.1	$0.336JMC + 1.594MZW - 1.139PAW + 0.245BL + 0.604SE - 0.295SA$ $- 1.004LM_3 - 1.363LM_{12} + 0.569HM_3 + 0.106JD^2 - 0.564$	5.391	0.918	0.157	81.61	4.62	$R_A = 2.72$ $R_B = -1.90$ $R_O = 0.41$
		4.2	$0.770JMC + 1.421MZW - 1.303PAW - 0.873LM_3 - 0.484LM_{12} - 1.170$	4.072	0.896	0.197	75.51	4.01	$R_A = 2.36$ $R_B = -1.65$ $R_O = 0.35$

Table 3. (cont.)

Group compared	n	Alg	Discriminant function	Eigen	r	λ	χ^2	D^2	R
Frugivores ^(A) vs browsers and mixed-feeders from closed habitats ^(B)	$n_A = 8$ $n_B = 44$	5.1	$2.043LPRL - 2.135JMC - 2.648PAW - 0.531SB - 1.347BL + 1.137SD - 5.038SE + 13.623JD - 0.363SA + 0.955SC + 0.106CA - 1.313LM_{12} + 4.561HM_3 - 22.478WM_3 + 0.062BL^2 + 0.663SE^2 - 1.389JD^2 + 2.727IWB^2 - 0.658HM_3^2 + 12.247WM_3^2 - 0.002TTV^2 - 15.228$	3.945	0.893	0.202	61.54	5.35	$R_A = 0.84$ $R_B = -4.51$ $R_O = -1.84$
Browsers ^(A) vs mixed feeders from closed habitats ^(B)	$n_A = 24$ $n_B = 20$	6.1	$1.613JMB - 1.914MZW - 0.713SA - 1.373CA - 19.861IWB - 3.947HM_3 - 0.070JMC^2 + 0.044SB^2 + 0.114SD^2 + 0.005CA^2 + 7.901IWB^2 + 0.215LM_3^2 + 0.760HM_3^2 + 112.113$	3.035	0.867	0.248	48.13	3.42	$R_A = 1.51$ $R_B = -1.91$ $R_O = 0.20$
General browsers ^(A) vs high-level browsers ^(B)	$n_A = 19$ $n_B = 5$	7.1	$3.413LPRL + 2.139MZW - 1.868JD - 0.975SC - 0.057JLB^2 + 0.466HM_3^2 + 0.165$	10.016	0.954	0.091	45.59	7.46	$R_A = -5.91$ $R_B = 1.55$ $R_O = -2.18$

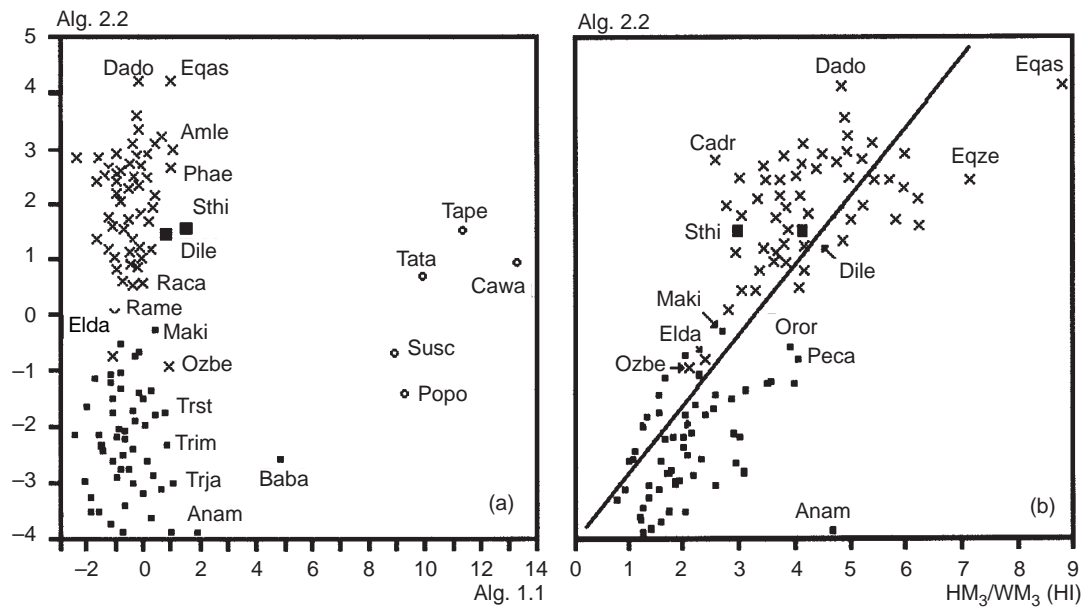


Fig. 4. Bivariate scatter-plots of ungulate projections on algorithm 2.2 vs: (a) projections on algorithm 1.1; (b) values of the hypsodonty index (HI). Open circles, omnivorous species (Cawa, *Catagonus wagneri*; Popo, *Potamochoerus porcus*; Susc, *Sus scrofa cristatus*; Tata, *Tayassu tajacu*; Tape, *Tayasu pecari*); crosses, species from open habitats (Amle, *Ammotragus lervia*; Cadr, *Camelus dromedarius*; Dado, *Damaliscus dorcas*; Elda, *Elaphurus davidianus*; Eqas, *Equus asinus*; Eqze, *Equus zebra*; Ozbe, *Ozotoceros bezoarticus*; Phae, *Phacochoerus aethiopicus*; Raca, *Raphicerus campestris*; Rame, *Raphicerus melanotis*); dotted squares, species from closed habitats (Anam, *Antilocapra americana*; Baba, *Babyrousa babyrussa*; Maki, *Madoqua kirki*; Oror, *Oreotragus oreotragus*; Peca, *Pelea capreolus*; Trim, *Tragelaphus imberbis*; Trja, *Tragulus javanicus*; Trst, *Tragelaphus strepsiceros*); large black squares, fossil species (Dile, *Dinohippus leidyianus*; Sthi, *Stenomylus hitchcocki*).

Herbivores vs omnivores

Most ungulates are herbivores, and only five out of 115 species used in this study have an omnivorous diet. The group centroids in the discriminant function between herbivores and omnivores (algorithm 1.1, Table 3) are placed far apart from each other, with a highly significant Mahalanobis distance. This function reclassifies correctly all species within each trophic group, showing no overlap between both distributions (Fig. 4a). According to the magnitude and sign of the unstandardized coefficients of the variables included in the discriminant function, omnivorous species are characterized by comparatively higher values of lower premolar tooth row length (LPRL), and of the third lower molar width (WM_3) in relation to palatal width (PAW), than those seen in herbivores.

The five omnivorous species belong to two closely related families, Suidae (two spp.) and Tayasuidae (three spp.). It could be argued that the result of the discrimination between omnivores and herbivores is due to taxonomic features unrelated to feeding adaptations. However, the suids analysed in this study also include a grazer (the warthog *Phacochoerus aethiopicus*) and a browser (the Celebes pig *Babyrousa babyrussa*). Both species are reclassified as herbivores. Thus, the good discrimination obtained (100% of correct reclassifications) suggests that the quadratic discriminant function is a successful combination of craniodental

features for discriminating between omnivores and herbivores across phylogenetic boundaries, although admittedly the sample size of omnivorous species used here is small.

Algorithm 1.1 involves eight variables. If the selection criterion required for the variables to be included in the function is slightly increased, all of them are excluded simultaneously. This implies that the overall morphological difference between both groups rests on this particular combination of morphological variables rather than on each variable on its own.

Open vs closed habitat species

Discriminant analysis was also used to evaluate differences in craniodental design between ungulates from open and closed habitats. This habitat division corresponds roughly to a feeding division, since each group includes particular feeding types (see above). It is worth mentioning here that Janis (1988) found significant differences ($P < 0.001$) in a pairwise comparison of the residuals of both groups around the regression line of body mass on third lower molar height (variables log-transformed).

Algorithm 2.1 (Table 3) is a quadratic discriminant function obtained from the data base with 134 species and 16 variables, which does not include molar height measurements. This algorithm involves 15 craniodental

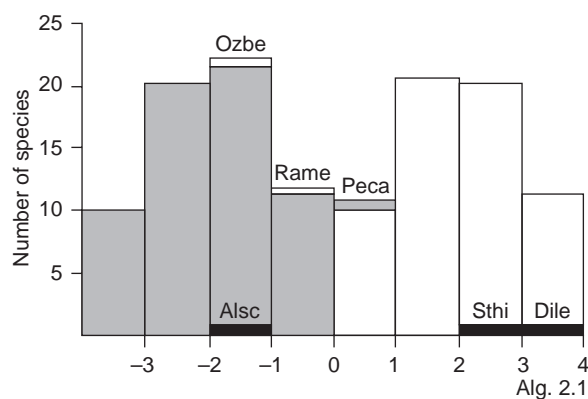


Fig. 5. Histogram of ungulate projections on algorithm 2.1. Grey, species from closed habitats; white, species from open habitats; black, extinct species (Alsc: *Aletomeryx scotti*, Dile: *Dinohippus leidyanus*, Sthi: *Stenomylus hitchcocki*). Key for misclassified species: Ozbe, *Ozotoceros bezoarticus*; Peca, *Pelea capreolus*; Rame, *Raphicerus melanotis*.

variables and reclassifies correctly 98% (126/129) of ungulates according with their feeding/habitat type. Figure 5 shows the histogram for the scores obtained by ungulate species on algorithm 2.1. The projections of those ungulates from open habitats that are correctly reclassified with this discriminant function range between 3.6 and 0.1, while the corresponding projections for closed habitat species range between -0.2 and -3.6 . *Raphicerus melanotis* (the grysbok), *Pelea capreolus* (the rhebok), and *Ozotoceros bezoarticus* (the Pampas deer) are the three species misclassified by algorithm 2.1. *Raphicerus melanotis*, an open habitat species misclassified as a closed habitat one, takes *c.* 30% of grass (Gagnon & Chew, 2000), a proportion close to 25% (i.e. that needed to be classified as browser). Moreover, this species dwells in dense bushland areas (Novak, 1999) and is placed by the discriminant function in a middle position between the group centroids for species from open and closed habitats. Thus, the misclassification of this species as a closed habitat dweller cannot be considered as a serious error. *Pelea capreolus* is the only browsing species in the database that dwells in open habitats; however, given its feeding behaviour, it was included with all browser species within the closed habitat group. Nevertheless, algorithm 2.1 reclassifies it as an inhabitant of un-forested environments, which indicates that this discriminant function gives more weight to the morphological features that characterize *P. capreolus* as an open habitat dweller than to those involved in its feeding adaptations. The pampas deer, however, is different. This cervid lives in open lowland and grassland habitats throughout South America and may be considered as a mixed-feeder, but it is reclassified by algorithms 2.1, 2.2 and 2.3 as a closed habitat species (i.e. as a browser or mixed-feeder from forested habitats). According to these algorithms, the Pampas deer shows a craniodental structure adapted to browsing habits or to a diet of

mixed-feeder in closed habitats. However, it is probable that its adaptation to eat grass in open environments was attained in a different way from that of the other species from open habitats. This possibility is suggested by the fact that *O. bezoarticus* and *Elaphurus davidianus* (Père David's deer), the latter also misclassified by algorithm 2.2, are the only cervid species from open habitats in the data base, and cervids in general occupy closed habitats. Thus, it is possible that the adaptation of cervids to a grazing niche in open habitats involves a set of characters different from that of other ungulates, which the algorithms do not take into account. Alternatively, these cervids may have adopted an open habitat mode of life comparatively recently (i.e. at the end of the Pleistocene), and their adaptive morphology does not yet reflect their behaviour.

