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Ecological generalization during adaptive radiation: evidence from Neogene mammals

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ABSTRACT

Question: How does the evolution of a key adaptation affect niche breadth during an adaptive radiation?

Organisms: Cenozoic horse and camel species, as well as Pleistocene ungulates.

Predictions: Niche breadth theoretically could increase, decrease or remain the same as attainment of a key adaptation facilitates a niche shift. Simpson predicted a decrease in niche breadth (ecological specialization) when key adaptations lead to adaptive radiations. I test Simpson's prediction by examining ecological response to attainment of high-crowned teeth (hypsodonty). The evolution of hyposdonty represents a key adaptation involved in many ungulate adaptive radiations.

Methods: To test whether hypsodont ungulates have potentially wider or narrower niche breadth in respect to their non-hypsodont, pre-adaptive radiation ancestors, I analysed $\delta^{13}C$ values in the tooth enamel of Pleistocene ungulates as a proxy for dietary breadth. For Cenozoic horses and camels, I measured the total number of biogeographic provinces and the total number of fossil localities in which individual taxa were found to assess breadth of habitat use. I considered these two parameters (dietary breadth and habitat breadth) as two major niche axes from which I qualitatively estimated niche breadth. I also compared taxon survival between low-crowned and high-crowned taxa, reasoning that if high-crowned taxa had less broad niches, their probability of extinction should be higher and their temporal duration shorter.

Results: The $\delta^{13}C$ values of herbivores from the Pleistocene of Florida revealed that high-crowned taxa fed on a diet of both C_3 and C_4 forage, while low-crowned taxa confined their feeding to C_3 plants. In the Cenozoic horse and camel clades, there was no statistically significant difference between high-crowned and low-crowned taxa in the number of biogeographic provinces or localities occupied. Nor were there significant differences between high-crowned and low-crowned taxa in the duration of time a particular species survived.

Conclusions: Simpson's prediction that key adaptations that lead to adaptive radiation also result in decreased niche breadth is not supported in the case of the evolution of hypsodonty by the ungulates. Instead, the attainment of hypsodonty in these taxa broadened niche space along one of the studied axes (dietary variety) and had no discernible effect on the other (habitat occupancy).

Keywords: adaptive radiation, diet, habitat, hypsodonty, key adaptation, mammal,
niche breadth, Ungulata

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INTRODUCTION

Key adaptations are the evolution of new traits that lead to increased diversification rates in an ensuing clade (Heard and Hauser, 1995; Hunter, 1998). It has been suggested that during an adaptive radiation, species become ecologically specialized (Simpson, 1944, 1953, 1967; Schluter, 2000), which implies that the derived taxa have narrower niches than the more ancestral taxa. The derived taxa are stenotopic compared with their eurytopic ancestors (Futuyma and Moreno, 1988). One potential consequence of ecological specialization is increased probability of extinction (Simpson, 1944, 1953, 1967; Schluter, 2000).

However, morphological adaptations can result in increased specialization (narrowing of ecological niche) or expansion of the suite of lifestyles available to an organism (increasing niche breadth). A practically and theoretically important question thus arises: Are key adaptations 'key' because they reduce or expand niche breadth? Addressing this question is the major focus of this study, which concentrates on niche effects of hypsodonty – high-crowned teeth – in now extinct ungulates.

Hypsodonty, or the condition of having high-crowned teeth, is implicated as a key adaptation for the Equidae because its appearance was one of the suite of features that characterized the adaptive radiation of horses during the early Miocene [ca. 20 million years ago (Ma)] of North America (MacFadden, 2000; Simpson, 1953). Hypsodonty qualifies as a key adaptation, as it 'relaxes the rules of trade-off' (Rosenzweig and McCord, 1991), permitting individuals with higher crowns to feed and survive longer on a particular resource than similar low-crowned individuals as the teeth of the former take longer to wear. Furthermore, hypsodonty has been interpreted as having evolved in response to specialization into a grazing niche from a browsing niche (Simpson, 1944, 1953; Stirton, 1947; Janis *et al.*, 2000, 2002; MacFadden, 2000), and/or a response to increasingly gritty foods (Janis, 1988, 1990).

Hypsodonty lends itself well to the proposed study:

- It clearly has an important function in feeding in ungulates (Fortelius, 1985).
- It has been implicated in the adaptive radiation of horses, noted above, as well as in many other herbivore clades (MacFadden, 2000).
- There is an inverse relationship between the number of brachydont and hypsodont taxa in the fossil record during the early Miocene (Janis *et al.*, 2000, 2002).
- Its evolution has been argued to indicate specialization on grasses or open habitat plants (niche narrowing) or generalization on wider forage varieties (niche broadening) (Simpson, 1944, 1953; Stirton, 1947; Feranec, 2003a, 2004).
- Teeth are commonly preserved in the fossil record and are amenable to relevant morphological and isotopic analyses.

This study uses the presence of hypsodonty to test the hypothesis that niche breadth decreases as this key adaptation spreads and intensifies during an adaptive radiation.

Hypothesis testing and predictions

Hypothesis 1 (H1): *There is a trend towards decreasing niche breadth (ecological specialization) during an adaptive radiation signalled by the attainment of hypsodonty.*

This study analyses niche breadth using two of the many potential axes that define niche hypervolumes, dietary variety and habitat occupancy. For H1 to be supported, three predictions must hold true.

Prediction 1: *Ungulate diet will shift and the degree of dietary variety will not increase in hypsodont taxa.*
Prediction 2: *Habitat occupancy, as defined by the number of biogeographic provinces and number of sites per province occupied, will not increase.*
Prediction 3: *Hypsodont taxa will have a higher probability of extinction than taxa that do not exhibit the key adaptation. This follows from the observation that taxa with narrow niches tend to become extinct more often than those with broad niches.*

To test these predictions, I examine:

- isotopic data in Pleistocene taxa from a restricted but well-studied geographic area (Florida);
- the correlation between hypsodonty index and number of habitats occupied by horse and camel taxa throughout the Cenozoic; and
- the relationship between species longevity and extinction in relevant taxa using a variety of statistical and phylogenetic techniques.

Data inconsistent with these three predictions lead to rejection of H1 that niche breadth decreased with attainment of hypsodonty, and opens the possibility for two alternative hypotheses:

Alternative hypothesis 1 (AH1): *Adaptive radiation resulting from hypsodonty has no effect on niche breadth. Predictions of this hypothesis are that no differences should be observed in ungulate diet, habitat occupancy or taxon longevity.*
Alternative hypothesis 2 (AH2): *Adaptive radiation resulting from hypsodonty increases niche breadth. Predictions of this hypothesis are that the range of ungulate diet and habitat occupancy should increase, and taxon longevity should not decrease in hypsodont taxa with respect to non-hypsodont taxa.*

BACKGROUND

Adaptive radiation, specialization, and generalization: definitions

In this study, the term 'ecological generalist' is used for taxa that are eurytopic (Futuyma and Moreno, 1988), and are able to utilize a wide range of resources. 'Ecological specialists', in contrast, are stenotopic (Futuyma and Moreno, 1988), and depend on certain subsets of resources. Generalists are able to eat a wide variety of resources, while specialists are constrained to a relatively narrow range of foods. Generalist taxa will also live in a wider variety of habitats than specialists. Using the niche model of Hutchinson (1958), generalist taxa have a wider niche breadth (Colwell and Futuyma, 1971) than do specialists.

Here I follow Simpson's (1953) concept of adaptive radiation. He suggested that much of evolutionary diversification occurred during adaptive radiations, which are defined by geologically rapid speciation from a single ancestor into many taxa. Furthermore, Simpson (1953) proposed that the radiations were the result of selection acting on generalist populations that moved into new adaptive zones. Speciation into this previously unexploited niche space was made possible by the attainment of key adaptations (Simpson, 1953).

The idea of generalist ancestors diversifying into specialist descendants has been contested by the reconstruction of ancestral ecological states (Schluter, 2000). This technique, which determines the ecology of ancestral taxa by working down a phylogeny from the states displayed by extant taxa and comparing sister taxa and nodes, assumes that fossils do not provide enough information to accurately describe ancestral ecologies (Schluter, 2000). However, recently developed online databases (e.g. The Paleobiology Database, Miomap) and analytical techniques (e.g. isotope geochemistry, functional morphological considerations) provide information on body mass, diet, longevity, as well as environment and location of deposition, allowing for the ecologies of many ancient taxa to be reasonably represented.

