

# Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat?

M. Mendoza<sup>1</sup> & P. Palmqvist<sup>2</sup>

<sup>1</sup> Instituto Catalán de Paleontología, Universidad Autónoma de Barcelona, Barcelona, Spain

<sup>2</sup> Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, Málaga, Spain

## Keywords

hypsodonty; ungulates; feeding preferences; habitat; grass consumption; knowledge discovery; decision trees; discriminant analysis.

## Correspondence

Manuel Mendoza, Institut Català de Paleontologia, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Facultat de Ciències, Universitat Autònoma de Barcelona. 08193-Barcelona, Spain.  
Email: mmendoza@fulbrightweb.org

Received 12 June 2007; accepted 20 June 2007

doi:10.1111/j.1469-7998.2007.00365.x

## Abstract

Hypsodont (i.e. high-crowned) teeth have been interpreted as an indicator of feeding preferences and habitat selection in ungulates. For this reason, the degree of hypsodonty has been used for estimating the diet of ancient taxa and in palaeoenvironmental reconstructions. The goal of this study is to elucidate the relative importance of grass consumption and open habitat foraging in the development of hypsodont teeth, using novel computer techniques of knowledge discovery applied to a dataset of 134 species of artiodactyls and perissodactyls distributed among thirteen families. The results obtained suggest that high-crowned teeth represent an adaptation for feeding in an open habitat, although the minimum threshold of hypsodonty seems to increase with the relative length of the anterior part of the jaw. On the contrary, there is no direct relationship between the degree of hypsodonty and the percentage of grass consumed, except for the correspondence between grazing and dwelling in open habitats. A relatively wide muzzle evidences an adaptation for grass foraging in open and mixed habitats, but there are some non-grazing species from a closed habitat that also show wide muzzles. Thus, the hypsodonty index, combined with the length of the anterior part of the jaw and the width of the muzzle, allows accurate inferences on the ecological preferences of extinct ungulates.

## Introduction

Among extant ungulates, grazing species usually have more hypsodont (i.e. high-crowned) teeth than others not specialized in grass consumption. The reason seems to be that an increase in tooth crown height represents an adaptation against tooth wear resulting from an abrasive diet consisting primarily of grasses with abundant silica-rich phytoliths, which represent 3–5% of dry matter in grass forage species (Van Valen, 1960; Brizuela, Detling & Cid, 1986; Solounias & Dawson-Saunders, 1988; Lucas *et al.*, 2000). In addition, those ungulate species that feed at the ground level in an open habitat often show more hypsodont teeth than those that forage similar amounts of grass in a closed habitat. In this case, the increase in tooth crown height would represent an adaptation against tooth wear resulting from the airborne grit and dust accumulated on the herbaceous plants of open environments (Stirton, 1947; Fortelius, 1985; Janis, 1988, 1995; Janis & Fortelius, 1988).

Hypsodonty has been extensively used in palaeontology as an indicator of the feeding preferences and/or habitat selection of extinct ungulates (e.g. Janis, Damuth & Theodor, 2000, 2002; Feranec, 2002, 2003; Jernvall & Fortelius, 2002; Fortelius *et al.*, 2003; Hopkins, 2003; Palmqvist *et al.*, 2003; Bargo, De Iuliis & Vizcaino, 2006; Strömberg, 2006). In fact, some classic examples of evolutionary change (e.g.

the development of the grassland biome and the diversification of equids in North America during middle Miocene times; Simpson, 1951; Shotwell, 1961) rely on the functional interpretation of hypsodonty. Similarly, the degree of hypsodonty has been used for estimating the habitat of ancient ungulates, in an attempt to reconstruct the environments of early hominids (e.g. Spencer, 1997; Reed, 1998; Harris & Cerling, 2002). However, in spite of the great ecological and evolutionary significance of this morphological innovation, to date only Williams & Kay (2001) have evaluated the relative importance of grass consumption and open-habitat foraging on the evolution of hypsodonty. In this article, we do not address the evolutionary, behavioural and climatic context of the development of high-crowned teeth during late Miocene times, as these issues have received a great deal of attention (see reviews in Janis, 1988, 1995; Mendoza, Janis & Palmqvist, 2002; Strömberg, 2004, 2006). Instead, we are concerned with testing in further depth the two hypotheses proposed for the functional significance of hypsodonty in the living ungulates: one based on their dietary preferences, and the other on their habitat choice.

Williams & Kay (2001) apply statistical analyses to 57 species of African ungulates and 55 species of South American rodents to test whether hypsodonty correlates with the mastication of grasses with high fibre and silica contents, external abrasives or both. In doing so, they take

into account the phylogenetic biases due to shared ancestry. The failure to recognize this source of constraint can lead to incorrect interpretations (i.e. we can conclude that there are significant morphological differences between a number of ecological groupings, useful for deriving palaeoecological inferences, when in fact there is no such relationship). This is a variant of the classic 'type I error' (i.e. the obtaining of a false positive) in statistics, where the apparent relationship between two variables is due to the operation of an extraneous variable (phylogeny, in this case; e.g. see Harvey & Pagel, 1991). However, in removing the effects of phylogeny, some important information about morphology and adaptation can be lost (Mendoza & Palmqvist, 2006a,b). Thus, while the goal of this study is similar to the one of Williams & Kay (2001), our approach is different. First, we apply novel computer techniques of knowledge discovery (Larose, 2004) to elucidate how hypsodonty is involved in the craniodental patterns that characterize the adaptations of ungulates for grass consumption and open habitat foraging. Second, we analyse a larger dataset of extant species. Third, we use other craniodental measurements apart from hypsodonty, as our previous studies have revealed that the ecological adaptations of ungulates often involve a rather complex covariation of morphological traits (Mendoza *et al.*, 2002; Mendoza, Janis & Palmqvist, 2006; Mendoza & Palmqvist, 2006a,b).