A problem with including cervids in this type of analysis is that 19 out of 22 cervids used in this study live in closed habitats feeding as browsers or mixed-feeders, and only the mixed feeding *O. bezoarticus*, the fresh-grass grazer *E. davidianus* and the frugivore *Mazama americana* (the brocket) have different feeding habits. These are the taxa that are misclassified by the discriminant functions. Note, however, that all grazing deer have at least a moderately high hypsodonty index (>2.0) (Janis, 1988).

Algorithm 2.2 (Table 3) involves 16 craniodental variables and reclassifies correctly 98% (108/110) of species (Fig. 4a,b). The two misclassified species are again *O. bezoarticus* and *E. davidianus*. According to the magnitude and sign of the unstandardized coefficients of the variables included in the discriminant function, open habitat species show comparatively higher values of length of the coronoid process (JD) in relation to both palatal width (PAW) and third lower molar width (WM_3) than closed habitat species. This indicates that species from open habitats (i.e. grazers and mixed-feeders) possess a greater area for insertion of the temporalis muscle than ungulates from closed habitats (i.e. frugivores, browsers and mixed-feeders), perhaps related to the processing of more fibrous food.

Algorithm 2.3 (Table 3) provides an interesting alternative discriminant function for evaluating differences in craniodental design between ungulates from open and closed habitats. This function was obtained using the stepwise procedure as described above, and involves only two variables: unworn lower third molar crown height (HM_3), with positive sign, and lower premolar tooth row length (LPRL), with negative one. This function correctly reclassifies the taxa into open and closed habitat species in 88% (97/110) of cases. HM_3 has frequently been used to determine feeding adaptations, although it is usually divided by another measurement for obtaining a size-independent adjustment (e.g. Janis (1988) divided unworn third molar crown height (HM_3) by third molar width (WM_3) to obtain her hypsodonty index in ungulates). Given the negative sign of LPRL, a variable which is positively correlated with body mass, algorithm 2.3 also behaves as an index of hypsodonty,

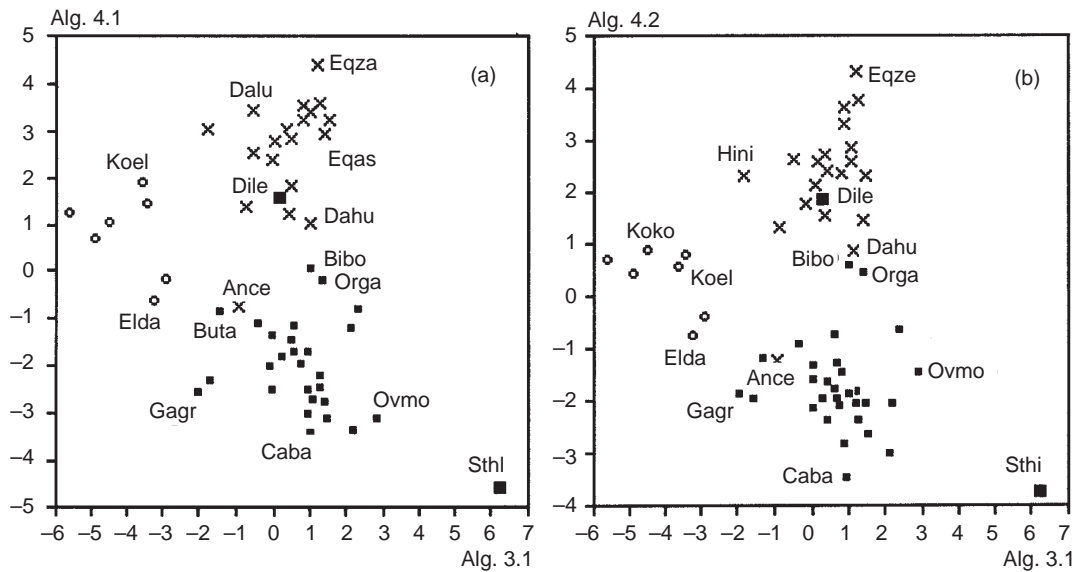


Fig. 6. Bivariate scatter-plots of ungulate projections on algorithm 3.1 vs projections on algorithms 4.1 (a) and 4.2 (b). Open circles, fresh-grass grazers (Elda, *Elaphurus davidianus*; Koel, *Kobus ellipsiprymnus*; Koko, *Kobus kob*); crosses, general grazers (Ance, *Antilope cervicapra*; Dahu, *Damaliscus hunteri*; Dalu, *Damaliscus lunatus*; Eqze, *Equus zebra*; Hini, *Hippotragus niger*); dots, mixed-feeders from open habitats (Bibo, *Bison bonasus*; Buta, *Budorcas taxicolor*; Caba, *Camelus bactrianus*; Gagr, *Gazella granti*; Orga, *Oryx gazella*; Ovm, *Ovibos moschatus*); black squares, extinct species (Dile, *Dinohippus leidymanus*; Sthi, *Stenomylus hitchcocki*).

since it is equivalent to the ratio of lower third molar height on lower premolar tooth row length.

If we use the distance to the centroid (i.e. the mean of each group in the discriminant function) to reclassify the 110 species of this study, the Janis hypsodonty index (i.e. $HI = HM_3/WM_3$) correctly assigns 87% (96/100) of them to their corresponding feeding/habitat type. This value is close to that obtained with algorithm 2.3, since with a single exception the same species are correctly reclassified. The distance between both centroids in the Janis index is also similar, 2.10 vs 2.32 with algorithm 2.3. Thus, there is a minor improvement of the percentage of correct reclassifications obtained with algorithm 2.3 with respect to the hypsodonty index. However, it is important to note that, starting from 22 variables (equally weighted *a priori*), the stepwise discriminant analysis provides a similar relationship to that described by the hypsodonty index, which is probably the best set of two variables for discriminating between these habitat groups. In spite of this, this combination of variables does not discriminate all species correctly, because the craniodental patterns that characterize the different feeding types clustered in both groups involve more variables. However, the analysis is able to identify more complex and less evident combinations of variables, as in algorithms 2.1 and 2.2, which allow discrimination of almost all the species and more closely describe the real craniodental patterns that underlie these trophic groups. On the other hand, although these discriminant functions do not provide 100% correct reclassifications, there is a small overlap between the range of values covered by ungulate species from open habitats and

closed habitats in the discriminant functions, while there is a great overlap between the hypsodonty values of ungulates from both habitat groups (e.g. algorithm 2.2 vs HI in Fig. 4b).

Fresh-grass grazers vs other herbivores from open habitats

Algorithm 3.1 (Table 3) was obtained for discriminating between fresh-grass grazers and other ungulates from open habitats, which are not specialized in feeding on fresh-grass (i.e. general grazers and mixed-feeding species). This quadratic discriminant function combines 10 craniodental variables and reclassifies correctly 97% (56/58) of species, thus providing a nearly perfect discrimination between both groups (Fig. 6a,b). Given the values for the unstandardized coefficients of the variables included in this algorithm, fresh-grass grazers have comparatively wider second incisors (*IWB*) while grazers and mixed-feeders from open habitats have a higher occiput (*SB*). This function also classifies across taxonomic categories, grouping the cervid *E. davidianus* with the bovids in the tribe Reduncini (kob, reedbuck, etc.).

Grazers vs mixed-feeders from open habitats

A function for discriminating between general grazers and mixed-feeders from open habitats is provided by algorithm 4.1 (Table 3), which involves 10 variables and reclassifies correctly 98% (50/51) of cases (Fig. 6a).

Antelope cervicapra (the blackbuck), which is considered to be a grazer, is the only species misclassified with this function, being identified as a mixed-feeder, although in fact in this algorithm it plots out between mixed-feeders and grazers. There are no clear data on the exact percentage of grass consumed by this species, but it has been considered by Janis (1988, 1990a) as a mixed feeder. As *A. cervicapra* is the only potentially grazing gazelle, the result obtained might be the result of phylogenetic effects. Unstandardized coefficients for the variables in this discriminant function (Table 3) indicate that grazers possess muzzles of greater width (MZW) in relation to both palatal width (PAW) and lower molars length (LM₁₂ and LM₃) than do mixed feeders.

Algorithm 4.2 involves only five variables and reclassifies correctly 94% (48/51) of species (Fig. 6b). The discrimination is almost perfect, since *A. cervicapra* is the only species that is clearly clustered within the other feeding group. Inspection of the magnitude of the unstandardized coefficients for the variables included in this discriminant function reveals that the two most contributing variables are muzzle width (MZW) and palatal width (PAW), the former with positive sign and the latter with negative one. Thus, this algorithm measures the relative width of premaxillae (i.e. premaxillary width/palatal width at molars), which is higher in grazers than in mixed-feeders and browsers (see Table 1).

Frugivores vs herbivores from closed habitats

The quadratic function for discriminating between frugivore species and both browsers and mixed-feeders from closed habitats (algorithm 5.1, Table 3) reclassifies correctly 98% (50/51) of species (Fig. 7a). Janis (1988) analysed differences in pairwise comparisons of different pairs of feeding groups, analysing the residuals around the regression line adjusted between the logarithms of body mass on the logarithms of three different molar measurements. Selective browsers were one of these feeding groups, which includes most of the frugivore species considered here. It is relevant to mention that this feeding group only showed significant differences from grazers and mixed-feeders from open habitats, but not from species from closed habitats, either browsers or mixed-feeders (Janis, 1988).

