

Characterizing adaptive morphological patterns related to diet in Bovidae (Mammalia: Artiodactyla)*

Manuel MENDOZA, Paul PALMQVIST**

Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, Málaga 29071, Spain

Abstract Morphological patterns in the craniodental structure of extant bovids indicative of ecological adaptations for feeding behavior were identified by stepwise discriminant analysis (SCDA). The analyses were carried out using 28 craniodental measurements from 72 extant bovid species. The discriminant functions obtained allow the characterization of six different types of dietary adaptations: general grazers, fresh-grass grazers, mixed-feeders from open habitat, browsers, mixed-feeders from closed habitat, and frugivores. The predictive ability of the algorithms was tested with 1 063 specimens, most of them lacking one or more measurements. The mean predictive ability of the discriminant functions over these specimens (94%) is only slightly lower than over the species used to obtain them (98%). Given that the algorithms involve small sets of craniodental measurements, they can also be applied to non-complete specimens from archaeological assemblages. These algorithms, combined with those obtained using postcranial measurements for estimating adaptations related to locomotor performance and habitat choice, are useful for deriving inferences on the autecology of ancient bovids and may be used in paleoenvironmental reconstruction [Acta Zoologica Sinica 52 (6): 988-1008, 2006].

Key words Bovidae, Ecomorphology, Feeding behavior, Stepwise canonical discriminant analysis

牛科(哺乳纲: 偶蹄目)动物与食物有关的适应形态模式*

Manuel MENDOZA Paul PALMQVIST**

Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, Málaga 29071, Spain

摘要 利用逐步分辨分析方法(Stepwise discriminant analysis, SCDA)检测了广义牛科动物的颅齿部结构, 这些结构特征可以作为采食行为生态适应特征。在本研究中, 测量了72种广义牛科动物的28个颅齿部结构。逐步分辨分析方法得出了6种采食方式适应类型: 一般粗食者、新鲜禾草粗食者、开阔生境混合型采食者、精食者、郁闭生境混合型采食者、食果者。用103个标本检测了分辨指标的预测能力, 所用标本为缺损标本, 大多数缺少一项或多项结构。从这些标本获得的分辨函数的平均预测能力为94%, 比用72种广义牛科动物标本建立的分辨函数的平均预测能力(98%)低一些。从一个颅齿部结构小样本建立的分函数可以用于考古发掘物中不完整标本的研究。这些指标与用颅下结构测量建立的运动能力和生境选择的指标相结合, 可以推断古牛科动物的个体生态学以及古环境重建[动物学报52(6): 988-1008, 2006]。

关键词 牛科 生态形态学 采食行为 逐步颅部分辨分析

With 140 species distributed over 49 genera (Nowak, 1999), bovids are today the most diverse family of hoofed mammals, inhabiting all the continents except Australia and Antarctica. They exhibit a range of body sizes that varies by nearly three orders of magnitude (Kingdon, 1982): from 4 kg in the

dik-dik *Madoqua guentheri*, to 600-800 kg in the African buffalo *Syncerus caffer*, and the Indian gaur *Bos gaurus*, and even 1 000 kg in some extinct species such as the long-horned African buffalo *Pelorovis antiquus*.

Bovids underwent an adaptive radiation in the

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** Corresponding author. E-mail: ppb@uma.es

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Old World during the Neogene, which may be seen as a response to changes in vegetation triggered by climatic and tectonic events (McNaughton and Georgiadis, 1986). As a result, bovids have shown consistently high levels of taxonomic diversity since the late Miocene, inhabiting a wide range of environments that stretch from mountain forest to arid desert. Perissodactyl equids (monogastric, hindgut fermenters) underwent a similar radiation in the New World during the Neogene, with the appearance of numerous species adapted to a fibrous diet and a cursorial lifestyle. The increased seasonality in the later Cenozoic, however, limited the quantity of vegetation available for ungulates and, given the higher digestive efficiency of foregut fermenters compared to hindgut herbivores, this resulted in an advantage for ruminants (Janis, 1989).

It is not easy to explain the greater diversity of bovids in comparison with other ruminant families such as cervids and giraffids. Historical factors have probably played an important role in their present-day patterns of diversity. For example, bovids are especially diverse today in Africa, where cervids have been virtually absent, and in addition to radiating into mixed-feeding and grazing savanna niches bovids also occupy woodland and forest cervid-like browsing niches (e.g., the tragelaphine antelopes). The extent of the bovids' relatively recent radiation is probably correlated with the development of the savanna-type ecosystems and the expansion of the grazing niche during the Plio-Pleistocene (Janis, 1993; Bodmer, 1990). There are also a number of bovid species in Eurasia, but here their diversity is similar to that of cervids. In addition, giraffids were also moderately diverse in Africa during the later Cenozoic, but their diversity was severely reduced in the Pleistocene, when most larger Old World browsers went extinct (e.g., the deinothere proboscideans and chalicothere perissodactyls, as well as large giraffids such as sivatheres; Janis, 1993; Agustí and Antón, 2002).

The diversity in dietary and habitat adaptations of bovids has been used for determining diet/habitat morphospaces (e.g., Kappelman et al., 1997; Spencer, 1995, 1997). As a result, bovids are probably the most useful indicators of Neogene-Quaternary paleoenvironments of early hominids in Africa (e.g., Bobe et al., 2002; Bobe and Behrensmeyer, 2004; Jousse and Scarguel, 2006).

The high diversity of bovids may also be related to a superior ability to partition the available plant resources, thereby avoiding competitive displacement among coexisting species [however, see Prins et al. (2006) for an alternative explanation based on niche segregation and Bowyer (2004) for a review on the role of both dietary specialization and habitat overlap

in sexual segregation]. Resource partitioning in present-day bovids (Spencer, 1995; Gagnon and Chew, 2000) includes choice of primary food (e.g., grass, leaves, and fruits), feeding-height preferences (e.g., grazing vegetation at ground level versus browsing from trees at a high-level), and habitat use (e.g., open plains, forests, and mountainous areas). A similar degree of resource partitioning is evidenced during Plio-Pleistocene times by the high number of bovid species found at many fossil localities of the Old World (e.g., Spencer, 1997; Palmqvist et al., 2003; Bobe and Behrensmeyer, 2004). These behavioral differences lead to the prediction that a bovid species practicing a given dietary strategy in a particular habitat will differ from other species in both craniodental and postcranial anatomy. Thus, the determination of the relationships between the craniodental morphology and dietary preferences, on the one hand, and between the postcranial adaptations and habitat choice, on the other, will allow the examination of the types of resource partitioning and habitat segregation that existed in past communities of bovids. This, in turn, may contribute additional evidence on past vegetation and environmental change over time (e.g., Spencer, 1995, 1997; Reed, 1987, 1998; Palmqvist et al., 2003; Bobe and Behrensmeyer, 2004; Mendoza et al., 2005; Mendoza and Palmqvist, 2006).

Univariate and bivariate studies of ungulate craniodental anatomy (summarized in Janis, 1995; Mendoza et al., 2002) have revealed a number of morphological correlates with feeding behavior (see Table 1). These morphological features are mainly related to the physical nature of the food (the dicotyledonous leaves consumed by browsers being less abrasive than the grass consumed by grazers), and its nutritional value (a fibrous grass diet being less nutritious, and thus needing to be eaten in greater bulk than a diet of browse). Using these morphological features it is possible to discriminate among grazers, mixed feeders and browsers, among extant species. Then, these features can be used to make inferences about the feeding adaptations of extinct species. However, overall differences between feeding types are not achieved by any single measurement; no variable allows for perfect discrimination by itself (i.e., the range of values for each group in any morphological measurement, whether untransformed or size adjusted, shows a considerable overlap with that of the other groups). Because of this, inferences about the feeding adaptations of extinct species from any of single value are often imprecise, which has been long recognized and is assumed to be the case even by those researchers who have used uni- and bivariate analyses (see reviews in Janis, 1995; MacFadden and Shock-

ey, 1997; Mendoza et al., 2002). Our hypothesis is that the main reason for this overlap is that the adaptation to a given trophic niche involves a complex set of covariant traits constrained by the phylogenetic legacy. Thus, the way that any morphological character is affected by a given adaptation will depend on the rest of the craniodental morphology and relatively complex craniodental patterns will often better char-

acterize different feeding adaptations than single measurements. These patterns, which represent the portions of ecospace inhabited by the bovids, correspond to different regions of the theoretical morphospace defined by the measurements used as variables in the morphological characterization of their dietary preferences.

Table 1 Summary of some correlates of craniodental morphology with dietary behavior in bovids and other ungulates (but see Mendoza et al. 2002 for differences among groups)

Morphological feature	Browser ($<25\%$ grass)	Mixed feeder ($25\% - 75\%$ grass)	Grazer ($>75\%$ grass)	Probable functional correlate
Height of cheek teeth	Brachydont (low)	Mesodont/hypsodont (medium)	Hypsodont (high)	Relates to abrasive nature of food (silica in grass or grit on herbage in open habitats)
Premaxillary width	Narrow	Variable	Broad	Relates to food selectivity (greater in browsers)
Premaxillary row length	Long	Intermediate	Short	May relate to degree of initial food preparation
Depth of mandibular angle	Shallow	Intermediate	Deep	Relates to size of masseter muscle (more developed in grazers)
Depth of mandibular corpus	Shallow	Intermediate	Deep	Height of lower cheek teeth and resistance to bending in sagittal plane
Position of orbit	Approx. above M^2	Intermediate	Posteriorly and vertically	Height of upper cheek teeth and flexion of face on basicranium
Flexion of face on basicranium	Broad angle	Intermediate angle	Acute angle (highly flexed)	May relate to position of head during feeding
Length of face	Short	Intermediate	Long	May relate to position of head during feeding
Length of paraoccipital process	Short	Intermediate	Long	Cropping behavior and movement of head at atlanto-occipital joint

Given its multidimensional nature, this morphospace can not be directly represented over a bidimensional surface, but it can be simplified using different techniques of multivariate statistics (i.e., discriminant analysis). We have shown elsewhere (Mendoza et al., 2002) that a multivariate approach to craniodental variables in ungulates, in general, can distinguish combinations of morphological features that are associated with various dietary habits (e.g., browsers versus grazers, etc.). In this study we apply a similar approach to bovids alone to determine if diet can be more finely distinguished within this more restricted taxonomic grouping.