## Materials and methods

One hundred and thirty-four extant ungulate species from two orders (Artiodactyla and Perissodactyla) and 13 families were analysed (see Appendix S1 Supplementary Material). These species were classified among the following three habitat categories (Mendoza, Janis & Palmqvist, 2005): (1) open habitats (i.e. treeless or scarcely wooded savannas, grasslands, dry deserts and semi-desert steppes); (2) mixed habitats (i.e. wooded savannas, bush land, open forests and species dwelling both in closed and open habitats); (3) closed habitats (i.e. closed woodlands, riverine, moist deciduous and evergreen forests). Concerning diet, species were classified among the following five feeding categories: (1) grazers, feeding mainly on grasses; (2) mixed feeders, including those species in which grass and leaves are consumed depending on their availability; (3) browsers, feeding predominantly on dicotyledonous plants; (4) omnivores, eating non-fibrous vegetal matter, mushrooms and animal tissues; (5) ungulates with specific ecological adaptations (e.g. high-level browsers from an open habitat;). In Mendoza *et al.* (2002, 2006), grazers, browsers and mixed feeders were classified according to the percentage of grass in the diet (<25% for browsers, 25–75% for mixed feeders and >75% for grazers). Although these cut-off values allowed classifying most ungulates unequivocally, Mendoza *et al.* (2002) noted that different studies reported marked differences in the amount of grass consumed for a number of mixed feeders. For this reason, we performed an exhaustive analysis of the bibliography on the diet of modern ungulates (see Appendix S1 Supplementary Material), which helped us

identify those species in which the percentage of grass varies through the year or between different localities, and this is the criterion upon which the category of mixed feeders is based.

Thirty-two craniodental measurements were used (see Mendoza *et al.*, 2002, 2006). The hypsodonty index (HI) (relative tooth crown height, estimated by dividing the third molar height by width at the tooth base) is a size-independent variable, but the other measurements were size-adjusted by dividing each of them by the lower molar tooth row length, measured along the base of the teeth (Mendoza & Palmqvist, 2006b).

Two novel computer techniques for knowledge discovery were used: (1) discriminant analysis (DA) (2) decision trees (DTs). DA is a technique of multivariate statistics that allows classifying new samples within predefined groups using the discriminant functions adjusted for maximizing the between-groups to within-groups ratio of variance. It is worth noting that we do not perform statistics in this work, and so we use DA following a novel approach for knowledge discovery (Cios, Pedrycz & Świniarski, 1998) based on the evaluation of changes in the significance of the variables throughout a stepwise process. The rationale of the procedure is as follows: the statistical significance of each variable before any other is incorporated into the discriminant function measures its independent contribution to the characterization of the groups compared. Those variables that increase their significance considerably when another has first been included contribute to the characterization of the groups in combination with that variable. The distribution of the species in the morphospace defined by the combination of these variables will reveal that it is their relationship that characterizes the groups compared rather than their independent contributions. Different exploratory analyses may be performed including or excluding each time variables that, alone or combined with others, show a high significance. Once the best set of predictive variables is selected, the bivariate plots that combine them will provide insights into the relationship between the ecological categories (i.e. those defined by the degree of tree coverage and grass consumption) and the craniodental measurements (for further details, see Mendoza & Palmqvist, 2006b).

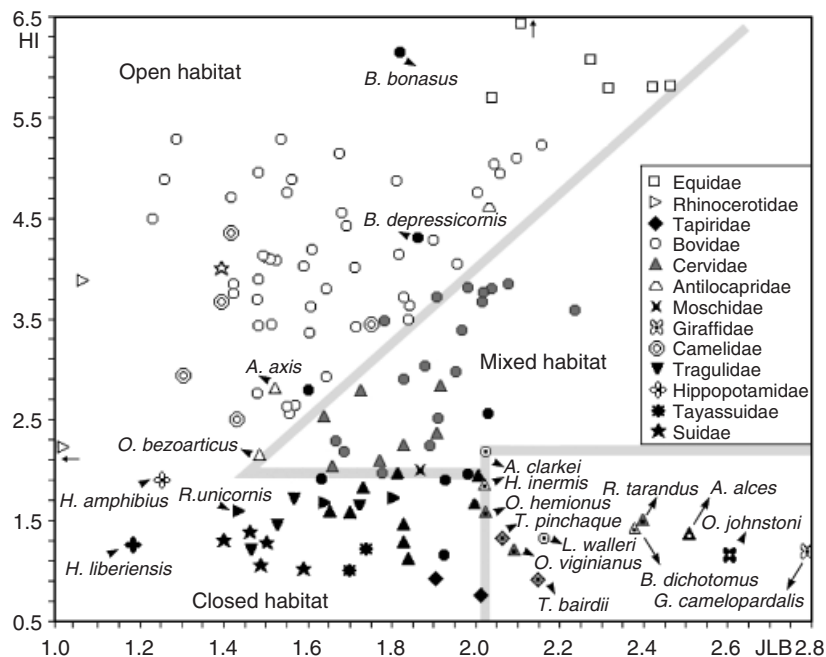
DTs are a technique of knowledge discovery (Larose, 2004) that stems from the realm of machine learning (Michie, Spiegelhalter & Taylor, 1994; Mendoza, 2007), whereby computer systems acquire knowledge inductively from the input of a large number of samples (e.g. ungulate species and craniodental measurements). The product of this learning is a piece of procedural knowledge that can assign a hitherto-unseen object (e.g. an extinct species whose palaeoecology is unknown) to one of a specified number of disjoint classes (e.g. habitat and feeding categories) based on the iterative division of the multidimensional space defined by the input variables. The result is a bifurcating tree pattern or dichotomous key with decisions at each branching point that combines the information provided by the craniodental measurements in a logical way. This tree allows evaluating the best sequence of variables for discriminating the

ecological groups compared (and, of course, for characterizing the autecology of any extinct ungulate in which such measurements are available). Knowledge discovery using machine learning is especially interesting because it has the potential to describe patterns in a compact and understandable form that 'lets the data suggest the pattern'. It schematizes knowledge in a manner resembling how experts think and classify information (Van Someren & Urbancic, 2005).