Niche breadth and ecological variability

The breadth of niche space occupied by a taxon at any one time may never represent the total breadth that the taxon could occupy, or that it may occupy through time. In other words, a taxon's realized niche (*sensu* Hutchinson, 1958) at any one place in time probably only reflects a portion of that taxon's fundamental niche (*sensu* Hutchinson, 1958). This could be caused by biotic interactions with other organisms, or the result of particular environmental conditions affecting the ecosystem at a particular time (Jackson and Overpeck, 2000). The niche space utilized in different places and at different times can be summed to help determine the total possible niche space. The part of the niche that a taxon actually uses at a specific time and place can be expressed as the observed range of values that a taxon displays for a relevant characteristic (i.e. morphological or ecological) at that time and place. Variability is the sum of all the observed ranges in the given measurement over time and space (Gould, 2002). In this study, it is detection of the summed variability in niche breadth, or sum total of realized niche space, that is required to test the hypotheses. It is impossible to analyse every portion of an *n*-dimensional niche, but the two axes examined in this study (aspects of diet and habitat occupation) are important proxies for resource utilization and niche occupation for particular species (Schoener, 1974).

Carbon isotopes and diet

Carbon isotope values are analysed as a proxy for ancient herbivore diet. The carbon isotope values found in fossil mammal tooth enamel are useful in determining diet in ancient animals because three different photosynthetic pathways used by plants, C_3, C_4, and crassulacean acid metabolism (CAM), impart different ratios of $^{13}C/^{12}C$ in different kinds of plants. Teeth of animals that feed on different kinds of plants will reflect the isotope ratio ($^{13}C/^{12}C$) ingested (DeNiro and Epstein, 1978; Quade *et al.*, 1992). Tropical, warm-season grasses and sedges using the C_4, or Hatch-Slack, photosynthetic pathway are enriched in the heavy carbon isotope (^{13}C). On the other hand, C_3, or Calvin cycle plants, including most trees and shrubs (browse) as well as high-latitude grasses, are enriched in the light carbon isotope (^{12}C). The third pathway, the CAM pathway, is characteristic of succulents (e.g. cacti) and incorporates intermediate ratios of ^{12}C and ^{13}C (O'Leary, 1988; Ehleringer *et al.*, 1991; Ehleringer and Monson, 1993).

The results in isotopic studies are compared using the following equation: $\delta^{13}C = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$. All isotope values are reported relative to the V-PDB standard. The $\delta^{13}C$ value of tooth enamel is further enriched by a consistent amount, which is +14.1 ±0.5‰ for medium- to large-bodied mammals (Cerling and Harris, 1999). Although post-depositional diagenesis can overprint carbon isotope values in bone (Schoeninger and DeNiro, 1982), tooth enamel is not prone to diagenetic alteration, and will reliably reflect stable-isotope values derived from feeding (Quade *et al.*, 1992; Wang and Cerling, 1994; Koch *et al.*, 1997).

In general, non-selective feeders of grasses and sedges (grazers) are predominantly C_4 feeders, the more selective tree and shrub foliage feeders (browsers) are predominantly C_3 foragers, while intermediate feeders that eat grasses as well as leaves on trees and shrubs will incorporate isotopic values from both C_3 and C_4 plants. Caution must be used when interpreting carbon isotope values from herbivore tissue because some grasses typically found above 43°N latitude use the C_3 pathway, some shrubs and trees (browse) use the C_4 pathway, especially in lower latitudes and more arid climates, and animals that feed on succulents (CAM plants) can show $\delta^{13}C$ values similar to either C_3 or C_4 feeders (Teeri and Stowe, 1976; Stowe and Teeri, 1978; O'Leary, 1988; Tieszen *et al.*, 1997). Interpretations presented below take these caveats into account.

I assume that herbivores did not make succulents a significant part of their diet, and consider the isotopic effects of CAM photosynthesis but only briefly. This is because CAM photosynthesis is typically found in xeric habitats that are generally not widespread (Ehleringer *et al.*, 1991). Moreover, a very small percentage of extant large ungulates browse on succulents (Janis and Ehrhardt, 1988).

Stable carbon isotope values in paleoecology

Herbivores will generally reflect the carbon isotope values of plants ingested. Trees, shrubs, and high-latitude grasses, which are C_3 plants, have mean $\delta^{13}C$ values of −27.0 ±3.0‰. This figure contrasts with tropical grasses and sedges, C_4 plants, which have mean isotopic values of −13.0 ±2.0‰ (O'Leary, 1988; Koch, 1998; Kohn and Cerling, 2002). Setting the fractionation from plant material to tooth enamel at +14.0‰ in large mammalian herbivores (Cerling and Harris, 1999), extant taxa that feed solely on C_3 plants will display enamel carbon isotope values between −16.0‰ and −10.0‰, while modern taxa that feed solely on C_4 plants exhibit isotopic values between −1.0‰ and +3.0‰. The plant and ultimately enamel isotope values are derived from the $\delta^{13}C$ value of the modern atmosphere, which has decreased −1.5‰, from −6.5‰ to about −8.0‰, due to fossil fuel burning over the last 200 years (Friedli *et al.*, 1986; Marino and McElroy, 1991; Marino *et al.*, 1992). For this reason, enamel isotope values from prehistoric specimens are expected to be about 0.5–1.3‰ more positive than the modern taxa due to $\delta^{13}C$ differences in the atmosphere during past glacial and interglacial periods compared with the modern (Koch, 1998). For fossil taxa, a diet of pure C_3 plants would not have an isotopic value more positive than −8.7‰, while a diet of pure C_4 plants would not have an isotopic value more negative than −0.5‰. Using these values as endpoints in a continuum between 100% C_3 feeding and 100% C_4 feeding, values more negative than −7.9‰ are interpreted to indicate primarily browsing (defined as < 10% C_4 diet), values more positive than −1.3‰ are interpreted to signal primarily grazing (here defined as < 10% C_3 diet), and values between −7.9‰ and −1.3‰ result from intermediate feeding strategies (defined as > 10% C_4 diet but < 90% C_4 diet).

MATERIALS AND METHODS

Stable carbon isotope values in herbivores

To test Prediction 1, which concerns the variability in the diet of hypsodont versus non-hypsodont herbivores, I concentrated on a discrete geographic region, Florida, and a time period for which abundant specimens and data were available, the Rancholabrean (the last part of the Pleistocene, currently thought to extend from 210,000 to 9500 years B.P.) (Bell *et al.*, 2004). I tabulated previously published $\delta^{13}C$ values from 198 individuals from the Rancholabrean of Florida (MacFadden and Cerling, 1996; Koch *et al.*, 1998; Feranec and MacFadden, 2000; Feranec, 2003a; Hoppe and Koch, 2006). The data comprise nine herbivore (and possibly omnivore) taxa including the four hypsodont taxa *Bison antiquus, Equus* sp., *Hemiauchenia macrocephala*, and *Mammuthus columbi*, and the five brachyodont taxa *Mammut americanum*, *Mylohyus fossilis*, *Odocoileus virginianus*, *Platygonus compressus*, and *Tapirus veroensis*. The analysis focuses on the generic level for *Equus* because species identifications were not available from utilized literature, and because the dental remains that were sampled may not be identifiable at the species level.

Isotopic data from the Rancholabrean of Florida is ideal for testing Prediction 1 for four reasons:

1. The taxa mentioned above are abundant during this time period throughout the entire state, making robust statistical analyses on the isotopic data possible.
2. The sample is spatially and temporally averaged to the extent necessary to appreciate fully the range of vegetation that the taxa were eating. Florida covers a wide range of habitat types, which should allow the total variability in diet to be represented (Feranec, 2004). Also, the variations in climate and vegetation structure that occurred throughout the Rancholabrean should sample a fuller representation of a taxon's potential dietary variability, as compared to relying on data from more temporally restricted slices of time.
3. Nearly all present-day browse in Florida is C_3 [> 97% (Stowe and Teeri, 1978)], and most of the grasses and many sedges (e.g. the plants that grazers eat) are C_4 [> 63% for Poaceae and up to 43% for Cyperaceae (Teeri and Stowe, 1976; Sage *et al.*, 1999)]. Therefore, interpretation of browsing versus grazing based solely on isotopic values is relatively straightforward. Although C_3 grasses and sedges are present, representing up to 40% of the species richness of grasses, these are unlikely to confound interpretations, because those plants are of low abundance and occur only in restricted areas. That has been demonstrated by studies on the modern floral composition of two sites positioned near pertinent fossil localities (Easley and Judd, 1990; Huffman and Judd, 1998). The C_3 grasses and sedges appear restricted to wetter areas – not habitats where one would expect to find the cursorial ungulates studied in this report (Easley and Judd, 1990; Huffman and Judd, 1998).

