A Comparative Test of Adaptive Explanations for Hypsodonty in Ungulates and Rodents

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Hypsodonty has long been recognized as an adaptation for grazing: grazing is suggested to increase tooth wear due to endogenous (e.g., fiber, silica) and/or exogenous (e.g., dust, grit) properties of ingested food. However, it is unknown whether tooth crown height is correlated with the mastication of high fiber or silica in grasses, the ingestion of external abrasives, or both. Furthermore, comparative studies of hypsodonty have not explicitly taken into account phylogenetic biases due to shared ancestry in tooth morphology and/or feeding behavior. This study highlights the relationship between molar crown height and feeding habits in African ungulates and South American rodents when phylogenetic effects are controlled. Among ungulates, high hypsodonty indices are significantly associated with specific plant and foraging height preferences, while habitat and climate show no correlation with tooth crown height. For rodents, grass-eating species are significantly more hypsodont than frugivorous or folivorous species, and arboreal rodents are less hypsodont than terrestrial species. These results as well as those of *a posteriori* analyses controlling for aspects of the behavioral ecology (e.g., grass-eating, substrate preference) of the sample species confirm the role of both diet and grit in shaping the evolution of cheek tooth crown height in herbivorous mammals.

KEY WORDS: Hypsodonty; ungulates; rodents; comparative methods; independent contrasts.

INTRODUCTION

The evolution of hypsodonty, the case in which cheek tooth crown height exceeds its anteroposterior length, in mammals has long been considered one of the best examples of a macroevolutionary trend. Simpson (1953) recognized an increase in crown height in the evolutionary history of a variety of mammals, including rodents, ungulates, marsupials, and lagomorphs. Its convergent evolution in various clades is considered evidence of an adaptation for an abrasive herbivorous diet usually consisting primarily of grasses. Indeed, Romer (1949, p. 306) notes that "grazing habits present a 'serious' problem to an ungulate, for grass is a hard, gritty material which rapidly wears down the surface of a grinding tooth." In particular, researchers (e.g., Osborn, 1910; Simpson, 1951, 1953; McNaughton *et al.*, 1985; MacFadden, 1997) point to horse evolution to show that increasing molar crown height beginning in the early Miocene coincided with the spread of grasslands and equids adopting grasses as their principal food.

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In hypsodont mammals, the base of the tooth crown is contained within the jaw and the tooth is gradually erupted over the lifespan of the animal as the tooth is worn down (see Figure 1). Hypothesized selective pressures for the development of hypsodonty, or more broadly, of relatively high-crowned teeth, in mammals all suggest a link with prolongation of the functional life of the teeth under conditions of rapid tooth wear (Romer, 1949; Van Valen, 1960; Rensberger, 1975; Fortelius, 1981, 1985; Janis, 1988; Janis and Fortelius, 1988). The physical properties of the food material or of exogenous substances attached to the food and the extent to which food is processed are all factors which can cause rapid tooth wear (Fortelius, 1985; Janis, 1988; Janis and Fortelius, 1988). With respect to the physical properties of plant foods, nutrients are contained within cells protected by cell walls containing cellulose, hemicellulose, and sometimes lignin. For an herbivore to make use of these nutrients, each cell wall must be broken down mechanically by mastication before the food material can be chemically broken in the digestive tract (Bell, 1971; Van Soest and Robertson, 1976). Additionally, many grasses contain abrasive phytoliths (opaline silica) in the internal structures of their organs (e.g., sheaths, stems, and roots), possibly as a defense mechanism against herbivory (McNaughton *et al.*, 1985). The abrasive qualities of fiber and phytoliths are thought to contribute to an increased rate of wear on the teeth. Another factor suggested to increase tooth wear is the presence of exogenous abrasive particles (dust or grit) that are ingested and masticated along with the plant material. Stirton (1947) observed that sand particles on grass blades and stems do indeed actively wear down the teeth of equids as they consume grass and roughage. Healy and Ludwig (1965) were among the first to test empirically the effects of differences in soil abrasives on teeth and documented that, in sheep, an increase in the amount of ingested soil measured from fecal samples resulted in increased incisor wear. More recently, Kay and Covert (1981, 1983) used controlled dental microwear experiments to show that grit has similar abrasive effects on the tooth as grasses with opal phytoliths.

The relative importance of intrinsic food abrasives *per se* and exogenous grit in shaping the evolution of high-crowned teeth has been debated. MacFadden and Cerling (1994) argue that grit is not a likely factor influencing the evolution of hypsodonty because not all hypsodont fossil equids are found in the same sedimentary environments. In the Northern Hemisphere, the contemporaneous appearance in geologic time of numerous hypsodont mammalian species in different clades coincident with the spread of grasses is cited as further evidence in favor of diet over exogenous abrasives (Webb, 1977, 1983; MacFadden, 1997).

Finally, dietary requirements associated with nutritional quality of the foods have also been implicated as a selective pressure to increase tooth hypsodonty. It is argued that having a "bulk diet" of low nutritional value might require an increase in total masticatory effort to break down foods. While there is no evidence that ungulates which consume primarily grasses have to produce higher masticatory forces, they may have prolonged oral breakdown of the plant material to aid in digestion (Axmacher and Hofmann, 1988). Furthermore, the volume of food consumed by an herbivore in a given time period is dependent on its method of digestion. Compared to ruminating ungulates, non-ruminating herbivores, such as horses, process a greater volume of plant material to extract comparable nutritional value and use more chews for a given quantity of food for initial processing (Janis, 1976; Janis and Constable, 1993). Ruminants, on the other hand, are limited in the amount of food they can consume. The ruminant digestive system
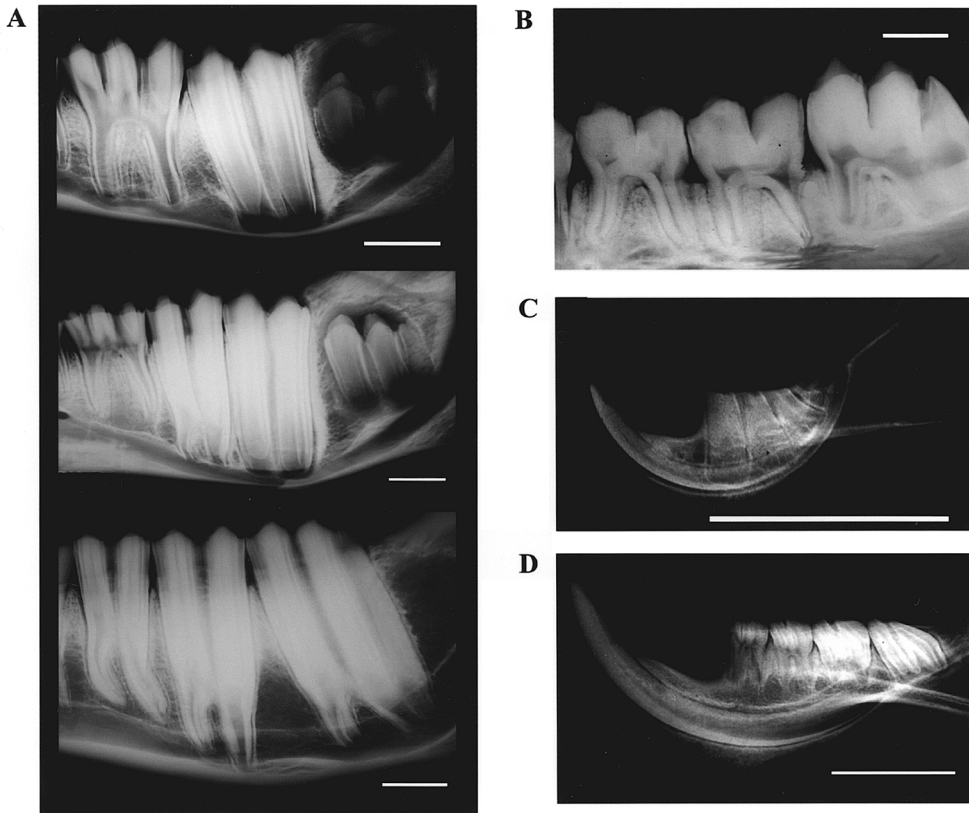
Fig. 1. Lateral radiographs of mandibles showing the variation in crown height in ungulates and rodents. (A) Growth series showing the eruption of hypsodont molars in *Connochaetes taurinus* (blue wildebeest) (USNM 251803, 181856, and 200860). (B) Relatively low-crowned (brachydont) molars of *Giraffa camelopardalis*. (C) Ever-growing cheek teeth (hypselodont) of *Ctenomys magellanicus* (tuco-tuco). (D) Hypsodont cheek-teeth of *Myocastor coypus* (nutria). Each scale bar represents 2 cm.

requires that plant material be broken down sufficiently through mastication and rumen fermentation before it can pass through the valve between the reticulum and omasum (Janis, 1976). Ruminants process ingested food more than once through the chewing of the cud, cud is probably mechanically softer due to breakdown by rumen microorganisms prior to regurgitation (Fortelius, 1981). Thus, chewing of cud may not lead to a substantially increased tooth wear.