In our case, the morphospace was divided into boxes containing as many species of each predefined group as possible (Quinlan, 1985; Michie *et al.*, 1994), which provided trees with decisions at each branching point (see Fig. 1 in Mendoza, 2007). The analysis of these trees supports valuable information about the relationship between the habitat/trophic categories and the craniodental variables (Mendoza & Palmqvist, 2006b; Mendoza, 2007): while DA is especially useful for characterizing those groups or categories that differ in the relationship between the variables, DT perform a better characterization of those groups placed in a concrete region of the multidimensional space defined by the variables. In this way, DA and DT are complementary, being used here as exploratory tools for knowledge discovery, as they do not only specify the patterns below the ecological adaptations but also simultaneously perform variable selection and data mining.

Ecological adaptations often involve morphological patterns that combine different traits (Mendoza *et al.*, 2002, 2006). These patterns represent different regions of the

theoretical morphospace for the craniodental anatomy of ungulates defined by the measurements used as variables. Knowledge discovery techniques are useful in the search for these patterns. In most cases, however, an ecological group includes species from several taxonomic subgroups with different phylogenetic legacy, which may obscure the general pattern involved in their common adaptation. In the search for 'taxon-free' patterns, we tried to minimize the effects of phylogeny. In doing so, we maximized the diversity of the sample in terms of the number of taxonomic groupings (ungulate families in this case) analysed and their evenness. Evenness is maximized overweighting in the analyses the species of those families poorly represented in the dataset of living species (e.g. antilocaprids, moschids or giraffids), which forces the analyses to take into account the information contributed by these species at the same level as that provided by the species from those families more abundantly represented in the dataset (e.g. bovids and cervids). Otherwise, the patterns identified would mainly reflect the relationship between the craniodental anatomy of the most diverse families and their ecological adaptations, instead of revealing the morphological traits that are common to all ungulates (Mendoza *et al.*, 2006). The probability of obtaining a phylogenetic patterning may be evaluated from the distribution of taxonomic groupings in the morphospace. It is worth noting that our approach differs from the techniques of phylogenetic contrast (e.g. Pérez-Barberia & Gordon, 2001), which are used for testing whether an



**Figure 1** Distribution of 134 extant ungulate species in the morphospace depicted by the hypsodonty index (HI) and the relative length of the anterior part of the jaw (JLB), which allows characterization of the craniodental morphology of those species from an open habitat (white symbols), a mixed habitat (grey symbols) and a closed habitat (black symbols). Dotted symbols: species with special adaptations (high-level browsers, riparian and extremely adaptable species). For a description of the morphological variables, see text and Fig. 1 in Mendoza & Palmqvist (2006b).

apparent relationship between the ecological groups compared remains or becomes significant after removing the effects of phylogenetic correlations. However, such a procedure is not appropriate here, as our approach is not based on statistics.

## Results

### Tree coverage

DA and DT led to the identification of a simple morphological pattern that allows a good discrimination between ungulate species that feed in open, mixed and closed habitats (Fig. 1). According to this pattern, the HI seems to play a major role in the adaptation of ungulates to habitats with different degrees of tree coverage. The bivariate plot of Fig. 1 shows that, with the only exception of several species with specific ecological adaptations (e.g. high-level browsers; see below), HI allows an almost complete discrimination between ungulates from forest ( $HI \leq 2$ ) and those from open and mixed environments ( $HI \geq 2$ ). HI does not discriminate the species from open and mixed habitats because the minimum threshold of hypsodonty for feeding in open habitats increases with the relative length of the anterior part of the jaw (JLB, size-adjusted distance between the base of the first incisor and the limit between the premolars and molars). Thus, what makes possible a good characterization of those ungulates adapted to feed in habitats with different degrees of tree coverage is a combination of HI and JLB (Fig. 1).

There is a group of species, however, which, according to their low values of HI, could be tentatively identified as forest species, although most of them live in open or mixed habitats. They cluster in the bottom-right region of the morphospace depicted in Fig. 1. Among them, the giraffe *Giraffa camelopardalis*, the dibatag *Ammodorcas clarkey* and the gerenuk *Litocranius walleri* live in open habitats and eat leaves at high levels above the ground. Although there are no data on grit and dust contents in the vegetation that grows at high and ground levels in open habitats, it is not unreasonable to expect lower levels of exogenous abrasives accumulating on tree leaves than on near-ground shrubs and herbs (Janis, 1988). This suggests that the difference in hypsodonty between high-level browsers and other ungulates from open habitats is motivated by differences in the amounts of airborne grit (Williams & Kay, 2001; Mendoza *et al.*, 2002). Two other high-level browsers of this region of the morphospace, the okapi *Okapia johnstoni* and the moose *Alces alces*, inhabit forest. Another species with high JLB and low HI values is the mountain tapir *Tapirus pinchaque*, which lives in forests and grasslands. This species mainly eats leaves of the myrtle tree, which grow far from the ground and probably also accumulate less grit. The caribou *Rangifer tarandus* inhabits subarctic (boreal) forest regions, but also lives in the arctic tundra; therefore, it was classified in the mixed tree-coverage category. Given that the snow covers the ground in the arctic tundra during part of the year, grit and dust do not