Mazama mazama is the species which is misclassified using algorithm 5.1. As indicated above, this species is the only frugivorous cervid included in the data base used in this study. Most cervids (19 spp.) are closed-habitat browsers or mixed feeders. As indicated previously, the homogeneity of feeding habits among cervid species is probably the reason why it is difficult to identify those cervids with different feeding habits. As was suggested for the Pampas deer *Ozotoceros*, this deer has only recently (Pleistocene, <2 Ma) adopted this mode of life, and its morphology may not yet reflect its behaviour. Thus, the craniodental features of cervids with frugivorous habits are probably different from

those of other frugivorous ungulates, and algorithm 5.1 does not describe them.

Algorithm 5.1 includes 16 variables; when the selection criterion for the variables to be included in the discriminant function is increased, 12 variables of those previously selected are rejected, and the percentage of correct reclassifications decreases significantly. This result suggests that the morphological pattern that differentiates between frugivores and browsers from closed habitats involves a large number of craniodental measurements, which would explain the low success rate of other researchers who tried to discriminate between these trophic groups using an univariate approach (Janis, 1988).

Browsers vs mixed-feeders from closed habitats

Algorithm 6.1 accounts for the discrimination between browsers and mixed feeders from closed habitats (Table 3). This function includes 10 variables and affords an almost perfect discrimination between both feeding types, since it reclassifies correctly 98% (41/42) of ungulates (Fig. 7a,b). The unstandardized coefficients of the variables indicate that browsing species show a greater depth of the mandibular angle (JMB), while mixed-feeders show wider muzzles (MZW) and second lower incisors (IWB), as well as third molars of greater height (HM₃) and a larger basicranial angle (CA).

Tragelaphus angasi (the nyala) is the only species which is misclassified by this algorithm. However, such misclassification does not represent a true error, because this species consumes ~30% of grass (Janis, 1992) and is thus placed near the limit (i.e. 25%) between both feeding groups. Additionally, further measurements of the molar crown height of this species suggest that the values used in this analysis were rather low. The high capability of prediction of this algorithm is evidenced by the fact that all frugivore species, in which grass constitutes <25% of diet, are classified as browsers; these species were not used to obtain the discriminant function.

If the criterion imposed to the variables in the stepwise procedure for entering within the discriminant function is increased slightly, then nine variables out of those 10 previously selected are rejected. This would explain the difficulties of other authors for discriminating these feeding groups without using a multivariate approach.

Browsers vs high-level browsers

The quadratic discriminant function between general browsers and high-level browsers (algorithm 7.1, Table 3) combines six craniodental variables and reclassifies correctly 100% of 24 cases (Fig. 7b), thus discriminating perfectly between general leaf-eaters from those species that browse at the higher levels of vegetation (e.g. the giraffe). According to the unstandardized

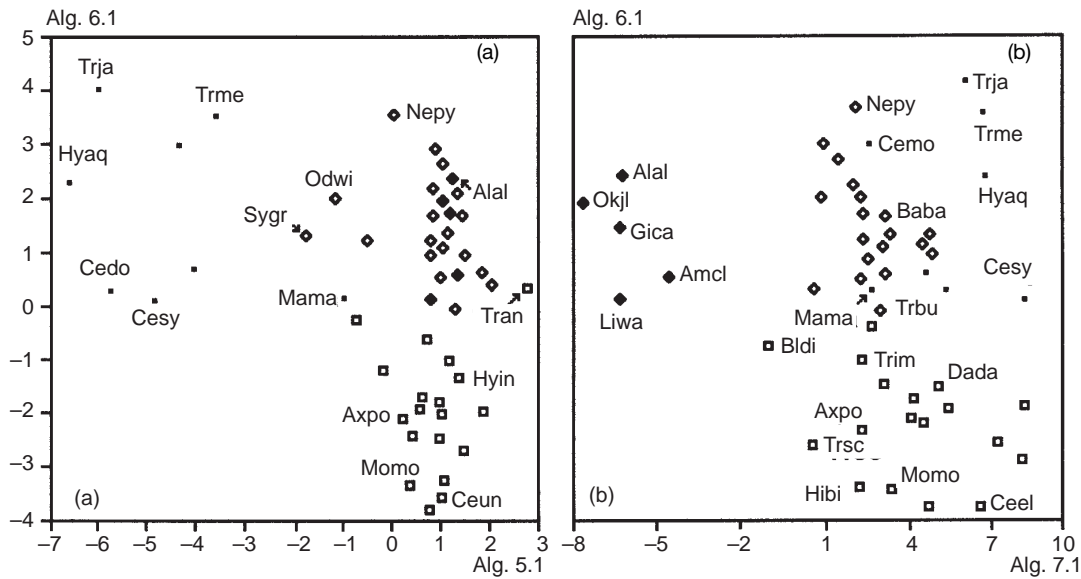


Fig. 7. Bivariate scatter-plots of ungulate projections on algorithm 6.1 vs projections on algorithms 5.1 (a) and 7.1 (b). Small dots, frugivores (Cedo, *Cephalophus dorsalis*; Cemo, *Cephalophus monticola*; Cesy, *Cephalophus sylvicultor*; Hyaq, *Hyemoschus aquaticus*; Mama, *Mazama mazama americana*; Trja, *Tragulus javanicus*; Trme, *Tragulus meminna*); open diamonds, general browsers (Baba, *Babyrousa babyrussa*; Maki, *Madoqua kirki*; Nepy, *Neotragus pygmaeus*; Odwi, *Odocoileus virginianus*; Sygr, *Sylvicapra grimmia*; Trbu, *Tragelaphus buxtoni*); open squares, mixed-feeders from closed habitats (Axpo, *Axis porcinus*; Bldi, *Blastocerus dichotomus*; Ceel, *Cervus elaphus scottius*; Ceun, *Cervus unicolor equinus*; Dada, *Dama dama*; Hibi, *Hippocamelus bisculus*; Hyin, *Hydropotes inermis*; Momo, *Moschus moschiferus*; Tran, *Tragelaphus angasi*; Trim, *Tragelaphus imberbis*; Trsc, *Tragelaphus scriptus*); dotted diamonds, high-level browsers (Alal, *Alces alces*; Amcl, *Ammodorcas clarkei*; Gica, *Giraffa camelopardalis*; Liwa, *Litocranius walleri*; Okjo, *Okapia johnstoni*).

coefficients of the variables in this discriminant function, general browsers have longer lower premolar tooth rows (LPRL) and wider muzzles (MZW), while high-level browsers have an enlarged coronoid process (JD) and a longer posterior portion of the skull (SC). Surprisingly, the basicranial angle (CA) is not included in algorithm 7.1, although Janis (1988) indicated that this variable was useful for discriminating between general browsers and high-level browsers; this probably implies that the morphological information of this variable is supplied by the combination of those selected in the discriminant function.

Only Janis (1988) has compared the craniodental morphology of these feeding groups. She found significant differences at $P < 0.05$ in a pairwise comparison of the residuals of both groups around the regression line between the logarithms of body mass and log-values of two metric variables, the height and volume of the third lower molar. A good indication of the predictive ability of algorithm 7.1 is that all frugivores and mixed-feeders that take the food at ground level, which were not used to obtain the algorithm, are classified as general browsers (Fig. 7b).

All feeding groups

Finally, discriminant analysis was also used for simultaneous comparison of all herbivores classified among

feeding categories. The ungulates from the data base with 115 species and 22 variables were included in one of the six following dietary groups: (1) general grazers, (2) fresh-grass grazers, (3) mixed-feeders from open habitats, (4) mixed-feeders from closed habitats, (5) browsers (including general browsers and high-level browsers), and (6) frugivores. Five quadratic discriminant functions were obtained (Table 4) which allow correct reclassification in 94% (108/115) of cases. Figure 8 shows three combinations of these discriminant functions. The misclassified species are those that were also misclassified with the two-groups algorithms plus *Blastocerus dichotomus* (the marsh deer) and *Sylvicapra grimmia* (the common duiker). *Antelope cervicapra* (a grazer) is misclassified as a mixed-feeder from open habitats, and *T. angasi* (a mixed-feeder from closed habitats) is misclassified as a browser. The misclassification of these species is justified in part, as explained above, given their intermediate position between the dietary groups considered in each case. *Sylvicapra grimmia* (a browser) is misclassified as a frugivore and *B. dichotomus* (a mixed-feeder from closed habitats) as a browser. The reason of the misclassification of *S. grimmia* may be the close relationship between this species and the other duikers included in the genus *Cephalophus*, all of them frugivores. *Blastocerus dichotomus* is a South American cervid which dwells in marshes and wet savannas with high grass, wooded islands and damp forests edges, feeding on fresh grass,

Table 4. Quadratic discriminant functions for extant ungulates clustered in feeding categories. Omnivore species were excluded from this analysis

