13. Terrestrial Mammalian Herbivore Response to Declining Levels of Atmospheric CO_2 During the Cenozoic: Evidence from North American Fossil Horses (Family Equidae)

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13.1 Introduction

The fossil record preserves a wonderfully rich sequence spanning 65 million years of Cenozoic mammals that lived in ancient terrestrial ecosystems. During this time in Earth history, major global climate changes undoubtedly affected the course of mammalian evolution. Similarly, countless biotic interactions, such as competition, contributed to the struggle for existence of particular species. One of the interesting challenges for the paleontologist is to understand the relative role of physical/climatic factors versus those of biological interactions in driving evolution. This challenge has been with us since Darwin, and is unlikely to be solved at any time in the near future. As more data and interpretations accumulate from the fossil record, we will have an enhanced understanding of these determinants of evolution.

The paleoecology of Cenozoic mammals has long been studied, mostly because these animals are abundant and many have living close relatives, which yield modern-day data that can be compared with paleontological data in order to reconstruct ancient ecosystems. With regard to the physical and climatic factors that structure ancient ecosystems, rainfall and seasonality are, classically, the best known. Other climatic parameters also have undoubtedly affected Cenozoic mammalian evolution. We now know, for example, that early Cenozoic Earth was a far more humid hothouse than it is today and that during a relatively short interval of several million years in the Eocene, this dominant climatic regime transformed into an "icehouse," that is, with significant global cooling that apparently affected the rate of extinctions (Prothero 1994). It has been asserted that, in a similar way, the late Cenozoic has undergone significant global change manifested by aridification, higher seasonality, and general cooling, particularly over the past 5 million years with the onset of Pleistocene glacial stages (Raymo 1994).

Over the past decade, studies of stable isotopes of ancient soils and fossil herbivore teeth (Cerling, Wang, and Quade 1993, Cerling et al. 1997) have demonstrated a major global change in the relative abundance of C_3 and C_4 photosynthesis in terrestrial ecosystems during the late Miocene. Prior to approx 7 million years ago, terrestrial ecosystems, even including tropical and temperate grasslands, were fundamentally C_3-based. After that time, approx the analogs of the older grasslands became C_4-based, which set the stage for modern C_4-based grassland biomes.

The purpose of this paper is to ask the question: How did mammalian herbivores living in late Cenozoic terrestrial ecosystems respond to declining levels of atmospheric CO_2? The short answer to the question might be that these herbivores were oblivious to this global climate change. However, as will be developed below, the long answer to this question is both more complex and certainly more interesting. As mammalian herbivores ate plants, and plants responded in fundamental ways to declining atmospheric CO_2, the primary consumers were indirectly affected by this global change. It should be noted that similar studies have been presented for browsing (Janis, Damuth, and Theodor 2000) and grazing ungulates (Janis, Damuth, and Theodor 2002).

Fossil horses (Family Equidae) from North America are chosen here as a model, or case example, because (1) this group was very abundantly represented in North America from the Eocene, approx 57 million years ago, until the last surviving genus *Equus* became extinct on this continent during the late Pleistocene, approx 10,000 years ago, (2) this group is a classic textbook example of morphological evolution related to adaptive change (e.g., Simpson 1951, 1953; MacFadden 1992), and (3) Recent work that analyzes stable isotopes of North American fossil horse teeth allow testing of previous morphological hypotheses concerning the dietary evolution related to the adaptive shift from browsing to grazing (Wang, Cerling, and MacFadden 1994; MacFadden and Cerling 1994; Cerling, Harris, and MacFadden 1998a; MacFadden, Solounias, and Cerling 1999).

This paper assumes that levels of atmospheric CO_2 declined during the Cenozoic and that this change, either fundamentally or partially (i.e., other factors such as increased aridity may also have been involved) affected the photosynthetic pathways used by grasses. There are some different interpretations about the exact timing of decreased levels of atmospheric CO_2 (e.g., Boucot and Gray 2001). Most authors (e.g., Cerling 1991; Berner 1991; 1994; Ekart et al. 1999; Pearson and Palmer 2000; Wallmann 2001) indicate low, or declining, levels to a point sometime during the Miocene that would have potentially favored C_4

photosynthesis, i.e., below approx 500 ppm (for an exception, see Pagani, Arthur, and Freeman 1999; Pagani, Freeman, and Arthur 1999).