accumulate on the plants consumed by caribous. Finally, the marsh deer *Blastocerus dichotomus*, the Chinese water deer *Hydropotes inermis*, the Baird's tapir *Tapirus bairdii* and the Indian rhino *Rhinoceros unicornis* live in grasslands or both in grasslands and forests, but they are usually found in marshy, swampy ground with standing water or waterside habitats. There are no data on the amounts of airborne grit adhering to the surface of riparian plants. However, given that they are frequently submerged, it is reasonable to expect lower levels than in the vegetation that grows in drier habitats. Riparian plants, however, are loaded with concentrations of phytoliths similar to those found in the vegetation from shrub steppes and savannas (Bremond *et al.*, 2005). Therefore, the low hypsodonty of those ungulates that feed on riparian plants supports the hypothesis that higher silica levels did not play an essential role in the evolution of hypsodonty.

The Indian rhino is the only riparian species with a relatively short anterior part of the jaw. However, other species of rhinos of open habitats such as the browsing black rhino *Diceros bicornis* and the grazing white rhino *Ceratotherium simum* also show very short anterior parts of the jaw (see Fig. 1). This morphological trait could be related to the fact that rhinos take food with their prehensile lips instead of using the incisor teeth.

The craniodental morphology of the common hippo *Hippopotamus amphibius* and the pygmy hippo *Hexaprotodon liberiensis* is unique among the living ungulates. Although both species live in different habitats, they have a very short anterior part of the jaw and brachydont teeth. In the case of *Hi. amphibius*, the reason for its low hypsodonty (which probably also applies to *He. liberiensis*) is most likely that it has a low metabolic rate, consuming less food per day than would be expected for an animal of its body size (Nowak, 2001). This means that the total amount of wear on the teeth is correspondingly less (Mendoza *et al.*, 2002). In addition, hippos feed in or near water habitats on grasses that are probably less abrasive as a result of being frequently immersed in water (Mendoza *et al.*, 2002). Moreover, a recent study of the isotopic composition of enamel in several populations of *Hi. amphibius* has shown that hippos have a more varied diet than usually believed, including significant amounts of  $C_3$  plants in closed to moderately open environments (Boisserie *et al.*, 2005).

Two other species that have specific ecological adaptations also show a combination of low HI and high JLB values: the mule deer *Odocoileus hemionus* and the white tailed deer *Odocoileus virginianus*. Both live in an extremely wide range of habitats in North America, including deserts, grasslands, chaparral, forests, mountains, rainforests, scrub forest and swamps. Thus, their low hypsodonty cannot be explained by the absence of grit on the plants consumed.

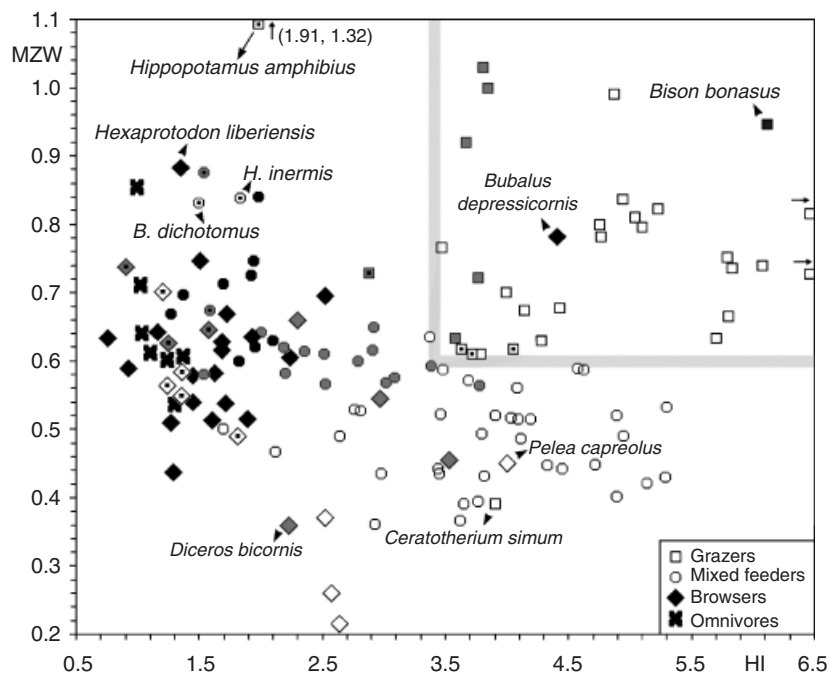
Finally, there are two ungulates that show an unexpected combination of HI and JLB values in relation to the degree of tree coverage of their habitat: the European bison *Bison bonasus* and the lowland anoa *Bubalus depressicornis*. The European bison, also called the wisent, is the largest herbivore in Europe. Historically, the wisent was distributed

through western, central and south-eastern Europe, but its range was severely shortened by the beginning of the 20th century, and now only small populations remain in a few isolated areas. The largest concentration lives in the temperate coniferous forests of Bialowieza Natural Park in Poland, and so the wisent was classified as a closed forest dweller. Although wisents browse in this closed habitat, they graze where grasses are available. In fact, Borowski & Kossak (1972) revealed that in wisents, leaves and shrubs constitute 33% of the diet, while grasses, sedges and herbs comprise up to 67% of the diet. Analysis of the rumen contents has confirmed that the wisent's basic diet contains grasses, sedges and herbs, which constitute 90% of the rumen capacity (Gebczynska, Gebczynski & Martynowicz, 1991). Wisents living in anthropogenic landscapes feed mostly on grass and agricultural crops, and browse usage is restricted mainly to winter (Balciauskas, 1999). Among modern ungulates, there are no grazing species in closed, forested habitats. This suggests that the European bison probably evolved in grasslands or mixed habitats.