Direct evidence for the adaptive relationship between tooth crown height and habitat and/or dietary variables in mammals comes from ecological studies of reindeer. Skogland's (1984, 1985, 1988, 1990) field studies of female reindeer found that when food is limited, reindeer ingest short lichens along with higher amounts of soil particles compared to individuals in good forage areas and low population densities. They report that females living in these conditions have an increased rate of tooth wear, a decrease in body weight, and a decrease in body fat reserves. This led to a significant decrease in reproductive fitness of these animals as indicated by a slowed fetal growth, increased

offspring mortality, and decreased reproductive success. Similarly, Kojola *et al.* (1998) document that increased tooth wear does indeed limit the extent to which female reindeer can process foods, and this, in turn, limits their body-fat reserves during winter months.

Although hypsodonty has been proposed as an adaptation to some or all factors listed above, there is little conclusive support for any single hypothesis or for the relative importance of several factors. With respect to diet, not all hypsodont species are grazers. For example, Janis (1988) shows that *Antilocapra americana*, the pronghorn, which consumes both grass and browse material, has higher molar crowns than some ungulate species that eat abrasive dry grass material (e.g., *Hippotragus niger* and *Ceratotherium simum*). In this case, higher molar crowns in the pronghorn could be attributed to the fact that this species lives in deserts and open grasslands where dust could be a factor. Nor are all exclusively grass-eating species similar in their degree of hypsodonty. For example, the grazing warthog *Phacochoerus aethiopicus* has lower molar crowns than other more omnivorous or browsing suids but lower crowns than grazing bovids of the tribe Alcelaphini, suggesting a phylogenetic effect (Janis, 1988).

If hypsodonty is indeed an adaptation for increasing the functional life of the dentition to guard against wear in herbivorous mammals, what is the relative importance of endogenous plant abrasives and exogenous grit in determining tooth wear? Only one study to date (Janis, 1988) has evaluated the relationship between hypsodonty and feeding behavior. Janis (1988) compared crown heights of ungulates with different diets and different habitat preferences. The former was assumed to be a proxy for the physical properties of the food itself (e.g., fiber and phytolith content) and the latter (e.g., the environment where the animal forages) was used as a means of expressing the amount of exogenous dust or grit. She concluded that habitat preference (and therefore dust and grit) is the primary selective factor in determining tooth crown height. She found that animals living in open, dry regions tend to be more hypsodont than species living in "closed" (wetter and more forested) habitats. However, there have been no studies in ungulates which look at the correlation between hypsodonty and other behavioral factors, such as feeding height, which also may be related directly to the ingestion of exogenous grit rather than the mastication of abrasive plant matter. While Kay *et al.* (2001) have shown that there is indeed a correlation between cheek tooth-crown height and substrate preference in Old World monkeys, with terrestrial species having relatively higher molar crowns, there are no similar analyses of the mammalian orders which have developed the extreme forms of increased tooth crown height such as hypsodonty and hypselodonty (evergrowing cheek-tooth crowns).

The factors cited above—specifically, dietary abrasiveness and exogenous grit—should lead to testable predictions about the relative crown height of herbivorous species. If diet is a significant selective factor, species with more abrasive diets should be subject to an increased rate of tooth wear and would selectively evolve higher tooth crowns compared to species with less abrasive diets. If so, we would expect to find increasing crown height along a vector leading from low-fiber foods, through high-fiber foods to high-fiber, phytolith-rich foods. Likewise, if exogenous grit is a significant selective factor, species with diets containing more abrasive exogenous grit substances should evolve higher crowns compared to those that eat foods with less exogenous grit adhering to it. The latter hypothesis would be supported if it were shown that species living in drier, more dust-laden environments had higher crown heights than species living in wetter,

more dust-free environments. Similarly, more arboreal species should be exposed to less exogenous grit and have lower molar crowns than more terrestrial species.

The goal of this study is to understand the relative importance of the selective force or forces hypothesized above that may lead to increased hypsodonty. Specifically, we examine the evolution of increased molar crown height in relation to ecological and behavioral variables, using phylogenetically "normalized" data on extant African ungulates and South American rodents.

MATERIALS AND METHODS

Independent Contrasts Method

To test the relationship between tooth morphology and relevant behavioral and ecological data, we used a phylogenetically-sensitive approach—the "independent contrasts" method developed by Felsenstein (1985)—to control for the confounding effects of phylogeny. Phylogenetically-sensitive comparative methods stress the need to take phylogeny into account when looking at traits or behaviors across numerous taxa. Because similar characters found in closely related taxa could just as likely be due to shared ancestry as to adaptive convergence, species cannot be assumed to be statistically independent. The consequence of the confounding effects of phylogeny is that statistical tests will overestimate the number of degrees of freedom, and thus p-values and confidence intervals are miscalculated when applied to data in which phylogenetic relationships have not been taken into account (Harvey and Pagel, 1991; Pagel, 1992). More simply and possibly more importantly, using a phylogenetic framework in interspecific analyses provides a means of understanding correlated evolution of two traits and instances of convergence across numerous related and unrelated taxa. Phylogenies are an important component of these comparative analyses because they show the distribution of traits among various species.

The independent contrast method calculates the standardized difference between the values of traits of sister taxa in a phylogeny (Felsenstein, 1985; Purvis and Rambaut, 1995). A "contrast" quantifies the amount of evolutionary change that has occurred in a trait after the divergence of sister taxa from a common ancestor. Contrasts are calculated at all levels of a phylogeny by using reconstructions of ancestral states for internal nodes.

Contrast values for the behavioral and morphological data are calculated from phylogenies for ungulates and rodents using the program *Comparative Analysis by Independent Contrasts (CAIC) Version 2.0.0* (Purvis and Rambaut, 1995). The program relies on various input data—a phylogeny for the taxa to be analyzed, behavioral data (either continuous or dichotomous), and continuous morphological data—each of which is discussed below. In the CAIC package, the CRUNCH algorithm calculates contrasts for continuous data whereas the BRUNCH algorithm calculates contrasts for dichotomous variables. In this study, the states are ordered and represent a continuum from the most abrasive to the least abrasive habitat and diet, so the CRUNCH algorithm of CAIC was used to calculate contrasts. Branch lengths corresponding to the temporal duration between speciation events are recommended; however, as in this study, they are not always known. Therefore, a punctuational model of evolution is assumed by assigning all branches the same length (Purvis and Rambaut, 1995).

A phylogeny for extant ungulate taxa used in the present study is presented in Fig-

ure 2. The topology of the ordinal branches is based on Shoshani and McKenna (1998). Species-level relationships for bovids are based on rDNA and morphological data from Gatesy *et al.* (1997). Additional species for which we have ecological and morphological data are added as sister taxa to form a polytomy of congeners with species included in the Gatesy *et al.* (1997) phylogeny. For example, additional species of the tribe Cephalophini for which ecological and behavioral data are known were incorporated as a polytomy with *Cephalophus maxwelli.*

The phylogeny for the South American rodents used in the present study (Figure 3) is derived from several sources. The topology for the species of the suborder Hystricognathi comes from Nedbal *et al.* (1994). The phylogeny for the paraphyletic taxon Sciurognathi includes the families Sciuridae and the Muridae. While the Sciuridae are simply arranged as a polytomy containing species of the genus *Sciurus* with *Microscuirus* as the sister taxon, the topology for the Muridae is based on Myers *et al.* (1995) and on the phylogeny compiled on the *Tree of Life* webpage (http://phylogeny.arizona.edu/tree).