13.2 Ancient Grasslands and Paleobotanical Evidence for C_3 and C_4 Plants During the Cenozoic

In the broad scheme of life on this planet, with land plants known to have existed at least since the Devonian, approx 300 million years ago (Behrensmeyer et al. 1992), grasses are a relatively recent arrival on the global ecological landscape. Today, grasslands constitute a major ecological biome type and cover about 25% of the Earth's land. They exist in a wide variety of climatic regimes ranging from mean annual temperatures between 0 and 20°C and between 250 and 1000 mm of annual precipitation. Grassland types vary from tropical savannas, to temperate tall and mixed-grass prairies, shrub steppe, high-latitude cold steppes and arid short-grass steppes, and montane grass communities (Shantz 1954; Lauenroth 1979). Grasses, therefore, contribute greatly to primary productivity and represent a considerable food resource for terrestrial herbivores.

With regard to the origin of Poaceae, Kellogg (1999, p. 431) states: "We can comfortably date the origin of the grasses at approximately 65 mya based on pollen grains from the Upper Maastrichtian" (Linder 1987). The earliest evidence of grasses during the Cenozoic comes from Paleocene pollen, approx 65 to 55 million years ago (Muller 1981), and the earliest plant macrofossil comes from the Paleocene/Eocene of Tennessee, approx 55 million years ago (Crepet and Feldman 1991). Thereafter, the fossil record lacks good evidence of grasses until the middle Cenozoic (Jacobs, Kingston, and Jacobs 1999). Based on the abundance of precocious (relative to, e.g., horses in North America; Shockey 1997) high-crowned, presumed grazing, mammalian herbivores during the late Eocene and Oligocene in South America, Stebbins (1981) suggested that grasses may have arisen, or spread, earlier there than in the Northern Hemisphere; fossil evidence for this assertion, however, is scanty. In the Northern Hemisphere, the next definitive evidence for fossil grasses includes paleofloras of the Great Plains that are approx 15 million years old and come from middle Miocene (MacGinitie 1962; Gabel, Backlund, and Hafner 1998) and dumb-bell shaped (panicoid) phytoliths (Fig.13.1), preserved from the 14-million-year-old Fort Ternan hominoid site in East Africa (Dugas and Retallack 1993; Jacobs, Kingston, and Jacobs 1999). It is not otherwise known whether middle Miocene grasses were principally C_3 or C_4, but proxy evidence from fossil high-crowned, presumed grazing, herbivores suggests that they were mostly C_3 (Wang, Cerling, and MacFadden 1994; MacFadden, Cerling, and Prado 1996; Cerling et al. 1997, Cerling, Ehleringer, and Harris 1998b).

The first definitive evidence for C_4 grasses, that is, with preserved Krantz anatomy, comes from the late Miocene (~12.5 Ma) Ricardo Formation from the

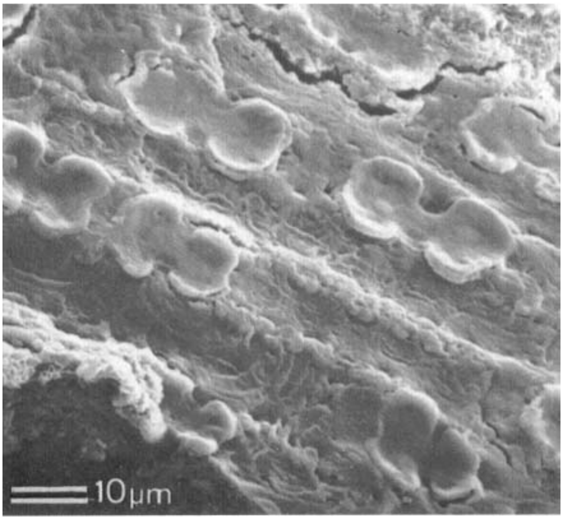

Figure 13.1. Middle Miocene dumb-bell shaped (panocoid) phytoliths from Fort Ternan, Kenya. From Dugas and Retallack (1993) and reproduced with permission of the Paleontological Society.

Mojave desert in southern California (Tidwell and Nambudiri 1989). There also is a late Miocene occurrence (~7 Ma) from Kansas (Thomasson, Nelson, and Zakrzewski 1986). Considerable discussion in the literature addresses the extent of and biogeographic distribution of C_4 grasses prior to the late Miocene (see Cerling 1999; Kellogg 1999). Based on carbon isotopic evidence from fossil herbivores and ancient soil carbonates, it seems that if C_4 grasses were present prior to this time, they were relatively rare in terrestrial ecosystems. A large body of carbon isotopic data from tooth enamel and ancient soil carbonates during the late Miocene (Fig. 13.2) demonstrates that C_4-based ecosystems became widespread globally in a relatively short period of time after about 7 million years ago (Cerling et al. 1997; 1999).