The lowland anoa *B. depressicornis* also shows the craniodental morphology of an ungulate from an open habitat (Fig. 1). Little is known about the original habitat and feeding behaviour of this domesticated bovid, although it is thought to be a solitary browser that inhabits lowland forests, including secondary formations and swampy areas, and it was once common along the coasts (Whitten, Mustafa & Henderson, 1987). However, a recent study of diet

digestibility and ingesta passage times in captive anoas has revealed a comparatively high fibre digestibility and high selective particle retention in the forestomach, which suggests that this species is adapted to feed significant amounts of grasses (Flores-Miyamoto *et al.*, 2005). In addition, its jaw morphology is the one typical of a grazer. Thus, the combination of HI and JLB values depicted by the lowland anoa, typical of those ungulates from open environments, could reveal the original habitat of this species before its domestication.

The representation of the taxonomic affinities of the species in the morphospace of HI and JLB (Fig. 1) shows that the patterning is not related to the phylogeny. Some ungulate families are only present in one of the categories (e.g. equids and tragulids) and do not allow testing whether the phylogenetic legacy hides the adaptive morphological patterns. Other families, however, are mostly represented in one of the ecological categories but have one or two species that belong to another guild. The warthog *Phacochoerus aethiopicus* is perhaps the clearest example: it is the only suid that lives in open habitats, feeding mainly on grasses (Harris & Cerling, 2002), and is clearly more hypsodont than the other suids, which all dwell in forests and show the typical morphology of closed habitat species (Fig. 1). Cervids are present in the four ecological categories, and all of them are correctly classified. Only two species forage in open habitats: the chital *Axis axis* and the pampas deer *Ozotoceros bezoarticus*. Even the pampas deer, which has one of the



**Figure 2** Distribution of 134 extant ungulate species in the morphospace defined by the hypsodonty index (HI) and the relative width of the muzzle (MZW), which allows characterizing aspects of the craniodental morphology of grazers compared with non-grazing species, including mixed feeders, browsers and omnivores. White symbols: species from an open habitat; grey symbols: species from a mixed habitat; black symbols: species from a closed habitat; dotted symbols: species with special adaptations (see legend of Fig. 1). For a description of the morphological variables, see text and fig. 1 in Mendoza & Palmqvist (2006b).

most brachydont dentitions among the species of open and even mixed habitats (Mendoza *et al.*, 2002), is correctly classified because it also has a very short anterior part of the jaw (Fig. 1). The short-crowned teeth of *O. bezoarticus* and its bordering position could evidence that the habitat of the pampas deer also includes areas temporarily inundated by fresh or estuarine waters (Jackson, 1987). The moose is the only high-level browser among cervids and combines brachydont teeth with a long anterior part of the jaw, characteristic of the ungulates with this particular feeding behaviour. Bovids, the most diverse family among extant ungulates, are represented by 72 species in the dataset, and these species are present in the four ecological categories. It is worth noting that if they are represented alone (not shown here), the same morphological pattern emerges as in the case of all ungulates. All these cases provide clear support to the adaptive origin of the HI–JLB pattern, ruling out the effects of phylogeny and the possibility of a random patterning.

### Grass consumption

The use of DTs led to the identification of another simple morphological pattern (Fig. 2), which involves HI combined with the relative width of the muzzle (MZW, size-adjusted distance between the outer junctions of the boundary between the maxilla and premaxilla). Muzzle shape reflects the adaptations related to the 'cropping mechanism' of ungulates: selective browsers have narrow, pointed muzzles consisting of a rounded incisor arcade with the first incisor generally larger than the third; in contrast, grazers have broad, square-shaped muzzles with transversely straight incisor arcades, showing equal or sub-equal-sized incisor teeth. These features reflect decreasing selectivity in food foraging (Gordon & Illius, 1988; Janis & Ehrhardt, 1988; Solounias & Moelleken, 1993).

According to the pattern of Fig. 2, grazers have a wider muzzle than other ungulates from an open habitat. However, although this pattern provides an almost perfect characterization of the craniodental anatomy of grazers, their range of HI values (3.5–8.7) exhibits a considerable overlap (65% of species) with that of mixed feeders from an open habitat (HI = 1.5–5.3). This suggests that the level of hypsodonty is a relatively poor indicator of the percentage of grass consumed. Therefore, the comparatively high HI values of grazers could reflect that most species of this dietary group live in open habitat, which would be the main factor determining the degree of hypsodonty. On the contrary, MZW does allow an almost perfect discrimination between grazers and other species from open habitats such as mixed feeders and browsers. However, given that some species from closed habitats also show wide muzzles, it is only a combination of MZW and HI that makes possible the characterization of grazers with respect to other ungulates.

Browsers and mixed feeders from open habitats show, in general terms, a narrower muzzle than those species from mixed and closed habitats. In fact, with only the exception of the grey rhebok *Pelea capreolus*, the few browsers that live in habitats without tree coverage have some of the

narrowest muzzles among ungulates, visibly narrower than in the browsing and mixed-feeding species from forest (Fig. 2). This could reflect a higher selectivity of food, as the plants from open habitats (e.g. acacia trees) are tougher and thornier than those that grow in forested environments. However, while MZW is a good indicator of a grazing diet for those species from open and mixed habitats, it is not an ecological indicator of open habitats (Fig. 2).

Figure 2 shows that the common hippo has a remarkably wide muzzle, which reveals its grazing habits, and brachydont teeth. As explained above, its short-crowned teeth are not typical of a grazer from open habitats and may result from the low metabolic rate of this species.