Morphological and Behavioral Data

Data for ungulate hypsodonty indices are taken from Janis (1988). Rodent molar crown height data were collected from specimens at the National Museum of Natural History (Smithsonian Institution). Crown height in rodent species was measured from lateral radiographs of lower first molars (m1) in place within the mandible. A point was established at the apex of the fork between the mesial and distal roots. A line was projected from that point toward the crown's occlusal surface and orthogonal to its occlusal plane. The distance between the fork and the point where this projected line crossed the occlusal plane is defined as the crown height (see Figure 4). The mesiodistal length of the tooth was measured on the radiograph. The mesiodistal and buccolingual dimensions of the teeth were also measured on the tooth itself. From these dimensions the tooth crown area and relative crown height were calculated. Relative crown height was calculated as:

$$\frac{m1 \ crown \ height}{\sqrt{(m1 \ mesiodistal \ length)(m1 \ buccolingual \ width)}}$$
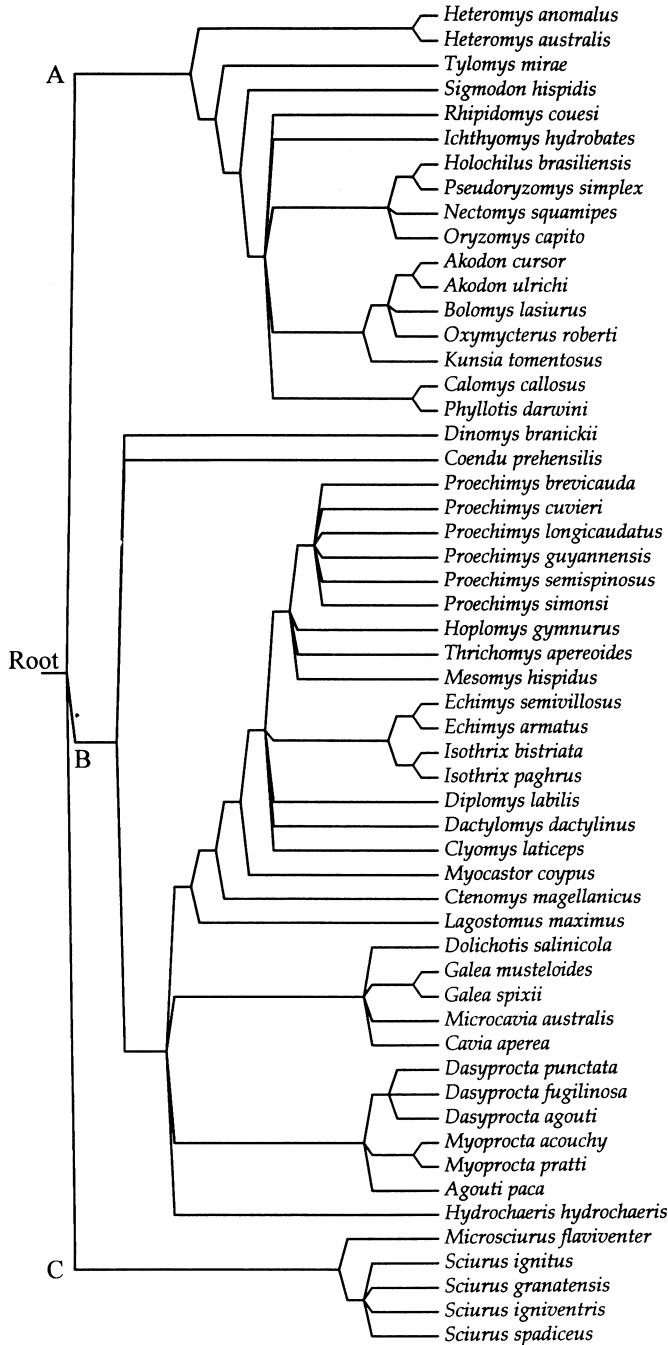
For brachydont species, only relatively unworn, newly erupted teeth were measured. Hypsodont species evince substantial crown wear before the root fork appears. For these species, the youngest specimens were selected whose roots have begun to form. For hypseledont species (i.e., species whose cheek teeth do not form roots and are evergrowing, as in *Cavia*), crown height is defined as the distance from the occlusal surface at midcrown mesiodistally to the base of the crown.

Behavioral and habitat data for ungulates (Appendix 1) are based on the literature and consist of several categories that attempt to capture a range of dietary, foraging, and habitat preferences. Theoretically, these categories may reflect the varying amounts of intrinsic and extrinsic abrasives incorporated into a species' diet, and therefore, may have affected natural selection for tooth crown height. These categories include diet, feeding height preference, habitat climate data, and grassland habitat preference, if applicable.

Ordered states for diet are treated as continuous variables and were scored as 0 =
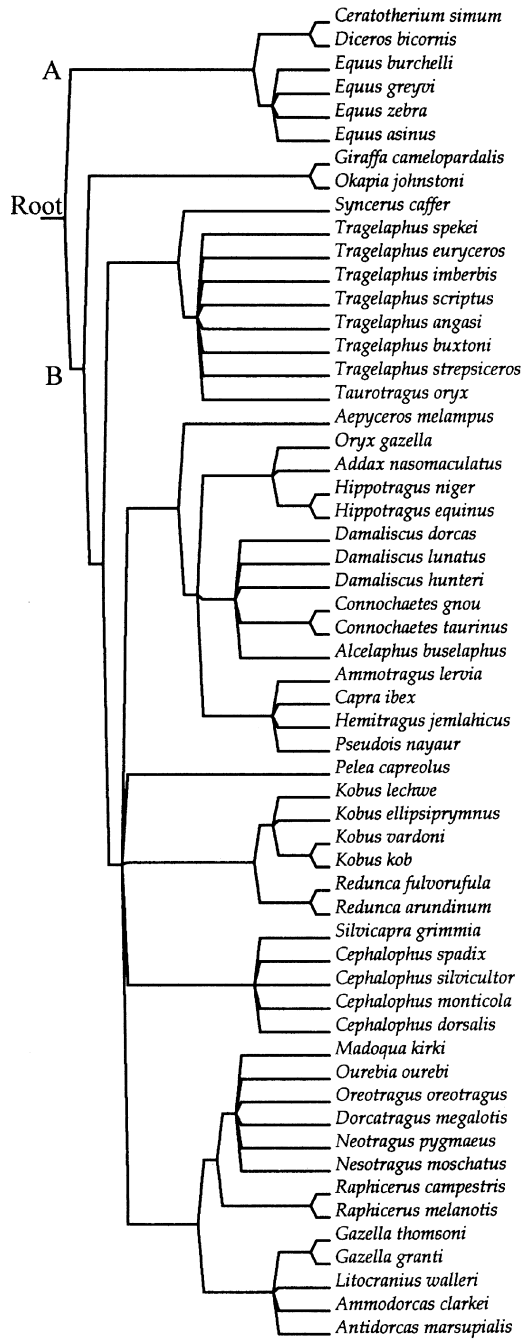
Fig. 2. A composite cladogram for extant perissodactyls and artiodactyls studied here, after Shoshani and McKenna (1998) and Gatesy *et al.* (1997). Contrasts for the root and for nodes A and B were excluded from some of the analyses. See text for explanation.