Other multivariate studies have been performed on African bovid dietary habits. Spencer (1995) used principal components analysis (PCA) on cranial and vertebral variables, and confirmed the dietary correla-

tions with cranial morphology of a number of different univariate studies (e.g., Gordon and Illius, 1988; Solounias and Dawson-Saunders, 1988; Janis, 1990). Spencer later (Spencer, 1997) extended this study to determine the dietary habits of some extinct bovids, with implications for the habitats used by Plio-Pleistocene hominids. PCA is a suitable methodology for describing the morphology of species from a multivariate perspective when no *a priori* hypothesis can be conducted on their groupings and the multidimensional structure of the morphospace. However, PCA it is not well designed for searching for particular morphological patterns. In contrast, stepwise canonical discriminant analysis (SCDA) is specifically designed to identify those variables involved in the differences between the groups compared, according to the criteria established for discriminating among

them (in this case, the feeding adaptations). In addition, SCDA allows the identification of combinations of small sets of measurements whose possibilities for specific applications are noticeably superior to PCA, which involves the full set of variables.

Gagnon and Chew (2000) evaluated bovid dietary behavior by analyzing the percentages of various food items in the diet, and performing cluster analyses to determine how these percentages related to both body size and taxonomic affiliation. They found evidence for both factors. With respect to body size, the percentage of grass in the diet correlated positively with body size while the proportion of fruit and dicotyledonous food material had a negative correlation. In addition, certain tribes tended towards certain dietary types (e.g., members of the tribe Alcelaphini were mostly grazers while members of the Cephalophini were mostly browsers).

The data presented in this paper constitutes a subset of extant bovid species of the data published in Mendoza et al. (2006: Appendix) and are analyzed using the novel approach of SCDA for pair wise comparisons of dietary/habitat groups using measurements of the craniodental morphology, a refinement of the procedure described in Mendoza et al. (2002). The results obtained by Mendoza et al. (2002) indicate that the characterization of aspects of craniodental structure, which are closely related to feeding behavior and habitat preferences in ungulates, is better addressed following a multivariate approach than with univariate methods, enabling the paleobiology of extinct ungulates to be reconstructed. Specifically, the discriminant functions developed by Mendoza et al. (2002) for pair wise comparisons of dietary/habitat groups in modern ungulates allowed the correct reclassification of 98% of species according to their environmental preferences (i.e., open vs. closed habitat), and between 97% in the less favorable case (fresh-grass grazers vs. other herbivores from open habitat) and 100% in the most favorable ones (e.g., browsers vs. high-level browsers) for feeding behavior. Given that bovids show a lower taxonomic and morphological diversity than the whole set of ungulates, it is expected that these functions will give better predictions than those adjusted by Mendoza et al. (2002) for all ungulates.

SCDA generates discriminant functions that can be considered to be mathematical algorithms (i.e., detailed sequences of actions to accomplish a task, in this case, the inference of the feeding habits of extinct bovid species). These algorithms make it possible to produce a more precise morphological characterization of different types of feeding adaptation, which in turn allows a more accurate determination of the feeding habits of extinct species (Mendoza et al.,

2002).

Multivariate statistical techniques, however, are not employed in this article to perform statistical analyses; instead they are used primarily to explore the relationship between morphology and adaptation. In fact, statistical analysis, *sensu stricto*, cannot be performed in analyses of this nature because species do not represent independent samples of a statistical distribution as a consequence of their phylogenetic interrelationships (Felsenstein, 1985; Harvey and Pagel, 1991), as discussed in depth below.

1 Materials and methods

1.1 Morphological variables and feeding categories

Craniodental patterns related to feeding adaptations were carried out using 28 craniodental variables (represented in Fig. 1 and described in Appendix I) measured on 72 extant bovid species. In 57 out of 72 species the full set of craniodental measurements was available for several adult individuals of both sexes and only complete specimens were used for these species (see Appendix II). We have used species means instead of individual data because although different individuals from the same species will show second-order morphological differences related to intraspecific variability (e.g., sexual dimorphism, individual variation and age), we expect that they will share a common, first-order morphological pattern in their craniodental structure, indicative of the dietary adaptations of the species. Our hypothesis is that distinct patterns of craniodental morphology will characterize different feeding adaptations in bovids and that SCDA is the best tool for unraveling them. As far as these patterns arise from the correlations among the variables, the use of non-complete specimens showing slight differences in shape and dimensions could affect such correlations. Thus, we considered the anatomical completeness of the specimens measured more important than their number for obtaining the discriminant functions. For this reason, non-complete individuals (i.e., crania or mandibles isolated, skulls fragmented) were discarded in these species. However, given that the algorithms obtained involve small sets of craniodental variables and that alternative algorithms were developed for each comparison of feeding groups (see below), in most cases they can be applied also to non-complete specimens from archaeological assemblages.

For 15 additional species only one or two complete specimens were available. In these cases, non-complete skulls and jaws were also used in order to increase their sample size. However, this procedure may represent a potential source of error: given the differences in the degree of completeness between the anatomical regions of the skull and mandibles, the use

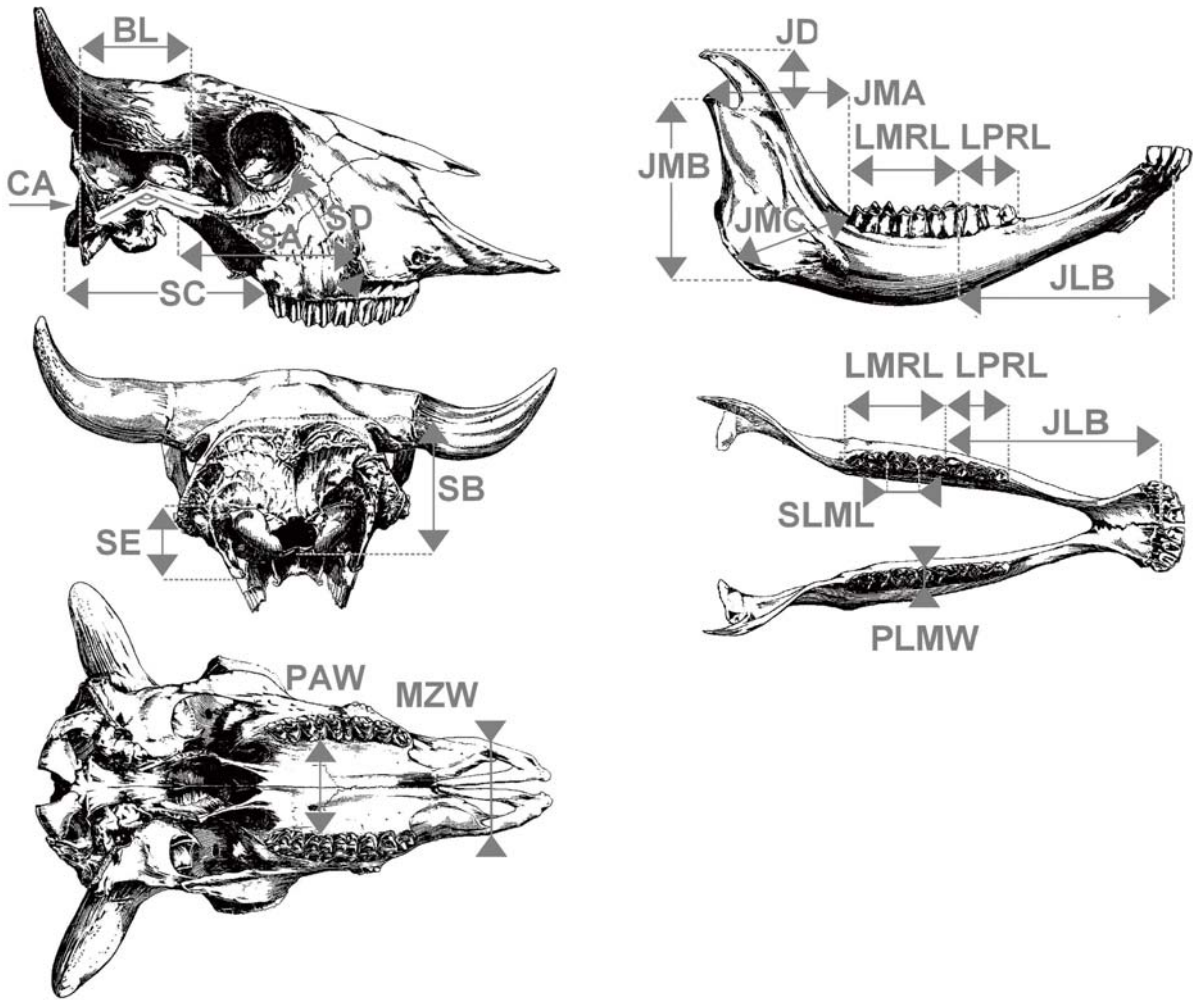


Fig. 1 Selected craniodental measurements used in this study

Measured in cm, with the exception of the basicranial angle, measured in degrees; see Appendix I for details on these measurements.

of fragmentary crania may result in different numbers (randomly distributed) of specimens of different sex and age measured for each morphological variable, thus biasing the averages obtained for the species. For this reason, the 15 additional species were included in the analyses because in all cases we could measure more than 20 specimens of both sexes lacking only a few variables. Thus, we also expect, for these species, that the estimated averages will be close to the real mean values.

The hypsodonty index (HI) or relative tooth crown height, is estimated by dividing the height of the third lower molar by its width at tooth base (Janis and Ehrhardt, 1988). HI was obtained independently from single individuals that showed little or no dental wear using X-ray photographs (see Janis and Ehrhardt, 1988). Thus, only individuals showing unworn teeth can be used for estimating the feeding adaptations of ancient bovids preserved in archaeological assemblages. Although this procedure entails some limitations on the sample size available from most fos-

sil localities, it is necessary because the hypsodonty index plays an essential role in the feeding adaptations of ungulates (see review in Mendoza et al., 2002).