The common rhebok shows a muzzle width typical of a mixed feeder from an open habitat (Fig. 2). It is, however, predominantly a browser, as faecal analysis shows that dicotyledonous material comprises 88% of its diet (Mills & Hes, 1997). This species lives among rocks and tangled growth on mountain sides and plateaus. However, where protected it ventures to grassy valleys and probably frequented such valleys regularly before being driven out by human activity (Nowak, 2001). This recent change in habitat could have translated into an increase in browsing. In addition, the subspecies known as Vaal Rhebuck shows a mixed diet of grasses and leaves (Nowak, 2001), which indicates that the craniodental morphology of this species also allows regular consumption of grass.

The white rhino is a typical grazer, but its muzzle is relatively narrower than in most mixed feeders (Fig. 2). This can be a consequence of its strategy for food foraging, as the wide, square-shaped lips of white rhinos are ideally suited for swathing short grasses.

Finally, the lowland anoa and the European bison show the typical muzzle morphology of those grazing ungulates that forage in an open habitat (Fig. 2), although both species live, at present, in forested areas. Therefore, these results confirm their adaptation to graze in open environments.

### Discussion

The goal of this article was to identify the morphological patterns that characterize the ecological adaptations of the living ungulates, using techniques of knowledge discovery with an expanded database that includes 134 species and 32 craniodental measurements. However, we primarily focused on understanding the relationship between these adaptations and the craniodental morphology, instead of obtaining algorithms for deriving inferences on the ecological preferences of extinct taxa, as in Mendoza *et al.* (2002). Specifically, we are concerned here with the role played by hypsodonty in determining the dietary preferences and habitat choice of extant ungulates. For this reason, DA and DT are not used as tools of classification. Instead, they are used for generating new ecomorphological knowledge, which can provide clues on the palaeoecology of ancient taxa.

Mendoza (2007) shows that different ecological adaptations may be characterized by morphological patterns

involving different numbers of measurements. However, given the variable numbers of species included in each ecological group, only those patterns that combine a few craniodental variables were considered here. Starting from 32 measurements, there are 5488 possible plots combining three or less of them. Using these combinations, DT identified a very simple pattern that involves only two variables: HI and JLB. This pattern allows discriminating between the species from closed environments and those that live in mixed or open habitats. In addition, the pattern is useful for characterizing those ungulates with special adaptations, such as high-level browsers and riparian species. DA was used for separating the species from open and mixed habitats, which could not be characterized with the DTs. Surprisingly, the same combination of variables, HI and JLB, was obtained. As the number of variables involved in a morphological pattern is lower, the probability of obtaining such a patterning by chance is also lower and, of course, its interpretation is easier. Therefore, obtaining a pattern that combines only two variables and allows characterizing four ecological categories is a highly satisfactory result. In addition, a tree involving only two craniodental measurements, HI and MZW, allowed a perfect characterization of grazers. These results revealed the role of hypsodonty in the adaptation of ungulates to different habitats and feeding behaviours, which can be considered as knowledge discovery in a literal sense.

Our results support the fact that hypsodonty represents a key adaptation of ungulates for consuming herbaceous plants in open environments where the vegetation that grows at ground level accumulates airborne grit. However, it is difficult to explain why the minimum threshold of hypsodonty required for consuming more abrasive foods increases with the relative length of the anterior part of the jaw. Thus, JLB seems to play a secondary but essential role in the adaptation of ungulates to forage in habitats with different degrees of tree coverage. Its importance is not only because the minimum threshold of HI for feeding in open habitats increases with JLB but also because those species that show specific adaptations (e.g. high-level browsers and riparian species) have comparatively high JLB values (see Fig. 1). In the case of high-level browsers, their long anterior part of the jaw facilitates to reach higher levels of the tree canopy (Mendoza, 2007). However, there is no simple biomechanical reason behind the high JLB values of the other species. The existence of this group of species, all with brachydont teeth and a long anterior part of the jaw, does not allow inferring the habitat adaptations of an extinct ungulate showing a similar combination of HI and JLB values. However, the finding of such a combination of features would indicate, at least, that such species was probably not a typical ungulate from open, mixed or closed habitats.

Several studies have indicated a relationship between grass consumption and muzzle width in the living ungulates, and premaxillary shape has been used as evidence of grazing habits for extinct ungulates (e.g. Janis & Ehrhardt, 1988; Solounias & Moelleken, 1993; MacFadden & Shockey,

1997). However, these studies do not mention that such a relationship does not hold among those species from closed habitats and some brachydont ungulates from mixed habitats.

The results presented here contradict those obtained by Williams & Kay (2001), who concluded that habitat and climate variables played no significant role in the development of hypsodont teeth. However, we show here that a combination of HI and JLB allows good discrimination between open and mixed habitat species, and leaving aside those ungulates with specific ecological adaptations such as high-level browsers, almost all the forest species are less hypsodont than those living in open and mixed habitats (Fig. 1). Williams & Kay (2001) also concluded that HI correlates well with the variations in diet and in preferences of feeding height. In what concerns the second aspect, our study reaches the same conclusions. Although we did not analyse directly the effects of feeding height, we found that all high-level browsers are brachydont, with independence of the degree of tree coverage of their foraging habitat. Moreover, other species that consume food with lower airborne grit (e.g. riparian species) also have short-crowned teeth. The only explanation for this is that hypsodonty relates closely to the presence of external abrasives. Thus, contrary to the conclusions of Williams & Kay (2001), we postulate that habitat and climate variables did play a major role in the development of high-crowned teeth.