Heteromys anomalus
Heteromys australis
Tylomys mirae
Sigmodon hispidis
Rhipidomys couesi
Ichthyomys hydrobates
Holochilus brasiliensis
Pseudoryzomys simplex
Nectomys squamipes
Oryzomys capito
Akodon cursor
Akodon ulrichi
Bolomys lasiurus
Oxymycterus roberti
Kunsia tomentosus
Calomys callosus
Phyllotis darwini
Dinomys branickii
Coendu prehensilis
Proechimys brevicauda
Proechimys cuvieri
Proechimys longicaudatus
Proechimys guyannensis
Proechimys semispinosus
Proechimys simonsi
Hoplomys gymnurus
Thrichomys apereoides
Mesomys hispidus
Echimys semivillosus
Echimys armatus
Isothrix bistriata
Isothrix paghrus
Diplomys labilis
Dactylomys dactylinus
Clyomys laticeps
Myocastor coypus
Ctenomys magellanicus
Lagostomus maximus
Dolichotis salinicola
Galea musteloides
Galea spixii
Microcavia australis
Cavia aperea
Dasyprocta punctata
Dasyprocta fugilinosa
Dasyprocta agouti
Myoprocta acouchy
Myoprocta pratti
Agouti paca
Hydrochaeris hydrochaeris
Microsciurus flaviventer
Sciurus ignitus
Sciurus granatensis
Sciurus igniventris
Sciurus spadiceus

Fig. 3. A composite cladogram for South American rodents studied here, after Nedbal *et al.* (1994), and Myers *et al.* (1995), and the *Tree of Life* webpage (http://phylogeny.arizona.edu/tree). Contrasts for the root and for nodes A, B, and C were excluded from some of the analyses. See text for explanation.
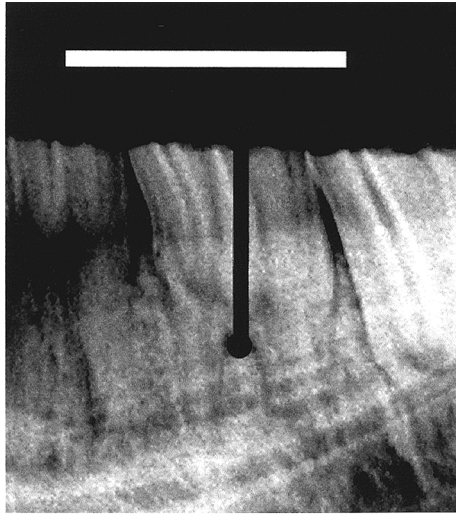
Fig. 4. Lateral radiograph of the lower first molar of *Myocastor coypus*. The line extending from the point at the apex of the fork between the mesial and distal roots represents the crown height measurement used to calculate relative crown height. See text for explanation. Scale bar represents 1 cm.

preferring dicots (browse); 1 = mixed feeder preferring dicots; 2 = mixed feeder preferring monocots (grasses); and 3 = preferring monocots. Species were scored based on their preferred diet according to published sources (Hofmann and Stewart, 1972; Estes, 1992; Spencer, 1995; Stuart and Stuart, 1997). Species scored as 0 consume more than 90% of their diet in dicots while those scored as 3 consume greater than 90% of their diet in monocots; mixed feeders consume less than 90% of their diets as purely monocot or dicot plant material.

Feeding height data for bovids is that compiled by Spencer (1995) and is supplemented here by accounts in Du Toit (1990) and Estes (1992). Foraging height preferences, treated as continuous, were coded as follows: 0 = tall plants and trees; 1 = medium level; 2 = ground. Species scored as 0 regularly feed at the level of their head or higher. All species considered as high browsers by Janis (1988) were given a score of 0 in this analysis. Medium level feeders are those species feeding on tall grasses and those bovids weighing between 70 kg and 300 kg feeding at their "knee level" as listed in Spencer (1995). While this is a substantial size range, it is assumed here that the knee level of species weighing less than 70 kg would be equivalent to feeding on the ground. Ground level feeders are those consuming low-lying grasses, forbs, herbs, sedges, fallen fruit, and tubers. Because the feeding height preferences for ungulates are difficult to determine from the literature, only specific references to feeding height were used and numerous taxa were omitted from the analyses.

The habitat data consists of two categories: climate and grassland preference. We compiled climate data from Estes (1974, 1992) and Stuart and Stuart (1997) and broadly

categorized the ungulate species as belonging to one of three climate categories: wet (coded as 0), mesic (coded as 1), and arid (coded as 2). Grassland habitat preference, taken from Estes (1992), Spencer (1995), and Stuart and Stuart (1997), is based on whether an ungulate species primarily inhabits edaphic or secondary grasslands, coded 0 and 1, respectively. Secondary grasslands are produced when fire and/or grazing impedes the growth of woody plants. Edaphic grasslands are found in drainage areas and valleys of river and lake systems as well as in floodplains where seasonal rainfall is poorly drained (Vesey-Fitzgerald, 1963).

For rodents, behavioral data (Appendix 2) used are diet and substrate preferences compiled by Kay and Madden (1997). For our analyses, rodent diets are partitioned into three ordered states as follows: 0 = fruit or animal food; 1 = leaves and/or seeds; 2 = grass. Substrate preference, used as a proxy for the possible amount of exogenous dust that can be ingested, was scored similarly as: 0 = arboreal; 1 = semi-arboreal; and 2 = terrestrial/semi-aquatic.

Data Analysis

Prior to statistical analyses of the data, the statistical assumptions of the independent contrasts method were tested to determine whether transformation of the data was required (see Purvis and Rambaut, 1995). Contrasts calculated by CAIC were regressed on the estimated values at the node also calculated by CAIC for each of the analyses. A slope significantly different from zero would indicate that the evolution of the characters is not random, as Felsenstein's (1985) model assumes. None of these regressions was significant and, therefore, data for both groups were not log-transformed. Heterogeneity of variances was tested by regressing the absolute value of the contrasts for both the independent and dependent variable on the square root of the contrasts variance produced by CAIC. In no cases were the statistical assumptions of CAIC violated—that is, there is no correlation between the absolute values of the contrasts and the square root of the contrasts variance; thus, transformation of data was not undertaken.

Statistical analysis of the data is limited to the contrasts produced by CAIC. For all of the analyses using continuous behavioral data, a simple linear regression through the origin of the contrasts tests for a relationship between the morphological and behavioral data (see Garland *et al.*, 1992). This provides a slope which shows the relationship between the independent and dependent variable when phylogenetic effects are controlled for (Pagel, 1993). Additionally, the sign of the slope provides information about the direction of change in the dependent variable, in this case the crown height contrast, versus the independent (behavioral) variable. Slopes are tested to determine if they were significantly different from zero. For dichotomous variables, the null hypothesis is that the dependent or continuous variable is not linked to changes in the independent variable. Because contrast values for the dependent variable can be either positive or negative when the independent variable is dichotomous, the mean value of the contrasts is expected to be 0. If the mean of the contrast values for the dependent variable is significantly greater than zero, as determined by a one-tailed t-test, the evolutionary increase in the dependent variable is significantly correlated with an evolutionary increase in the independent variable (Purvis and Rambaut, 1995).

A priori analyses. Table I summarizes the analyses undertaken. The first analysis

Table I. Summary of Analyses

Data set	Test #	Variables	CAIC option
Ungulate	*A priori:*	1 H.I.,[a] diet	CRUNCH
		2 H.I., feeding height	CRUNCH
		3 H.I., climate	CRUNCH
	↓	4 H.I., grassland type	BRUNCH
	A posteriori:	5 H.I., diet excluding grazers	CRUNCH
		6 H.I., feeding height excluding grazers	CRUNCH
	↓	7 H.I., diet, feeding height	CRUNCH
Rodent	*A priori:*	1 Relative crown height, diet	CRUNCH
	↓	2 Relative crown height, substrate preference	CRUNCH
	A posteriori:	3 Relative crown height, diet excluding grass-eaters	BRUNCH
		4 Relative crown height, substrate preference excluding grass-eaters	CRUNCH
	↓	5 Relative crown height, diet, substrate preference	BRUNCH

[a] H.I. = Hypsodonty Index as determined by Janis (1988).

for ungulates (test 1) is based on a categorization of their diet, reflecting an increase in the abrasiveness of the actual plant material ingested. Grazers consume primarily grasses (monocots), which are high in fiber and have thicker sheath cell walls, and they can also be more abrasive than other plant material because of the presence of abrasive silica phytoliths in their organs (Walker *et al.*, 1978; Kay and Covert, 1983). Thus, grazing species would be hypothesized to have the highest hypsodonty indices while those species feeding on browse material and minimal amounts of grasses are hypothesized to have the lowest hypsodonty indices. The second ungulate analysis (test 2) uses variation in feeding height among the ungulate species to determine the relationship between hypsodonty indices and the amount of inferred exogenous grit in the diet. Animals feeding close to the ground are expected to ingest more grit than animals feeding on plant material found in higher levels of the canopy (Ungar *et al.*, 1995), and therefore, are predicted to have higher molar crown height. The third analysis for the ungulate data set (test 3) more accurately determines the effects of grit and dust on tooth crown height by using habitat data, with species living in arid regions hypothesized to ingest more grit and therefore to have higher hypsodonty indices than those inhabiting wetter environments. Finally, we hypothesize that because edaphic grasslands likely contain less dust and grit compared to relatively drier secondary grasslands, ungulate species living in the former will have relatively lower molar crowns (test 4).