Canonical discriminant functions	I	II	III	IV	V
Eigenvalues	8.367	3.097	1.603	1.030	0.760
Variance explained (%)	56.32	20.85	10.79	6.93	5.12
Cumulative percentage	56.32	77.16	87.95	94.88	100.00
Canonical correlation	0.945	0.869	0.785	0.712	0.657
Wilks' lambda	0.003	0.026	0.108	0.280	0.568
χ^2	514.295	318.538	195.137	111.436	49.484
Statistical significance (<i>P</i>)	<0.00001	<0.00001	<0.00001	0.0007	0.0321
Factor loadings of variables	I	II	III	IV	V
LPRL	0.4133	-1.4202	1.1836	0.2426	-1.1849
JLB	-0.8342	-1.2958	-0.6002	-0.0253	-0.4007
JMB	1.4363	0.4810	-2.5130	0.2041	-1.4052
JMC	-0.9974	-1.6752	2.7647	-0.4814	-1.8607
MZM	-0.1385	-1.6608	4.4486	-0.8296	-0.3449
PAW	-1.9287	-1.7083	-0.9891	-2.8647	1.8163
SB	-0.5423	-0.6328	-1.7462	2.5603	1.0427
SD	0.8746	0.8184	-1.8836	0.8595	-0.8145
JD	3.8012	3.1913	0.4226	5.7631	5.0679
SA	-0.4546	-0.0499	1.3566	0.2253	-1.4478
SC	-0.0297	1.0295	-1.0386	-1.0624	1.6395
CA	-0.2752	-0.5739	1.0571	-0.5147	0.0938
IWA	4.2101	-1.3967	7.7408	2.9018	-0.0886
IWB	-0.1931	0.6368	7.1583	-7.9799	1.3791
LM ₃	-1.1595	1.9715	1.4088	-1.1566	1.4591
LM ₁₂	-1.3711	0.9249	2.1263	-3.6593	-0.3308
HM ₃	0.3360	-0.3241	0.6739	0.2545	0.7453
TTV	0.0876	-0.1124	-0.0475	0.0543	-0.0866
LPRL ²	-0.1017	0.1448	-0.0890	0.0031	0.2066
JLB ²	0.0385	0.0287	0.0286	0.0044	0.0231
JMA ²	-0.0368	0.0002	-0.0150	-0.0347	0.0180
JMB ²	-0.0463	-0.0050	0.0606	-0.0131	0.0406
JMC ²	0.0389	0.0856	-0.0973	-0.0158	0.1219
MZW ²	0.0877	0.0320	-0.2640	0.0334	0.0972
PAW ²	0.0114	0.2313	-0.0049	0.1959	-0.1597
SB ²	0.0193	0.0269	0.0774	-0.1245	-0.0480
BL ²	0.0115	-0.0123	0.0034	0.0180	-0.0081
SD ²	0.0026	-0.0099	0.0850	-0.0291	0.0443
SE ²	0.0540	-0.0695	-0.0499	0.2121	0.0577
JD ²	-0.2686	-0.3508	0.0124	-0.5085	-0.5154
SA ²	0.0097	-0.0001	-0.0441	-0.0003	0.0292
SC ²	0.0111	-0.0256	0.0209	0.0285	-0.0584
CA ²	0.0009	0.0018	-0.0035	0.0017	-0.0001
IWA ²	-1.9968	0.3167	-3.0517	-1.4584	-0.0291
IWB ²	-0.8706	1.5185	-1.7402	1.9890	0.3879
LM ₁₂ ²	0.0024	0.0972	-0.0726	0.3073	0.1153
TTV ²	-0.0001	0.0002	0.0002	-0.0001	0.0000
Constant	20.6805	46.9621	-87.0023	36.9933	-15.2291
Group centroids	I	II	III	IV	V
General grazers	4.8299	-1.2962	-0.1004	-0.7241	0.3500
Fresh-grass grazers	1.9104	-1.8602	-0.2987	2.8409	-1.8429
Mixed-feeders from open habitats	0.5439	2.7077	0.2253	-0.0088	-0.2570
Mixed-feeders from closed habitats	-2.2947	-1.0368	2.1252	0.2495	0.5514
Browsers (high level and general browsers)	-2.2871	-0.3384	-1.7397	0.3150	0.7507
Frugivores	-3.7919	-1.5167	-0.4137	-2.1208	-1.9731

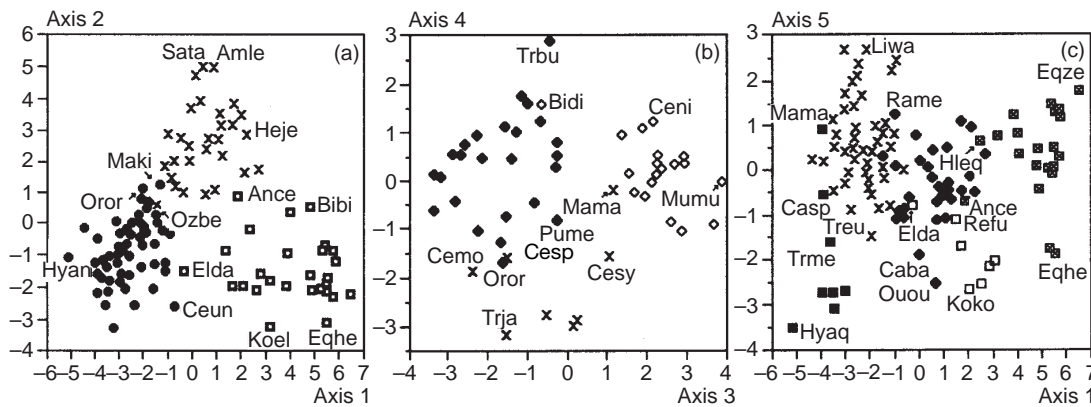


Fig. 8. Bivariate scatter-plots of ungulate projections on canonical discriminant functions for comparison of all feeding groups. (a) Scores on the first two discriminant functions for all grazers (squares), mixed feeders from open habitats (crosses) and mixed feeders from closed habitats, frugivores and browsers (circles). (b) Scores on the third and fourth discriminant functions for frugivores (crosses), browsers (dotted diamonds), and mixed feeders from closed habitats (open diamonds). (c) Scores on the first and fifth discriminant functions for general grazers (squares with crosses), mixed feeders from open habitats (small diamonds), mixed feeders from closed habitats and browsers (crosses), frugivores (dotted squares), and fresh-grass grazers (open squares). Key for ungulate species: Amle, *Ammotragus lervia*; Ance, *Antelope cervicapra*; Bibi, *Bison bison*; Bldi, *Blastocerus dichotomus*; Caba, *Camelus bactrianus*; Cemo, *Cephalophus monticola*; Ceni, *Cervus nippon*; Ceun, *Cervus unicolor equinus*; Cesp, *Cephalophus spadix*; Cesy, *Cephalophus sylvicultor*; Elda, *Elaphurus davidianus*; Eqhe, *Equus hemionus*; Eqze, *Equus zebra*; Heje, *Hemitragus jenghlagicus*; Hieq, *Hippotragus equinus*; Hyan, *Hippopotamus amphibius*; Hyaq, *Hyemoschus aquaticus*; Kobe, *Kobus ellipsiprygmus*; Koko, *Kobus kob*; Liwa, *Litocranius walleri*; Maki, *Madoqua kirkii*; Mama, *Mazama mazama americana*; Mumu, *Muntiacus muntjak vaginalis*; Oror, *Oreotragus oreotragus*; Ouou, *Ourebia ourebi*; Ozbe, *Ozotoceros bezoarticus*; Pume, *Pudu mephistopheles*; Rame, *Raphicerus melanotis*; Refu, *Redunca fulvorufula*; Sata, *Saiga tatarica*; Trbu, *Tragelaphus buxtoni*; Treu, *Tragelaphus euryceros*; Trja, *Tragulus javanicus*; Trme, *Tragulus meminna*.

reeds and numerous aquatic plants. The three other misclassified species, *E. davidianus* (a fresh-grass grazer), *O. bezoarticus* (a mixed-feeder from open habitats) and *M. mazama* (a frugivore), are also cervids, being misclassified by these discriminant functions as mixed-feeders from closed habitats. As explained before, the reason of these four misclassifications is probably that the craniodental adaptations of cervids involve a set of morphological characters different from that of other ungulates.

Inferences about extinct taxa

The algorithms described above were applied to three extinct North American ungulates, the equid *Dinohippus leidymanus*, the camelid *Stenomylus hitchcocki*, and the dromomerycid *Aletomeryx scotti*. Previous speculations on the diets of these species are as follows (see chapters in Janis, Scott & Jacobs, 1998). *Dinohippus* is a late Miocene equid, closely related to modern horses. It has usually been considered to be a grazer, due to its high degree of hypsodonty, but results obtained in recent morphological and biogeochemical studies on dental microwear and carbon isotopes, respectively, have been interpreted as indicative of a browsing or mixed-feeding diet (MacFadden *et al.*, 1999). *Stenomylus* is a late Oligocene/early Miocene 'gazelle camel'. It has extremely hypsodont third molars, leading some workers to consider it to be a grazer. However, it also has a very

narrow muzzle, and existed before the extensive spread of grasslands in North America, thus it would more likely be a mixed-feeder. *Aletomeryx* belongs to the cervid-related family Dromomerycidae, whose members are usually considered to be browsers. However, *Aletomeryx* is more hypsodont than other species in this family. Additionally, it is the only species where horns are apparent in both sexes, which among modern ungulates is indicative of an open habitat existence, its limb proportions are also suggestive of a preference for open habitats, and its dental microwear is typically that of a mixed-feeder.

Results obtained with the discriminant functions provide inferences on the feeding behaviour of these fossil species. *Dinohippus leidymanus* and *S. hitchcocki* are unambiguously classified by algorithm 1.1 as herbivores (Fig. 4a). Algorithm 2.1 identifies them as ungulates from open habitats (i.e. as grazers or mixed-feeders inhabiting an open environment). Algorithm 2.2, which is based on a different set of variables, also classifies them unequivocally as species from open habitats (Fig. 4a); note here that the hypsodonty index does not allow to determine the habitat adaptations of these species, since their intermediate values greatly overlap between species from open and closed habitats (Fig. 4b). Algorithm 3.1 indicates that *D. leidymanus* and *S. hitchcocki* were not fresh grass-grazers (Fig. 6a, b). Finally, algorithms 4.1 and 4.2 help to more accurately identify the trophic behaviour of these species: these discriminant functions classify *D. leidymanus* as a general

grazer and *S. hitchcocki* as a mixed-feeder from open habitats (Fig. 6a). Concerning *Dinohippus*, some authors (e.g. MacFadden *et al.*, 1999) have estimated a mixed-feeding niche for it (i.e. < 90% grass in diet); however, given the limit used in this study for discriminating between mixed feeders and grazers (75% grass instead of 90% grass), algorithms 4.1 and 4.2 indicate a grazing niche for *D. leidymanus*, which suggests that the percentage of grass ingested comprised between 75% and 90%. This is further indicated by the fact that, although the projections of *D. leidymanus* on these algorithms unequivocally classify it as a grazer, the values obtained are closer to those of modern mixed-feeders than the corresponding ones for equids (Fig. 6), thus suggesting that *Dinohippus* incorporated more browse in its diet than extant horses.

In *A. scotti*, algorithm 2.1 classifies it as a species from closed habitats (i.e. as a browser or a mixed-feeder dwelling in forested habitats, Fig. 5); some of the variables included in algorithm 2.2 were not available for *A. scotti*. Thus this animal is potentially misclassified with respect to its habitat preference. However, note that a similar problem was apparent with the open-habitat cervids, as previously discussed. As with the related cervids, if *Aletomeryx* was indeed an open habitat species, then it would have been unusual among its family. In instances such as this, additional information from limb proportions (e.g. Scott, 1985, 1987) would probably be useful.

Discriminant functions for simultaneous comparison of all feeding groups could not be applied to these extinct ungulates because many morphological variables included in them were not available.

