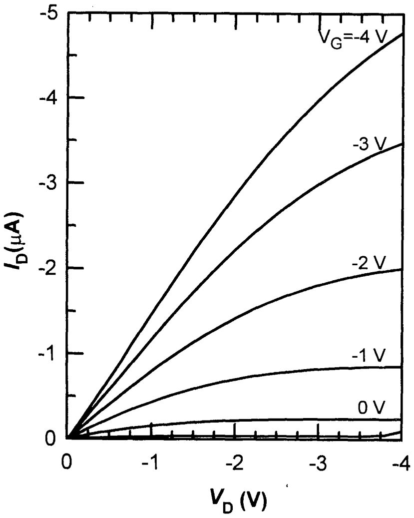

Fig. 4. Plot of I_D versus V_D at various V_G from an organic IGFET on polycarbonate.

ative gate bias increases, the Fermi level approaches the delocalized band edge and more traps are filled. At an appropriately high voltage, all of the trap states are filled, and any subsequently injected carriers are free to move with the microscopic mobility associated with carriers in the delocalized band. In devices with a 0.12-μm-thick SiO_2 gate insulator, the negative gate bias required to reach such carrier concentration levels was above 70 to 80 V. As shown in Fig. 2, the mobility saturates above this gate bias, indicating that all localized states are occupied. By using higher dielectric constant insulators, a sufficient number of carriers to fill all these traps are generated by the field effect at much lower gate voltages, and this is the reason that high mobilities are observed at such low voltages compared with the SiO_2-based devices. Several localized trap levels have been reported for thin polycrystalline vapor-deposited films of pentacene at depths ranging from 0.06 to 0.68 eV (*23*), which could account for the aforementioned localized states. Brown *et al.* (*17*) have used an alternative model, based on hopping polaron transport processes, to explain the gate bias dependence in organic semiconductor IGFETs.

On a more practical note, all of the steps in the fabrication process of our low operating voltage BZT-pentacene–based devices were performed entirely at RT. Initially, we used sol-gel–deposited BST films as the high ε gate insulator (*19*), which required annealing at 400°C, and although they produced excellent low-voltage device characteristics, they were not compatible with transparent plastic substrates. The RT fabricated devices we now report are compatible with transparent plastic substrates. Given their operating characteristics, which are very close to the characteristics of the widely used a-Si:H TFT, they are good candidates for applications involving AMLCD or AMOLED displays on plastic substrates. Several efforts in the past to develop a-Si:H TFT-based liquid crystal displays on plastic have not been successful because of deterioration of the performance of those TFTs when a-Si:H was grown at temperatures below 150° to 200°C.

To demonstrate the feasibility of the above idea, we successfully fabricated pentacene-based TFT on very transparent plastic substrates (polycarbonate). The BZT gate insulator was 0.128 μm thick. Their performance was similar to devices fabricated on quartz or SiO_2/Si substrates. Figure 4 shows the characteristics of such a device (W = 1500 μm and L = 69.2 μm). Mobility was 0.2 $cm^2\ V^{-1}\ s^{-1}$, as calculated in the saturation region. Mobility values as high as 0.38 $cm^2\ V^{-1}\ s^{-1}$ were measured from devices with a W/L ratio of 4. These are the highest reported mobilities from devices fabricated on plastic substrates, and they are obtained at a maximum gate voltage of only 4 V. The highest mobility reported before for organic IGFET on plastic substrates was up to 0.1 $cm^2\ V^{-1}\ s^{-1}$, and it required the operating voltage to be modulated between 0 and −100 V (*24*).

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Ancient Diets, Ecology, and Extinction of 5-Million-Year-Old Horses from Florida

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Six sympatric species of 5-million-year-old (late Hemphillian) horses from Florida existed during a time of major global change and extinction in terrestrial ecosystems. Traditionally, these horses were interpreted to have fed on abrasive grasses because of their high-crowned teeth. However, carbon isotopic and tooth microwear data indicate that these horses were not all C_4 grazers but also included mixed feeders and C_3 browsers. The late Hemphillian Florida sister species of the modern genus *Equus* was principally a browser, unlike the grazing diet of modern equids. Late Hemphillian horse extinctions in Florida involved two grazing and one browsing species.