Twenty eight craniodental measurements were used for defining 54 morphological variables, of which 26 were size-adjusted by dividing each measurement by the lower molar row length (LMRL). The transformed variables have the same abbreviations as the original ones, but with the addition of the prefix R (e.g., JMB/LMRL = RJMB). Given the ranges of body size exhibited by the species of most dietary/habitat groups compared, the size-transformation helps to find the best combinations of morphological variables for separating these dietary/habitat groups. The hypsodonty index (HI, estimated as HM_3/WM_3) and the basicranial angle (CA, measured as the angle between the basioccipital bone and the palate) are the only variables that were not size-transformed, because both are size-independent ratios (i.e., HI is calculated dividing two morphological variables and CA is an angle whose estimation implies

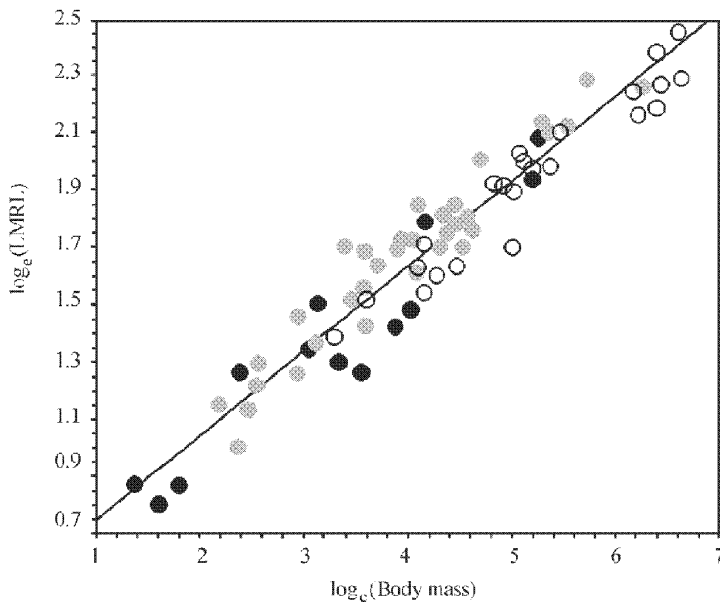


Fig. 2 Least-squares regression between the logarithms of the lower premolar tooth row length (LMRL, in cm) and the body mass (BM, in kg) of 72 bovid species used in this study

Filled circles: Browsers and frugivores; Grey circles: mixed feeders from open and closed habitats; White circles: general grazers and fresh-grass grazers. $\text{Log}_e(\text{LMRL}) = 0.451 (\pm 0.043) + 0.296 (\pm 0.010) \text{Log}_e(\text{BM})$, $r^2 = 0.931$, s.e.e. = 0.104.

a proportion between three distances).

These size-transformed variables could be considered to be simple ratios, and the use of ratios in morphometric studies is strongly discouraged by many authors because ratios are rarely normally distributed and may be affected by allometric growth (e.g., Reyment et al., 1984). The lower molar row length (LMRL) is, however, one of the craniodental variables that is best correlated with body mass in bovids (Janis, 1990a, b) and scales isometrically with r^2 values of approximately 0.93. In addition, of those measurements that are well correlated with body size (Janis, 1990a, b), LMRL is the one most frequently available in fossil specimens, as it is often possible to measure it in jaw fragments (Arribas and Palmqvist, 1998), and it is unrelated with dietary types in ungulates (Janis, 1995; Mendoza et al., 2002) and also in our bovid dataset (Fig. 2). Thus, according to these criteria, LMRL is the most appropriate measurement for creating size-transformed variables.

Information on the feeding preferences of bovid species (Appendix II) was obtained from Janis (1990a, b, 1993), Nowak (1999), Gagnon and Chew (2000) and Mendoza et al. (2002).

Species were classified into the following categories and subcategories: (1) species from open habitat (*OH*, $n = 50$), including general grazers (*GG*, $n = 17$), feeding predominately on grasses for most of the year, fresh-grass grazers (*FG*, $n = 4$), feeding predominately on fresh grass close to water, and mixed-feeders (*MO*, $n = 29$), feeding on both grass and dicotyledonous plants, depending on their avail-

ability; and (2) species from closed habitat (*CH*, $n = 22$), including browsers (*Br*, $n = 11$), feeding predominately on dicotyledonous plant leaves for most of the year, mixed-feeders (*MC*, $n = 6$), and frugivores (*Frg*, $n = 5$), feeding predominately on fruits and other non-fibrous soft material.

The categories of “open” and “closed” habitat as employed here (and also by Mendoza et al., 2002) do not strictly correspond to habitat categories, but to broad feeding categories.

The feeding categories of grazing, mixed-feeding and browsing herbivores were initially characterized by Hofmann and Stewart (1972), where they showed that feeding behavior also correlated with stomach anatomy. Subsequent studies have also shown these feeding categories to be correlated with different modes of digestive physiology (e.g., Clauss et al., 2002, 2003).

These same feeding categories have been used by a number of authors in many studies of correlations of craniodental morphology with diet (e.g., Janis, 1988, 1990a, b, 1995; Mendoza et al., 2002; Pérez-Barbería and Gordon, 2001; Semperebon et al., 2004), and they have also been widely accepted by ecologists as representing the most coherent functional dietary classification of ungulates (Owen-Smith, 1982; Spalinger and Hobbs, 1992; Iason and Van Wieren, 1999).

1.2 Statistical analyses and phylogenetic contrast

Patterns of combinations of craniodental variables characterizing each dietary group were identified using comparisons with discriminant analysis, follow-

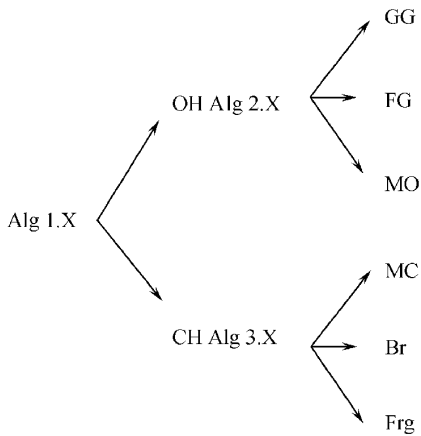


Fig.3 Sequence of discrimination for characterizing feeding behavior in bovids

OH: open habitat feeding categories; CH: closed habitat feeding categories; GG: general grazer; FG: fresh-grass grazer; MO: mixed feeder from open habitat; MC: mixed feeder from closed habitat; Br: browser; Frg: frugivore.

ing the sequence of discrimination depicted in Fig.3. A large number of variables were used at the beginning of the analysis, but only a few of them were finally included in the algorithms.

SCDA allows the derivation of the linear combination of variables that best distinguishes the differences between the groups compared (Mendoza et al., 2002). In this study, each group is composed of species that share a common feeding adaptation. The variables involved in the discriminant functions are those that contribute to minimize the within-group variance relative to the between-groups variance (Davis, 1986). In those cases where a good discrimination between the groups (e.g., grazers and browsers) is obtained, it is expected that the resultant discriminant function will capture the morphological patterns that characterize the morphological adaptations of both groups with regard to each other (e.g., grazers versus browsers). However, the number of species available in ecomorphological studies such as the one presented here is often limited, and the probability of obtaining good discrimination between the groups compared merely by chance increases with the number of variables involved in the discriminant function. The possibility that the correlations are not merely obtained by chance is usually tested with the statistical significance of the discriminant functions, estimated using the Mahalanobis distance between the group centroids and the value of Wilk's lambda.

Our hypothesis is that distinct morphological patterns emerge from the relationship between craniodental morphology and feeding behavior. Under any statistical approach, the null hypothesis assumes a random distribution of the samples (bovid species in

our case) in the morphospace. As with other statistical techniques, SCDA assumes the statistical independence of the samples within the groups compared. However, in a strict sense these samples (e.g., bovids that share a feeding adaptation) are non-independent, which provides the expectation that the predefined groupings are, in some sense, real. In addition, species do not represent independent samples of a statistical distribution as a consequence of their phylogenetic interrelationships (Felsenstein, 1985; Harvey and Pagel, 1991).

The existence of phylogenetic relationships among the species of a taxonomic grouping represents a serious violation of the concept of independence. The effect of these structured relationships is to impose a correlation between the metric variables that is solely attributable to the phylogenetic patterning and does not necessarily reflect the relationship between morphology and feeding behavior. Thus, the effects of a common phylogenetic legacy may potentially obscure the adaptive signal that will allow us to derive autecological inferences from craniodental morphology (e.g., species of the same genus or tribe are bound to share some morphological traits by virtue of their shared common ancestry, despite the variation in their dietary preferences). The failure to recognize this source of constraint on variation within biological systems can lead to incorrect interpretations (i.e., it can be concluded that a significant relationship exists between the morphological variables and the ecological groupings, useful for deriving paleoecological inferences, when in fact there is no such relationship). For example, the craniodental patterns that help to discriminate between herbivorous and omnivorous ungulates are biased by the fact that all living ungulates with an omnivorous diet are suids (Mendoza et al., 2002). This is a variant of the classic "type I error" in statistics, where the apparent relationship is due to the operation of an extraneous variable (phylogeny in this case) on the observed variables (see Harvey and Pagel, 1991).

For these reasons, statistical analysis cannot be performed in studies of this nature, although this has been the most common approach during previous decades (e.g., Janis, 1995; Spencer, 1995, 1997; Kappelman et al., 1997; Mendoza et al., 2002; DeGusta and Vrba, 2005a). There are several methodologies whereby continuous variable data can be corrected for the effects of phylogenetic patterning (e.g., phylogenetic autocorrelation, see Gittleman and Kot, 1990). However, in removing the effect of the phylogeny, some important information about morphology and adaptation can be lost (e.g., the lower premolar tooth row is enlarged in grazing perissodactyls and shortened in grazing ruminants, which

reflects the differences in the way food is orally processed in foregut and hindgut fermenters, precluding the use of this variable in the ecomorphological study of ungulates; Mendoza et al., 2002). Using a non-statistical approach, however, SCDA can be used in a way that allows the recognition of a possible phylogenetic patterning, and thus compensating for its effect (see below).

In order to minimize the effects of phylogeny, it is possible to maximize the taxonomic evenness of the sample of bovids analyzed by overweighting the species of those taxonomic groups (e.g., subfamilies and tribes) that are under-represented in it with respect to those that are better represented. This is achieved by multiplying each species by $1/N$, where N is the number of species of the taxonomic group in which this species is classified. In this way, the analyses are performed with an equitable contribution from all of the groups compared. It could be argued, however, that this procedure may increase the influence of rare taxa that have unusual craniodental specializations and would, therefore, obscure the morphological patterns we are looking for. However, this is not the case, because the discriminant functions adjusted using this procedure provided similar percentages of correct reclassifications among dietary/habitat categories for all taxonomic groups, irrespective of their simple sizes. It is also possible to minimize the probability of a random patterning, by minimizing the number of variables involved in the discriminant functions, which is achieved by increasing the level of significance required for their incorporation within the functions. Thus, SCDA can be used merely to identify the morphological patterns that involve the lowest possible number of variables, making it possible to characterize particular ecological adaptations (e.g., grazers). These patterns do not usually allow a perfect discrimination, but they are sufficiently robust so that very often the same patterns even emerge when some of the species used as samples are excluded to perform the same analyses. The morphological patterns characterizing each ecological category correspond to the region of the multidimensional morphospace defined by the variables occupied by the included species. SCDA is used in this fashion to outline these regions of the morphospace, identifying those combinations of variables involved in the boundaries between different ecological groupings.