Studies of the relative proportions of C_3 and C_4 plant foods eaten by mammalian herbivores in the New World during the latest Miocene through late Pleistocene indicate that latitudinal gradients of C_3 and C_4 distributions, as we know them from the present-day, were established during this time, as shown in Fig. 13.3 (MacFadden, Cerling, and Prado 1996; MacFadden et al. 1999). In the context of the present discussion, the proximate cause for the advent of C_4 grasses during the late Miocene approx 7 million years ago seems to have been the decrease in atmospheric CO_2 to below levels (<400 ppm) that would favor C_4 photosynthesis as an adaptive strategy for grasses (Ehleringer, Cerling, and Harris 1997; Cerling 1999).

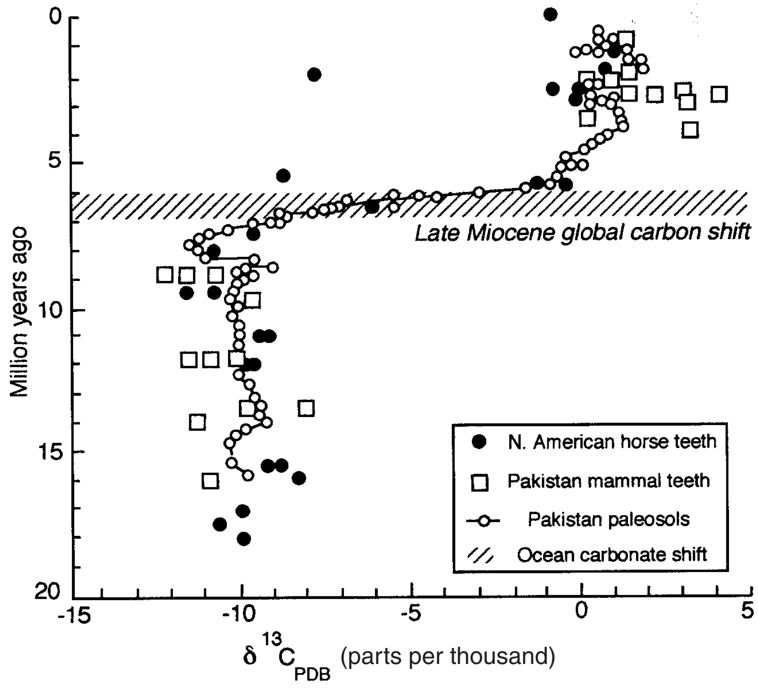

Figure 13.2. Late Miocene global carbon shift based on data from fossil teeth, paleosols, and the deep-sea carbonate record. The carbon isotopic content is expressed in $\delta^{13}C$ (parts per thousand) = $(R_{sample}/R_{standard} - 1) \times 100$, where R = $^{13}C/^{12}C$, sample is unknown and standard is PBD Cretaceous belemnite. Modified from Cerling, Wang and Quade (1993) and reproduced with permission of Macmillan.

13.3 Reconstruction of Ancient Diets: General Background for Mammalian Herbivores

Traditionally, the diets of ancient herbivores have been interpreted through study of dental morphology. This stems from a classic study of fossil horses from Europe (Kowalevsky 1873) but is also based on an extensive body of modern literature (e.g., Janis and Fortelius 1988). Recent studies also have added paleodietary information from the study of cranial morphology (Janis and Ehrhardt 1988; Solounias and Moelleken 1993) and enamel-wear patterns (Solounias and Hayek 1993; Fortelius and Solounias 2000; Solounias and Semprebon 2001) of fossil mammalian herbivores.

Based on study of extant mammalian herbivores with known diets and habitat preferences, the feeding adaptations of corresponding extinct species can be modeled from the fossil record. For example, extant mammals such as the white-tailed deer (*Odocoileus virginianus*) and tapir (*Tapirus*) have a feeding mor-

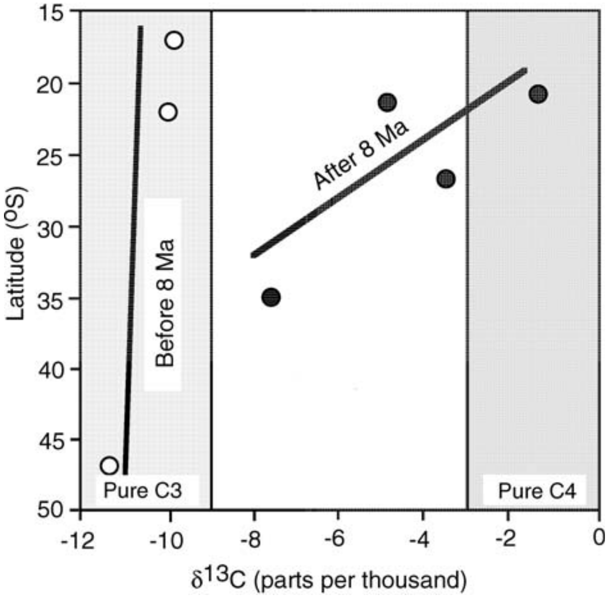

Figure 13.3. Variation in tooth enamel carbonate $\delta^{13}C$ of terrestrial mammalian grazers from South America, showing the development of latitudinal gradients in the distribution of C_3 and C_4 grasses after 8 million years ago (Ma). Modified from MacFadden, Cerling and Prado (1996) and reproduced with permission of the Society for Sedimentary Geology.