The fossil record of horses (family Equidae) over the past 55 million years is a classic example of macroevolution. In the traditional interpretation, during the Eocene through early Miocene [~55 to 20 million years ago (Ma)], horses had short-crowned teeth, indicating a browsing diet of leafy and soft plants. After ~20 Ma, fossil horses underwent an explosive adaptive radiation resulting in numerous clades with high-crowned (hypsodont) teeth adapted for grazing on abrasive plants, particularly grasses. This connection between observed tooth crown height and interpreted diets of extinct horses is a widely accepted model of long-term adaptation and evolution (*1*).

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Traditional morphological studies of tooth crown height integrated with isotopes and microwear provide a powerful method for testing and refining previous hypotheses about fossil horse diets and macroevolution. Carbon isotopic ratios measured from fossil tooth enamel indicate the relative proportions of C_3 (plants in which the first product of photosynthesis is a 3-carbon acid) and C_4 (plants in which the first product of photosynthesis is a 4-carbon acid) plants in diets of extinct herbivores (*2*). In modern terrestrial ecosystems, C_3 plants include most leafy, woody, and other soft plants (browse) and cool growing season or aquatic grasses, whereas C_4 plants include most tropical and temperate grasses. These differences in C_3 (Calvin) and C_4 (Hatch-Slack) photosynthetic pathways produce different proportions of stable carbon isotopes (^{12}C and ^{13}C) incorporated into plant tissues. C_3 plants have $\delta^{13}C$ values ranging from -36 to -22 per mil (*3*), with a mean of ~ -27 per mil, whereas the $\delta^{13}C$ values of C_4 grasses range from -16 to -9 per mil, with a mean of ~ -13 per mil (*4*). With the use of tooth enamel microwear, diets can be determined by analysis of distinctive microscopic patterns of scratches and pits on fossil herbivore teeth that indicate the mastication of different plant foodstuffs (that is, grass versus browse) (*5*).

Here we present carbon isotope, tooth crown height, and enamel microwear data for six contemporaneous and apparently sympatric fossil horse species from the late Hemphillian (latest Miocene to early Pliocene, ~5 Ma) Bone Valley deposits of central Florida. The Bone Valley horses are an excellent group to study because they (i) have a rich and well-sampled fossil record, (ii) represent two diverse clades of advanced hypsodont horses with similar dental morphologies and body sizes, (iii) existed during a time of major global change in terrestrial ecosystems (*6*), and (iv) preceded a terrestrial mammal extinction event at ~4.8 Ma (*7*).

The six late Hemphillian Bone Valley horses include four species of three-toed hipparionines, that is, tiny *Pseudhipparion simpsoni*, small *Nannippus minor*, and medium-sized *Cormohipparion emsliei* and *Neohipparion eurystyle*, and two one-toed equines, that is, medium-sized *Astrohippus stockii* and large *Dinohippus mexicanus* (*8*). All of the Bone Valley horses had high-crowned teeth (Fig. 1), and traditionally they would be interpreted as grazers (*1*, *9*). However, one problem with this interpretation is that all six closely related and sympatric species would be competing for the same general food resource.

Hypsodonty indices (HI; Table 1) range from 2.1 for *C. emsliei* to >3.5 for *P. simpsoni*, which indicate species with high-crowned to very high-crowned teeth. Mean $\delta^{13}C$ values range from -9.0 to -1.7 per mil, indicating a range in the proportion of C_3 and C_4 plants in the ancient diets. Microwear indices (MI) range from browsers (MI $< \sim 1.5$; Fig. 2) to principally grazers (MI $> \sim 1.5$). In our interpretations of Bone Valley horse diets, the combination of $\delta^{13}C$ values and microwear patterns is the most informative (*10*). Body size is also of considerable interest in understanding species interactions within communities. Estimated body sizes range from the very small *P. simpsoni* (51 kg) and *N. minor* (63 kg), to intermediate-sized *A. stockii* (101 kg), *C. emsliei* (105 kg), and *N. eurystyle* (141 kg), to large *D. mexicanus* (268 kg) (*11*).

The ancient diets interpreted for the Bone Valley horses include a broad spectrum from C_4 grazers, to C_4-C_3 grazers–mixed feeders, to principally C_3 browsers (Fig. 3). An MI of 3.6 and $\delta^{13}C$ of -1.7 per mil indicate that the medium-sized *N. eurystyle* fed almost exclusively on C_4 grasses. An MI of 4.1 and $\delta^{13}C$ of -5.7 per mil indicate that the tiny *P. simpsoni* fed on C_4 and C_3 grasses in roughly equal proportions. Likewise, an MI of 2.5 and $\delta^{13}C$ of -5.1 per mil indicate that the tiny *N. minor* was a mixed C_4-C_3 grazer. With an MI of 1.6 and $\delta^{13}C$ of -3.6 per mil, the interpretation of the diet of *C. emsliei* remains enigmatic. It seems to have been a mixed feeder but with both browse (low MI) and C_4 plants (high $\delta^{13}C$ value), which is a combination rarely encountered in modern ecosys-