Concerning grass consumption, both studies also reach opposite conclusions. Knowledge discovery techniques allowed us to decipher the morphological pattern that characterizes grazing ungulates. This pattern reveals that while grazers have a wider muzzle than other open habitat species, there is considerable overlap of HI values between grazers and mixed feeders from open environments (Fig. 2). Therefore, the relationship between grass consumption and hypsodonty deduced by Williams & Kay (2001) and other authors (e.g. Janis, 1988; Solounias & Dawson-Saunders, 1988; MacFadden, 2000) most likely arises from the correspondence between grazing and foraging in open habitats. Our results indicate that HI discriminates primarily between ungulates from open and closed habitats (Fig. 1), and secondarily among dietary categories (Fig. 2). The latter is so because most species from open habitats are grazers or mixed feeders. This indicates that HI correlates indirectly with the diet because it correlates directly with the habitat type. Williams & Kay (2001) controlled the phylogenetic effects to avoid obtaining a significant correlation between grass consumption and hypsodonty due to the external operation of phylogeny. However, they did not control the effects of habitat type. Grazing ungulates have statistically higher HI values than other non-grazing species (Janis, 1988, 1995; Williams & Kay, 2001), even if we rule out the effects of phylogeny, but this merely indicates that most grazers live in an open habitat. This is, according to our results, the main factor determining the degree of hypsodonty.

Knowledge discovery techniques are particularly useful for ecomorphological studies. Instead of identifying

correlations between variables, they assume that there is a pattern behind each ecological adaptation and try to search for it. These techniques do not generate complex functions, whose interpretation is often confusing, as in the case of multivariate statistics. Rather, what they generate is new ecomorphological knowledge, which can provide reliable inferences on the ecological adaptations of extinct species.

## Acknowledgements

One of the authors (M.M.) received a postdoctoral grant from the Spanish CICYT and the Fulbright Visiting Scholar Program. This research was funded in part by project CGL2004-01615/BTE. We gratefully acknowledge constructive remarks from Christine Janis and three anonymous reviewers.

## References

- Balciauskas, L. (1999). European bison (*Bison bonasus*) in Lithuania: status and possibilities of range extension. *Acta Zool. Lituan.* **9**, 3–18.
- Bargo, M.S., De Iuliis, G. & Vizcaíno, S.F. (2006). Hypsodonty in Pleistocene ground sloths. *Acta Palaeont. Polon.* **51**, 53–61.
- Boisserie, J.R., Zazzo, A., Merceron, G., Blondel, C., Vignaud, P., Likius, A., Taïso-Mackaye, H. & Brunet, M. (2005). Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **221**, 153–174.
- Borowski, S. & Kossak, S. (1972). The natural food preferences of the European bison in seasons free of snow cover. *Acta Theriol.* **17**, 151–169.
- Bremond, L., Alexandre, A., Peyron, O. & Guiot, J. (2005). Grass water stress estimated from phytoliths in West Africa. *J. Biogeogr.* **32**, 311–327.
- Brizuela, M.A., Detling, J.K. & Cid, M.S. (1986). Silicon concentration of grasses growing in sites with different grazing histories. *Ecology* **67**, 1098–1101.
- Cios, K., Pedrycz, W. & Świniarski, R.W. (1998). *Data mining methods in knowledge discovery*. Boston: Kluwer Publishers.
- Feranec, R.S. (2002). Key adaptations creating ecological generalization through morphological specialization: evidence from hypsodonty and stable isotopes. *J. Vertebr. Paleont.* **22** (Suppl.), 52A.
- Feranec, R.S. (2003). Stable isotopes, hypsodonty, and the paleodiet of *Hemiauchenia* (Mammalia: Camelidae): a morphological specialization creating ecological generalization. *Paleobiology* **29**, 230–242.
- Flores-Miyamoto, K., Clauss, M., Ortman, S. & Sainsbury, A.W. (2005). Nutrition of captive lowland anoa (*Bubalus depressicornis*): a study on ingesta passage, intake, digestibility, and a diet survey. *Zool. Biol.* **24**, 125–134.
- Fortelius, M. (1985). Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zool. Fenn.* **180**, 1–76.
- Fortelius, M., Eronen, J., Liu, L.P., Pushkina, D., Tesakov, A., Vislobokova, I. & Zhang, Z.Q. (2003). Continental-scale hypsodonty patterns, climatic paleobiogeography and dispersal of Eurasian Neogene large mammal herbivores. In *Distribution & migration of tertiary mammals in Eurasia*. Reumer, J.W.F. & Wessels, W. (Eds). *Deinsea* **10**: 1–11.
- Gebczynska, Z., Gebczynski, M. & Martynowicz, E. (1991). Food eaten by free-living European bison. *Acta Theriol.* **36**, 307–313.
- Gordon, I.J. & Illius, A.W. (1988). Incisor arcade structure and diet selection in ruminants. *Func. Ecol.* **2**, 5–22.
- Harris, J.M. & Cerling, T.E. (2002). Dietary adaptations of extant and Neogene African suids. *J. Zool. (Lond.)* **256**, 45–54.
- Harvey, P.H. & Pagel, M.D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hopkins, S.S.B. (2003). Parallel adaptive radiations in four lineages of Aplodontoid rodents: a case study in the evolution of hypsodonty. *Geol. Soc. Am. Abstr. Prog.* **34**, 418.
- Jackson, J.E. (1987). *Oxtocherus bexoarticus*. *Mammal. Species* **295**, 1–5.
- Janis, C.M. (1988). An estimation of tooth volume and hypsodonty indices in ungulate mammals. In *Teeth revisited: 371–391*. Russell, D.E., Santoro, J.P. & Sigogneau-Russel, D. (Eds). Proceedings of the 7th International Congress of Dental Morphology. *Mem. Mus. Hist. Nat.* **53**: 367–387.
- Janis, C.M. (1995). Correlations between craniodental morphology and feeding behaviour in ungulates: reciprocal illumination between living & fossil taxa. In *Functional morphology in vertebrate paleontology: 76–98*. Thomason, J.J. (Ed.). Cambridge: Cambridge University Press.
- Janis, C.M., Damuth, J. & Theodor, J.M. (2000). Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proc. Nat. Acad. Sci. USA* **14**, 7899–7904.
- Janis, C.M., Damuth, J. & Theodor, J.M. (2002). The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **177**, 183–198.
- Janis, C.M. & Ehrhardt, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool. J. Linn. Soc.* **92**, 267–284.
- Janis, C.M. & Fortelius, M. (1988). On the means whereby mammals achieve increased functional durability of their dentitions, with especial reference to limiting factors. *Biol. Rev.* **63**, 197–230.
- Jernvall, J. & Fortelius, M. (2002). Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature* **417**, 538–540.