phology that includes short-crowned (brachydont) teeth (Fig. 13.4) and a rounded incisor cropping mechanism (Janis and Fortelius 1988; Janis and Ehrhardt 1988; Solounias and Moelleken 1993). These species are known to be principally forest-dwelling browsers, that is, feeding on relatively soft leafy plant foods (Walker 1975).

In contrast, the extant North American Bison, *Bison bison* or African zebras (e.g., *Equus burchelli*) have high-crowned (hypsodont) teeth and relatively straight incisor cropping mechanisms. These species are known to be principally open-country grazers, that is, feeding principally (>90%, Janis and Ehrhardt 1988) on grasses. The primary adaptive explanation for the increased crown height in grazers is the accelerated tooth wear rate resulting from chewing abrasive grasses, which contain phytoliths—silica plant parts that function to deter herbivory (McNaughton et al. 1985; Piperno 1988). To a lesser extent, another factor potentially contributing to tooth wear could be the introduction of contaminant grit in herbivore diets, either from feeding close to the ground, or from abrasive dust particles on plant foodstuffs.

The radiation of Cenozoic mammals during the past 65 million years is characterized by increasing taxonomic and morphological diversification and by re-

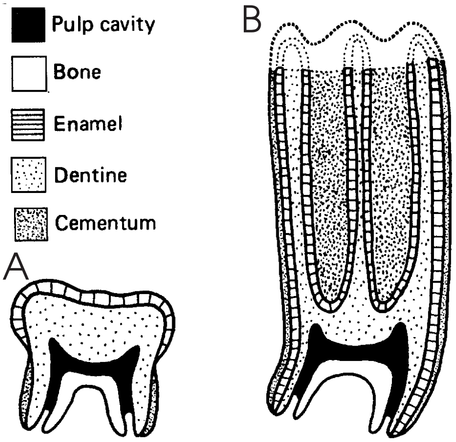

Figure 13.4. Comparisons of tooth crown height represented by cross-sectioned teeth. A. a short-crowned (brachydont) molar from a human. B. High-crowned (hypsodont) molar from a horse. From Janis and Fortelius (1988) and reproduced with permission of Cambridge University Press.

placement, since some clades radiated into new "adaptive zones" (*sensu* Simpson 1953), or guilds (*sensu* Root 1967). With a few very rare exceptions (e.g., archaic mammalian orders Taeniodontia and Tillodontia), early Tertiary (Paleocene through Oligocene) terrestrial mammalian herbivores are universally characterized by short-crowned, or brachydont, teeth, as shown in Fig. 13.4 (Janis 2000). This morphology is interpreted as a generalized browsing adaptation, either for folivory or for frugivory. This is also consistent with paleoecological reconstructions in which Earth's terrestrial ecosystems during the early Tertiary had a relatively high proportion of forested and woodland biomes available as food resources to these ancient browsers (Webb 1977).

During the Miocene there was a widespread change in the dental morphology of terrestrial mammalian herbivores. Notwithstanding what occurred in South America (to be discussed below), there was a widespread and geologically simultaneous (i.e., all within a period of a several million years) increase in crown height in these mammals. This dramatic evolution of hypsodont, or high-crowned, teeth is interpreted as a response to the advent of widespread grassland communities during the Miocene and corresponding adaptive radiation of terrestrial mammalian grazers. Correspondingly, many mammal groups that during the earlier Tertiary were represented by brachyodont species (e.g., Artiodactyla and Perissodactyla) evolved into clades consisting of grazers.