It is likely that C_3 grasses and sedges were even less abundant on Pleistocene landscapes. Grimm *et al.* (1993) showed that during glacial stages, local flora fluctuated from drier, *Quercus*-dominated vegetation to wetter, *Pinus*-dominated vegetation but did not include significant numbers of plants that are not still on the landscape. Vegetation models for the Last Glacial Maximum (for about 20 ka) suggest an overall spread of open vegetation (grasslands) and an increase in the dominance of grasses and sedges using C_4 photosynthesis due to decreasing CO_2 levels (Webb, 1991; Ehleringer *et al.*, 1997; Cowling, 1999; Jackson and Overpeck, 2000). This would suggest that percentages of C_3 grasses in Florida are unlikely to have been significantly greater during the past, assuming the vegetation model is representative for all glacial periods and that the current interglacial is characteristic of past interglacials. Since C_4 browse is rare, it is unlikely that these percentages have changed significantly either. These considerations suggest that the conclusions about Prediction 1 are conservative in using the modern flora as an interpretive analogue in this study, because I am likely underestimating the abundance of C_4 grass that was available to taxa through the late Pleistocene.

4. The Rancholabrean represents an 'end-point' of the adaptive radiation that the key innovation of hypsodonty triggered beginning in the Miocene. Therefore, taxa have had ample time to evolve a broad range of potential life-history strategies (i.e. for selective pressures to turn ancestral generalized taxa into descendent specialists).

Habitat occupation: biogeographic provinces and localities

It is generally difficult to determine the type of habitat (vegetation assemblage) present at a particular vertebrate fossil locality. Different requirements for preservation generally preclude fossil bone and ancient plant material occurring together in integrated deposits (Schopf, 1975; Ferguson, 1986; Lyman, 1994; Burney, 1999). Fossils also could have been transported from some distance from the habitat in which the animal lived. Cenogram analysis, a graphic examination of the rank-size distribution of mammal species within a community, is one technique that has been used to identify major habitats in which animals represented by vertebrate fossils lived (Legendre, 1986), but this technique has been criticized on several grounds (Legendre, 1986; Rodriguez, 1999; Alroy, 2000). Many other types of analyses, besides cenograms, have also been used to provide insight into aspects of the habitats occupied by vertebrates, especially food availability and amount of openness in vegetation structure. Such studies, including mean hypsodonty at a locality (Fortelius *et al.*, 2002), overall mammalian community composition (Fernandez and Pelaez-Campomanes, 2003), or the diversity of a particular taxon at a locality (Montuire *et al.*, 1997), have each been correlated to aspects of climate or vegetation type. However, it has been particularly difficult to use fossil vertebrates themselves to distinguish between specific and clear-cut habitat types such as grasslands, woodlands or a closed canopy.

Testing Prediction 2 relies only on determining comparable estimates of the range of habitats occupied by certain taxa, not specific aspects of the habitats. Such information is easier to infer than details about habitat *per se*. To determine range of habitat occupation in this study, the number of North American biogeographic regions, together with the total number of localities in which a fossil is found, are used as a proxy for habitat number of habitats occupied – the more biogeographic regions or localities in which a taxon is present, the more habitats it is assumed to occupy. Modern taxa provide support for this assumption, as they are related to particular vegetation assemblages by their association with flora in biotic provinces (Brown *et al.*, 1998) or ecoregions (Ricketts *et al.*, 1999). The presence of a taxon in a higher number of biogeographic regions would signify occurrence in a higher number of biotic provinces or ecoregions and consequently a larger variety of vegetation assemblages.

The taxa involved in testing Prediction 2 are Miocene in age; therefore, I used the biogeographic provinces delineated in Janis *et al.* (1998), as modified from Tedford *et al.* (1987). Those provinces take the distribution of ancient ungulates, especially Miocene ungulates, into consideration. Roughly they correspond to provinces defined by modern mammals

(Hagmeier and Stults, 1964), although clearly the attributes and position of boundaries of each region were different in the Miocene with respect to the modern regions (Barnosky and Carrasco, 2002; Barnosky *et al.*, 2005).

Analyses were done by plotting hypsodonty in horses and camels taxa against the number of biogeographic provinces and localities in which taxa were found. Hypsodonty is generally measured and expressed as the hypsodonty index (HI = tooth crown height/tooth crown length), which standardizes the height of the tooth with body size (Van Valen, 1960). If the more specialized, hypsodont taxa indeed do show less habitat variability, as predicted by the hypotheses, they should be found in fewer biogeographic provinces and localities than the ecologically generalized brachyodont taxa.

Upper first molar (M1) hypsodonty indices for horses were obtained from the original data of MacFadden (1988, personal communication April 2002), as well as from Forsten (1975), MacFadden (1984), and Hulbert (1987, 1988a, 1988b). Camel hypsodonty indices for upper second molars (M2) were obtained from measurements I took on specimens in the University of California Museum of Paleontology and the University of Florida Museum of Natural History, and represent the maximum measured hypsodonty indices for the studied camel taxa. In many cases, these measurements for camels still represent worn teeth; thus the hypsodonty index is a minimum value. M2 rather than M1 hypsodonty indices were measured for camels to increase sample size.

Species longevity and extinction

One of the potential consequences of specialization is an increased probability of extinction (Simpson, 1944, 1953, 1967; Schluter, 2000). To determine whether the attainment of hyposodonty represented such a specialization, I used data from raw data files of the North American Paleofaunal Database (Alroy, 2002), now part of the Paleobiology Database (www.paleodb.org). I derived the first and last appearance dates of species from the localities in which they occur. If a species was found in only one locality, or when all locality dates were the same, a value of 0.1 million years was set as the species longevity. Prediction 3 claims that more hypsodont taxa should survive for a shorter length of time than brachydont taxa.

Phylogenetic inheritance and analyses using phylogenetically independent contrasts

Taxa, and consequently the morphological characteristics that a taxon displays, are linked by their phylogenetic history (Felsenstein, 1985; Harvey and Pagel, 1991). Because of the relationship between the morphological characteristics of ancestors and descendants, values for morphological features do not represent independent variables when comparisons are made among taxa. Using the values as independent variables in traditional statistical methods results in the inflation of the degrees of freedom, which results in increased acceptance of hypotheses when they are false (Type I errors) (Martins and Garland, 1991; Garland *et al.*, 1992, 1993). Attempting to take phylogenetic history into account, I employed the phylogenetically independent contrasts (PIC) methodology (Felsenstein, 1985; Martins and Garland, 1991; Garland *et al.*, 1992, 1993). Independent contrasts were obtained utilizing the comparative analysis by independent contrasts (CAIC) statistical package for the Apple Macintosh, version 2.0 (Purvis and Rambaut, 1995).

A detailed method for calculating independent contrasts is provided in Felsenstein (1985) and Garland *et al.* (1999). Very briefly, independent contrasts are calculated by subtracting the value of a particular characteristic between sister taxa or nodes, followed by dividing that value by the square root of the sum of its branch lengths (Garland *et al.*, 1999). In a phylogeny with no polytomies having X taxa, there will be $X-1$ independent contrasts. Independent contrasts were calculated for species longevity using the horse phylogeny (Fig. 1) and camel phylogeny (Fig. 2). The species level horse phylogeny was adapted from Hulbert (1987, 1988a, 1988b), Hulbert and MacFadden (1991), and MacFadden (1992). The camel phylogeny was modified from Honey *et al.* (1998). Because using a species' longevity as representative of branch length was not possible, I allowed the CAIC program to assign branch lengths with the assumption of punctuational change (Purvis and Rambaut, 1995). The assumption of punctuational change is supported by rapid cladogenesis occurring during the early radiation of the Equidae (MacFadden and Hulbert, 1988; Hulbert and MacFadden, 1991).

Fig. 1. Species level horse phylogeny used to determine phylogenetically independent contrasts in hypsodonty and species longevity. The phylogeny was adapted from Hulbert (1987, 1988a, 1988b), Hulbert and MacFadden (1991), and MacFadden (1992).

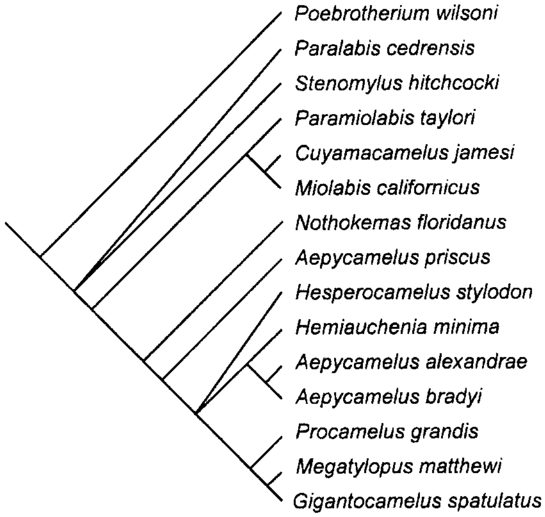

Fig. 2. Species level camel phylogeny used to determine phylogenetically independent contrasts in hypsodonty and species longevity. The camel phylogeny was modified from Honey *et al.* (1998).