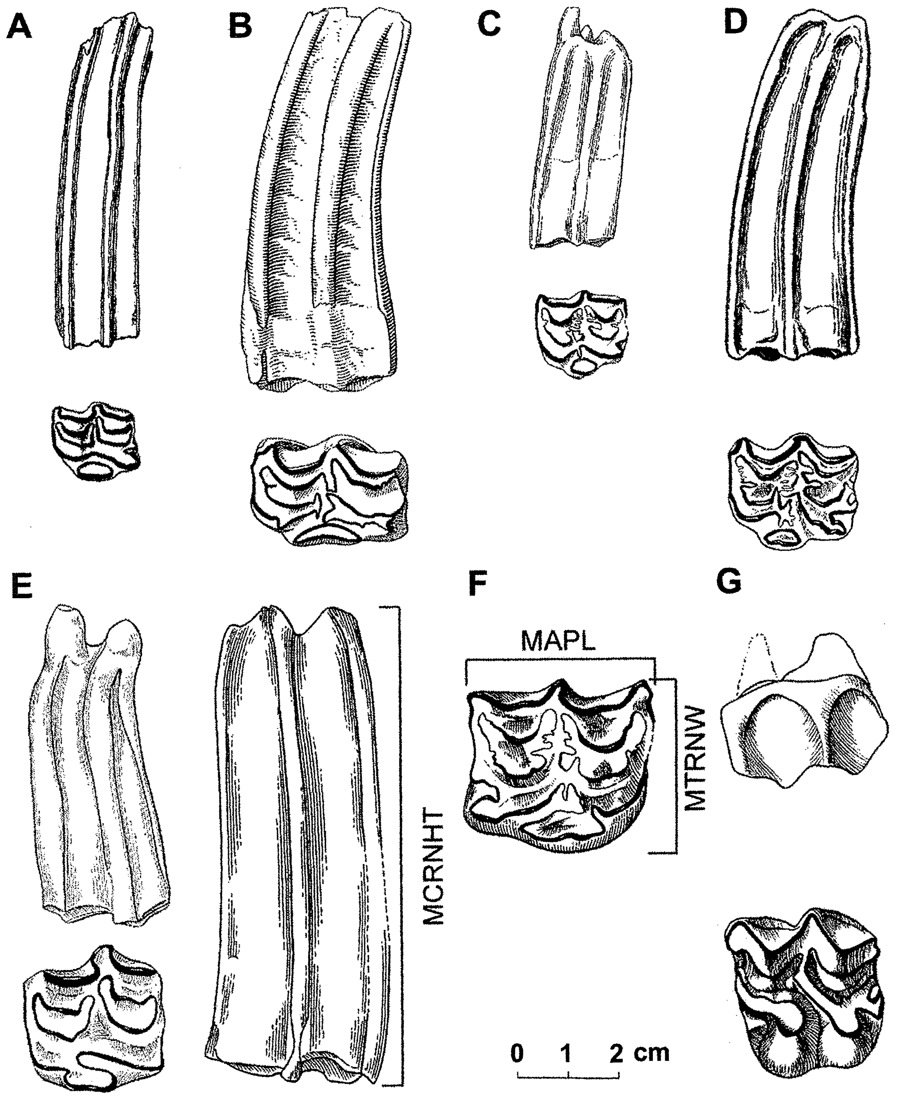


Fig. 1. Upper molars of the six Bone Valley horse species (**A** to **F**) in early to middle wear, external (top) and occlusal (bottom or right) views. *Pseudhipparion simpsoni* (A), *N. eurystyle* (B), *N. minor* (C), *C. emsliei* (D), *A. stockii* (E), and *D. mexicanus* (F). *Hypohippus chico* (**G**) is a middle Miocene Florida horse from older (~15 Ma) Bone Valley levels that shows a short-crowned, presumed browsing tooth. HI is the maximum molar crown height (MCRNHT) divided by the greatest length (MAPL). Compiled from original illustrations and specimens in the University of Florida Vertebrate Paleontology collection.

tems. A $\delta^{13}C$ of −9.0 per mil and low MI of 0.8 for *A. stockii* indicate that it was a browser. Likewise, a $\delta^{13}C$ of −7.7 per mil and low MI of 0.4 indicate that *D. mexicanus* was principally a browser (although not as specialized as other browsers in the Bone Valley fauna) (*12*).