Although this rapid and widespread (both taxonomically and geographically) increase in hypsodonty occurred throughout Holarctica and Africa during the Miocene, a different pattern is observed for extinct South American mammalian herbivores. Mammalian faunas from the late Eocene, and particularly the De-

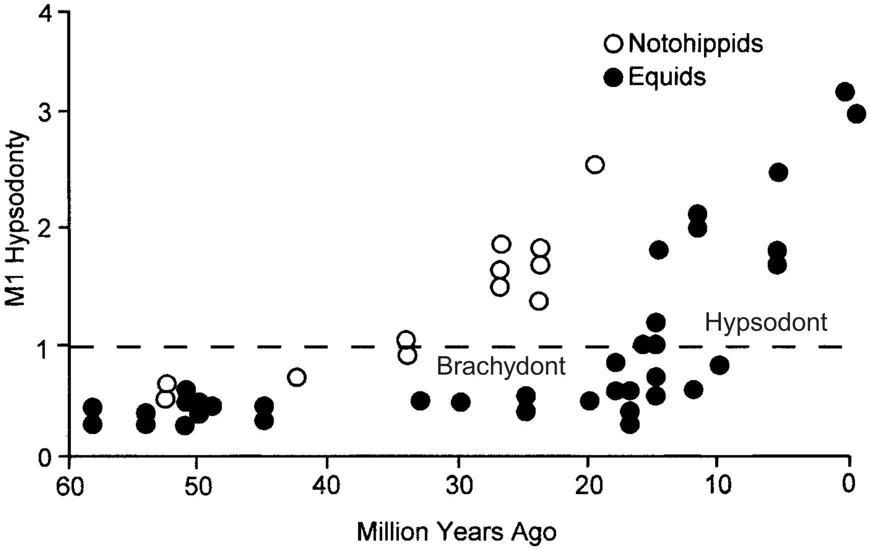

Figure 13.5. The timing of increased crown height (hypsodonty) in South American notoungulates (Family Notohippidae) as compared to North American horses (Family Equidae). Hypsodonty, or the hypsodonty index (HI), is the ratio of molar occlusal length to unworn molar crown height. Mammals with HIs of <1 are short-crowned, or brachydont, whereas those with HIs of >1 are high-crowned, or hypsodont. From Shockey (1997) and reproduced with permission of the Society of Vertebrate Paleontology.

seadan late Oligocene, approx 30 million years ago, show a large diversity of the high-crowned, endemic notoungulates. The stage of evolution seen in the dentition of these terrestrial mammalian herbivores is comparable to that of North American clades, such as horses approx 20 million years ago, thus giving rise to the concept of "precocious hypsodonty" in South America (Fig. 13.5). Several workers have asserted that the advent of precocious hypsodonty indicates an earlier origin of grasses in South America than in the Northern Hemisphere (Patterson and Pascual 1972; Stebbins 1981; Jacobs, Kingston, and Jacobs 1999) by approx 10 million years ago.

13.4 Fossil Horses, Diets, and Climate: Case Example from North America

Fossil horses (Family Equidae) have an abundant fossil record in North America spanning most of the Cenozoic, that is, for the past 57 million years. For this reason, and probably because of their close association with humans, fossil horses have been a classic example of long-term macroevolution (e.g., Simpson

1951, 1953; MacFadden 1992). In this section, fossil horses will be presented as a case example of patterns of morphological evolution, extinction, and possible climatic influences, particularly during the late Cenozoic, that is, the past 25 million years, within the Family Equidae (Fig. 13.6).

Like other early Cenozoic terrestrial mammalian herbivores, Eocene through early Miocene horses are characterized by brachydont (short-crowned) dentitions. During the middle Miocene, approx 20 million years ago, horses underwent a dramatic morphological evolution of their dentitions (MacFadden and Hulbert 1988), resulting in a rapid diversification of hypsodont (high-crowned) taxa. This Great Transformation has been interpreted to represent the advent of grass-dominated ecosystems and the corresponding onset of grazing by horses and other herbivores (Simpson 1951; Webb 1977; MacFadden 1992). Given that the carbon isotopic composition of plant foods are incorporated into the enamel mineral lattice of teeth, Wang, Cerling, and MacFadden (1994) investigated the carbon isotopic composition of fossil horse teeth to determine if there was an isotopic shift corresponding to a dietary shift from C_3 to C_4 plant foods during the Great Transformation.

Interestingly, the results were somewhat unexpected in terms of the original hypothesis to be tested. Wang, Cerling, and MacFadden (1994) found that although the increase in hypsodonty occurs during the middle Miocene, starting at approx 20 million years ago, the isotopic shift from C_3 to C_4 plant foods did not occur until the late Miocene, approx 7 million years ago (Fig. 13.7).