Punctuational change was also assumed in the camels for statistical consistency. Furthermore, Diaz-Uriarte and Garland (1998, p. 654) have shown that even if there are branch length errors, 'independent contrasts are a robust method for testing hypotheses of correlated evolution'.

Other statistical tests

Standard linear regression, a non-phylogenetically based statistical test, was applied to the species longevity data for comparison with the results obtained from the PIC method. This technique was also applied to the biogeographic province and locality occupation data. Analyses of variance (ANOVA), together with *post-hoc* Tukey-Kramer honest significant difference tests (HSD) (SAS Institute, 2005), were performed among taxa for the stable isotope data. The HSD tests are similar to *t*-tests, but take multiple comparisons into account reducing the probability of Type I error. Statistical significance for all tests was set at $P < 0.05$. Statistics were completed using JMP IN 5 for Students and MS Excel OS X.

RESULTS AND DISCUSSION

Stable isotopes and dietary variability in herbivores from Florida

There is no significant relationship between the number of specimens sampled and either the observed range in carbon isotope values ($P > 0.49$) or the standard deviation from the mean isotope value ($P > 0.9$). The isotope data indicate that hypsodont taxa had a wider dietary array than the more brachydont taxa (Fig. 3; Tables 1, 2). This rejects Hypotheses H1 and AH1, but is consistent with AH2. The significant differences in $\delta^{13}C$ values reinforce the idea that food resources were being partitioned in the late Pleistocene of Florida (Koch *et al.*, 1998; Feranec and MacFadden, 2000; Feranec, 2004). The brachydont taxa, with isotope values

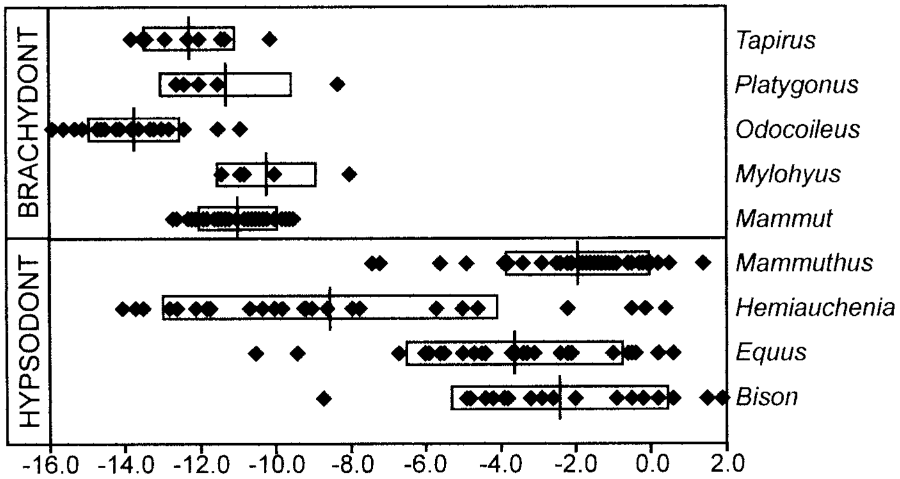

Fig. 3. Stable carbon isotope values from the Rancholabrean herbivore genera from Florida. Vertical lines represent means, while boxes around the mean represent one standard deviation. Hypsodont taxa show wider variability in $\delta^{13}C$ values than do brachydont taxa.

Table 1. Total number, mean, and standard deviation of stable carbon isotope values for herbivore genera from the Rancholabrean of Florida

Genera	*n*	Mean (‰)	Standard deviation (‰)
Hypsodont taxa			
Bison	19	−2.3	2.7
Equus	27	−3.8	2.7
Hemiauchenia	25	−8.5	4.4
Mammuthus	40	−1.9	2.0
Brachydont taxa			
Mammut	45	−11.1	0.9
Mylohyus	5	−10.2	1.3
Odocoileus	22	−13.8	1.2
Platygonus	5	−11.4	1.8
Tapirus	10	−12.4	1.2

below −7.9‰, are confined to feeding on a diet solely of C_3 plants, presumably browse. However, the hypsodont taxa are not confined to any of the dietary categories, having individuals capable of feeding on either C_3 browse or C_4 grasses and sedges, and appear to be more flexible in their dietary requirements. This result is supported by more ancient data where hypsodont horses from the Miocene of Florida were also found to have diets inclusive of both browse and grasses (MacFadden *et al.*, 1999).

A latitudinal gradient has been noted in the diversity of C_4 grasses in Florida, with a higher percentage of C_4 grasses occurring at lower latitudes (Sage *et al.*, 1999). A similar gradient is noted in the $\delta^{13}C$ values of large herbivore tooth enamel over the latest Pleistocene (Koch *et al.*, 1998; Feranec, 2004). A consequence of this gradient makes it difficult to determine if the

Table 2. Significant differences in carbon isotope values among genera based on *post-hoc* Tukey-Kramer HSD tests

	Bison	*Equus*	*Hemiauchenia*	*Mammuthus*	*Mammut*	*Mylohyus*	*Odocoileus*	*Platygonus*	*Tapirus*
Bison	–								
Equus	–	–							
Hemiauchenia	+	+	–						
Mammuthus	–	+	+	–					
Mammut	+	+	+	+	–				
Mylohyus	+	+	–	+	–	–			
Odocoileus	+	+	+	+	+	–	–		
Platygonus	+	+	–	+	–	–	–	–	
Tapirus	+	+	+	+	–	–	–	–	–

Note: $P \leq 0.05$: +, significant difference; –, no significant difference.

more negative $\delta^{13}C$ enamel isotope values, especially in samples from northern Florida, are due to the ingestion of C_3 grasses or C_3 browse. Based on the vegetation models and modern distribution of C_3 and C_4 plants, I assume that the individuals that have $\delta^{13}C$ values more negative than −7.9‰ are feeding on C_3 browse rather than C_3 grasses. Even so, it has been shown that C_3 plants have higher C:N and C:P ratios, making them more nutritious than C_4 forage (Caswell *et al.*, 1973; Heckathorn *et al.*, 1999). The wider array of $\delta^{13}C$ values displayed by hypsodont taxa would then imply a greater ability to forage on more nutritious or less nutritious plants, while the brachydont taxa are restricted to feed on the more nutritious plants. Similarly, if some of the more positive individual enamel isotope values are due to the ingestion of succulents using CAM photosynthesis, it supports the idea that hypsodont taxa had a wider dietary variability than did the brachydont taxa. However, as stated earlier, I presume that fossil taxa did not use succulents as a significant dietary component, which appears to be the case in modern ungulates (Janis and Ehrhardt, 1988).

The isotopic results for these Pleistocene taxa indicate that hypsodont taxa are ecological generalists, not specialists, in comparison to brachydont taxa. It would be desirable to conduct isotopic studies on early to middle Miocene faunas to attempt to bracket how closely in time the shift from restricted to more generalized diets corresponded with the development of hypsodonty within selected clades. Unfortunately, isotopic studies have generally been confined to fossils geologically younger than the C_4 global carbon shift that occurred worldwide 5–7 Ma. The lack of studies on pre-7 Ma taxa is because prior to the global carbon shift, pure C_3 environments prevailed, making it difficult to characterize isotopically dietary differences. However, recent studies (Wang and Cerling, 1994; MacFadden and Cerling, 1996; MacFadden *et al.*, 1996) have laid the groundwork for dietary analysis in pure C_3 environments and hint that it may become possible (Feranec, 2003b; Stewart *et al.*, 2003; Cerling *et al.*, 2004; MacFadden and Higgins, 2004; Feranec and MacFadden, 2006).