The first rodent analysis (test 1) is based on the hypothetical relationship between molar crown height and diet. The hypothesis for this test is that species feeding on grasses will have higher m1 crown heights than those feeding on leaves and/or seeds and those feeding on fruits and/or animals. The second rodent analysis (test 2) tests whether substrate preferences are linked to changes in m1 crown heights in rodents. Arboreal species are assumed to ingest the least amount of dust while terrestrial/semi-aquatic species are assumed to ingest the most. When there was uncertainty as to the behavioral data, taxa were omitted from the analysis.

A posteriori analyses. Several *a posteriori* analyses were conducted for both the ungu-

late and rodent data sets to control for variables that may confound the results of the analyses presented above (Table I). First, using a simple linear regression through the origin, we regressed the contrasts for each of the continuous behaviors (diet, feeding height, and substrate preference) against the contrast for the hypsodonty index or relative m1 crown height while omitting species with the most abrasive diet (e.g., grass) from the data set. While this makes the *a priori* assumption that diet is more importantly correlated with molar crown height, it allows us to determine, for example, whether terrestrial species with less abrasive diets still have higher molar crown heights. These tests (ungulate tests 5 and 6; rodent tests 3 and 4) were only done for those behaviors coded as continuous and for which a significant correlation with the morphological variable was found.

We more rigorously tested the relationship of the various behavioral variables with the morphological data by using a forward stepwise regression through the origin. Multiple regression techniques determine whether variation in multiple independent variables is correlated with variation in a dependent variable when their relationship with each other is controlled. Because we are interested in comparing the effects of diet and an additional behavioral or ecological variable, diet was considered to be the independent variable when calculating contrasts with the CAIC program for both the ungulate and rodent data (ungulate test 7 and rodent test 5). We used the default settings for a forward stepwise regression (0.25 to enter a variable and 0.10 to leave) in the statistical package *JMP* (SAS Institute, Cary, N.C.). Multiple regressions were conducted only for those ecological and behavioral variables which showed significant correlations with the morphological data in the *a priori* analyses.

Lastly, because the tooth measurements used in this study may be inherently affected by phylogeny, we performed a series of *a posteriori* analyses in which contrasts for nodes at the more basal levels within the ungulate and rodent phylogenies are excluded. The rationale for these analyses is that differences in dental morphology between higher level taxa may be influenced by phylogenetic biases due to overall differences in the morphology and/or function of the masticatory apparatus. For example, in rodents, members of the family Muridae all lack a p4 and the m1 is elongated at its anterior end. Because relative molar crown height is based in part on the mesiodistal length of m1, any measure of tooth crown height may be underestimated for muroid rodents as compared to the other rodent species used in this study. To determine whether phylogenetic bias in the hypsodonty indices in ungulates and relative molar crown height measurements influence the comparative tests, we performed each of the tests described above while excluding the contrasts for the most internal nodes in the phylogenies. For ungulates, these include the contrasts calculated for the root of the phylogeny as well as for those at the base of the clades containing the Perissodactyla and Artiodactyla (labeled A and B in Figure 2). For rodents, contrasts at the root of the phylogeny and those at the base of the clades containing the Muridae, the caviomorph rodents, and the Sciuridae (labeled A, B, and C in Figure 3) were excluded.

RESULTS

Ungulates

A priori results. Results for the simple linear regressions are presented in Table II. In test 1, diet is found to be significantly correlated with ungulate hypsodonty indices (*p*

Table II. Summary of Results

| Data set	Test #	p	F-ratio	Slope
UNGULATE	1	0.001	13.491	0.654
	2	0.004	10.313	0.483
	3	0.831 (n.s.[a])	0.047	−0.064
	4	0.286 (n.s.)	NA[b]	NA
	5	0.014	2.791	0.721
	6	0.014	2.912	0.651
	7	Diet 0.002;	13.101;	NA
		Feeding height 0.016	7.000	
RODENT	1	0.004	10.245	0.642
	2	0.032	2.247	0.305
	3	0.0002	NA	NA
	4	0.021	2.462	0.128
	5	Diet 0.004;	7.79	NA
		Substrate 0.099	2.938	

[a] (n.s.) = not significant, [b] NA = not applicable.

$= 0.0001$) when phylogenetic effects are controlled for. Furthermore, the slope for this regression is in the predicted direction as determined by the coding of the behavioral data. That is, because species feeding on grass having a higher code than browsers, a positive slope of 0.654 indicates that species feeding on more intrinsically abrasive plant materials have higher hypsodonty indices than those feeding on less abrasive foods (see Figure 5A).

The second variable tested for ungulates is feeding height preference (test 2). Despite the limited data set for this variable, the regression of the hypsodonty index contrasts on the feeding height contrasts is significant ($p = 0.004$). Once again, the coding of the variables, with ground feeders having a higher code, and the slope of the regression line (0.483) indicate that as feeding height decreases, hypsodonty index increases, as is predicted. This relationship is shown in Figure 5B.

The results for test 3, which looked at the effects of climate on ungulate hypsodonty indices, are not significant ($p = 0.831$). A closer look at the contrasts produced for various nodes of the phylogeny, as shown in Figure 5C, shows that in many cases, while there is no change in the climate variable (resulting in a contrast of 0 on the x-axis), there was substantial change in the hypsodonty indices yielding contrasts that were widely scattered along the y-axis.

In the fourth analysis (test 4), contrasts in grassland type, which were treated as categorical, have no significant relationship with contrasts in hypsodonty indices ($p = 0.286$). This would be expected if most of the species living in secondary grasslands were browsers. However, this is not the case, as purely grass-eating species comprise nearly 50% of the edaphic versus secondary grassland data set. These results suggest, on the other hand, that the amount of grit on ingested plant material in edaphic grasslands is not significantly reduced despite the seasonal flooding of these environments.

A posteriori results. In the first *a posteriori* test, when grazers are removed from the diet data set (Table II, test 5), the correlation between diet and hypsodonty index in African ungulates remains significant ($p = 0.014$), and the slope of the line (0.721) indicates that those species feeding on more abrasive plant foods (e.g. mixed feeders
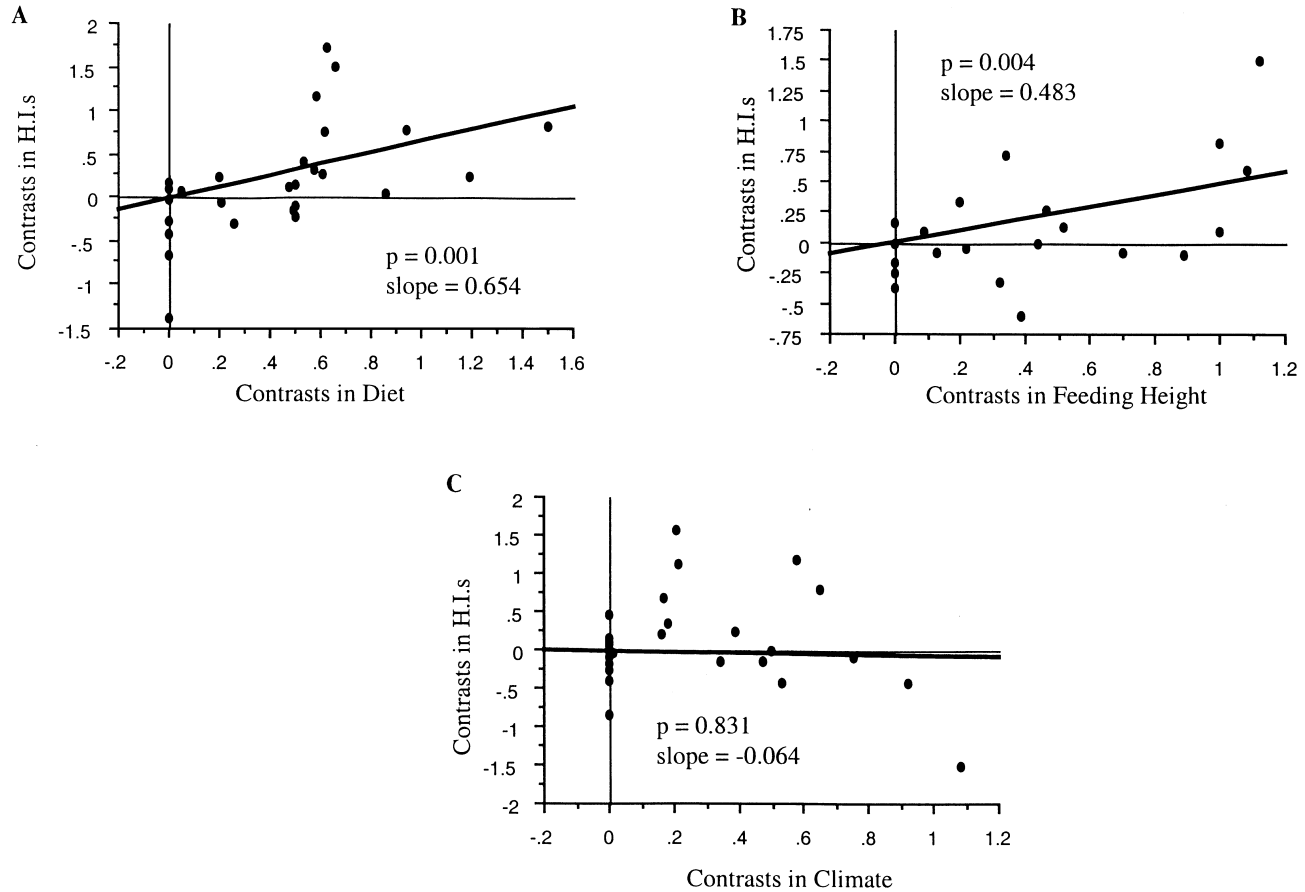
Fig. 5. Bivariate plots of reconstructed contrasts for hypsodonty indices (H.I.s) at various nodes in the ungulate phylogeny shown in Figure 2 versus the reconstructed behavioral data: A, diet preference; B, feeding height preference; and C, climate.