Several subsequent studies have confirmed that the carbon isotopic shift in diets from C_3 to C_4 plants recorded in extinct terrestrial grazing-mammal teeth also did not occur until the late Miocene in South America, Africa, and Eurasia (Cerling 1999; Cerling et al. 1997, 1998b), thus indicating a global phenomenon (see Fig. 13.2). This observation has direct relevance here because this global carbon shift preserved in fossil grazing-mammal teeth is a response to changes in grass photosynthesis, that is, predominantly C3 prior to approx 7 million years ago to predominantly C_4 thereafter (in temperate and tropical grassland biomes). Although other factors (such as increased aridity) may have been involved, this change in photosynthesis seems related to declining atmospheric CO_2 to levels less than approx 500 ppm—the threshold below which C_4 photosynthesis becomes advantageous as a physiological adaptation (Ehleringer et al. 1991; Ehleringer, Cerling, and Helliker 1997).

The macroevolution of fossil horses during the browsing/grazing transition was part of the widespread change in overall standing diversity of terrestrial mammalian herbivores (Janis, Damuth, and Theodor 2000). During the middle Miocene, this terrestrial herbivore diversity reached its peak in the Clarendonian Chronofauna (Webb 1977; 1984) between approx 15 million to 12 million years ago. This time is characterized by high-productivity terrestrial biomes that supported a rich ancient biodiversity, including both browsing and grazing herbivore taxa. For example, a dozen genera, many of which were sympatric, of fossil horses lived in North America during this time. Beginning 12 million years ago,

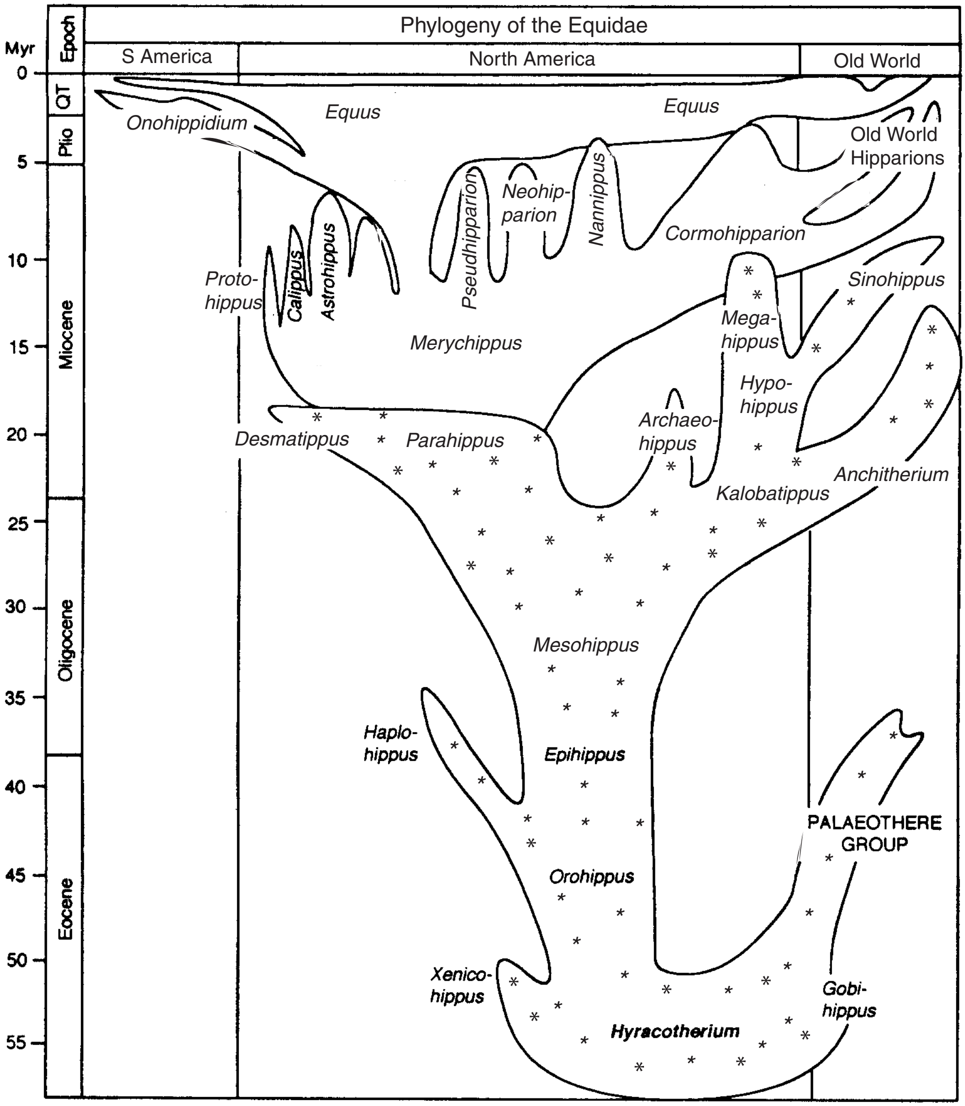

Figure 13.6. Phylogeny of the Equidae, with emphasis on the North American radiation. Principally browsing taxa are represented by the region of the phylogeny between 57 and 20 million years ago with "*" symbols. Modified from MacFadden (1992) and reproduced with permission of Cambridge University Press.