CONCLUSIONS

The results obtained in this study indicate that the characterization of aspects of craniodental structure, which are closely related to feeding behaviour in ungulates, is better addressed following a multivariate approach than with the previously employed univariate methods. Such characterization should allow for confidence in the determination of the feeding adaptations of extinct ungulates, as we can demonstrate correct assignment for living species of known diet not used for obtaining the algorithms.

A further feature of these analyses is that the discriminant functions developed for one pairwise comparison of feeding groups can also be used to assign species from a third group. In this case the species in the third group will be assigned to whichever feeding group in the original pairwise comparison is most similar to its own, which indicates the robustness of these algorithms. For example, frugivorous species (in which grass constitutes < 25% of diet) were not used for obtaining the discriminant function between browsers and mixed feeders from closed habitats (algorithm 6.1), but they all were classified as browsers with this algorithm (Fig. 7). Similarly, algorithm 7.1 allows the discrimination of general

browsers from high-level browsers; this function also classifies as general browsers those frugivorous species and mixed-feeders from closed habitats, both of which feed at low levels, and no species is assigned to the group of high-level browsers (Fig. 7b). Finally, although fresh-grass grazers consume > 75% of grass, fresh grass is a less abrasive resource than regular grass; all fresh-grass grazing ungulates are placed by the discriminant function between general grazers and mixed-feeders from open habitats (algorithm 4.1), in an intermediate position between both groups which reflects their intermediate feeding ecology (Fig. 6a).

However, problems exist with the trophic characterization of cervids. This is probably due to the homogeneity of feeding habits shown by members of this family, since most of them are browsers or mixed-feeders from closed habitats. Many of the misclassified forms are from South America, representing a relatively recent (< 2 Ma) adaptive radiation, where morphology may not have had time to catch up with novel feeding behaviour such as grazing or frugivory. Thus, a methodological conclusion is that, in spite of the great ability of canonical discriminant analysis for identifying complex craniodental patterns indicative of feeding behaviour in ungulates, the groups that are the object of discrimination must be heterogeneous in their trophic diversity.

These algorithms will presumably have the same predictive properties over extinct species as with modern ones. Although the Ungulata, as currently defined, represents a monophyletic clade (although there is some dispute over this from molecular data), given the morphological and taxonomic diversity of living hoofed mammals it is to be expected that this set of discriminant functions will be applicable over a large number of fossil taxa. Preliminary results have been obtained on the probable diets of three extinct species, the equid *Dinohippus leidymanus*, the camelid *Stenomylus hitchcocki*, and the dromomerycid *Aletomeryx scotti*. *Dinohippus leidymanus* and *S. hitchcocki* are classified by algorithm 1.1 as herbivores, and by algorithms 2.1 and 2.2 as species dwelling in open habitats. Concerning their feeding adaptations, algorithm 4.1 identifies *D. leidymanus* as a general grazer and *S. hitchcocki* as a mixed-feeder. Finally, algorithm 2.1 classifies *A. scotti* as a mixed feeding or browsing ungulate from closed habitats.

There is, however, a major problem with the multivariate approach proposed here for characterizing the ecomorphological adaptations of extinct taxa: the skeletal remains of ungulates used to be very fragmentary in many fossil assemblages (e.g. those collected by hyaenids, due to the bone-cracking activities of these carnivores; see Palmqvist, Martínez & Arribas, 1996; Arribas & Palmqvist, 1998; Palmqvist & Arribas, 2001) and only small pieces of the skull and mandible are available. In such cases it is impossible to measure all the morphological variables included in the discriminant functions, and the only possibility would be to look at individual variables.

Finally, a second problem of this methodology is the

impossibility of applying it to handle extinct taxa with a unique morphological pattern which does not resemble that of any living ungulate (e.g. the South American xenarthrans, litopterns, and notoungulates). In such situations, even those inferences obtained using single variables have proved to be controversial (see Fariña, Vizcaíno & Bargo, 1998; Vizcaíno, Iuliis & Bargo, 1998).

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Appendix. Ungulate species and craniodental measurements (cm) used in this study. BM, body mass (in kg); DHC, dietary/habitat categories (Omn, omnivores; Frg, frugivores; GBr, general browsers; HBr, high-level browsers; GGr, general grazers; FGr, fresh-grass grazers; CMf, mixed-feeders from closed habitats; OMf, mixed-feeders from open habitats). LPRL to TTV, morphological variables (see description in Table 2)

Species	Code	BM	DHC	LPRL	JLB	JMA	JMB	JMC	MZW	PAW	SB	BL	SD	SE	JD	LMRL	SA	SC	CA	IWA	IWB	LM ₃	LM ₁₂	HM ₃	WM ₃	TTV
<i>Addax nasomaculatis</i>	Adna	111	OMf	3.7	7.5	7.8	11.4	8.1	3.9	4.8	6.9	10.1	9.3	4.9	4.4	7.5	15.6	14.3	155	1.25	0.78	3.25	4.20	4.17	1.02	28.5
<i>Aepyceros melampus</i>	Aeme	53	OMf	2.6	6.1	5.9	7.0	5.8	3.1	3.8	5.1	7.8	6.6	3.2	3.7	5.7	11.5	10.6	150	1.27	0.29	2.35	3.31	3.52	0.72	15.0
<i>Alcephalus buselaphus</i>	Albu	136	GGr	3.2	11.4	11.1	11.3	9.1	5.6	5.2	8.0	8.5	12.3	5.3	4.8	6.7	17.2	17.9	147	1.26	0.62	2.62	4.10	4.60	0.88	32.2
<i>Alces alces</i>	Alal	384	HBr	7.5	16.8	11.9	14.7	10.3	6.0	8.2	11.7	12.6	10.4	6.6	6.9	9.7	22.7	19.1	168	1.26	1.02	4.09	5.63	2.48	1.85	66.6
<i>Ammodorcas clarkei</i>	Amcl	28	HBr	1.8	5.7	3.9	4.9	4.2	1.8	2.9	4.3	7.1	3.3	2.4	2.8	3.7	8.4	8.2	162	0.92	0.22	1.54	2.19	1.25	0.56	2.6
<i>Ammotragus lervia</i>	Amle	86	OMf	3.0	6.0	6.8	7.2	5.9	2.9	4.5	6.3	8.0	9.1	3.2	3.7	6.4	12.8	11.3	135	0.81	0.64	2.73	3.68	3.88	0.87	23.4
<i>Anoa depressicornis</i>	Ande	150	CMf	2.6	7.5	6.4	7.5	5.6	4.2	5.0	7.0	9.9	5.9	3.4	3.5	5.5	13.0	10.7	146	–	–	–	–	–	–	–
<i>Antidorcas marsupialis</i>	Anma	31	OMf	1.4	5.1	5.7	7.1	5.6	2.1	3.3	4.7	6.5	6.1	2.9	3.4	5.2	9.8	8.9	155	1.40	0.21	2.15	3.05	3.18	0.65	10.3
<i>Antilocapra americana</i>	Anam	50	GBr	2.5	8.5	6.4	6.5	5.3	3.2	4.7	11.7	6.1	7.4	2.7	3.6	5.4	11.7	10.0	160	0.82	0.63	2.27	3.09	3.64	0.79	16.0
<i>Antilope cervicapra</i>	Ance	37	GGr	1.7	5.9	4.7	7.2	5.3	2.3	3.3	4.4	8.0	5.3	2.9	3.5	4.9	10.1	9.0	155	1.28	0.28	1.96	2.92	3.65	0.71	11.5
<i>Axis porcinus</i>	Axpo	42	CMf	2.8	5.0	4.2	6.1	4.6	2.6	4.0	5.1	7.1	3.9	2.9	3.3	4.9	10.4	8.2	160	1.03	0.32	2.17	2.69	1.85	0.73	7.4
<i>Babyrousa babyrussa</i>	Baba	85	GBr	2.6	6.6	6.1	8.9	7.2	3.6	2.3	8.9	5.6	5.5	7.0	1.7	5.5	8.5	9.9	180	0.61	1.37	2.26	3.27	1.11	1.08	6.4
<i>Bison bison</i>	Bibi	675	GGr	5.8	11.9	13.8	15.1	11.6	9.4	9.9	15.2	15.1	13.8	6.8	4.5	10.3	25.1	21.7	145	1.16	1.15	4.26	6.00	7.30	1.50	120.6
<i>Bison bonasus</i>	Bibo	625	OMf	5.9	11.9	12.9	14.0	10.6	8.6	9.2	14.8	15.3	13.3	6.2	4.6	10.3	24.7	21.7	149	1.37	1.26	3.76	6.51	7.28	1.19	91.0
<i>Blastoecerus dichotomus</i>	Bldi	130	CMf	3.9	8.6	6.3	8.0	6.4	3.6	4.8	6.8	10.2	6.5	3.9	4.4	5.7	12.3	11.7	158	0.65	0.41	2.19	3.47	1.52	1.02	10.1
<i>Bos banteng (javanicus)</i>	Boba	600	OMf	5.8	12.1	11.0	15.5	10.9	7.2	8.2	12.8	14.9	10.4	6.8	4.7	8.8	22.9	18.1	151	–	–	–	–	–	–	–
<i>Bos gaurus</i>	Boga	755	GGr	6.1	13.3	12.2	17.0	11.6	8.9	9.1	17.7	16.6	12.3	7.8	5.4	9.7	25.4	20.7	156	1.52	1.40	3.94	5.78	6.20	1.68	102.0
<i>Bos indicus</i>	Boin	600	GGr	5.4	11.2	12.1	15.1	10.3	7.4	7.6	13.3	13.8	12.1	6.5	5.5	9.3	23.2	19.5	156	1.45	1.02	3.66	5.68	5.75	1.30	73.1
<i>Boselaphus tragocamelus</i>	Botr	210	CMf	4.8	11.1	8.7	11.4	9.0	4.9	5.8	8.1	11.2	9.0	5.4	4.5	8.0	18.0	14.4	165	1.34	0.84	3.10	4.85	3.70	1.22	35.4
<i>Bubalus bubalis</i>	Bubu	725	FGr	7.1	16.0	13.8	17.8	13.0	10.7	9.2	16.4	18.9	13.4	7.2	7.3	11.0	28.6	22.3	156	–	–	–	–	–	–	–
<i>Budorcas taxicolor</i>	Buta	250	OMf	4.7	9.6	9.4	11.4	8.7	5.6	7.2	10.0	13.6	11.2	5.3	5.2	8.4	19.2	16.1	132	1.27	1.15	3.36	5.04	4.43	1.29	47.1
<i>Camelus bactrianus</i>	Caba	550	OMf	2.9	15.3	9.7	17.3	9.5	5.4	6.5	11.1	14.9	8.9	6.0	7.9	13.7	26.0	19.0	180	1.80	2.11	5.44	8.21	5.87	1.97	133.3
<i>Camelus dromedarius</i>	Cadr	550	OMf	2.2	14.3	9.3	16.4	9.9	4.9	5.8	10.8	13.3	7.9	6.2	6.5	11.7	20.2	17.9	182	1.85	2.13	5.35	6.37	5.25	2.08	125.7
<i>Capra ibex</i>	Caib	87	OMf	2.4	6.1	6.1	7.0	5.7	2.8	4.4	6.1	9.3	7.9	3.5	3.9	5.8	12.1	11.2	137	0.69	0.64	0.85	4.94	4.71	1.00	18.3
<i>Capreolus capreolus</i>	Caca	30	Gbr	3.1	5.0	4.2	6.1	4.5	2.6	3.9	5.1	6.5	4.3	2.7	3.5	4.5	10.0	8.0	163	0.53	0.20	1.51	2.96	1.56	1.05	7.0
<i>Capricornis sumatraensis</i>	Casu	102	CMf	4.0	7.5	6.4	8.0	6.6	3.3	5.5	6.4	9.9	6.9	3.8	4.2	6.1	13.4	11.3	159	0.83	0.61	2.58	3.50	3.73	0.95	21.7
<i>Catagonus wagneri</i>	Cawa	36	Omn	3.7	6.2	4.1	8.3	6.2	4.2	2.7	9.3	5.7	8.9	1.7	2.4	6.7	9.0	9.3	157	0.63	0.36	4.59	2.06	1.40	1.32	14.5
<i>Cephalophus dorsalis</i>	Cedo	20	Frg	2.7	4.8	3.4	5.5	4.2	2.5	3.3	4.6	6.9	3.4	1.9	2.1	4.0	7.3	6.8	156	0.63	0.22	0.98	2.98	1.30	1.13	4.6
<i>Cephalophus monticola</i>	Cemo	6	Frg	1.6	3.0	2.3	3.1	2.6	1.2	2.2	2.9	3.3	1.9	1.2	1.3	2.4	4.8	4.0	146	0.46	0.12	0.89	1.51	0.80	0.42	0.9