The environmental and biotic context in which the Bone Valley horses lived as well as comparisons with modern ecological analogs provide a framework for understanding late Hemphillian ecology and extinctions. Paleoecological reconstructions of central Florida at 5 Ma indicate low-elevation floodplain and estuarine environments with a mosaic of local closed-canopy forests, woodlands, and open-country grasslands (*7*). Recent carbon isotopic analyses of the entire late Hemphillian Bone Valley mammalian herbivore fauna indicate a combination of C_3 browsers, possible C_3 grazers, isotopically mixed feeders, and C_4 grazers (*12*). The Bone Valley flora and fauna have similarities to diverse C_3-C_4-based modern communities in regions such as East Africa. Modern terrestrial plant communities in Florida include C_3 browse and aquatic plants year-round with a predominance of C_4 grasses, although some C_3 grasses occur naturally during the winter (*13*). Given paleoenvironmental reconstructions for the Bone Valley, the explanation for some C_3 grasses in the diets of *P. simpsoni* and *N. minor* is not straightforward. It could represent feeding on abrasive C_3 aquatic plants such as reeds, rushes, and sedges [all of which are well represented in modern Florida ecosystems (*13*)]. It is perplexing how one of the least hypsodont Bone Valley horses, *N. minor* (HI = 2.4), could have been principally a grazer. *Nannippus minor* probably compensated for feeding on abrasive foodstuffs, but not being very hypsodont, by having a small body size and hence probable short potential individual life-span (*14*).

Body size is extremely important to understanding dietary adaptations and niche specializations. Within extinct grazing guilds of terrestrial herbivores, body size tends to span a large range (*15*). This is not the case with the Bone Valley grazing horses. The small to medium body sizes (Table 1) of these horses are probably due to the presence of other large-bodied mammalian grazers or grazers–mixed feeders in the Bone Valley fauna, including rhinoceroses and proboscideans (*12*). The larger body sizes seen in subsequent Plio-Pleistocene *Equus* may represent a morphological shift after the extinction of late Hemphillian grazing megaherbivores such as rhinoceroses.

Table 1. Data for the six species of late Hemphillian Bone Valley horses from Florida and, as appropriate, comparisons with modern ungulates with known diets. Univariate and comparative statistics are presented elsewhere (*22*).

Species/ taxon	HI*	$\delta^{13}C$ (per mil)†	MI‡	Estimated body mass (kg)§	Interpreted diet‖	Clade history after ~4.8 Ma
N. eurystyle	2.4	−1.7	3.6	141	C_4 grazer	Extinct
P. simpsoni	>3.5	−5.7	4.1	51	C_3-C_4 grazer	Extinct
N. minor	2.4	−5.1	2.5	63	C_3-C_4 grazer	*N. peninsulatus*
C. emsliei	2.1	−3.6	1.6	105	?C_4 grazer/ browser	*C. emsliei* in Florida
A. stockii	3.1	−9.0	0.8	101	Browser	Extinct
D. mexicanus	2.3	−7.7	0.4	268	Browser	*Equus* spp.
Modern grazers¶	>1	>~−2.0	>~1.5	–	–	–
Modern browsers#	<1	<~−8.0	<~1.5	–	–	–

*Mean hypsodonty index (HI) = molar crown height (MCRNHT) divided by the greatest anteroposterior occlusal length (MAPL) (Fig. 1), with late tooth wear removed. HI for *P. simpsoni* is a minimum because of ever-growing teeth. †Mean values for each species. ‡Ratio of microwear scratches to pits per unit occlusal surface area. §With the use of regression equations to calculate body mass with highly correlated ($r > 0.9$) variables (*11*). ‖With the use of $\delta^{13}C$ and microwear data as principal determinants. ¶$\delta^{13}C$ expected range based on previous studies of fossil mammalian herbivores (*2, 12*). MIs were calculated from the following extant species known to be principally grazers (*21*): *Alcelaphus buselaphus* (Ab, Coke's hartebeest), *Axis axis* (Ax; Axis deer), *Bison bison* (Bb; North American bison), *Cervus duvauceli* (Cd; swamp deer), *Connochaetes taurinus* (Ct; wildebeest), *Equus burchelli* (Eb, Grant's zebra), *E. grevyii* (Eg; Grevy's zebra), and *Kobus ellipsiprymnus* (Ke; waterbuck). Mean MI for grazers [$N = 8$, $x = 3.2$, $s = 1.8$, observed range (O.R.) = 1.6 to 7.1] is statistically different ($P < 0.002$, Wilcoxon test; $P < 0.01$, analysis of variance and t test) from browsers ($N = 7$, $x = 0.72$, $s = 0.5$, O.R. = 0.3 to 1.7). #$\delta^{13}C$ expected range based on previous studies of fossil mammalian herbivores (*2, 12*). MIs were calculated from the following extant species known to be principally browsers (*21*): *Boocercus eurycerus* (Be; bongo), *Cephalophus dorsalis* (Cdo; duiker), *C. niger* (Cn; black-fronted duiker), *Giraffa camelopardis* (Gc; giraffe), *Litocranius welleri* (Lw; gerenuk), *Tragelaphus imbaris* (Ti; lesser kudu), and *T. strepsiceros* (Ts; greater kudu).