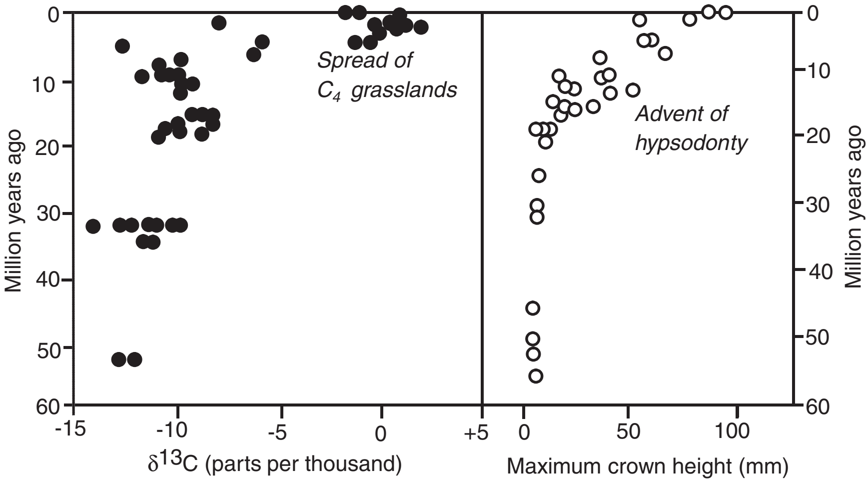

Figure 13.7. The shift in tooth enamel carbonate $\delta^{13}C$ (left) versus increased crown height (right) in Cenozoic horses from North America. From Wang, Cerling and MacFadden (1994) and reproduced with permission of Elsevier.

terrestrial mammalian herbivore diversity has declined, so that today it is the lowest it has been during the late Cenozoic. During this interval, the decrease in herbivore diversity occurred within different feeding guilds and apparently for different reasons.

The relatively high diversity of browsing taxa during the early and middle Cenozoic correlates with widespread and abundant forested and woodland communities, providing extensive browsing plant food resources (Webb 1977; Janis, Damuth, and Theodor 2000). By the middle Miocene, forested and woodland biomes decreased as grasslands expanded. Correspondingly, the number of browsing mammals declined and grazers increased in their diversity (Webb 1977), although Janis, Damuth, and Theodor (2000, 2002) assert that these changes were unrelated. Thereafter, overall standing herbivore diversity declined steadily, and this is even seen within the grazing mammals such as horses (Fig. 13.8) and therefore cannot be simply explained by the decline of browsers.

The interpretation for this decline in the diversity of grazing herbivore has been a global deterioration of climate, including increased aridity, higher seasonality, and general global cooling resulting in lower productivity ecosystems supporting lower biodiversity (Webb 1977; MacFadden 1997; Janis, Damuth, and Theodor 2000). While these previously recognized climatic parameters undoubtedly affected the diversity of grazing mammals during the late Cenozoic, the decrease in atmospheric CO_2 also undoubtedly played a part in this equation, as will be discussed in the next section.