<i>Cephalophus spadix</i>	Cesp	57	Frg	2.9	5.7	3.5	6.1	4.4	2.8	4.0	5.2	8.1	3.7	2.2	2.5	4.4	8.1	7.6	160	0.55	0.24	1.67	2.70	1.48	0.76	5.4
<i>Cephalophus sylvicultor</i>	Cesy	61	Frg	4.0	7.2	5.2	9.4	6.5	3.6	4.7	6.1	9.4	5.1	3.2	3.1	6.0	12.1	9.5	162	0.80	0.32	2.24	3.77	2.32	1.04	14.9
<i>Cervus</i>	Ceca	325	CMf	6.1	11.0	9.2	12.3	8.0	7.1	6.8	10.2	12.9	8.8	5.4	5.7	9.3	18.3	16.5	158	1.22	0.64	3.43	5.84	2.76	1.41	39.7
<i>Cervus elaphus canadensis</i>	Ceel	153	CMf	4.3	7.7	6.6	8.2	5.9	4.5	5.0	6.6	9.7	6.0	3.9	4.0	6.8	12.7	11.3	166	1.06	0.51	2.58	4.25	2.17	1.03	17.0
<i>Cervus scottius</i>	Ceni	53	CMf	3.2	5.3	4.9	6.6	5.1	3.0	3.9	5.6	7.3	4.2	3.1	3.6	5.0	10.6	8.9	165	0.93	0.31	1.93	3.02	2.18	0.78	9.1
<i>Cervus nippon</i>	Ceun	188	CMf	4.9	9.5	7.4	10.3	7.8	5.1	5.7	8.1	11.6	7.4	4.4	5.0	7.3	15.8	13.8	161	1.26	0.63	3.04	4.22	2.75	1.25	29.7
<i>Cervus unicolor equinus</i>	Chli	240	GBr	6.3	3.5	8.2	12.1	10.9	7.5	3.6	9.8	10.3	7.1	3.6	6.3	8.4	14.7	13.0	161	-	-	-	-	-	-	-
<i>Choeropsis liberitensis</i>	Cogn	136	GGr	2.6	9.4	10.9	11.6	8.9	6.1	5.4	10.1	10.7	10.9	5.9	5.3	7.4	18.0	18.2	161	1.80	0.97	2.87	4.48	4.85	1.02	39.0
<i>Comochaeetes gnou</i>	Cota	216	GGr	2.8	12.6	12.3	13.4	10.1	6.3	5.9	9.7	10.9	14.0	6.2	5.1	7.9	20.3	20.0	148	1.80	1.08	3.23	4.70	5.63	1.14	49.1
<i>Comochaeetes taurinus</i>	Dada	55	CMf	3.5	5.6	5.2	6.6	5.4	3.6	4.5	6.0	8.2	5.1	3.1	3.6	5.6	11.0	9.5	162	0.91	0.25	2.14	3.41	1.85	0.92	9.8
<i>Dama dama</i>	Dado	69	GGr	2.2	8.9	8.5	10.3	7.7	4.3	3.9	5.7	8.4	9.2	4.6	4.6	5.6	13.5	12.9	146	1.29	0.54	2.26	3.38	3.90	0.82	21.6
<i>Damaliscus dorcas</i>	Dahu	88	GGr	2.6	9.7	10.2	9.8	7.6	4.6	4.6	6.6	8.7	11.0	5.2	4.7	6.8	15.8	15.5	150	1.15	0.61	2.77	4.06	4.02	0.97	26.2
<i>Damaliscus hunteri</i>	Dalu	150	GGr	3.2	11.0	10.3	12.4	9.6	5.3	4.9	7.6	9.1	11.4	5.5	4.9	6.7	16.6	16.3	147	1.62	0.70	3.76	2.98	4.60	0.90	37.6
<i>Damaliscus lanatus</i>	Dedo	5	GBr	2.0	1.1	1.5	4.6	3.6	1.4	1.7	2.6	3.6	1.2	1.4	0.9	1.9	4.6	4.3	188	-	-	-	-	-	-	-
<i>Dendrohyrax dorsalis</i>	Disu	800	GBr	7.9	9.2	12.9	18.9	15.3	6.7	7.7	17.2	25.8	9.8	7.8	4.5	11.7	20.4	23.7	202	-	-	-	-	-	-	-
<i>Dicrohinus sumatrensis</i>	Dome	9	OMf	1.9	3.5	3.0	4.1	3.5	1.2	2.3	3.2	5.0	2.8	1.7	2.3	3.3	6.8	5.6	157	0.70	0.20	1.30	1.98	1.20	0.41	2.0
<i>Dorcotragus megalotis</i>	Elce	18	CMf	2.8	5.0	3.6	4.5	3.9	2.7	3.8	4.4	6.1	3.5	1.8	2.9	3.8	8.3	6.6	161	0.58	0.24	1.55	2.21	1.23	0.73	3.9
<i>Elaphodus cephalodus</i>	Elda	175	FGr	5.4	9.6	8.8	11.3	7.4	5.4	6.1	8.0	11.7	8.8	5.2	5.6	8.0	18.1	13.7	156	1.34	0.64	3.10	4.89	2.84	1.21	36.8
<i>Elaphurus davidianus</i>	Eqas	220	GGr	7.7	7.6	10.2	18.7	9.9	5.0	5.7	8.8	12.2	10.3	4.3	5.4	7.1	17.6	16.2	163	1.03	1.48	2.92	4.22	6.90	0.79	115.5
<i>Equus asinus</i>	Eqbu	235	GGr	8.1	10.5	6.1	22.2	12.0	6.3	6.5	10.2	10.3	10.7	5.1	5.9	7.5	21.6	20.3	170	1.17	1.50	2.68	4.80	6.76	1.16	111.9
<i>Equus burchelli</i>	Eqgr	400	GGr	9.0	13.2	14.4	25.1	13.6	5.9	7.2	11.0	18.4	14.4	5.4	6.8	8.8	26.6	24.9	169	1.41	1.67	3.00	5.82	7.90	1.36	171.9
<i>Equus grevyi</i>	Eqhe	290	GGr	7.9	9.6	12.2	21.6	11.8	5.7	6.7	8.8	13.1	10.8	4.8	6.2	7.6	22.0	19.6	170	1.25	1.52	2.69	4.88	7.47	1.29	159.0
<i>Equus</i>	Eqki	300	GGr	8.6	9.3	12.2	21.0	11.8	6.0	6.8	9.6	12.3	11.0	5.0	5.3	8.0	23.2	19.9	170	1.41	1.68	2.76	5.24	7.90	1.30	172.4
<i>Equus thomsonii</i>	Eqpr	350	GGr	9.5	10.8	12.4	22.4	12.9	6.0	7.0	9.8	15.3	12.2	5.5	6.4	8.8	24.0	20.1	170	1.53	1.62	3.01	5.78	7.64	1.34	207.2
<i>Equus zebra</i>	Eqze	260	GGr	8.1	10.3	12.4	23.7	12.8	6.4	6.5	10.3	10.4	12.5	5.1	6.1	7.8	23.8	21.3	168	1.24	1.69	2.84	4.94	8.75	1.24	171.9
<i>Gazella dorcas</i>	Gado	23	OMf	2.1	3.7	3.6	4.4	4.1	1.5	2.7	3.9	7.0	3.7	2.4	2.5	3.8	7.5	8.2	152	0.89	0.21	1.60	2.18	1.88	0.52	4.1
<i>Gazella granti</i>	Gagr	62	OMf	2.6	5.7	5.6	7.1	6.2	2.4	3.9	5.6	9.1	5.8	3.2	3.6	5.7	12.2	10.9	153	1.21	0.30	2.39	3.26	2.83	0.82	11.7
<i>Gazella thomsonii</i>	Gath	20	OMf	2.1	4.0	3.9	5.5	4.3	1.7	3.0	4.3	6.9	4.4	2.1	3.0	4.3	8.9	8.2	151	1.00	0.24	1.82	2.47	2.26	0.60	9.3
<i>Gingifa camelopardalis</i>	Gica	1075	HBr	7.1	16.7	12.9	16.3	12.6	7.9	9.0	14.2	16.8	10.7	7.3	6.8	10.5	22.6	22.3	168	1.51	0.91	3.90	6.58	2.26	1.88	60.9
<i>Hemitragus jenghlabicus</i>	Heje	91	OMf	2.5	5.8	5.9	6.9	5.3	2.8	4.3	5.5	8.2	8.1	3.2	4.0	5.6	12.0	9.6	141	0.67	0.61	2.41	3.16	4.11	0.83	19.0
<i>Heterohyrax brucei</i>	Hebr	3	GBr	1.6	1.0	1.1	3.4	2.9	1.0	1.4	2.6	2.9	1.1	1.2	0.8	1.7	3.7	3.2	173	-	-	-	-	-	-	-
<i>Hippocamelus bisulcus</i>	Hibi	50	CMf	3.6	7.3	5.9	6.5	5.3	3.4	4.3	6.3	8.0	6.1	2.9	3.7	5.6	12.2	10.1	150	0.70	0.43	2.13	3.48	1.61	0.83	8.6
<i>Hippopotamus amphibius</i>	Hiam	3200	FGr	11.2	10.4	14.7	32.7	25.3	23.2	6.5	19.4	14.7	18.7	7.0	5.4	16.6	27.7	21.8	167	-	-	-	-	-	-	-