Habitat occupation: biogeographic provinces and localities

For the horses, there is no significant relationship between the level of hypsodonty and the number of biogeographic provinces ($r = 0.20$; $P > 0.11$) or localities ($r = 0.21$; $P > 0.12$) in which a taxon is found (Table 3, Fig. 4). In camels, the relationship is unclear. Camels show a significant relationship between the hypsodonty index and the number of biogeographic

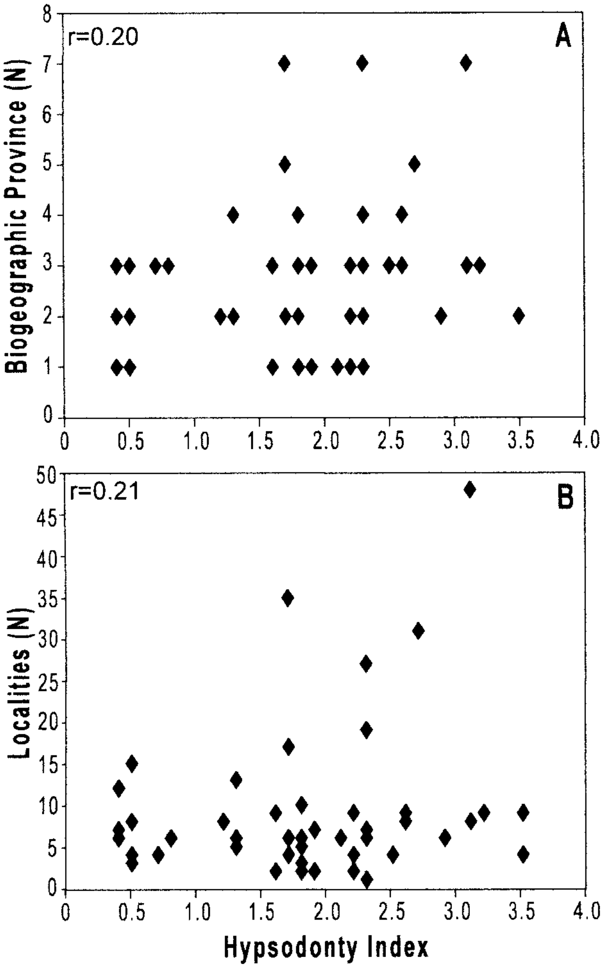

Fig. 4. Number of biogeographic provinces (A) and localities (B) in which horse taxa were found as a function of hypsodonty index. One single data point represents one particular species. The relationship among the data points is not significant.

provinces ($r = 0.64$; $P > 0.009$) and localities ($r = 0.53$; $P > 0.04$) occupied (Table 4, Fig. 5). This trend, however, is driven by one taxon, *Procamelus grandis*, which is found in many biogeographic provinces and localities. When *Procamelus grandis* is removed from the analysis, the statistical significance disappears. These analyses reject H1 – they contradict the prediction that habitat occupancy should decrease in specialized taxa. The trend in slopes portrayed in the data is consistent with AH2 (decreasing habitat specialization with hypsodonty), which predicts the more hypsodont horses and camels should be found in more biogeographic provinces and localities. The data also are consistent with AH1 (no difference in hypsodont versus non-hypsosdont taxa). Distinguishing whether the data support AH1 over AH2 is difficult, since the lack of significant correlations in the data implies support for AH1, while the trend in the data is highly suggestive of supporting AH2. More data will be needed to distinguish between these two alternatives.

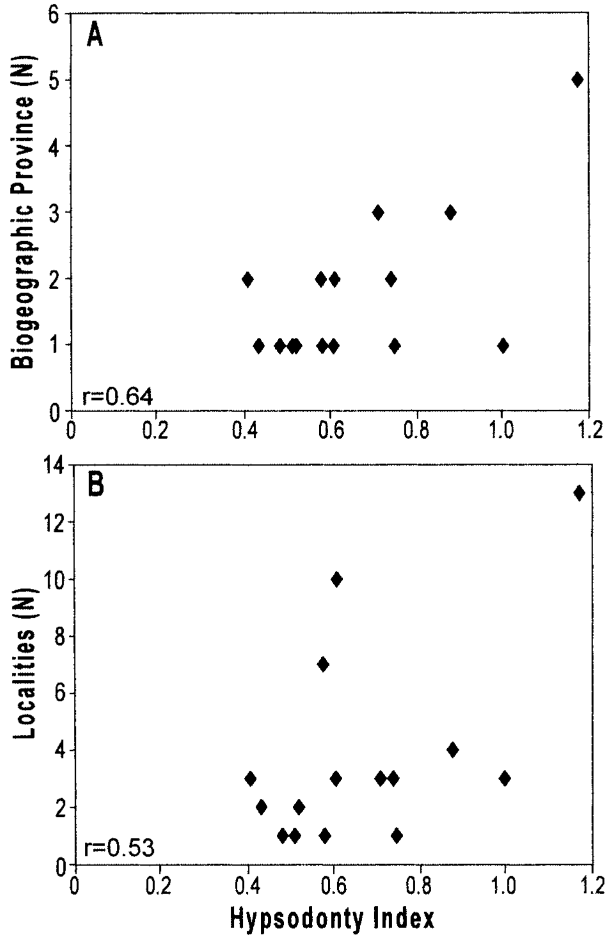

Fig. 5. Number of biogeographic provinces (A) and localities (B) in which camel taxa were found as a function of hypsodonty index. One single data point represents one particular species. Similar to the horses, the relationship among the data points is not significant.

Species longevity in horses and camels: probability of extinction

There is no significant relationship between the level of hypsodonty and the duration a taxon survived in the horses ($r = 0.17$; $P > 0.26$) and camels ($r = 0.44$; $P > 0.09$) analysed. Although the slopes in the non-phylogenetically based regressions suggest that hypsodont horses do have shorter longevities than brachydont taxa (Fig. 6A), the opposite pattern is shown for the camels (Fig. 7A). The phylogenetically independent contrasts also show no significant relationship in the horse ($r = 0.08$; $P > 0.94$) or camel ($r = 0.21$; $P > 0.14$) data, and refute any trend indicating that hypsodont taxa and brachydont taxa have the same probability of survival (Figs. 6, 7). As was the case in the other analyses, this too is the opposite of the expected result if evolution of hypsodonty led to ecological specialization, leading to rejection of H1. It is consistent with AH1 and AH2.

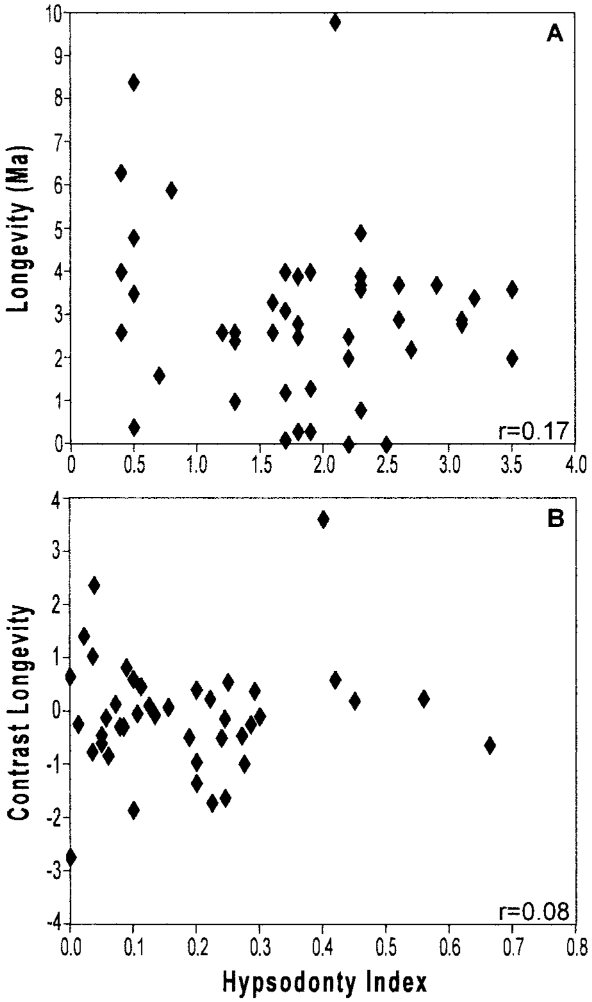

Fig. 6. Horse species longevity as a function of hypsodonty index using non-phylogenetically based methods (A) and phylogenetically independent contrasts (B). There is no significant relationship among data points using either methodology.