- Larose, D.T. (2004). *Discovering knowledge in data: an introduction to data mining*. New York: John Wiley & Sons Inc.
- Lucas, P.W., Turner, I.M., Dominy, N.J. & Yamashita, N. (2000). Mechanical defences to herbivory. *Ann. Bot.* **86**, 913–920.
- MacFadden, B.J. (2000). Cenozoic mammalian herbivores from the Americas: reconstructing ancient diets & terrestrial communities. *Annu. Rev. Ecol. Syst.* **31**, 33–59.
- MacFadden, B.J. & Shockey, B.J. (1997). Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiology* **23**, 77–100.
- Mendoza, M. (2007). Decision trees: a machine learning methodology for characterizing morphological patterns resulting from ecological adaptations. In *Automated Taxon Identification in Systematics: Theory, Approaches and Applications*: 261–276. MacLeod, N. (Ed.) London: Taylor & Francis.
- Mendoza, M., Janis, C.M. & Palmqvist, P. (2002). Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. *J. Zool. (Lond.)* **258**, 223–246.
- Mendoza, M., Janis, C.M. & Palmqvist, P. (2005). Patterns in the trophic-size structure of mammal communities: a taxon-free characterization. *Evol. Ecol. Res.* **7**, 505–530.
- Mendoza, M., Janis, C.M. & Palmqvist, P. (2006). Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *J. Zool. (Lond.)* **270**, 90–101.
- Mendoza, M. & Palmqvist, P. (2006a). Characterizing adaptive morphological patterns related to habitat use and body mass in Bovidae (Mammalia, Artiodactyla). *Acta Zool. Sin.* **52**, 971–987.
- Mendoza, M. & Palmqvist, P. (2006b). Characterizing adaptive morphological patterns related to diet in Bovidae (Mammalia, Artiodactyla). *Acta Zool. Sin.* **52**, 988–1008.
- Michie, D., Spiegelhalter, D.J. & Taylor, C.C. (Eds). (1994). *Machine learning, neural & statistical classification*. New York: Ellis Horwood.
- Mills, G. & Hes, L. (1997). *The complete book of Southern African mammals*. Cape town, South Africa: Struik Publishing Group.
- Nowak, R. (2001). *Walker's mammals of the world*. 6th edn. Baltimore: Johns Hopkins University Press.
- Palmqvist, P., Gröcke, D.R., Arribas, A. & Fariña, R.A. (2003). Paleocological reconstruction of a lower Pleistocene large mammals community using biogeochemical ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\delta^{18}\text{O}$ , Sr: Zn) and ecomorphological approaches. *Paleobiology* **29**, 205–229.
- Pérez-Barbería, F.J. & Gordon, I.J. (2001). Relationships between oral morphology and feeding style in the Ungulata: a phylogenetically controlled evaluation. *Proc. Roy. Soc. Lond. Ser. B – Biol. Sci.* **268**, 1021–1030.
- Quinlan, J.R. (1985). Introduction to decision trees. *Machine Learning* **1**, 81–106.
- Reed, K.E. (1998). Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. *Paleobiology* **24**, 384–408.
- Shotwell, J.A. (1961). Late Tertiary biogeography of horses in the northern Great Basin. *J. Paleontol.* **35**, 203–217.
- Simpson, G.G. (1951). *Horses: the story of the horse family in the modern world and through sixty million years of history*. Oxford: Oxford University Press.
- Solounias, N. & Dawson-Saunders, B. (1988). Dietary adaptations and palaeoecology of the late Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **65**, 149–172.
- Solounias, N. & Moelleken, S.M.C. (1993). Dietary adaptation of some extinct ruminants determined by premaxillary shape. *J. Mammal.* **74**, 1059–1071.
- Spencer, L.M. (1997). Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. *J. Hum. Evol.* **32**, 201–228.
- Stirton, R.A. (1947). Observations on evolutionary rates in hypsodonty. *Evolution* **1**, 34–41.
- Strömberg, C.A.E. (2004). Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **207**, 239–275.
- Strömberg, C.A.E. (2006). Evolution of hypsodonty in equids: testing a hypothesis of adaptation. *Paleobiology* **32**, 236–258.
- Van Someren, M. & Urbancic, T. (2005). Applications of machine learning: matching problems to tasks and methods. *Knowledge Eng. Rev.* **20**, 363–402 (Published online by Cambridge University Press; 17 May 2006).
- Van Valen, L. (1960). A functional index of hypsodonty. *Evolution* **14**, 531–532.
- Whitten, A.J., Mustafa, M. & Henderson, G.S. (1987). *The ecology of Sulawesi*. Yogyakarta, Indonesia: Gadjah Mada University Press.
- Williams, S.H. & Kay, R.F. (2001). A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. *J. Mammal. Evol.* **8**, 207–229.

## Supplementary material

The following material is available for this article online:

**Appendix S1** This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-7998.2007.00365.x>

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.