Table III. Summary of Results for *a posteriori* Analyses Controlling for Phylogenetic
Bias in Crown Height Measurements.

Data set	Test #	p	F-ratio	Slope
UNGULATE	1	0.008	8.335	0.467
	2	0.008	8.842	0.446
	3	0.370 (n.s.[a])	0.838	−0.221
	4	0.594	NA[b]	NA
	5	0.027	6.198	0.674
	6	0.034	6.286	0.609
	7	Diet 0.004;	10.715;	NA
		Feeding height 0.026	5.918	
RODENT	1	0.010	7.955	0.628
	2	0.048	4.282	0.297
	3	0.002	NA	NA
	4	No internal nodes[c]	—	—
	5	Diet 0.024;	5.913;	NA
		Substrate preference 0.122	2.583	

[a] (n.s.) = not significant.

[b] NA = not applicable.

[c] Because all of the contrasts produced by CAIC were above the nodes of the clades containing the
Muridae, Sciuridae, and caviomorph rodents, this analysis was not performed.

preferring monocots) have higher hypsodonty indices. These results suggest that some-
thing other than a diet of exclusively grasses is associated with increased hypsodonty.
To test this second possibility, we removed grazers from the feeding height data (test 6)
and found that once again, the correlation between hypsodonty index and feeding height
is significant ($p = 0.014$; Table II) with no change in the direction of the slope (0.651).
Therefore, we conclude that shifts in feeding height are correlated with changes in hyp-
sodonty indices among African ungulates.

In the third *a posteriori* analysis for the ungulate data, diet and feeding height were
both entered into a stepwise multiple regression (test 7; Table I). Contrasts in diet were
highly correlated with hypsodonty indices ($p = 0.002$; see Table II). Feeding height was
also independently correlated with hypsodonty indices in this analysis with a p-value of
0.016. In short, this means that the effects of diet and feeding height are additive and that
variation in hypsodonty indices is associated with variation in habitat when the relation-
ship of both of these variables with diet is controlled. Because climate and grassland type
are not significantly correlated with hypsodonty values, we did not enter these variables
into the stepwise regressions.

Results for the analyses in which contrasts for internal nodes of higher level taxa
were excluded are presented in Table III. While significance levels are different for each
of these tests as compared to those in which all contrasts are included (Table II), any
phylogenetic bias in the hypsodonty indices themselves does not alter the overall pattern
of significant results. Thus, an abrasive diet due to either the properties of the foods them-
selves and/or exogenous dust still appears to be correlated with increases in hypsodonty
indices in ungulates.

Rodents

A priori results. Results for the South American rodent analyses are similar to those presented above for African ungulates. Test 1 found that diet and molar crown height are significantly correlated ($p = 0.004$) (Table II). Because grass is ranked as the highest value of the diet preferences, a positive slope of 0.642 indicates that when there is a shift to a more abrasive diet, relative molar crown height increases when phylogeny is accounted for (see Figure 6A). Likewise, results for the substrate preference (test 2) show that this variable is significantly correlated ($p = 0.032$) with molar crown height so that terrestrial rodents have higher relative m1 crown heights compared to semi-arboreal or arboreal species (see Figure 6B).

A posteriori results. We performed two *a posteriori* analyses to determine if a significant relationship remained when grass-eaters were removed from both the diet and substrate preference data sets. Because the removal of grass-eating species resulted in only two remaining variables, contrasts in relative crown height produced by CAIC using the BRUNCH option were tested for significance using t-tests. Interestingly, although diet was more strongly correlated with relative crown height in the rodent sample, removal of the most intrinsically abrasive dietary items (test 3) still results in a highly significant correlation between the remaining diet categories and the morphological variable ($p = 0.0002$; Table II). To test the possibility that species feeding at ground level are eating more abrasive exogenous materials than species feeding in arboreal environments regardless of diet, we removed grass-eaters from the substrate preference data set (test 4) and once again produced contrasts in relative crown height using the CRUNCH option in CAIC. A linear regression through the origin was significant ($p = 0.021$), indicating that terrestriality is indeed a significant variable in molar crown height evolution in rodents even when the effects of grass-eating are controlled for.

The third *a posteriori* test for the rodent data set consisted of a multiple stepwise regression to determine the relationship between relative m1 height and substrate preference when the relationship of both variables with diet is taken into consideration (test 5). In this analysis, we found that diet (the independent variable) is still significantly correlated with molar crown height ($p = 0.004$) but that substrate preference is not significantly linked with molar crown height ($p = 0.099$) (see Table II). Examination of the raw contrasts produced for substrate preference shows that once diet is accounted for, changes in substrate preference were often 0 between the taxa being compared. Ideally, for these results to be significant, substrate preference would also have to vary in the predicted direction when diet preferences are also shifting, although they would vary independent of each other.

Results for the analyses in which internal contrasts were excluded to control for phylogenetic bias in relative molar crown height measurements, presented in Table III, are similar to those in which all contrasts are included (Table II). Thus, there is no evidence that differences in dental morphology between higher level rodent taxa have a bearing on the overall relationship between grass-eating or terrestriality and increased molar crown height.