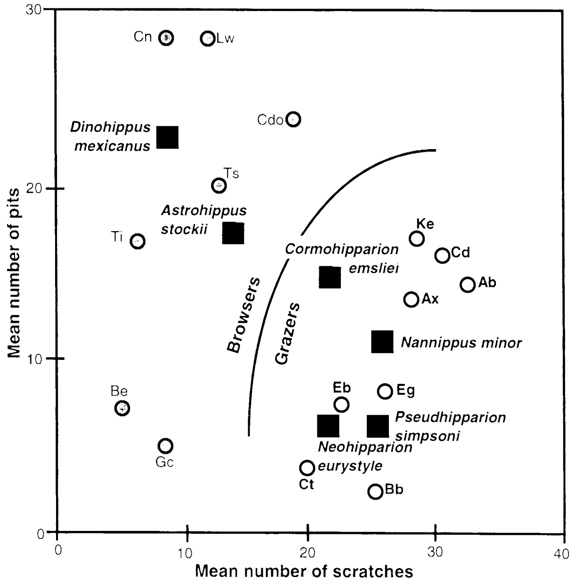
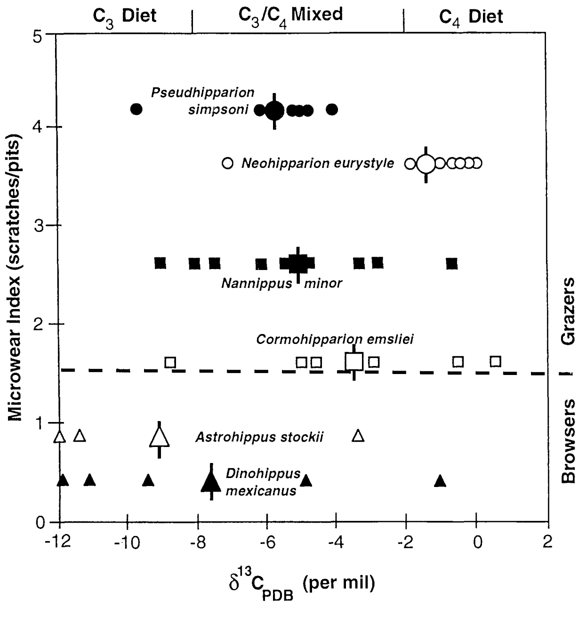


Fig. 2. Microwear is analyzed by plotting the mean number of scratches versus pits per unit area (0.5 mm^2). Abbreviations of modern browsers (shaded circles) and grazers (open circles) are given in the footnotes to Table 1. Extant grazers have, on average, more scratches and less pits than browsers.

The Bone Valley late Hemphillian represents the latest occurrence of the equid grazing genera *Pseudhipparion* and *Neohipparion*. The genus *Cormohipparion*, previously widespread in North America during the Miocene, became extinct throughout the continent by the end of the Hemphillian (4.8 Ma), except for the local persistence of *C. emsliei* into the Plio-Pleistocene of Florida (*16*), when a single $\delta^{13}C$ value of −6.3 per mil suggests a mixed C_3-C_4 mixed diet (*12*). The sister species of Bone Valley *Nannippus*, *N. peninsulatus*, survives into the Plio-Pleistocene throughout North America where it had a principally grazing diet (*17*). The genus *Astrohippus* became extinct by the end of the Hemphillian, whereas *D. mexicanus* is the closest sister taxon of the earliest recognized species of the extant genus *Equus*, for example, *E. "simplicidens*," from the Pliocene of North America (*18*).