Overweighting the species of a taxonomic group under-represented in the dataset of modern bovids does not mean that the discriminant functions are forced to include these few species within their correct ecomorphological grouping. Instead, this implies that the analysis is forced to take into account the information contributed by these few species at the same level

as that provided by the species from other groups more abundantly represented in the dataset. Otherwise, the adjusted algorithms would mainly reflect the relationship between the morphology of those groups better represented in the dataset and the ecological adaptation under study; obviously, this relationship is not always the same in the groups analyzed and may involve different morphological traits. In other words, we are maximizing the taxonomic evenness of the sample, a procedure which increases its taxonomic diversity. As the taxonomic spectrum discriminated by the resulting algorithm is wider, the morphological pattern that it captures will be more general. Fig.4 shows a theoretical example of the results that may be obtained using this procedure.

The main conclusion is that statistics, *sensu stricto*, based on the significance of the patterning cannot be applied in studies of this nature. This is the reason why we followed a non-statistical approach, using SCDA only for identifying the region of the morphospace occupied by each ecological grouping. The probability that these groupings are the consequence of a common adaptation or derive from phylogeny cannot be assessed unequivocally. However, the effects of phylogeny can be minimized by increasing the diversity of the dataset in two ways: (i) using a sample as large and diverse as possible; and (ii) maximizing the taxonomic evenness; as explained above, the latter is achieved by overweighting the species of those taxonomic groups poorly represented in the sample with respect to those that are more numerous. The success of the resulting discriminant functions may be evaluated by estimating the percentage of correct reclassifications obtained and how this percentage rises when the species of those groups under-represented in the dataset are overweighted. In addition, the probability of obtaining a random patterning can be minimized by minimizing the number of variables involved in the discriminant functions, which is achieved by increasing the level of significance required for their incorporation within the functions. In any case, the taxonomic composition of the feeding groups must be evaluated in order to detect and avoid phylogenetic patterning.

For each algorithm, the distribution of taxa along the discriminant axes was also tested according to phylogenetic affinities, following the classification proposed by Hassanin and Douzery (2003) (Table 2). This makes it possible to ascertain if there is a correspondence between ecological and phylogenetic groupings. For those cases where all the species sharing a particular ecological adaptation belong to the same group (e.g., all frugivorous bovids are members of the tribe Cephalophini), it is impossible to determine if the correlation between morphology and e-

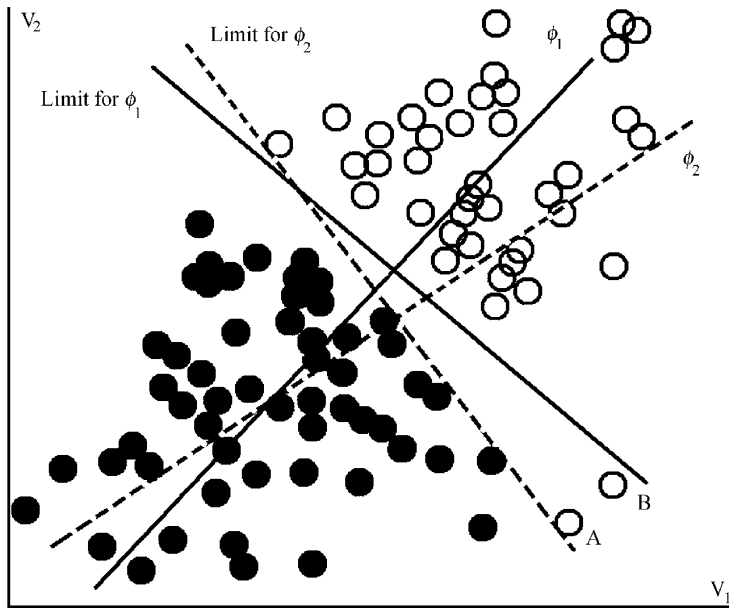


Fig. 4 Hypothetical distribution of two ecological groups of modern bovids (grazing species, open circles; browsing species, filled circles) in a theoretical morphospace defined by two variables, V_1 and V_2)

Although species A and B feed on grass, they belong to a taxonomic group poorly represented among grazing bovids, showing a morphology which is closer to that of browsing species. As a consequence, if these two species are not overweighed in the analysis, the discriminant function ϕ_1 for variables V_1 and V_2 will take the direction of the filled axis because their weight is small compared to the rest of grazing species; according to the limit between the groups compared, this function would misclassify species A and B as browsers. Given that these species provide relevant information on the alternative craniodental adaptations of bovids to a diet of grass, it is important to force the algorithms to capture this information, because there could be some extinct grazing species placed in the morphospace between them and the rest of grazing bovids that would be otherwise wrongly characterized. When species A and B are overweighed, the discriminant analysis is forced to take them into account and the limit between the groups for function ϕ_2 , depicted by the striped line, would reclassify them correctly as grazers.

ecology is a functional response, or just representative of a common phylogenetic legacy. However, in those cases in which the correspondence between ecological grouping and phylogenetic group was not absolute (e.g., many, but not all, grazers belong to the tribe Alcelaphini), the only algorithms selected were those that correctly reclassified all of the species.

Table 2 Phylogeny proposed by Hassanin and Douzery (2003)*

A. Subfamily Bovinae (three tribes)
1. Bovini: Bovina (oxen), Bubalina (buffaloes) and Pseudoryina (saolas)
2. Tragelaphini: spiral-horned bovines
3. Boselaphini: four-horned antelopes.
B. Subfamily Antilopinae (eight tribes)
1. Alcelaphini (bonteboks, topis, hartebeests, and gnus)
2. Caprini <i>sensu lato</i> (sheep, goats, muskox, and chamois)
3. Hippotragini (oryxes, addax, roan, and sable antelopes)
4. Reduncini (reedbucks and kobs)
5. Cephalophini (duikers)
6. Aepycerotini (impalas)
7. Neotragini (dwarf antelopes)
8. Antilopini (gazelles)
C. Subfamily Peleinae (one species)
1. <i>Pelea capreolus</i>

* *Pelea capreolus*, which was not included in the Hassanin and Douzery study, was classified according to Robinson et al. (1998).

1.3 Hypothesis

The relationship between the craniodental and postcranial morphology of bovids and their ecological adaptations in terms of feeding behavior and habitat preferences has been demonstrated by several workers (e.g., Spalinger and Hobbs, 1992; Spencer, 1995; Kappelman et al., 1997; Gagnon and Chew, 2000; DeGusta and Vrba, 2005a, b). However, our hypothesis is that the adaptation to a given trophic niche involves a pattern of covariation between different morphological variables, and so the way in which any morphological trait is affected by a given adaptation depends on the rest of the craniodental morphology. Thus, we propose here that those craniodental patterns that involve a combination of morphological variables will be more useful than single measurements for characterizing the differences in dietary adaptations.

1.4 Classification criteria and pattern verification

Table 3 shows the unstandardized coefficients for those variables incorporated into the discriminant functions; these values are the factor loadings of the variables when they are expressed in the original units of measurement (cm). Table 3 also includes the percentage of species and specimens reclassified correctly by each algorithm.

In SCDA, the reclassification of species is often performed according to their distance to the groups' centroids. However, this procedure assumes an equal morphological diversity for the groups compared (i.e., homogeneity of variances) and, if this condition does not apply, those species from one group can be classified in another. In addition, for those cases

in which different taxonomic or ecological groups showing the same feeding behavior occupy different regions of the multidimensional morphospace, the position of the centroid is affected by the number of species belonging to each group. For these reasons, we reclassify the species according to the region of the morphospace occupied by each group.

Table 3 Algorithms that allow characterization of the feeding behavior of bovids (CR%: percentages of correct reclassifications for species and individuals)

Groups	Algorithm	Discriminant function	CR% (# Spp.)	CC% (# Ind.)
OH vs. CH	1.1	$1.175HI + 0.913JD - 0.187JLB - 5.813$	93.1% (72)	96.7% (419)
	1.2	$0.981HI - 30.936RSUMW + 2.234RJMB + 0.475$	97.2% (72)	92.8% (391)
	1.3	$4.421RJMB - 31.205RTLmw - RJLB + 3.532RSA + 2.076$	93.1% (72)	88.7% (362)
	1.1/1.3		100% (72)	98.1% (271)
	1.3/HI		98.6% (72)	97.1% (362)
GG vs. MO	2.1.1	$12.811RMZW - 44.521RTLmw - 1.300$	100% (46)	96.5% (367)
	2.1.1/RJLB		100% (46)	97.3% (361)
GG vs. (FG and MO)	2.1.2	$6.293RMZW + 0.517HI + 2.074FLPL - 4.430PLMW + 0.315JMB - 7.415$	100% (50)	96.5% (227)
MO vs. FG	2.2	$7.037RJMB - 0.092CA + 4.054$	100% (33)	98.8% (252)
Fr vs. (Br and MC)	3.1	$5.825RJMB - 4.753RSA + 5.030RJLB - 6.918$	100% (22)	92.8% (125)
MC vs. (Br and Fr)	3.2.1	$1.392HI + 8.644RJMA - 12.038RSB + 2.131$	95.5% (22)	92.4% (119)
	3.2.2	$7.185FLPL - 2.861SB + 0.991SC - 1.634$	100% (22)	86.9% (107)
Fr vs. Br vs. MC	3.2.1/3.2.2		95.5% (22)	81.4% (102)

Morphological measurements from 1 063 specimens were available, but most of these specimens were not used for generating the algorithms because they lacked some measurements, as explained above. However, the algorithms identified here were applied to those non-included individuals for which the set of variables involved in that particular algorithm was available in order to test their predictive power. Appendix II shows the number of specimens used to obtain the mean values of variables for each species, as well as the total number of specimens available per species, including those not used for estimating the species means but employed in testing the predictive power of the morphological patterns depicted by the algorithms.

2 Results

2.1 Morphological adaptations for feeding in open and closed habitats

The open habitat category includes grazers and mixed feeders inhabiting unforested environments, while the closed habitat category includes frugivores, browsers, and mixed feeders that dwell in habitats with tree cover (see Fig.3). This division is the most

relevant to paleoautecology, because it makes it possible to simultaneously characterize feeding and habitat adaptations, and to archaeology, because it provides reconstructions of past vegetation.

With the exception of the single species of the tribe Peleini *Pelea capreolus* (the rhebok), the 72 bovid species used for this characterization belong to two subfamilies, Antilopinae and Bovinae, represented by 11 tribes (see Table 2). Both subfamilies are widely represented in the two ecological categories compared. Nine tribes are represented in the open habitat category, six in the closed habitat one, and four are present in both categories. Given such diversity, it is very difficult to identify phylogenetic patterns.

Three different sets of algorithms were obtained. The first used untransformed variables, the second was developed with size-transformed variables, and the third also involved size-transformed variables but excluded the hypsodonty index. The best algorithms from each set (1.1 to 1.3) were selected according to the percentage of species correctly reclassified, the number of variables involved in the discriminant functions and their significance (Table 3, Fig.5).