CONCLUSIONS AND BROADER IMPLICATIONS

The hypothesis that a key adaptation led to ecological specialization (decreasing niche breadth) during adaptive radiation can be rejected in the case of hypsodonty. In fact, hypsodonty seems to have permitted exploitation of broader niche space – ecological generalization – where taxa attained the ability to utilize a wide range of food resources and habitats. This is not to say that hypsodont taxa could not specialize on abrasive food resources when that became necessary; rather, it suggests that hypsodont taxa effectively expanded the range of food resources that they could utilize, and that they made full use of all those resources. Thus, although hyposdonty clearly was a key adaptation in that it allowed radiation into a number of previously unoccupied eco-spaces, the key adaptation

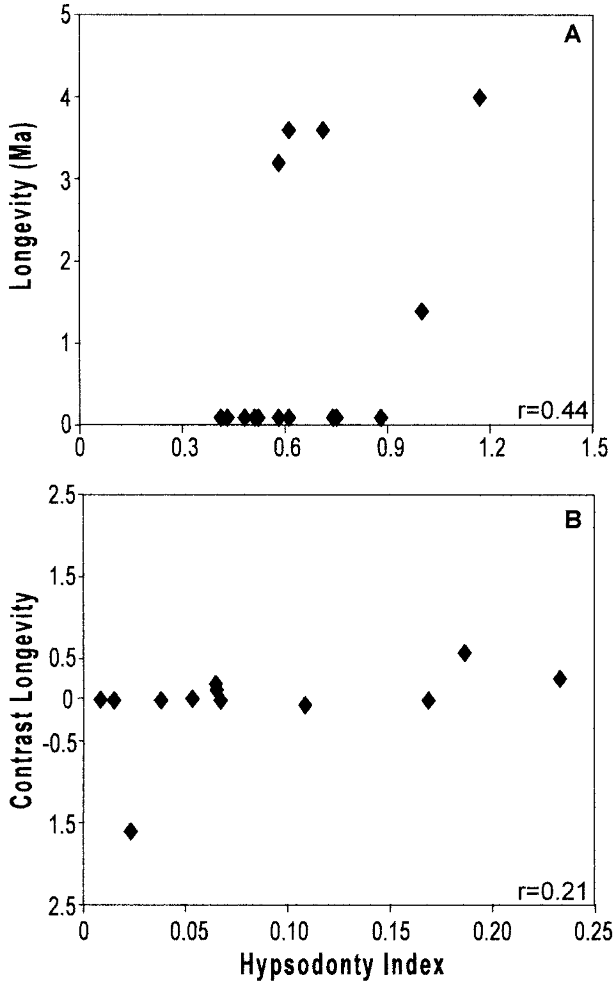

Fig. 7. Camel species longevity as a function of hypsodonty index using non-phylogenetically based methods (A) and phylogenetically independent contrasts (B). Similar to the horses, there is no significant relationship among data points using either methodology.

acted to increase the range of possible ecological niches, rather than shift taxa from one niche into another, more narrow one. This puts a new twist on an old story: rather than attainment of hypsodonty resulting in a shift from generalist browsing to specialist grazing, it resulted in a shift from obligate browsing to a more generalized strategy of browsing plus grazing.

This observation has subtle implications for using numbers of hypsodont taxa in various paleoenvironmental interpretations. A noteworthy trend in ungulates since the Miocene has been the proportional decline in numbers of brachyodont taxa relative to the increase in hypsodont taxa (Janis *et al.*, 2000, 2002). This trend has been suggested to result from the decline of forested habitats (spread of more open grassland environments), and from decreasing CO_2 levels that led to decreased productivity (Janis *et al.*, 2000). Similarly, the mean hypsodonty

Table 3. Hypsodonty, longevity, number of biogeographic provinces occupied, and number of localities occupied for horse taxa included in this study

Genus	Species	Hypsodonty index	Longevity (millions of years)	Biogeographic provinces (*n*)	Localities (*n*)
Archaeohippus	*blackbergi*	0.5	8.4	3	8
Astrohippus	*stocki*	3.2	3.4	3	9
Calippus	*cerasinus*	1.8	3.9	2	3
Calippus	*circulus*	2.3	0.8	1	1
Calippus	*elachistus*	2.2	2.5	1	4
Calippus	*hondurensis*	1.7	1.2	2	4
Calippus	*maccartyi*	1.8	0.3	1	2
Calippus	*martini*	1.6	3.3	3	9
Calippus	*placitus*	1.8	2.5	3	5
Calippus	*proplacitus*	2.3	3.6	2	6
Calippus	*regulus*	3.1	2.9	3	8
Cormohipparion	*emslei*	2.1	9.8	1	6
Cormohipparion	*occidentale*	1.7	0.1	7	35
Cormohipparion	*plicatile*	1.3	2.6	2	6
Dinohippus	*leidyanus*	2.9	3.7	2	6
Dinohippus	*mexicanus*	2.3	3.9	3	7
Epihippus	*gracilis*	0.4	6.3	3	7
Equus	*scotti*	3.5	3.6	2	9
Equus	*simplicidens*	3.1	2.8	7	48
Hipparion	*forcei*	1.8	2.8	4	10
Hipparion	*tehonense*	1.7	4.0	5	17
Hyracotherium	*vasacciense*	0.4	4.0	2	12
Megahippus	*matthewi*	0.7	1.6	3	4
Megahippus	*mckennai*	0.5	0.4	3	4
Merychippus	*gunteri*	1.2	2.6	2	8
Merychippus	*insignis*	1.3	2.4	4	13
Merychippus	*primus*	1.3	1.0	2	5
Mesohippus	*bairdi*	0.5	4.8	2	15
Mesohippus	*texanus*	0.5	3.5	1	3
Nannippus	*beckensis*	2.2	0.1	2	2
Nannippus	*ingenuus*	2.3	4.9	4	19
Nannippus	*morgani*	1.9	0.3	1	2
Nannippus	*peninsulatus*	2.7	2.2	5	31
Nannippus	*westoni*	1.6	2.6	1	2
Neohipparion	*eurystyle*	2.3	3.7	7	27
Neohipparion	*gidleyi*	2.5	0.1	3	4
Neohipparion	*leptode*	2.6	3.7	4	8
Neohipparion	*trampasense*	1.9	4	3	7
Orohippus	*pumulis*	0.4	2.6	1	6
Parahippus	*leonensis*	0.8	5.9	3	6
Pliohippus	*pernix*	2.6	2.9	3	9
Protohippus	*gidleyi*	1.8	3.9	2	6
Protohippus	*perditus*	1.7	3.1	2	6
Protohippus	*supremus*	2.2	2	3	9
Protohippus	*vetus*	1.9	1.3	1	2
Pseudhipparion	*simpsoni*	3.5	2	2	4

Table 4. Measured hypsodonty, longevity, number of biogeographic provinces occupied, and number of localities occupied for camelid taxa included in this study.

Genus	Species	Hypsodonty index	Longevity (millions of years)	Biogeographic provinces (*n*)	Localities (*n*)
Aepycamelus	*alexandrae*	0.41	0.1	2	3
Aepycamelus	*bradyi*	0.75	0.1	1	1
Aepycamelus	*priscus*	0.74	0.1	2	3
Cuyamacamelus	*jamesi*	0.48	0.1	1	1
Gigantocamelus	*spatulatus*	0.58	3.2	2	7
Hemiauchenia	*minima*	1.00	1.4	1	3
Hesperocamelus	*stylodon*	0.43	0.1	1	2
Megatylopus	*matthewi*	0.71	3.6	3	3
Miolabis	*californicus*	0.51	0.1	1	1
Nothokemas	*floridanus*	0.52	0.1	1	2
Paralabis	*cedrensis*	0.61	0.1	1	3
Paramiolabis	*taylori*	0.58	0.1	1	1
Poebrotherium	*wilsoni*	0.61	3.6	2	10
Procamelus	*grandis*	1.17	4.0	5	13
Stenomylus	*hitchcocki*	0.88	0.1	3	4

within a fauna has been used to interpret increasing continental-scale aridity (Fortelius *et al.*, 2002). The finding that hypsodonty leads to ecological generalization adds the information that hypsodont taxa feed on the same nutritious forage as obligate browsers (brachyodont taxa) when available, but are able to further support themselves on grass or other similar vegetation when necessary. While not obviating the usefulness of hypsodont /brachyodont proportions as proxies for productivity, aridity, and related parameters, this observation introduces an important caveat. It is the absence of brachyodont taxa, not the presence of hypsodont taxa, that is meaningful. Given their wide dietary variety, hypsodont taxa perform equally well in typical 'browsing' and 'grazing' environments; thus their presence alone says little about relative proportions of various plants. Brachydont taxa, however, simply cannot subsist in some places where hypsodont taxa can; thus, their low frequency compared with hypsodont taxa carries environmentally clear implications.