<i>Hippotragus equinus</i>	Hieq	270	GGr	5.5	10.7	9.0	15.4	10.3	5.7	6.2	9.1	13.2	10.8	5.7	5.7	8.1	17.7	17.4	153	1.65	0.94	2.85	5.22	4.41	1.03	36.3
<i>Hippotragus niger</i>	Himi	226	GGr	4.4	10.1	9.4	14.0	10.4	5.2	5.5	9.1	11.9	11.1	5.9	5.6	7.3	16.9	16.1	151	1.33	0.76	2.86	4.40	3.87	1.03	35.8
<i>Hydropotes inermis</i>	Hyin	11	CMF	2.2	4.4	2.9	3.9	3.6	2.5	3.0	3.9	5.0	2.7	2.0	2.8	3.4	7.6	5.5	163	0.35	0.20	1.32	2.06	1.05	0.57	2.6
<i>Hyemoschus aquaticus</i>	Hyaq	13	Frg	2.7	2.7	2.7	3.6	2.9	1.5	2.3	3.8	4.9	2.0	1.3	1.2	3.4	7.5	5.1	170	0.54	0.17	1.33	2.03	0.74	0.57	2.0
<i>Hylchoerus meinertzhageni</i>	Hyme	215	CMF	1.6	11.1	8.7	11.8	7.8	5.9	3.8	11.5	5.6	11.9	7.5	1.0	8.6	12.3	12.2	174	-	-	-	-	-	-	-
<i>Kobus</i>	Koel	205	FGr	3.7	10.8	8.0	12.2	8.1	5.2	5.6	8.2	12.2	9.4	5.3	5.2	7.1	16.5	16.2	152	1.86	0.53	2.83	4.24	3.82	1.10	30.9
<i>Kobus kob</i>	Koko	58	FGr	2.7	7.1	6.2	8.5	6.7	3.5	3.8	6.2	9.4	6.2	3.7	4.2	5.0	12.4	10.9	148	1.28	0.32	1.67	3.30	2.75	0.74	11.6
<i>Kobus lechwe</i>	Kole	87	FGr	7.3	7.3	6.7	9.6	7.1	3.7	4.0	6.1	10.1	6.6	4.4	4.4	5.3	13.1	11.9	152	1.34	0.35	2.20	3.13	2.90	0.80	13.9
<i>Kobus vardoni</i>	Kova	87	FGr	2.8	7.7	6.4	8.7	6.7	3.5	3.8	6.3	10.2	6.8	4.0	4.2	5.2	13.3	11.5	148	1.30	0.26	2.21	2.98	3.04	0.75	12.9
<i>Lama guanicoe</i>	Lagu	110	OMF	1.4	8.5	6.5	10.0	6.4	2.9	3.4	6.1	9.1	5.4	3.2	4.8	6.2	14.9	10.8	166	0.94	0.96	2.63	3.53	3.42	0.99	20.8
<i>Lama pacos</i>	Lapa	60	GGr	1.6	7.9	5.5	10.8	5.9	2.8	3.5	6.3	9.2	4.7	3.2	5.5	6.1	11.3	10.5	163	-	-	-	-	-	-	-
<i>Litocranius walleri</i>	Liwa	42	HBr	1.8	5.7	4.5	3.8	4.3	2.0	2.9	4.6	8.3	3.3	2.5	2.9	3.5	8.4	9.8	163	0.91	0.19	1.43	2.07	0.78	0.59	1.8
<i>Madoqua guentheri</i>	Magu	4	GBr	1.7	2.1	2.0	3.1	2.7	0.6	1.9	2.8	3.8	2.0	1.1	1.6	2.4	4.8	4.1	154	-	-	-	-	-	-	-
<i>Madoqua kirki</i>	Maaki	5	GBr	1.7	2.0	1.9	2.8	2.5	0.6	1.8	2.7	3.7	1.9	1.2	1.5	2.4	4.6	4.0	157	0.48	0.15	0.87	1.51	1.00	0.38	1.2
<i>Mazama mazama</i>	Mama	20	Frg	2.6	4.5	3.5	4.1	3.8	2.0	3.4	4.2	5.8	2.8	2.1	2.8	3.9	8.3	6.5	166	0.56	0.21	1.48	2.39	0.90	0.69	3.2
<i>Moschus moschiferus</i>	Momo	12	CMF	1.9	4.0	2.8	3.5	3.2	2.5	2.8	4.0	4.2	2.7	1.6	2.3	3.2	7.5	5.1	157	0.35	0.29	1.18	1.99	0.97	0.49	1.7
<i>Muntiac muntjak</i>	Mumu	25	CMF	2.9	4.8	3.5	4.4	3.8	2.5	3.5	4.5	6.1	3.2	1.8	3.0	4.3	8.7	6.5	155	0.72	0.22	1.62	2.71	1.34	0.74	4.7
<i>Muntiacus reevesi</i>	Mure	13	CMF	2.3	4.2	3.0	3.6	3.4	2.2	3.0	3.9	5.4	3.0	1.5	2.5	3.5	7.2	5.7	152	0.56	0.18	1.44	2.04	0.84	0.75	2.6
<i>Nemorhaedus goral</i>	Nego	27	OMF	2.6	4.6	4.3	6.1	4.7	2.3	3.7	4.7	7.0	5.0	2.6	3.0	4.4	9.3	7.6	147	0.62	0.47	1.84	2.60	2.90	0.72	10.8
<i>Neotragus moschatus</i>	Nemo	5	GBr	1.6	2.4	2.1	2.9	2.6	1.2	2.2	2.8	4.3	1.8	1.2	1.6	2.5	4.8	4.4	157	0.46	0.11	1.00	1.49	1.30	0.37	1.2
<i>Neotragus pygmaeus</i>	Nepy	4	GBr	1.3	3.0	1.5	2.7	2.2	1.1	1.9	2.4	4.4	1.6	1.0	1.3	2.4	4.2	3.4	171	0.58	0.13	0.99	1.45	1.06	0.36	0.8
<i>Odocoileus hemionus</i>	Odhe	74	GBr	3.9	7.5	5.2	7.7	5.6	3.8	4.9	6.5	8.7	5.3	3.6	3.8	5.4	11.9	10.8	168	0.76	0.40	3.44	2.00	1.17	0.74	9.7
<i>Odocoileus virginianus</i>	Odvi	52	GBr	3.5	7.4	5.7	6.6	5.3	3.2	4.3	6.3	7.3	5.0	3.3	3.3	5.1	11.4	10.3	167	0.66	0.18	1.81	3.31	1.17	0.95	6.4
<i>Okapia johnstoni</i>	Okjo	250	HBr	5.8	15.7	8.9	13.0	9.4	5.2	7.6	10.2	15.1	7.5	4.7	4.7	8.8	17.9	17.9	174	0.90	0.58	3.29	5.53	1.96	1.66	33.9
<i>Oreamnos americanus</i>	Oram	97	OMF	2.5	6.9	7.2	7.5	6.1	2.9	4.4	6.1	7.5	8.9	2.8	4.3	5.7	12.7	11.1	152	0.78	0.74	2.49	3.20	2.35	0.85	11.3
<i>Oreotragus oreotragus</i>	Oror	14	GBr	2.3	2.6	2.7	4.3	3.2	1.5	2.8	3.6	4.5	2.7	1.6	1.9	3.4	5.8	5.2	151	0.47	0.19	1.39	2.01	1.68	0.44	3.0
<i>Oryx gazella</i>	Orga	170	OMF	4.4	9.5	10.3	13.2	9.6	5.1	5.8	8.3	11.4	12.0	5.7	5.1	8.5	17.9	16.2	153	1.43	0.91	3.36	5.11	4.08	1.21	45.6
<i>Ourebia ourebi</i>	Ouou	18	OMF	1.8	4.1	3.2	5.2	3.8	1.8	2.6	3.6	5.1	3.7	2.0	2.6	3.5	8.3	6.0	147	0.91	0.31	1.56	1.92	2.05	0.54	4.3
<i>Ovis montanus</i>	Ovmo	395	OMF	5.0	9.8	10.6	12.3	10.3	5.4	7.2	10.7	12.2	12.5	5.7	4.3	9.7	18.7	20.2	157	0.78	0.82	4.20	5.54	4.50	1.22	61.4
<i>Ovis canadensis</i>	Ovea	59	OMF	2.8	7.1	6.7	7.1	5.7	3.2	4.9	5.9	8.6	8.5	3.7	3.6	6.4	13.0	11.1	146	0.76	0.69	2.65	3.75	3.82	0.93	21.7
<i>Ovis nelsoni</i>	Ovda	71	OMF	2.5	5.9	6.0	6.8	5.0	3.1	4.4	5.3	7.9	7.4	3.6	3.8	5.7	11.3	10.6	153	-	-	-	-	-	-	-
<i>Ozotoceros bezaarticus</i>	Ozbe	38	OMF	3.0	5.1	3.6	5.4	4.1	2.4	3.2	4.5	6.6	4.0	2.4	3.0	4.8	8.8	7.2	162	0.61	0.19	2.04	2.73	1.61	0.76	7.0
<i>Panthalops hodgsoni</i>	Palho	50	OMF	1.6	6.2	6.5	7.9	6.1	2.8	3.6	5.1	7.4	6.5	3.0	3.6	4.7	11.0	11.5	159	-	-	-	-	-	-	-
<i>Pelea capreolus</i>	Peca	32	GBr	1.8	6.1	4.2	5.0	4.1	2.2	3.3	4.2	5.5	5.0	1.9	2.6	4.3	8.7	7.6	146	0.75	0.20	1.88	2.46	2.67	0.67	6.8
<i>Phacochoerus aethiopicus</i>	Phae	100	GGr	1.3	8.7	10.4	14.6	8.4	5.7	3.4	12.6	6.3	18.4	9.0	0.6	7.8	15.6	13.1	158	0.65	0.80	3.93	3.90	4.96	1.24	31.7