DISCUSSION

The results from the above analyses clearly show that both diet *and* exogenous dust and grit play a role in shaping the evolution of tooth crown height in ungulates and
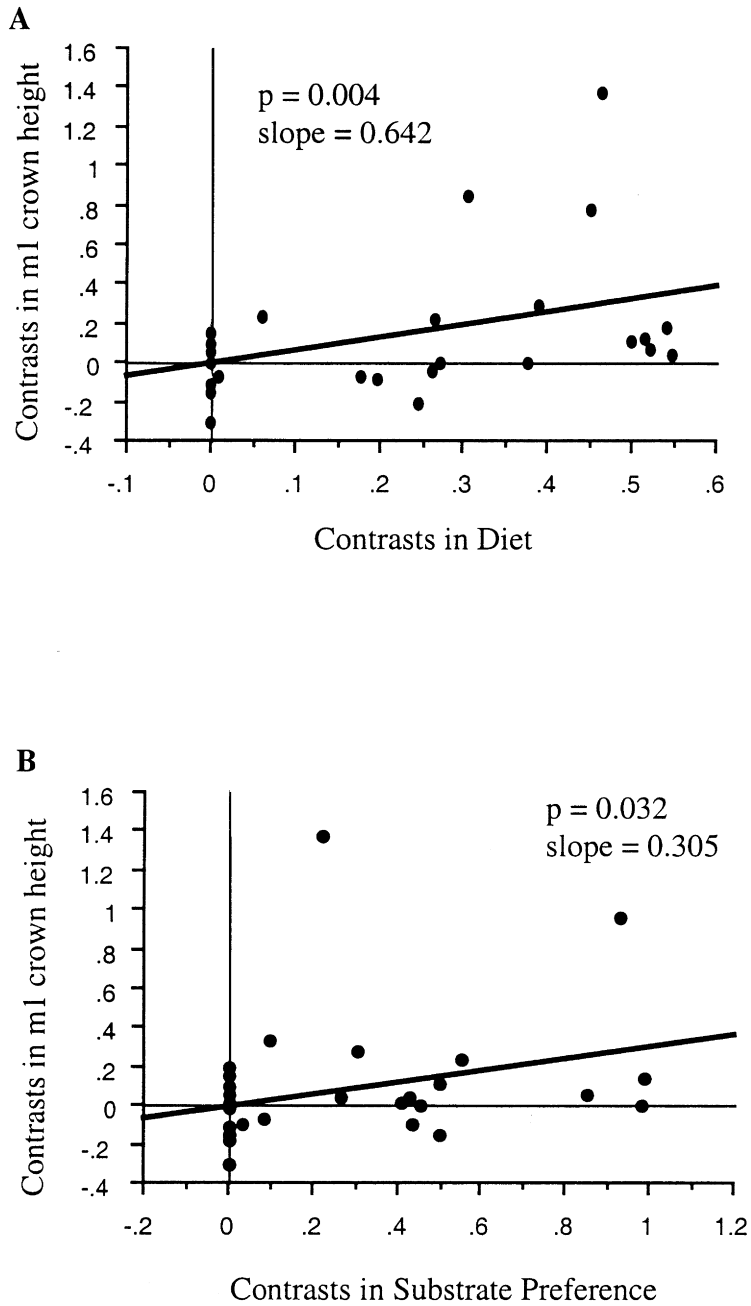
Fig. 6. Bivariate plots of reconstructed contrasts for relative m1 crown height at various nodes in the rodent phylogeny shown in Figure 3 versus the reconstructed behavioral data: A, diet preference; and B, substrate preference.

rodents. While not all tests were statistically significant, phylogenetically-controlled analyses still reveal the common trend of increasing hypsodonty with an increase in both intrinsic and extrinsic dietary abrasives and show that the effects of both variables are additive. Coupled with the studies discussed above by Skogland (1984, 1985, 1988, 1990) and Kojola *et al.* (1990) on female reindeer, the trends highlighted by our analyses are evidence of an adaptive relationship between tooth morphology and behavioral or ecological traits.

More specifically, for ungulates, our results indicate that while variation in diet and feeding height preferences are strongly correlated with variation in tooth crown height, habitat and climate variables play no detected role in the development of hypsodonty. On the surface, these results tend to counter those found by Janis (1988) who found no significant diet effect. However, we must point out that our habitat categories—climate and grassland type—are not the same as those used by Janis (1988), who used open versus closed habitats, and dry region and roughage grazers versus fresh grass grazers. While Janis' (1988) categories may be more appropriate for understanding the relationship between diet, habitat, and hypsodonty indices in ungulates, these categories are inappropriate for independent contrasts methodology for several reasons.

First, it is unclear whether these habitat categories represent an ordered continuum towards increased exogenous grit and dust or intrinsic dietary abrasives. Habitat structure is highly variable and climate and grassland preferences are "big picture" proxies for exogenous dust and thus may not be adequately representative of the actual situation. For example, there is little evidence that high browsers consume less intrinsically abrasive plant material than regular browsers. Second, coding these variables as continuous becomes an issue, and CAIC is unable to adequately deal with so many categorical variables. As Purvis and Rambaut (1995) explain, contrasts calculated between state 0 and state 1 may not be comparable with those calculated between state 1 and state 2. Finally, the relationship between grassland habitat and dust is unfounded. Healy and Ludwig (1965) found that sheep consumed more soil in areas where drainage was impeded compared to areas of good drainage.

Our finding that the directional relationship in ungulates between variation in feeding height and hypsodonty indices does suggest that differences in feeding height may reflect the amount of exogenous grit on ingested plant material. Unfortunately, an important confounding variable to consider in both the ungulate and rodent analyses is the fact that intrinsic abrasives are not necessarily the same in grasses versus browse found in the same feeding level, given the presence of greater amounts of silica phytoliths in grasses compared with browse. Furthermore, there is little control for the amount of internal abrasives and of cellulose contained within a cell wall that might require increased masticatory processing within a single grass plant. If one were to examine a single grass plant and the amount of internal abrasives compared with exogenous grit found along the height of the plant, one would probably find that these two features are inversely related. This is because new growth is short and interspersed by taller, tougher growth which has more cellulose and less protein in each cell wall (Bell, 1970). On the other hand, an animal that feeds on this new growth may also be ingesting more exogenous grit because it is closer to the ground. Because our results indicate that low-level feeders are indeed more

hypsodont than high level feeders, we hypothesize that the effect of intrinsic abrasives is negligible.

For rodents, the more clear-cut (and perhaps less precise) behavioral categories show that, independent of phylogenetic effects, diet and substrate preference are factors in the evolution of molar crown height. To further test the grit hypotheses in rodents, it would be helpful to include data on more fossorial species, particularly those that use their teeth to dig burrows (e.g., the mole rats). In the current data set, only *Ctenomys* is known to use its incisors for digging (Jarvis and Bennett, 1991), and this species has the highest relative molar crown of all species used in the analyses. Additionally, we cannot discount the influence of climatic variables as an additional explanation for evolutionary changes in molar crown height in rodents. Kay *et al.* (1999) report strong negative correlations between the proportion of species of hypsodont sigmodontine rodents at approximately 75 South American localities and mean annual precipitation, mean annual temperature, and the mean temperature of the coldest month, and a positive correlation with seasonal temperature amplitude.

Partitioning the effects of diet and grit on the evolution of tooth crown height provides a comparative method for understanding the selective forces leading to hypsodonty or hypseledonty. It is generally (and simplistically) accepted that while increasing tooth crown height is one mechanism to maintain a functional tooth in the face of intensive wear, crown height *per se* does not measure actual wear. Currently, there have been no comparative studies citing empirical evidence on the actual rate of tooth wear in relation to diet and other behavioral or habitat preferences in ungulates or rodents, nor is there any evidence for the rate of wear of the various dental tissues. Furthermore, quantification of the proportions of the various dental tissues exposed to wear at the occlusal surface in different species is an additional mitigating factor that has yet to be researched. Despite this, our study supports the conclusions of Janis (1988) that measures of tooth crown height alone are not sufficient for determining dietary preference in fossils because there are other factors which may select for maintaining or increasing tooth crown height. Given the results presented above, the timing of a trend towards increase in hypsodonty in many mammalian herbivores cannot be viewed solely as a response to the spread of grassland environments. Instead, additional of paleoecological and paleoclimatic information specifically relating to an increase in dust and grit on plant material (e.g., volcanism and wind-blown pyroclastic dust) need to be considered.