On the larger scale, the data support the findings of Schluter (2000), who showed that adaptive radiations do not always follow the pattern of an ecologically generalist ancestor evolving into ecologically specialized descendants. However, the case demonstrated here for hypsodonty and Schluter's examples does not necessarily imply that all morphologically based key adaptations result in ecological generalization. There are numerous indications that evolution of specialized morphology in mammals, key adaptation or not, can lead to obligate ecological specialization (Van Valkenburgh, 1991; Gingerich, 2001, 2003; Reiss, 2001; Van Valkenburgh *et al.*, 2004). It will be of interest to conduct similarly detailed studies on other key adaptations to determine whether any general patterns emerge.

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REFERENCES

Alroy, J. 2000. New methods for quantifying macroevolutionary patterns and processes. *Paleobiology*, **26**: 707–733.

Alroy, J. 2002. *North American Paleofaunal Database*, raw data files (available at: http://www.nceas.ucsb.edu/≈alroy/nam/data.html).

Barnosky, A.D. and Carrasco, M.A. 2002. Effects of Oligo-Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. *Evol. Ecol. Res.*, **4**: 811–841.

Barnosky, A.D., Carrasco, M.A. and Davis, E.B. 2005. The impact of the species–area relationship on estimates of paleodiversity. *PLOS*, **3**(8): e266.

Bell, C.J., Lundelius, E.L., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez, D.R., Jr. *et al.* 2004. The Blancan, Irvingtonian, and Rancholabrean mammal ages. In *Late Cretaceous and Cenozoic Mammals of North America* (M.O. Woodburne, ed.), pp. 232–314. New York: Columbia University Press.

Brown, D.E., Reichenbacher, F. and Franson, S.E. 1998. *A classification of North American biotic communities*. Salt Lake City, UT: University of Utah Press.

Burney, D.A. 1999. Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In *Extinctions in Near Time* (R. MacPhee, ed.), pp. 145–164. New York: Kluwer Academic/ Plenum Publishers.

Caswell, H., Reed, F., Stephenson, S.N. and Werner, P.A. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. *Am. Nat.*, **107**: 465–480.

Cerling, T.E. and Harris, J.M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia*, **120**: 347–363.

Cerling, T.E., Hart, J.A. and Hart, T.B. 2004. Stable isotope ecology in the Ituri Forest. *Oecologia*, **138**: 5–12.

Colwell, R.K. and Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. *Ecology*, **52**: 567–576.

Cowling, S.A. 1999. Simulated effects of low atmospheric CO_2 on structure and composition of North American vegetation at the Last Glacial Maximum. *Global Ecol. Biogeogr.*, **8**: 81–93.

DeNiro, M.J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta*, **42**: 495–506.

Diaz-Uriarte, R. and Garland, T. 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. *Syst. Biol.*, **47**: 654–672.

Easley, M.C. and Judd, W.S. 1990. Vascular flora of the southern upland property of Paynes Prairie State Preserve, Alachua County, Florida. *Castanea*, **55**: 142–186.

Ehleringer, J.R. and Monson, R.K. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annu. Rev. Ecol. Syst.*, **24**: 411–439.

Ehleringer, J.R., Sage, R.F., Flanagan, L.B. and Pearcy, R.W. 1991. Climate change and the evolution of C_4 photosynthesis. *Trends Ecol. Evol.*, **6**: 95–99.

Ehleringer, J.R., Cerling, T.E. and Helliker, B.R. 1997. C_4 photosynthesis, atmospheric CO_2, and climate. *Oecologia*, **112**: 285–299.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.*, **125**: 1–15.

Feranec, R.S. 2003a. Stable isotopes, hypsodonty, and the paleodiet of *Hemiauchenia* (Mammalia: Camelidae), a morphological specialization creating ecological generalization. *Paleobiology*, **29**: 230–242.

Feranec, R.S. 2003b. Determination of resource partitioning in a predominantly C_3 environment by the analysis of stable isotope values from herbivores in Yellowstone National Park. *J. Vert. Paleontol.*, **23**: 49A.

Feranec, R.S. 2004. Geographic variation in the diet of hypsodont ungulates from the Rancholabrean of Florida reveals more than discrete feeding categories. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **207**: 359–369.

Feranec, R.S. and MacFadden, B.J. 2000. Evolution of the grazing niche in Pleistocene mammals from Florida: evidence from stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **162**: 155–169.

Feranec, R.S. and MacFadden, B.J. 2006. Isotopic discrimination of resource partitioning among ungulates in C_3-dominated communities from the Miocene of Florida and California. *Paleobiology*, **32**: 190–205.

Ferguson, D.K. 1986. The origin of leaf-assemblages – new light on an old problem. *Rev. Palaeobot. Palynol.*, **46**: 117–188.

Fernandez, M.H. and Pelaez-Campomanes, P. 2003. The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations. *Global Ecol. Biogeogr.*, **12**: 507–517.

Forsten, A. 1975. Fossil horses of the Texas Gulf coastal plain: a revision. *Pierce-Sellards Ser., Texas Mem. Mus.*, **22**: 1–86.

Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zool. Fenn.*, **180**: 1–76.

Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J. *et al.* 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evol. Ecol. Res.*, **4**: 1005–1016.

Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U. and Stauffer, B. 1986. Ice core record of the $^{13}C/^{12}C$ ratio of atmospheric CO_2 in the past two centuries. *Nature*, **324**: 237–238.

Futuyma, D.J. and Moreno, G. 1988. The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.*, **19**: 207–233.

Garland, T., Harvey, P.H. and Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.*, **41**: 18–32.

Garland, T., Dickerman, A.W., Janis, C.M. and Jones, J.A. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.*, **42**: 265–292.

Garland, T., Midford, P.E. and Ives, A.R. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *Am. Zool.*, **39**: 374–388.

Gingerich, P.D. 2001. Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan. *Science*, **293**: 2239–2242.

Gingerich, P.D. 2003. Land-to-sea transition in early whales: evolution of Eocene Archaeoceti (Cetacea) in relation to skeletal proportions and locomotion of living semiaquatic mammals. *Paleobiology*, **29**: 429–454.

Gould, S.J. 2002. *The Structure of Evolutionary Theory*. Cambridge, MA: Belknap Press of Harvard University Press.

Grimm, E.C., Jacobson, G.L., Watts, W.W., Hansen, B.C.S. and Maasch, K.A. 1993. A 50,000-year record of climate oscillations from Florida and its temporal correlation with Heinrich Events. *Science*, **261**: 198–200.

Hagmeier, E.M. and Stults, C.D. 1964. A numerical analysis of the distributional patterns of North American mammals. *Syst. Zool.*, **13**: 125–155.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Heard, S.B. and Hauser, D.L. 1995. Key evolutionary innovations and their ecological mechanisms. *Hist. Biol.*, **10**: 151–173.

Heckathorn, S.A., McNaughton, S.J. and Coleman, J.S. 1999. C_4 plants and herbivory. In *C_4 Plant Biology* (R.F. Sage and R.K. Monson, eds.), pp. 285–312. New York: Academic Press.

Honey, J.G., Harrison, J.A., Prothero, D.R. and Stevens, M.S. 1998. Camelidae. In *Evolution of Tertiary Mammals of North America, Vol. 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals* (C.M. Janis, K.M. Scott and L.L. Jacobs, eds.), pp. 439–462. New York: Cambridge University Press.

Hoppe, K.A. and Koch, P.L. 2006. The biogeochemistry of the Aucilla River fauna. In *The First Floridians and the Last Mastodons: The Page-Ladson Site on the Aucilla River* (S.D. Webb, ed.), pp. 379–402. London: Springer.

Huffman, J.M. and Judd, W.S. 1998. Vascular flora of Myakka River State Park, Sarasota and Manatee Counties, Florida. *Castanea*, **63**: 25–50.

Hulbert, R.C. 1987. Late Neogene *Neohipparion* (Mammalia, Equidae) from the Gulf coastal plain of Florida and Texas. *J. Paleontol.*, **61**: 809–830.

Hulbert, R.C. 1988a. *Calippus* and *Protohippus* (Mammalia, Perissodactyla, Equidae) from the Miocene (Barstovian-Early Hemphillian) of the Gulf coastal plain. *Bull. Florida State Mus., Biol. Sci.*, **32**: 221–340.

Hulbert, R.C. 1988b. *Cormohipparion* and *Hipparion* (Mammalia, Perissodactyla, Equidae) from the late Neogene of Florida. *Bull. Florida State Mus., Biol. Sci.*, **33**: 229–338.

Hulbert, R.C., Jr. and MacFadden, B.J. 1991. Morphological transformation and cladogenesis at the base of the adaptive radiation of Miocene hypsodont horses. *Am. Mus. Nov.*, **3000**: 1–61.

Hunter, J.P. 1998. Key innovations and the ecology of macroevolution. *Trends Ecol. Evol.*, **13**: 31–36.