<i>Potamochoerus porcus</i>	Popo	78	Omn	3.8	6.3	7.9	11.2	7.3	4.2	2.7	11.6	10.0	9.8	7.0	1.1	6.9	9.0	10.5	166	0.62	0.90	2.76	4.18	1.62	1.21	12.9
<i>Procapra gutturosa</i>	Prgu	30	OMF	2.5	5.6	6.0	7.1	5.6	3.1	4.2	4.7	8.4	6.8	3.0	3.5	5.3	11.1	11.1	155	1.04	0.29	2.21	3.12	2.89	0.74	9.9
<i>Procapra capensis</i>	Prcu	4	CMF	1.3	0.5	1.3	3.9	3.0	1.1	1.4	2.7	2.9	1.1	1.1	0.4	2.1	3.8	3.4	166	—	—	—	—	—	—	—
<i>Pseudis nayaur</i>	Pсна	59	OMF	2.2	5.4	5.9	6.1	4.7	2.7	3.7	5.1	6.9	7.3	3.1	3.8	5.3	10.9	9.4	141	0.55	0.56	2.14	3.13	4.08	0.77	14.3
<i>Pudu mephistopheles</i>	Pume	9	GBr	2.2	2.7	2.5	3.5	3.3	1.7	2.9	3.3	5.0	1.8	1.8	2.3	2.8	6.0	5.1	167	0.34	0.19	1.03	1.81	0.90	0.56	1.5
<i>Pudu pudu</i>	Pupu	9	GBr	2.3	2.9	2.8	3.9	3.4	1.6	2.6	3.5	5.2	2.2	2.0	2.5	3.1	6.8	5.6	167	0.39	0.23	1.07	2.01	1.00	0.62	2.0
<i>Rangifer tarandus</i>	Rata	145	GBr	4.5	10.5	8.5	8.8	7.0	5.9	5.9	8.3	9.2	8.6	4.4	4.0	6.0	14.3	14.4	172	0.61	0.36	2.09	3.91	1.40	0.92	12.3
<i>Raphicerus campestris</i>	Raea	14	OMF	1.9	2.7	2.6	4.1	3.2	1.4	2.4	3.3	4.5	2.7	1.4	2.0	3.1	5.9	5.3	151	0.59	0.14	1.22	1.90	1.48	0.43	1.9
<i>Raphicerus melanotis</i>	Rame	10	OMF	2.0	2.3	2.2	3.5	2.9	1.4	2.5	3.3	4.7	2.2	1.4	2.2	3.0	5.9	5.4	155	0.57	0.15	1.26	1.78	1.11	0.42	1.7
<i>Redunca arundinum</i>	Rear	62	FGr	2.4	7.9	6.2	8.3	6.7	3.0	3.6	5.6	8.5	5.9	3.6	3.9	4.6	11.8	11.0	156	0.95	0.22	2.07	2.49	2.69	0.75	10.0
<i>Redunca fulvonifida</i>	Refu	31	FGr	1.9	6.3	4.9	6.4	5.1	2.5	3.1	4.6	7.2	4.8	2.6	3.4	4.1	9.9	8.8	154	1.09	0.21	1.67	2.40	2.77	0.73	8.0
<i>Rhinoceros sondaicus</i>	Rhso	1400	GBr	9.9	12.5	16.8	21.7	17.0	8.3	7.8	22.5	24.6	7.0	9.3	3.7	12.4	23.7	25.4	210	—	—	—	—	—	—	—
<i>Rhinoceros unicornis</i>	Rhun	2200	CMF	10.9	10.7	15.6	28.7	19.0	9.8	8.1	24.5	23.9	11.6	10.6	5.7	14.8	28.0	29.2	200	—	—	—	—	—	—	—
<i>Rapicapra rupicapra</i>	Ruru	39	OMF	2.1	4.6	4.4	5.2	4.1	2.2	3.3	4.3	6.0	5.6	2.6	2.9	4.2	9.1	7.7	145	0.50	0.42	1.63	2.59	2.47	0.59	6.2
<i>Saiga tatarica</i>	Sata	45	OMF	1.8	5.3	4.8	6.7	4.7	2.3	3.9	4.7	7.1	6.7	2.3	3.4	5.5	10.3	9.2	151	0.91	0.47	2.31	3.20	3.28	0.62	10.7
<i>Sus scrofa cristatus</i>	Susc	80	Omn	3.8	7.2	7.4	11.6	8.1	3.9	2.8	11.3	11.3	9.7	7.6	1.3	7.8	9.9	11.1	174	0.61	0.80	3.99	3.84	1.70	1.33	16.2
<i>Sylvicapra grinnia</i>	Sygr	13	GBr	2.4	4.4	2.8	4.8	3.6	1.9	3.0	4.2	5.9	2.8	1.8	2.0	3.5	6.6	6.0	159	0.63	0.17	1.47	2.02	1.72	0.58	4.4
<i>Syncerus caffer</i>	Syca	620	GGr	5.5	13.2	9.8	15.2	10.3	10.0	8.8	10.9	13.5	10.4	5.2	5.6	9.5	20.9	21.6	154	1.43	1.24	3.89	5.64	4.77	1.59	77.6
<i>Tapirus bairdii</i>	Taba	250	GBr	5.9	8.6	8.3	12.9	11.6	4.8	6.1	12.0	13.7	4.1	4.8	5.2	6.7	16.7	17.5	196	—	—	—	—	—	—	—
<i>Tapirus indicus</i>	Tain	275	GBr	7.4	8.7	9.1	15.0	12.7	4.9	6.6	11.6	16.8	4.6	5.1	7.2	8.0	18.4	17.7	191	1.19	0.65	2.86	5.12	1.60	2.11	41.8
<i>Tapirus pincbaque</i>	Tapi	250	CMF	6.2	7.8	7.8	11.9	10.3	4.4	5.6	9.6	13.9	3.3	4.2	4.9	6.9	15.6	14.6	190	—	—	—	—	—	—	—
<i>Tapirus terrestris</i>	Tate	240	GBr	6.1	7.5	8.1	12.2	11.2	4.2	5.7	12.1	13.5	3.9	4.7	6.1	6.9	15.8	16.7	195	0.92	0.70	2.47	4.40	1.64	1.78	28.8
<i>Taurotragus oryx</i>	Taor	511	OMF	5.3	9.9	9.9	11.8	8.7	6.5	8.0	10.1	11.4	13.0	5.9	5.3	9.6	18.6	18.4	155	2.12	0.74	4.10	5.46	4.43	1.52	63.8
<i>Tayassu tajacu</i>	Tata	22	Omn	2.7	5.0	3.6	6.6	5.1	2.7	1.7	7.9	5.9	4.7	1.5	2.3	4.3	7.2	7.5	160	0.44	0.37	1.81	2.53	0.97	0.97	5.1
<i>Tayassu pecari</i>	Tape	32	Omn	3.3	6.0	4.7	8.6	6.4	4.6	2.0	9.8	6.5	6.0	2.0	2.8	5.5	8.9	9.2	164	0.50	0.67	2.37	3.13	1.23	1.00	8.4
<i>Tetracerus quadricornis</i>	Tequ	17	CMF	2.9	4.4	3.2	4.8	3.6	2.1	2.9	4.1	5.7	2.9	2.2	2.5	3.9	8.2	6.7	163	0.69	0.28	0.52	3.40	2.89	1.00	3.8
<i>Tragelaphus angasi</i>	Tran	91	CMF	3.7	6.6	6.9	8.0	6.3	3.8	4.6	6.8	9.5	6.7	3.6	4.0	5.7	12.6	12.3	162	1.56	0.30	2.47	3.25	2.34	0.93	12.3
<i>Tragelaphus buxtoni</i>	Trbu	183	GBr	4.5	8.3	7.7	9.1	7.5	5.0	6.3	8.5	11.6	7.7	5.0	5.0	6.7	15.0	14.5	162	1.58	0.32	2.82	3.91	2.48	1.27	22.3
<i>Tragelaphus euryceros</i>	Treu	205	GBr	4.9	9.0	8.1	10.7	8.0	5.9	7.1	10.3	15.3	9.5	4.7	5.1	8.5	17.7	17.8	158	1.91	0.45	3.42	5.04	2.49	1.30	28.7
<i>Tragelaphus imberbis</i>	Trim	77	CMF	3.8	7.1	6.4	7.1	6.2	3.8	4.3	6.6	9.8	5.9	3.6	3.8	6.2	12.4	11.9	160	1.48	0.27	2.69	3.46	1.91	0.97	12.2
<i>Tragelaphus scriptus</i>	Trsc	58	CMF	2.5	5.7	4.3	5.1	4.4	2.9	3.7	5.2	6.9	3.9	2.7	2.9	4.1	11.2	9.5	164	1.14	0.20	1.88	2.20	1.73	0.68	5.1
<i>Tragelaphus spekei</i>	Trsp	74	CMF	3.4	6.9	5.2	6.6	5.7	3.4	4.2	6.2	9.3	5.1	3.0	3.6	5.5	11.8	10.8	158	1.27	0.25	2.06	3.48	2.29	0.79	9.5
<i>Tragelaphus strapsiceros</i>	Trst	215	GBr	4.9	8.4	8.9	10.1	8.0	5.2	6.0	9.7	10.1	8.8	4.6	4.9	8.0	18.1	16.2	158	1.65	0.38	3.30	4.73	3.07	1.34	35.6
<i>Tragulus javanicus</i>	Trja	3	Frg	1.8	1.7	1.6	2.3	2.0	1.2	1.6	2.7	3.8	1.2	0.8	0.7	2.2	4.1	3.2	170	0.40	0.13	0.94	1.29	0.53	0.36	0.6