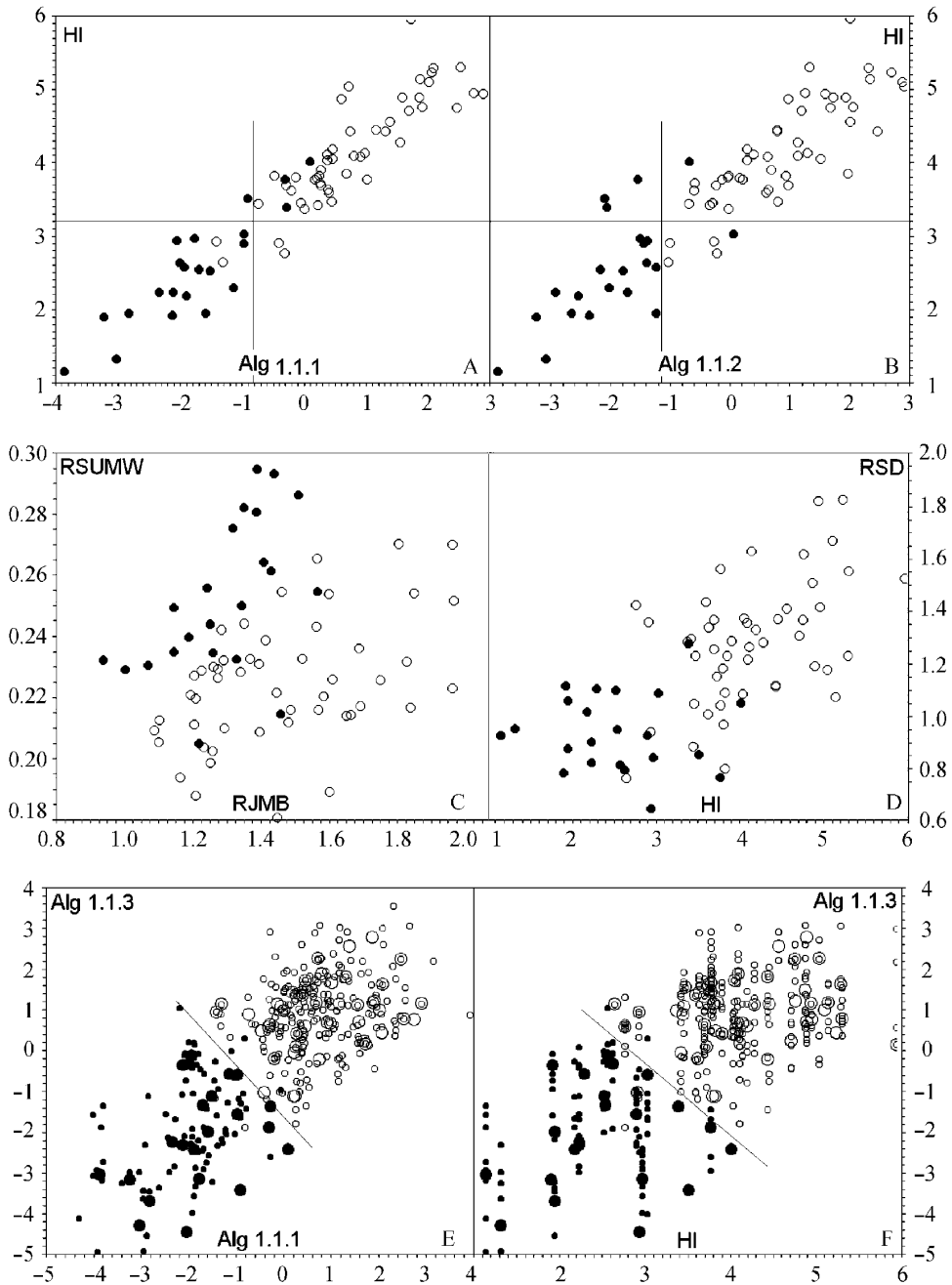


Fig. 5 Distribution of bovids in the morphospace reflected by the combinations of variables involved in those morphological patterns that characterize species feeding in open habitat (open symbols) and closed habitat (filled symbols)

A. Improvement of algorithm 1.1 compared to the hypsodonty index, which reduces the misclassifications from 8 to 5 cases. B. Improvement of algorithm 1.2 compared to the hypsodonty index, which reduces the misclassifications from 8 to 2 cases. C. Example of two variables that show a combined contribution to the discrimination. D. Example of two variables whose contribution is independent. E. Application of algorithms 1.1 and 1.3 to the full set of bovid species (large circles) and to those specimens for which the seven variables involved in this algorithm are available (small circles). F. Application of algorithm 1.3 and the hypsodonty index to those bovid species from open habitat (large circles) and those specimens for which the five variables involved in this algorithm are available (small circles); according to the number of individuals misclassified (Table 3), this combination of variables is almost as good as the one shown in E.

Algorithms 1.1 and 1.2 correctly reclassified 93.1% and 97.2% of species, respectively (Table 3, Figs. 5A, B). The percentages for individuals were 96.7% (Fig. 5E) and 92.8%, respectively (Table

3). The most significant variable in the first two algorithms was the hypsodonty index (HI), which alone provides discrimination of 89% of the species. Both algorithms combine HI with two other cranio-

dental measurements, which slightly improve the discrimination between these two broad categories of feeding and habitat preferences (Figs. 5A, B). Algorithm 1.2 makes an almost perfect discrimination between species from open and closed habitats possible, but the percentage of individuals correctly reclassified is lower than that obtained using algorithm 1.1. In addition, algorithm 1.2 misclassifies *Boselaphus tragocamelus* (the nilgai, Botr, Fig. 5B), a species which was correctly classified by the HI alone.

Algorithms 1.1 and 1.2 do not represent an essential improvement with respect to HI, but they are useful for illustrating the way in which any morphological trait (HI in this case) depends on (and co-varies with) other features of the craniodental morphology.

In comparison with species from closed habitats, open habitat bovids are more hypsodont and have a longer coronoid process relative to the length of the anterior jaw.

Similarly, in the generation of algorithm 1.2, the significance of RJMB (relative jaw depth) increases after the inclusion of RSUMW (relative second upper molar width). Thus, this algorithm involves a combined contribution of both variables, which may be observed clearly in Fig. 5C.

Although the basicranial angle (CA) and the relative depth of the face under the orbit (RSD) are two of the most significant variables for discriminating among bovids from open and closed habitats, none of them were included in any of the final algorithms because both are redundant when considered together with HI, losing their significance after its inclusion. Both variables allow the discrimination of the same percentage of species (83%). The combination of HI and CA increases this value to 93% and, if HI and SD are combined, the percentage of correct reclassifications raises to 92% (Fig. 5D).

Algorithm 1.3 involves four variables measured in the mandible: JMB (depth of mandibular angle), RTLMW (relative third lower molar width), RJLB (relative anterior jaw length), and RSA (relative length of the masseteric fossa). It correctly reclassifies 93% of the species, but only 89% of individuals (Table 3, Figs. 5E, F). Algorithm 1.3, which does not include HI, misclassifies a different set of species from those wrongly assigned by the hypsodonty index and the two first algorithms. It therefore seems to capture a different morphological pattern. In fact, the combination of algorithm 1.3 with algorithm 1.1 allows the best discrimination for species (100% correct reclassifications), while only five individuals are misclassified (98% correct reclassifications; Fig. 5E, Table 3). The combination of algorithm 1.3 with HI (Fig. 5F) allows the correct reclassification of 99% of

species (i.e., all except one) and 97% of individuals (Table 3), in spite of the fact that only five variables (which can be measured in most fossil specimens) are involved.

2.2 Morphological adaptations to different feeding strategies in open habitats

A more in-depth analysis of the open habitat species allowed the morphological characterization of general grazers, fresh-grass grazers and mixed-feeders.

Subfamilies Antilopinae and Bovinae are both represented in the general grazer (five and six tribes, respectively) and mixed-feeder categories (five and one tribes, respectively). Thus, both dietary categories are taxonomically diverse enough to rule out the possibility of a phylogenetic patterning of these feeding strategies. However, the situation with the fresh-grass grazers is different, because the four species included in this group all belong to the tribe Reduncini. One reduncine, the mountain reedbeek, *Redunca fulvorufula*, is a mixed feeder. The waterbuck *Kobus ellipsiprymnus*, less confined to wet areas than most other reduncines (Nowak, 1999), was considered as a general grazer in these analyses.

2.2.1 Morphological adaptations to feed primarily on grass of any type

Two sets of algorithms were generated. The first was adjusted to discriminate between general grazers and mixed feeders, and the second to differentiate general grazers from other species from open habitat (i.e., fresh-grass grazers and mixed feeders). The best algorithms from each set (2.1.1 and 2.1.2) were finally selected, according to the criteria mentioned above (Table 3, Fig. 6).

Algorithm 2.1.1 was adjusted to discriminate between general grazers and mixed feeders. However, it allowed us to differentiate general grazers from all other species from open habitats, since fresh-grass grazers were clearly placed by this algorithm among mixed feeders. The percentages of correct reclassifications for species and individuals are 100% and 96%, respectively (Table 3, Figs. 6A, F). Algorithm 2.1.1 involves only two variables (Table 3), the relative width of the muzzle (RMZW) and the relative width of the third lower molar (RTLMW), although RMZW is the variable with the greatest contribution. Throughout the generation of this algorithm, RTLMW was not significant prior to the inclusion of RMZW; however, once RMZW is included, RTLMW became much more significant, indicating that its contribution to the morphological pattern depicted by this algorithm is only in relation to RMZW. This is because general grazers have a muzzle which is relatively broader than those of other species from open habitats, but this feature is less pronounced in