ACKNOWLEDGMENTS

Appendix 1. Ungulate Behavioral and Habitat Data

Species	Diet	Foraging height	Climate	Grassland habitat
Addax nasomaculatus	mixed/monocots	—	arid	—
Aepyceros melampus	mixed/dicots	medium	mesic	—
Alcelaphus buselaphus	monocots	tall plants/trees	arid	secondary
Ammodorcas clarkei	dicots	tall plants/trees	arid	—
Ammotragus lervia	mixed/dicots	—	arid	—
Antidorcas marsupialis	mixed/dicots	ground	wet	secondary
Capra ibex	mixed/dicots	ground	arid	—
Cephalopus dorsalis	dicots	—	wet	edaphic
Cephalophuys monticola	dicots	—	wet	edaphic
Cephalophus silvicultor	dicots	ground	wet	edaphic
Cephalophus spadix	dicots	—	wet	edaphic
Ceratotherium simum	monocots	ground	mesic	—
Connochaetes gnou	monocots	—	mesic	—
Connochaetes taurinus	monocots	ground	mesic	secondary
Damaliscus dorcas	monocots	medium	mesic	secondary
Damaliscus hunteri	mixed/monocots	—	arid	secondary
Damaliscus lunatus	monocots	medium	mesic	edaphic
Diceros bicornis	dicots	tall plants/trees	mesic	—
Dorcatragus megalotis	mixed/dicots	—	arid	—
Equus asinus	monocots	—	arid	secondary
Equus burchelli	monocots	—	mesic	secondary
Equus greyvi	monocots	—	mesic	secondary
Equus zebra	monocots	—	arid	secondary
Gazella granti	mixed/dicots	ground	arid	secondary
Gazella thomsoni	mixed/monocots	ground	arid	secondary
Giraffa camelopardalis	dicots	tall plants/trees	mesic	—
Hemitragus jehmlahicus	mixed/monocots	—	arid	secondary
Hippotragus equinus	monocots	medium	mesic	secondary
Hippotragus niger	monocots	medium	mesic	—
Kobus ellipsiprymnus	monocots	medium	mesic	edaphic
Kobus kob	monocots	ground	mesic	edaphic
Kobus lechwe	monocots	ground	mesic	edaphic
Kobus vardoni	monocots	ground	mesic	edaphic
Litocranius walleri	dicots	tall plants/trees	arid	—
Madoqua kirki	dicots	tall plants/trees	arid	—
Neotragus pygmaeus	dicots	—	wet	—
Nesotragus moschatus	dicots	—	wet	—
Okapia johnstoni	dicots	tall plants/trees	wet	—
Oreotragus oreotragus	dicots	ground	mesic	—
Oryx gazella	mixed/monocots	—	arid	secondary
Ourebia ourebi	mixed/monocots	ground	mesic	edaphic
Pelea capreolus	mixed/monocots	—	arid	—
Pseudois nayaur	—	—	arid	—
Raphicerus campestris	mixed/dicots	ground	arid	secondary
Raphicerus melanotis	mixed/dicots	—	arid	—
Redunca arundinum	monocots	tall plants/trees	mesic	edaphic
Redunca fulvorufula	mixed/monocots	ground	mesic	secondary
Silvicapra grimmia	dicots	ground	—	—
Syncerus caffer	monocots	tall plants/trees	—	edaphic
Taurotragus oryx	mixed/dicots	—	arid	secondary
Tragelaphus angasi	mixed/dicots	—	mesic	—
Tragelaphus buxtoni	dicots	—	mesic	—
Tragelaphus euryceros	dicots	ground	wet	edaphic
Tragelaphus imberbis	dicots	tall plants/trees	mesic	—
Tragelaphus scriptus	dicots	medium	wet	edaphic
Tragelaphus spekei	dicots	tall plants/trees	wet	edaphic
Tragelaphus strepsiceros	dicots	tall plants/trees	mesic	secondary

Diet and habitat data for ungulate species are taken from Du Toit (1990), Estes (1974 and 1992), Hofmann and Stewart (1972), Spencer (1995), and Stuart and Stuart (1997). —: unknown.

Appendix 2. Rodent Molar Crown Heights and Behavioral Data

Species	Relative m1 crown height	Diet	Substrate preference
Agouti paca (2)	1.34	leaves/seeds	terrestrial/semi-aquatic
Akodon cursor (2)	0.60	fruits/animals	terrestrial/semi-aquatic
Akodon ulrichi (2)	0.60	fruits/animals	terrestrial/semi-aquatic
Bolomys lasiurus (2)	1.01	leaves/seeds	terrestrial/semi-aquatic
Calomys callosus (2)	0.77	fruits/animals	semi-arboreal
Cavia aperea (2)	2.80	grass	terrestrial/semi-aquatic
Clyomys laticeps (2)	0.80	leaves/seeds	terrestrial/semi-aquatic
Coendu prehensilis (3)	0.57	leaves/seeds	arboreal
Ctenomys magellanicus (2)	4.15	grass	terrestrial/semi-aquatic
Dactylomys dactylinus (2)	0.46	leaves/seeds	arboreal
Dasyprocta agouti (2)	1.37	leaves/seeds	terrestrial/semi-aquatic
Dasyprocta fugilinosa (2)	1.54	leaves/seeds	terrestrial/semi-aquatic
Dasyprocta punctata (2)	1.17	leaves/seeds	terrestrial/semi-aquatic
Dinomys branickii (2)	0.72	leaves/seeds	arboreal
Diplomys labilis (1)	0.61	—	arboreal
Dolichotis salinicola (3)	3.79	grass	terrestrial/semi-aquatic
Echimys armatus (2)	0.81	leaves/seeds	arboreal
Echimys semivillosus (2)	0.81	leaves/seeds	arboreal
Galea musteloides (2)	3.36	grass	terrestrial/semi-aquatic
Galea spixii (2)	3.57	grass	terrestrial/semi-aquatic
Heteromys anomalus (2)	1.25	leaves/seeds	terrestrial/semi-aquatic
Heteromys australis (2)	1.36	leaves/seeds	terrestrial/semi-aquatic
Holochilus brasiliensis (2)	0.77	leaves/seeds	semi-arboreal
Hoplomys gymnurus (2)	0.85	leaves/seeds	terrestrial/semi-aquatic
Hydrochaeris hydrochaeris (3)	2.80	grass	terrestrial/semi-aquatic
Ichthyomys hydrobates (2)	0.39	fruits/animals	terrestrial/semi-aquatic
Isothrix bistriata (2)	0.87	—	arboreal
Isothrix paghrus (2)	0.86	—	arboreal
Kunsia tomentosus (1)	0.47	leaves/seeds	terrestrial/semi-aquatic
Lagostomus maximus (2)	2.78	grass	terrestrial/semi-aquatic
Mesomys hispidus (1)	0.63	fruits/animals	arboreal
Microcavia australis (2)	3.52	grass	terrestrial/semi-aquatic
Microsciurus flaviventer (2)	0.50	fruits/animals	arboreal
Myocastor coypus (2)	1.23	leaves/seeds	terrestrial/semi-aquatic
Myoprocta acouchy (2)	1.45	leaves/seeds	terrestrial/semi-aquatic
Myoprocta pratti (2)	1.16	leaves/seeds	terrestrial/semi-aquatic
Nectomys squamipes (2)	0.67	fruits/animals	terrestrial/semi-aquatic
Oryzomys capito (2)	0.95	leaves/seeds	semi-arboreal
Oxymycterus roberti (1)	1.01	fruits/animals	terrestrial/semi-aquatic
Phyllotis darwini (2)	1.01	leaves/seeds	terrestrial/semi-aquatic
Proechimys brevicauda (3)	1.16	leaves/seeds	terrestrial/semi-aquatic
Proechimys cuvieri (2)	1.00	leaves/seeds	terrestrial/semi-aquatic
Proechimys guyannensis (2)	0.96	leaves/seeds	terrestrial/semi-aquatic
Proechimys longicaudatus (2)	1.02	leaves/seeds	terrestrial/semi-aquatic
Proechimys semispinosus (3)	0.98	leaves/seeds	terrestrial/semi-aquatic
Proechimys simonsi (3)	0.89	leaves/seeds	terrestrial/semi-aquatic
Pseudoryzomys simplex (1)	0.47	—	terrestrial/semi-aquatic
Rhipidomys couesi (2)	0.62	leaves/seeds	arboreal
Sciurus granatensis (2)	0.49	leaves/seeds	semi-arboreal
Sciurus ignitus (2)	0.44	fruits/animals	semi-arboreal
Sciurus igniventris (2)	0.46	leaves/seeds	semi-arboreal
Sciurus spadiceus (2)	0.65	leaves/seeds	semi-arboreal
Sigmodon hispidis (2)	0.72	fruits/animals	terrestrial/semi-aquatic
Thrichomys apereoides (2)	1.01	leaves/seeds	semi-arboreal
Tylomys mirae (2)	0.57	—	semi-arboreal

Sample sizes indicated in parentheses. Diet and substrate preference data are from Kay and Madden (1997).
—: unknown.

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