Hutchinson, G.E. 1958. Concluding remarks. *Cold Springs Harbor Symp. Quant. Biol.*, **22**: 415–427.

Jackson, S.T. and Overpeck, J.T. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. In Deep Time: Paleobiology's Perspective (D.H. Erwin and S.L. Wing, eds.). *Paleobiology*, **26** (suppl. to #4): 194–220.

Janis, C.M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. In *Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology* (D.E. Russell, J.-P. Santoro and D. Sigogneau-Russell, eds.), pp. 367–387. Paris: Memoires du museum National d'Histoire Naturelle C.

Janis, C.M. 1990. Correlation of dental and cranial variables with body size in ungulates and macropodids. In *Body Size in Mammalian Paleobiology: Estimation and Biological Implications* (J. Damuth and B.J. MacFadden, eds,), pp. 255–300. Cambridge: Cambridge University Press.

Janis, C.M. and Ehrhardt, D. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference. *Biol. J. Linn. Soc.*, **92**: 267–284.

Janis, C.M., Scott, K.M. and Jacobs, L.L. 1998. *Evolution of Tertiary Mammals of North America*. New York: Cambridge University Press.

Janis, C.M., Damuth, J. and Theodor, J.M. 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proc. Natl. Acad. Sci. USA*, **97**: 7899–7904.

Janis, C.M., Damuth, J. and 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.

Koch, P.L. 1998. Isotopic reconstruction of past continental environments. *Annu. Rev. Earth Planet. Sci.*, **26**: 573–613.

Koch, P.L., Tuross, N. and Fogel, M.L. 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *J. Archaeol. Sci.*, **24**: 417–429.

Koch, P.L., Hoppe, K.A. and Webb, S.D. 1998. The isotopic ecology of late Pleistocene mammals in North America Part 1. Florida. *Chem. Geol.*, **152**: 119–138.

Kohn, M.J. and Cerling, T.E. 2002. Stable isotope compositions of biological apatite. In *Phosphates: Geochemical, Geobiological and Materials Importance* (M.J. Kohn, J. Rakovan and J. Hughes, eds.), pp. 455–488. Washington, DC: Mineralogical Society of America.

Legendre, S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeovertebrata*, **16**: 191–212.

Lyman, R.L. 1994. *Vertebrate Taphonomy*. Cambridge: Cambridge University Press.

MacFadden, B.J. 1984. Systematics and phylogeny of *Hipparion, Neohipparion, Nannippus*, and *Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. *Bull. Am. Mus. Nat. His.*, **179**: 1–195.

MacFadden, B.J. 1988. Fossil horses from 'Eohippus' (*Hyracotherium*) to Equus: 2. Rates of dental evolution revisited. *Biol. J. Linn. Soc.*, **35**: 37–48.

MacFadden, B.J. 1992. *Fossil Horses: Systematics, Paleobiology, and the Evolution of the Family Equidae*. Cambridge: Cambridge University Press.

MacFadden, B.J. 2000. Cenozoic mammalian faunas from the Americas: reconstructing ancient diets and terrestrial communities. *Annu. Rev. Ecol. Syst.*, **31**: 33–59.

MacFadden, B.J. and Cerling, T.E. 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million-year sequence from the Neogene of Florida. *J. Vert. Paleontol.*, **16**: 103–115.

MacFadden, B.J. and Higgins, P. 2004. Ancient ecology of 15-million-year-old browsing mammals within C_3 plant communities from Panama. *Oecologia*, **140**: 169–182.

MacFadden, B.J. and Hulbert, R.C., Jr. 1988. Explosive speciation at the base of the adaptive radiation of Miocene grazing horses. *Nature*, **336**: 466–468.

MacFadden, B.J., Cerling, T.E. and Prado, J. 1996. Cenozoic terrestrial ecosystem evolution in Argentina: evidence from carbon isotopes of fossil mammal teeth. *Palaios*, **11**: 319–327.

MacFadden, B.J., Cerling, T.E. and Solounias, N. 1999. Ancient diets, ecology and extinction in 5-million-year-old horses from Florida. *Science*, **283**: 824–827.

Marino, B.D. and McElroy, M.B. 1991. Isotopic composition of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. *Nature*, **349**: 127–131.

Marino, B.D., McElroy, M.B., Salawitch, R.J. and Spaulding, W.G. 1992. Glacial-to-interglacial variations in the carbon isotopic composition of atmospheric CO_2. *Nature*, **357**: 461–466.

Martins, E.P. and Garland, T. 1991. Phylogenetic analysis of the correlated evolution of continuous characters: a simulation study. *Evolution*, **45**: 534–557.

Montuire, S., Michaux, J., Legendre, S. and Aguilar, J.-P. 1997. Rodents and climate. 1. A model for estimating past temperatures using arvicolids (Mammalia: Rodentia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **128**: 187–206.

O'Leary, M.H. 1988. Carbon isotopes in photosynthesis. *BioScience*, **38**: 328–336.

Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comp. Appl. Biosci.*, **11**: 247–251.

Quade, J., Cerling, T.E., Barry, J.C., Morgan, M.E., Pilbeam, D.R., Chivas, A.R. *et al.* 1992. A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. *Chem. Geol.*, **94**: 183–192.

Reiss, K.Z. 2001. Using phylogenies to study convergence: the case of the ant-eating mammals. *Am. Zool.*, **41**: 507–525.

Ricketts, T.H., Dinerstein, E., Loucks, C.J., Eichbaum, W., Dellasala, D., Kavanaugh, K. *et al.* 1999. *Terrestrial Ecoregions of North America: A Conservation Assessment*. Wahington, DC: Island Press.

Rodriguez, J. 1999. Use of cenograms in mammalian palaeoecology: a critical review. *Lethaia*, **32**: 331–347.

Rosenzweig, M.L. and McCord, R.D. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology*, **17**: 202–213.

Sage, R.F., Wedin, D.A. and Li, M. 1999. The biogeography of C_4 photosynthesis: patterns and controlling factors. In *C_4 Plant Biology* (R.F. Sage and R.K. Monson, eds.), pp. 313–373. New York: Academic Press.

SAS Institute. 2005. *JMP IN*, Version 5. Cary, NC: SAS Institute, Inc.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. New York: Oxford University Press.

Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science*, **185**: 27–39.

Schoeninger, M.J. and DeNiro, M.J. 1982. Carbon isotope ratios of apatite from fossil bone cannot be used to reconstruct diets of ancient animals. *Nature*, **297**: 577–578.

Schopf, J.M. 1975. Modes of fossil preservation. *Rev. Palaeobot. Palynol.*, **20**: 27–53.

Simpson, G.G. 1944. *Tempo and Mode in Evolution*. New York: Columbia University Press.

Simpson, G.G. 1953. *The Major Features of Evolution*. New York: Columbia University Press.

Simpson, G.G. 1967. *The Meaning of Evolution*. New Haven, CT: Yale University Press.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Dick, B.L. and Ben-David, M. 2003. Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? *Ècoscience*, **10**: 297–302.

Stirton, R.A. 1947. Observations on evolutionary rates in hypsodonty. *Evolution*, **1**: 32–41.

Stowe, L.G. and Teeri, J.A. 1978. The geographic distribution of C_4 species of the Dicotyledonae in relation to climate. *Am. Nat.*, **112**: 609–623.

Tedford, R.H., Skinner, M.F., Fields, R.W., Rensberger, J.M., Whistler, D.P., Galusha, T. *et al.* 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene epochs) in North America. In *Cenozoic Mammals of North America: Geochronology and Biostratigraphy* (M.O. Woodburne, ed.), pp. 153–210. Berkeley, CA: University of California Press.

Teeri, J.A. and Stowe, L.G. 1976. Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia*, **23**: 1–12.

Tieszen, L.L., Reed, B.C., Bliss, N.B., Wylie, B.K. and DeJong, D.D. 1997. NDVI, C_3 and C_4 production, and distribution in Great Plains grassland land cover classes. *Ecol. Appl.*, **7**: 59–78.

Van Valen, L. 1960. A functional index of hypsodonty. *Evolution*, **14**: 531–532.

Van Valkenburgh, B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. *Paleobiology*, **17**: 340–362.

Van Valkenburgh, B., Wang, X. and Damuth, J. 2004. Cope's rule, hypercarnivory, and extinction in North American canids. *Science*, **306**: 101–104.

Wang, Y. and Cerling, T.E. 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **107**: 281–289.

Webb, S.D. 1991. Historical biogeography. In *Ecosystems of Florida* (R.L. Myers and J.J. Ewel, eds.), pp. 70–100. Orlando, FL: University of Central Florida Press.