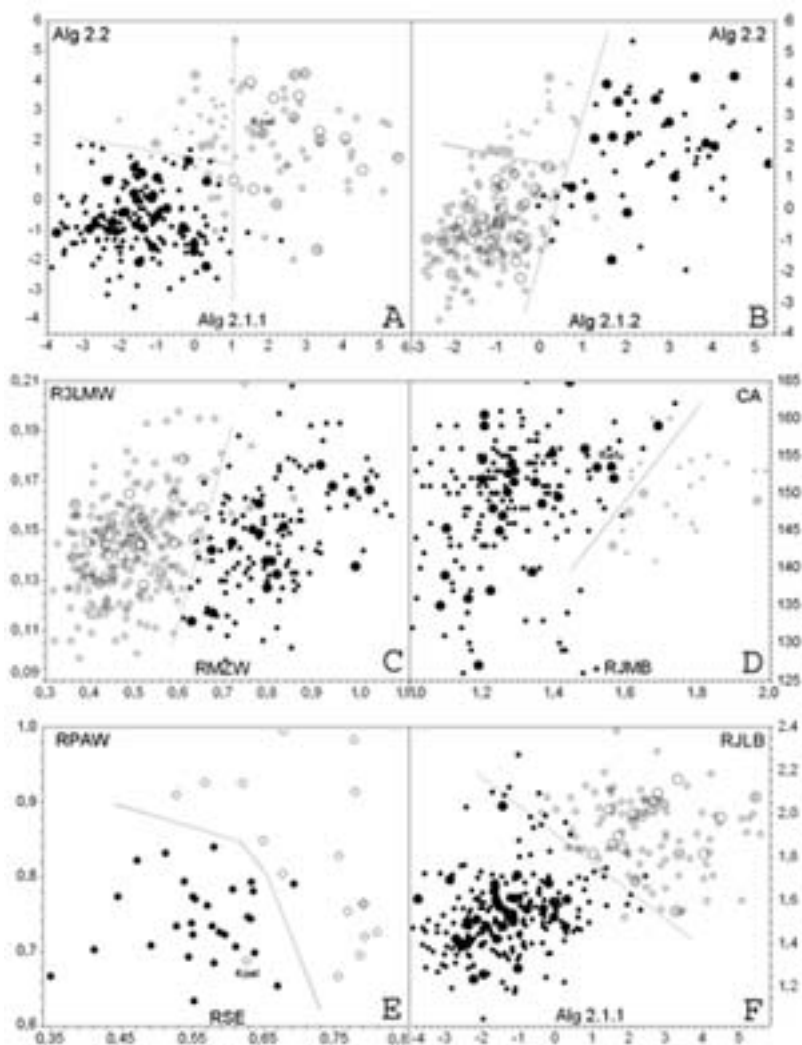


Fig.6 Distribution of bovids in the morphospace reflected by the combinations of variables involved in those morphological patterns that characterize species feeding in open habitat: general grazers (open symbols), fresh-grass grazers (gray symbols), and mixed feeders (filled symbols)

A. Application of algorithms 2.1.1 (generated for discriminating general grazers from mixed feeders) and 2.2 (adjusted for differentiating fresh-grass grazers from mixed feeders); a complete discrimination among the three groups of species is obtained in spite of the fact that both algorithms jointly involve only four variables. B. Application of algorithms 2.1.2 (generated for discriminating general grazers from fresh-grass grazers and mixed feeders) and 2.2. C, D. Combined contribution of the two variables of algorithms 2.1.1 and 2.2, respectively (Refu, *Redunca fulvorufula*). E. Application of a pattern not related with algorithms 2.1.x, which allows also a good discrimination between general grazers and mixed feeders (Koel, *Kobus ellipsiprymnus*). F. Bivariate plot of algorithm 2.1.1 and the relative length of the anterior jaw in bovid species (large circles) and individuals (small circles). This diagram involves only three variables and allows reclassifying correctly 97% of individuals.

those species that have narrower third lower molars, according to the negative loading of the latter variable in the algorithm. Thus, it is only a combination of both morphological variables which allows for a perfect discrimination (see Fig.6C).

The combination of algorithm 2.1.1 with the relative length of the anterior lower jaw (RJB), which is one of the most significant variables before the inclusion of RMZW, also allows the correct re-

classification of 100% of the species from the categories of general grazers and mixed feeders, and the percentage of individuals correctly reclassified increases to 97% (Table 3, Fig.6F). This indicates that bovids feeding mainly on grass (but not exclusively on fresh grass) also have a relatively longer anterior jaw than fresh-grass grazers or mixed feeders from open habitats. There is another morphological pattern that characterizes these two feeding groups: general graz-

ers have wider palatals and/or a longer paraoccipital process than mixed feeders (see Fig. 6E).

Algorithm 2.1.2 was derived for discriminating between general grazers and other species from open habitats (i.e., fresh-grass grazers and mixed feeders). It involved five variables and allowed for 100% correct reclassifications of species and 96% for individuals (Fig. 6B). The combination of algorithm 2.1.1 with RJLB involved two variables less than algorithm 2.1.2 and allowed for a slightly higher percentage of specimens to be reclassified correctly when general grazers were compared only with mixed feeders, without the inclusion of fresh-grass grazers as with algorithm 2.1.2.

Another morphological pattern that was seemingly related to grazing involves the combination of only two variables, relative palatal width (RPAW) and relative length of the paraoccipital process (RSE) (Fig. 6E).

It is worth mentioning that HI alone showed a poor correlation with the combination of craniodental variables identified to characterize different types of open habitat feeders. This is because all of these bovids were highly hypsodont, and hypsodonty alone could not distinguish between them (see Janis and Ehrhardt, 1988).

2.2.2 Morphological differences between fresh-grass grazers and mixed feeders from open habitat

Only one algorithm was selected for this comparison (2.2, Table 3), involving two variables (RJMB and CA). According to this algorithm (Table 3, Fig. 6D), which allows a full discrimination between both groups of species, fresh-grass grazers differ from mixed-feeding bovids from open habitat in having a relatively deeper mandibular angle (reflected in higher RJMB values), although both groups show a certain degree of overlap for this variable. However, the limit between both groups for RJMB seems to depend on the value of the basicranial angle (Fig. 6D), showing that it is the combination of both variables that allows for a perfect discrimination.

Given the low number of fresh-grass grazers in the sample and their phylogenetic homogeneity (all belonging to the tribe Reduncini), the probability of this discrimination being the consequence of their shared evolutionary legacy must be considered. However, note that the mixed feeding reduncine (*R. fulvorufula*, Refu), and the general grazing reduncine (*K. ellipsiprymnus*, Koel) are correctly reclassified within their respective feeding groups. This shows that the phylogenetic signal of reduncine tribal affinities does not overpower ecomorphological classifications, although caution must still be applied when considering either the feeding habits of extinct reduncines, or the possibility of extinct bovids being

fresh-grass grazers.

Algorithm 2.2 reclassifies correctly 100% of the species and 99% of the individuals (Table 3, Figs. 6A, B). Thus, the combination of algorithms 2.1.1 and 2.2, which jointly involve only four variables, makes a complete characterization of the dietary preferences of open habitat bovids possible (Fig. 6A). Given that algorithm 2.1.2 was the only algorithm specifically designed for discriminating between general grazers and other species from open habitats, its combination with algorithm 2.2 provides the best means for obtaining a complete characterization of the feeding habits of those bovids from open habitats (e.g., compare Figs. 6A, B).

2.3 Morphological characterization of the feeding categories from closed habitats

Members of the subfamilies Antilopinae and Bovinae are both represented in the dietary categories of mixed feeders (one and two tribes, respectively) and browsers (one tribe for both subfamilies). A third subfamily, Peleinae, is monotypic, and comprises the browser *Pelea capreolus*.

2.3.1 Morphological adaptations of frugivores

The only algorithm selected for discriminating between frugivores and other species from closed habitat (i.e., browsers and mixed feeders) involves three variables (Table 3). It correctly reclassifies 100% of the species and 93% of the individuals (Table 3, Fig. 7A). Frugivores have a relatively shorter masseteric fossa (RSA) in comparison with the relative depth of the mandibular angle (RJMB) and the relative length of the anterior jaw (RJLB). However, all of the frugivorous species are duikers (tribe Cephalophini) and none of these small bovids consume other resources. Thus, any morphological pattern that identifies bovid frugivores could result from phylogenetic associations alone.

2.3.2 Morphological characterization of mixed feeders from closed habitats

Two algorithms, 3.2.1 and 3.2.2, were selected for differentiating mixed feeders from browsers or frugivores.

Algorithm 3.2.1 involves three variables (Table 3) and reclassifies correctly 95% of the species and 92% of the individuals (Table 3, Fig. 7A, C). *P. capreolus* is a hypsodont browser misclassified by algorithms 1.1 and 1.2 within the feeding categories of open habitat, so it was expected that algorithm 3.2.1, which also involves HI, would classify this species as an extreme mixed feeder (see Figs. 7A, C, E). Note, moreover, that *P. capreolus* also shares with the rest of mixed feeders a relatively short occipital (RSB, see Figs. 7E, F). For these reasons *P. capreolus* was not used for quantifying the percentage of specimens correctly reclassified.

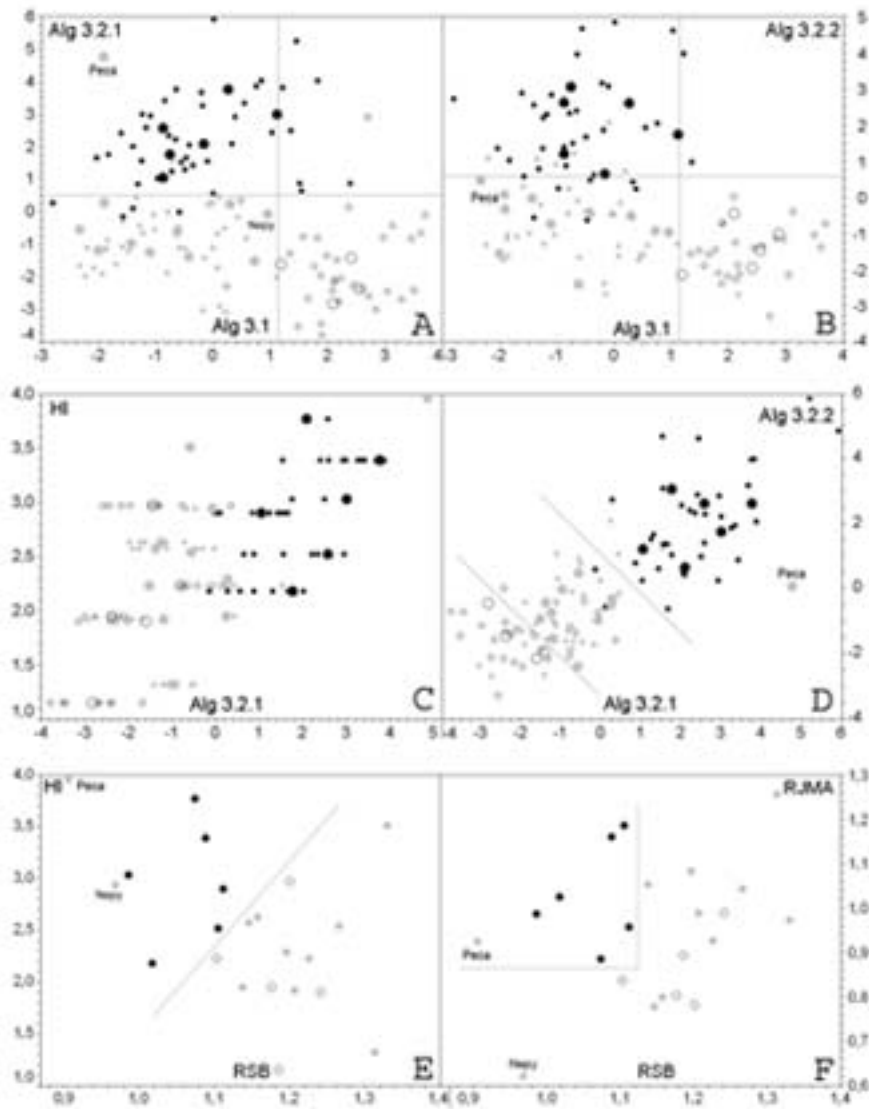


Fig. 7 Distribution of bovid species (large circles) from closed habitat and individuals (small circles) in the morphospace reflected by several combinations of algorithms 3.1, 3.2. x (A–D) and different combinations of the variables involved in algorithm 3.2.1 (E–F)

Open symbols: frugivores; Filled symbols: mixed-feeders; Gray symbols: browsers (*Peca Pelea capreolus*; *Nepy Neotragus pygmaeus*).