After explosive speciation, apparently in response to global climate change and the spread of grasslands, the family Equidae reached its maximum diversity of a dozen genera in North America during the middle Miocene, about 15 Ma (*7*). Thereafter, North American horse diversity declined. During the earlier part of this decline in the middle

Fig. 3. Mean $\delta^{13}C$ versus MI for the Bone Valley horses (large symbols with vertical lines, data from Table 1; individual $\delta^{13}C$ sample data are indicated by small symbols).



Miocene (~15 to 10 Ma), more primitive, short-crowned (HI < 1) clades became extinct [including "browsing" anchitheres such as *Hypohippus* (Fig. 1G)]. These extinctions apparently resulted from a loss of forested habitats as grasslands spread (*7*, *19*). Late Miocene (~10 to 5 Ma) horse extinctions resulted from a different cause, apparently related to expansion of C_4 terrestrial ecosystems (*20*). The Bone Valley horses existed shortly before a major extinction event at ~4.8 Ma. This event resulted in a drop in diversity from eight horse genera in North America during the late Miocene to three genera in the succeeding Pliocene (*7*). Three separate equid clades, *Nannippus*, *Cormohipparion*, and *Dinohippus/Equus*, all related to the Bone Valley horses, survived locally in Florida into the Plio-Pleistocene after ~4.8 Ma. Fossil and extant species of *Equus* have been almost exclusively grazers (*12*, *17*, *21*), and, as such, there was a major dietary shift from the browsing seen in late Hemphillian *D. mexicanus* from Florida. This dietary transition may already have occurred elsewhere in North America because $\delta^{13}C$ data indicate that some local populations (Mexico) of late Hemphillian *Dinohippus* were principally grazers (*17*). Although we interpret Florida *D. mexicanus* as principally a browser, the presence of two individual $\delta^{13}C$ values of -4.7 and -1.5 per mil (Fig. 3) suggests that some individuals of the Bone Valley population were feeding on C_4 grasses. The subsequent transition to widespread grazing in *Equus* apparently occurred rapidly during the early Pliocene in North America between ~4.8 and ~4.5 Ma.

The ancient environmental context of Bone Valley horses also allows a better understanding of late Hemphillian horse diversity elsewhere in North America at ~5 Ma. Relative to other contemporaneous sites in North America, (i) Bone Valley horses exhibited a greater overall diversity of six, rather than four, species (*7*, *19*), and (ii) one species (*C. emsliei*) survived the late Hemphillian extinction event locally in Florida. Modern ecological studies indicate that greater herbivore diversity can be supported by more diverse plant communities. Along with the Hemphillian grasslands that were widespread in North America, the ancient Florida landscape also included additional plant diversity in marsh and estuarine communities. This greater habitat and plant diversity in ancient Florida apparently supported a more diverse horse fauna.

Before this study, traditional hypotheses about horse evolution would have asserted that the Bone Valley hypsodont horses indicated a grazing adaptation. This now must be modified in light of the carbon isotope and microwear evidence. Our study indicates that the Bone Valley horses partitioned their available food resources across a broad spectrum from almost pure C_4 grazers to principally C_3 browsers. The Bone Valley horses remained hypsodont, even though they were not all grazers, because of phylogenetic constraint and the irreversibility of macroevolution. The ancestral clades from which Bone Valley horses descended probably evolved high-crowned teeth adapted for grazing. Once hypsodonty evolved, it was impossible to return to being short-crowned browsers, even though the descendent Bone Valley horses had markedly changed their diets.

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3. $\delta^{13}C_{PDB}$ (per mil) = $[(R_{sample}/R_{standard}) - 1] \times 1000$, where R is the ratio of ^{13}C to ^{12}C, sample is unknown, and standard is Pee Dee belemnite. A third photosynthetic pathway, CAM (Crassulacean acid metabolism), found in plants such as succulents (Cactaceae), is not considered relevant here.
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9. A grazer is defined as having a diet predominantly of grass, but the diet can also include other short C_3 plants forming low grasslike ground cover.
10. HI is a less reliable dietary indicator because it is influenced by ancestral morphology (that is, descending from high-crowned species) and possibly other factors such as degree of open habitat or contaminant grit (or both) in diet [C. M. Janis, in *Teeth Revisited*, D. E. Russell, J.-P. Santoro, D. Sigogneau, Eds., *Mem. Mus. Natl. Hist. Ser. C.* **53**, 367 (1988)].
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