According to this algorithm (Table 3, Figs. 7E, F) mixed feeders are characterized by a relatively short occipital height (RSB), higher values of hypsodonty (HI) and a relatively longer posterior jaw (RJMA). *Neotragus pygmaeus* (Nepy, Figs. 7E, F) is a browser that shows a relation between RSB and HI typical of mixed feeders, although it is reclassified correctly by algorithm 3.2.1 given its low value of RJMA (see Figs. 7E, F).

Algorithm 3.2.2 correctly reclassifies 100% of the species but only 87% of the individuals (Table 3, Fig. 7B). The decrease in the predictive capacity of this algorithm for individual specimens, in spite of its high capacity of discrimination for species, could be a consequence of the fact that the variables included in

the discriminant function have a lower level of significance than in the other algorithms. According to this algorithm, mixed feeders are also characterized by a long fourth lower premolar (FLPL) and a long posterior portion of the skull (SC) in relation to the occipital height (SB, Table 3). Algorithm 3.2.2, which does not include HI but incorporates SB, reclassifies correctly *P. capreolus* among browsers (Fig. 7B) although close to the mixed feeding category.

Although algorithms 3.2.1 and 3.2.2 were generated for discriminating between mixed feeders and other feeding categories from closed habitat (i.e., browsers and frugivores), the bivariate plot of the relationship between these two algorithms (Fig. 7D) shows that the three groups are arranged along a con-

tinuum, with browsers in an intermediate position between mixed feeders and frugivores. This agrees with Bodmer's interpretation of the feeding adaptations of herbivores (Bodmer, 1990), at least for closed habitat species. Moreover, this arrangement supports the validity of both algorithms, which allow the correct reclassification of 95% of the species and 81% of the individuals. In addition, the indirect characterization of frugivores is not, in this case, the result of a phylogenetic pattern exclusive of the tribe Cephalophini, given that the species of this tribe were not used for the generation of these algorithms.

3 Discussion

3.1 Problems in the morphological characterization of species and specimens

In some cases, the region of the morphospace occupied by the species from each feeding group is not clearly defined. In addition, the percentages of correct reclassifications are influenced by the number of specimens available for those species which were misclassified or placed close to the boundary between the groups compared. Therefore, these percentages are not an exact estimate of the goodness of fit of the morphological patterns revealed by SCDA.

It is always difficult to find a complete skull of any extinct species (e.g., see Arribas and Palmqvist, 1998), rather, in most cases only a small set of measurements from the same specimen are available. However, if different morphological patterns, such as the ones proposed here, are available, and these patterns involve few measurements, the probability of finding a particular combination of metric variables that allows the characterization of the feeding adaptations of a given extinct species increases. Moreover, if several patterns involving different combinations of variables predict the same feeding adaptation for an ancient species, the reliability of such a determination increases.

It is not easy to assess why some specimens belonging to a species that is reclassified correctly by a given algorithm are misclassified with this same algorithm. When different discriminant functions with different combinations of variables misclassify these individuals in the same way, the most probable explanation is that the species shows a morphological range that overlaps a range of feeding behavior, and that those specimens misclassified would be actually more adapted to the feeding habits of the group to which they are assigned. For example, the lesser kudu *Tragelaphus imberbis* shows one of the widest morphological ranges according to algorithms 3.2.1 and 3.2.2, and several of the individuals misclassified by these algorithms are members of this species. The lesser kudu lives in the Arabian Peninsula, Sudan,

Ethiopia, Somalia, Uganda, Kenya, and Tanzania (Nowak, 1999), dwelling in dry, flat, and densely thicketed areas, woodlands and hilly land (Roosevelt and Heller, 1914). This species was considered to be a mixed feeder in the analyses because different authors estimated that its diet included quite different percentages of grass and browse, but some of the misclassified specimens are placed among browsers. According to Lamprey (1963) and Kingdon (1982), *T. imberbis* is a mixed feeder, but Chen et al. (1998) and Nowak (1999) consider it to be an almost exclusive browser. It would be very interesting to test if there is a correspondence between the feeding behavior of different populations and their craniodental morphology according to the morphological patterns that characterize these two feeding adaptations.

If this is the main reason for the misclassification of individuals, they would not actually be misclassified. However, if a species and all the individuals belonging to this species are misclassified by a given algorithm but correctly reclassified by another, it is more likely that the first algorithm did not precisely capture the morphological pattern that characterizes the feeding adaptations which it was intended to discriminate. In such a case, other factors such as the allometric effects of body size differences, the constraints posed by the phylogenetic legacy, or other types of ecological adaptations may affect the variables involved in the algorithm.

The misclassification of some specimens has important implications for assigning extinct bovid species to diet/habitat based categories, because if a given extant species is optimally adapted for a particular ecospace but also occupies a different ecospace, then this might also be true for an extinct one but would be very difficult-if not impossible-to detect, unless other indicators of feeding and habitat preferences apart from the craniodental morphology are available (e.g., analysis of carbon-and nitrogen-isotope ratios in bone collagen and hydroxylapatite, as used in the dual ecomorphological and biogeochemical approach developed by Palmqvist et al., 2003).

The analysis of the percentage of specimens from each species that are correctly reclassified by each algorithm, as well as the taxonomic affiliation of the species that are correctly or incorrectly classified as a consequence of the inclusion or exclusion of each variable, provide important information about the particular morphological adaptations of each species and taxonomic grouping. However, such in depth analysis goes beyond the scope of this paper.

3.2 Autecological inferences on extinct taxa

The adjusted discriminant functions (Table 3, Figs. 4–7) allow the characterization of six different

types of dietary adaptations in bovids: general grazers, fresh-grass grazers, mixed-feeders from open habitat, browsers, mixed-feeders from closed habitat, and frugivores. These algorithms involve small sets of craniodental measurements, showing a high predictive ability over the species means used in their adjustment (98%) and also when applied to specimens (94%). The low number of measurements involved in each algorithm opens up the possibility of using them with isolated and even non-complete specimens from archaeological assemblages. In order to estimate the dietary preferences of an ancient bovid, what an archaeologist needs to do is to measure the craniodental variables in the specimens available and incorporate these measurements in the discriminant functions of Table 3, following the sequence of discrimination depicted in Fig. 3.

The results of this study confirm those obtained by Mendoza et al. (2002) about the suitability of a multivariate approach, and especially SCDA, for identifying the morphological patterns in the craniodental structure that make it possible to characterize trophic adaptations in both extant and extinct mammalian species.

The morphological patterns identified with SCDA, such as those proposed in this paper, show a predictive capacity for specific individuals that is only slightly lower than their discrimination capacity for the species used for obtaining them. This indicates that the mean values for a given bovid species can be used for characterizing its morphological adaptations, in spite of a variable amount of intraspecific morphological diversity related to individual variability, age and sex differences.

3.3 Morphological characterization of ecological adaptations

Compared with the species that have feeding habits typical of closed habitat (i.e., frugivores, browsers, and mixed feeders), those bovids with trophic adaptations characteristic of open habitat (i.e., grazers and mixed feeders) are more hypsodont, have a braincase which is more flexed on the craniofacial axis, and show a deeper face under a more posteriorly positioned orbit. These are features shared with other ungulates, as already noted in previous studies (e.g., Janis, 1995; Spencer, 1995; Mendoza et al., 2002). However, a better morphological characterization of these two broad ecological categories of bovids is only possible if, together with the hypsodonty index, other morphological features are taken into account. These are, for example, the relation between the length of the coronoid process and the length of the anterior jaw portion, or the relation between the depth of the mandibular angle and the width of the second upper molar. Moreover,

there is a more complex morphological pattern that involves the depth of the mandibular angle, the relative width of the third lower molar, the relative length of the anterior jaw, and the relative length of the masseteric fossa. This morphological pattern discriminates bovid species with dietary preferences typical of open habitats from those with trophic adaptations characteristic of forested environments. This pattern, combined with others that involve the hypsodonty index, or used in combination only with the hypsodonty index, allows the best characterization of these two broad ecological categories of bovids.

According to these results, general grazers have a broader muzzle than other species from open habitat such as fresh-grass grazers and mixed feeders. This feature is related to the "cropping mechanism" (i.e., grazers have transversely straight incisor arcades with equal, or subequal sized incisors; in contrast, browsers have relatively narrow muzzles consisting of a rounded incisor arcade with the first incisor generally being larger than the third incisor; Gordon and Illius, 1988; Janis and Ehrhardt, 1988; MacFadden and Shockey, 1997). Muzzle width, however, is a little less pronounced in those species that have a relatively narrow third lower molar. The anterior jaw portion is also longer in general grazers, the mandibular angle is deeper and the molar teeth are wider. In addition, these bovids have wider palatals and/or a longer paraoccipital process than mixed feeders. Thus, the morphological discrimination of open habitat bovids, whose diet is mainly restricted to grass, from those that feed on grass or browse according to the availability of both resources, involves a number of morphological traits among which hypsodonty does not play a particularly important role.

The differences between fresh-grass grazers and mixed feeders from open habitat are, however, more subtle. Fresh-grass grazers differ from mixed-feeding bovids in having a relatively deeper angle of the mandible, which is less pronounced in those species that show a more acute basicranial angle.

The morphological characterization of the dietary strategies of closed habitat bovids is less straightforward, because their discrimination requires six variables in spite of the low number of species in two of the three feeding groups (five frugivores and six mixed-feeders) and their taxonomic homogeneity. For this reason, the application of those patterns identified as characteristic of these feeding categories to extinct bovids has a higher level of uncertainty.

Frugivores (all duikers) have a shorter masseteric fossa in relation to the depth of the mandibular angle and the length of the anterior portion of the jaw. Mixed feeders are differentiated from other closed habitat species by at least two different morphological

patterns; a relatively shorter occipital height, combined with higher values of hypsodonty and a longer posterior portion of the jaw; or with a longer fourth lower premolar and more developed posterior portion of the skull. A remarkable and unexpected result was that combining both patterns, closed habitat bovids are arranged along a continuous morphological gradient, as anticipated by Bodmer (1990), with browsers occupying an intermediate position between mixed-feeders and frugivores. Given that frugivores (duikers) were not used for identifying these patterns, their position supports the ecological reason behind these patterns, ruling out the possibility that they reflect the effects of a common phylogenetic legacy.

3.4 Conclusions

In this study we have classified 72 extant bovid species among six dietary and habitat categories (general grazers, fresh-grass grazers, mixed-feeders from open habitat, browsers, mixed-feeders from closed habitat, and frugivores), using stepwise canonical discriminant for identifying the morphological patterns of the craniodental structure involved in these ecological adaptations. The discriminant functions obtained reclassify correctly 98% of those species used in their statistical adjustment and provide accurate predictions for 94% of non-complete specimens lacking one or more craniodental variables. Given that the discriminant functions involve small sets of measurements and that alternative functions based on different combinations of variables are provided for each dietary/habitat comparison, this opens the possibility of applying them to non-complete, fragmented specimens as those preserved in most archaeological assemblages. Therefore, the discriminant functions based on the craniodental anatomy of extant bovids, combined with those obtained using postcranial measurements for estimating adaptations related to locomotor performance and habitat choice, are a useful tool for deriving autecological inferences on the paleobiology of extinct bovids and may also be used in paleoenvironmental reconstruction.

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Appendix I Description of craniodental measurements used in this study

 Craniodental Measurements

- HI: hypsodonty index, estimated by dividing the height of the third lower molar (measured from the base of the crown to the tip of the protoconid) by its width (measured at the occlusal surface of the tooth, between the outer surfaces of the protoconid and the entoconid)
- LMRL: lower molar tooth row length, measured along the base of the teeth
- LPRL: lower premolar tooth row length, measured along the base of the teeth
- CA: basicranial angle, measured as the angle between the basioccipital bone and the palate
- FLPL: fourth lower premolar length, measured at the occlusal surface as the maximum labial excursion of the tooth
- FLPW: fourth lower premolar width, measured at the occlusal surface of the tooth, between the outer surfaces of the protoconid and the entoconid
- PLML: first lower molar length, measured at the occlusal surface as the maximum labial excursion of the tooth
- PLMW: first lower molar width, measured at the occlusal surface of the tooth, between the outer surfaces of the protoconid and the entoconid
- SLML: second lower molar length, measured at the occlusal surface as the maximum labial excursion of the tooth
- SLMW: second lower molar width, measured at the occlusal surface of the tooth, between the outer surfaces of the protoconid and the entoconid
- TLML: third lower molar length, measured at the occlusal surface as the maximum labial excursion of the tooth
- TLMW: third lower molar width, measured at the occlusal surface of the tooth, between the outer surfaces of the protoconid and the entoconid
- SUML: second upper molar length, measured at the occlusal surface as the maximum labial excursion of the tooth
- SUMW: second upper molar width, measured at the occlusal surface of the tooth, between the outer surfaces of the protocone and the entocone
- JLB: anterior jaw length, measured from the base of the first incisor to the premolar/molar boundary
- JMA: posterior jaw length, measured as the horizontal distance from the back of the jaw condyle to the posterior border of the third molar
- JAW: jaw length (JLB + LMRL + JMA)
- 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 base of the jaw condyle to the tip of the coronoid process
- SA: length of the masseteric fossa, 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 condyle 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 to 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
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Appendix II Bovid species used in this study

Species	# <i>n</i> (<i>m</i>)	Tribe	Subf	DC	Species	# <i>n</i> (<i>m</i>)	Tribe	Subf	DC
<i>Addax nasomacultus</i>	3 (8)	Hippotragini	Ant	MO	<i>Kobus kob</i>	4 (11)	Reduncini	Ant	FG
<i>Aepyceros melampus</i>	8 (20)	Aepycerotini	Ant	MO	<i>Kobus vardoni</i>	5 (10)	Reduncini	Ant	FG
<i>Alcelaphus buselaphus</i>	0 (40)	Alcelaphini	Ant	GG	<i>Litocranius walleri</i>	6 (20)	Antilopini	Ant	Br
<i>Ammodorcas clarkei</i>	2 (9)	Antilopini	Ant	Br	<i>Madoqua guentheri</i>	5 (10)	Antilopini	Ant	Br
<i>Ammotragus lervia</i>	3 (9)	Antilopini	Ant	MO	<i>Madoqua kirki</i>	6 (11)	Antilopini	Ant	Br
<i>Antilope cervicapra</i>	3 (10)	Antilopini	Ant	MO	<i>Nemorhaedus goral</i>	3 (7)	Caprini	Ant	MO
<i>Anoa depressicornis</i>	6 (7)	Bovini	Bov	GG	<i>Neotragus moschatus</i>	0 (27)	Antilopini	Ant	Br
<i>Antidorcas marsupialis</i>	0 (25)	Antilopini	Ant	MO	<i>Neotragus pygmaeus</i>	5 (5)	Antilopini	Ant	Br
<i>Bos banteng</i>	4 (6)	Bovini	Bov	GG	<i>Ovis canadensis nelsoni</i>	5 (7)	Caprini	Ant	MO
<i>Bison bonasus</i>	2 (5)	Bovini	Bov	GG	<i>Oreamnus americanus</i>	5 (10)	Caprini	Ant	MO
<i>Bison bison</i>	9 (11)	Bovini	Bov	GG	<i>Oreotragus oreotragus</i>	0 (20)	Antilopini	Ant	MO
<i>Bos gaurus</i>	6 (8)	Bovini	Bov	GG	<i>Oryx gazella</i>	0 (26)	Hippotragini	Ant	MO
<i>Bos indicus</i>	3 (5)	Bovini	Bov	GG	<i>Ourebia ourebi</i>	9 (11)	Antilopini	Ant	MO
<i>Boselaphus tragocamelus</i>	6 (13)	Boselaphini	Bov	MC	<i>Ovis dalli</i>	6 (6)	Caprini	Ant	MO
<i>Bubalus bubalis</i>	1 (7)	Bovini	Bov	GG	<i>Ovibos moschatus</i>	6 (7)	Caprini	Ant	MO
<i>Budorcas taxicolor</i>	5 (10)	Caprini	Ant	MO	<i>Panthelops hodgsoni</i>	2 (2)	Antilopini	Ant	MO
<i>Capricornis sumatrensis</i>	6 (11)	Caprini	Ant	MC	<i>Pelea capreolus</i>	1 (14)	Antilocapriini	Pel	Br
<i>Cephalophus dorsalis</i>	7 (9)	Cephalophini	Ant	Fr	<i>Procapra gutterosa</i>	8 (8)	Antilopini	Ant	MO
<i>Cephalophus monticolor</i>	0 (27)	Cephalophini	Ant	Fr	<i>Pseudois nayeur</i>	6 (10)	Caprini	Ant	MO
<i>Capra ibex</i>	4 (16)	Caprini	Ant	MO	<i>Raphicerus campestris</i>	0 (26)	Antilopini	Ant	MO
<i>Cephalophus silvicultor</i>	4 (15)	Cephalophini	Ant	Fr	<i>Raphicerus melanotis</i>	1 (20)	Antilopini	Ant	MO
<i>Cephalophus spadix</i>	1 (5)	Cephalophini	Ant	Fr	<i>Redunca arundinum</i>	3 (33)	Reduncini	Ant	FG
<i>Connochaetes gnou</i>	1 (11)	Alcelaphini	Ant	GG	<i>Redunca fulvorufula</i>	0 (29)	Reduncini	Ant	MO
<i>Connochaetes taurinus</i>	1 (36)	Alcelaphini	Ant	GG	<i>Rupicapra rupicapra</i>	6 (8)	Caprini	Ant	MO
<i>Damaliscus dorcas</i>	0 (21)	Alcelaphini	Ant	GG	<i>Saiga tatarica</i>	8 (10)	Antilopini	Ant	MO
<i>Damaliscus hunteri</i>	7 (10)	Alcelaphini	Ant	GG	<i>Sylvicapra grimmia</i>	9 (11)	Cephalophini	Ant	Fr
<i>Damaliscus lunatus</i>	0 (35)	Alcelaphini	Ant	GG	<i>Syncerus caffer</i>	0 (21)	Boselaphini	Bov	GG
<i>Dorcatragus megalotis</i>	4 (8)	Antilopini	Ant	MO	<i>Tetraceras quadricornis</i>	2 (14)	Boselaphini	Bov	MC
<i>Gazella dorcas</i>	3 (3)	Antilopini	Ant	MO	<i>Tragelaphus euryceros</i>	4 (10)	Tragelaphini	Bov	Br
<i>Gazella granti</i>	6 (9)	Antilopini	Ant	MO	<i>Taurotragus oryx</i>	0 (26)	Tragelaphini	Bov	MO
<i>Gazella thomsoni</i>	11 (26)	Antilopini	Ant	MO	<i>Tragelaphus angasi</i>	4 (14)	Tragelaphini	Bov	MC
<i>Hemitragus jehmlahicus</i>	2 (9)	Caprini	Ant	MO	<i>Tragelaphus buxtoni</i>	4 (7)	Tragelaphini	Bov	Br
<i>Hippotragus equinus</i>	8 (19)	Hippotragini	Ant	GG	<i>Tragelaphus imberbis</i>	9 (14)	Tragelaphini	Bov	MC
<i>Hippotragus niger</i>	0 (21)	Hippotragini	Ant	GG	<i>Tragelaphus scriptus</i>	0 (33M)	Tragelaphini	Bov	Br
<i>Kobus ellipsiprymnus</i>	1 (29)	Reduncini	Ant	GG	<i>Tragelaphus spekei</i>	6 (11)	Tragelaphini	Bov	MC
<i>Kobus lechwe</i>	6 (9)	Reduncini	Ant	FG	<i>Tragelaphus strepsiceros</i>	0 (32)	Tragelaphini	Bov	Br

DC: dietary categories (GG: General grazers; FG: Fresh-grass grazers; MO: Mixed-feeders from open habitat; MC: Mixed-feeders from closed habitat; Br: Browsers; Fr: Frugivores). Subf: subfamily (Ant: Antilopinae, Bov: Bovinae, Pel: Peleinae). # *n* (*m*): *n* is the number of complete individuals used for obtaining the average values for the species, *m* is number of non-complete individuals used for testing the patterns (in those cases in which *n* = 0, *m* is the number of non complete individuals used for calculating the average values for the species).