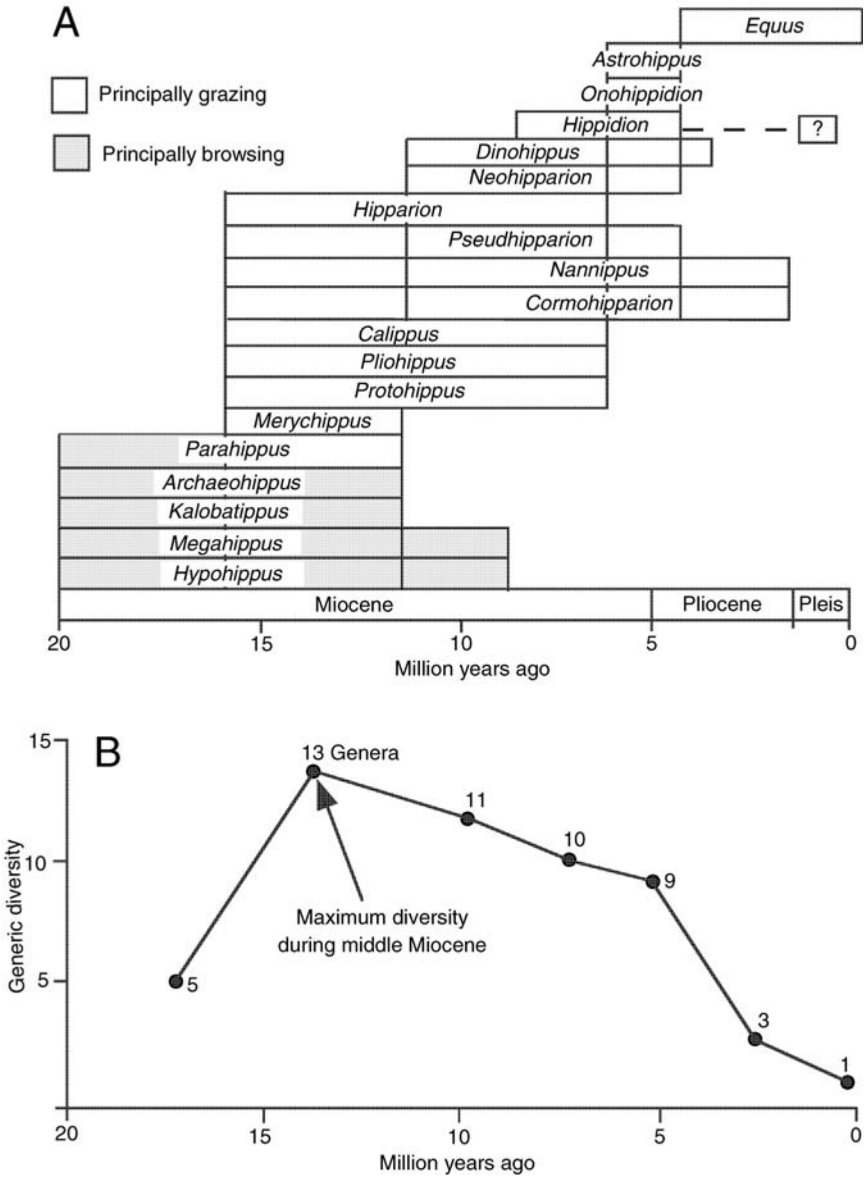

Figure 13.8. Decline in horse diversity since the middle Miocene, approx 15 Ma ago. **(A)** Time ranges of principally browsing and grazing genera. **(B)** Plot of generic diversity. Modified from MacFadden (1992) and reproduced with permission of Cambridge University Press.

13.5 The Present Is the Key to the Past

The proximate result of the decrease in atmospheric CO_2 during the late Miocene to levels below approx 500 ppm (the C_3/C_4 adaptive crossover) was the proliferation of C_4 grasses at the expense of C_3 grasses in temperate and tropical regions. Using modern analogs, we might ask what are the differences between C_3 versus C_4 grasses as food resources for grazers? The following potential factors are relevant in this context:

1. Lower ecosystem productivity. Studies have demonstrated that many C_4 grassland ecosystems generally have lower productivity than do corresponding C_3 grasslands. This does not result from an inherent lowered productivity of the grass species, per se, but rather because they exist in climates that support lower productivity. Along with this, lower productivity ecosystems support a lower biomass and lower biodiversity (Dyer et al. 1982; Lauenroth 1979; McNaughton et al. 1989), including the consuming herbivores. While this may be a general rule for grasslands, an exception is the higher mammalian herbivore diversity seen in some C_4 grasslands, for example, African savannas.
2. Lower nutritive value. C_4 grasses have a lower percentage of digestible plant parts than do C_3 grasses: for example, a greater percentage of bundle sheaths (Heckathorn, McNaughton, and Coleman 1999). Herbivore species feeding on this low-nutritive, low-digestibility food resource will "need" to evolve adaptive strategies to extract more nutrition from their diet per unit volume. This could be done by one or more ways, including higher digestibility and/or increased intake of plant foods.
3. Greater plant defenses. Plants potentially have the following dominant antiherbivory adaptations: physical, that is, the presence of abrasive materials (phytoliths) and or other structures, such as thorns; and chemical, that is, toxic or unpalatable compounds within their leaves. Grasses, characteristically have neither secondary chemical compounds (Heckathorn, McNaughton, and Coleman 1999) nor thorns. The primary antiherbivory mechanism in grasses, therefore, consists of internal silica phytoliths. Phytoliths vary significantly between C_3 and C_4 grasses (Piperno 1988; Twiss 1992; Piperno and Pearsall 1998). These differences may have affected the consuming herbivores in two ways: C_4 grasses have a greater phytolith content than do C_3 grasses; and generally C_4 grasses have more elongated (panicoid) phytoliths, whereas in C_3 grasses these structures are more rounded or equidimensional (e.g., pooid). These differences potentially affected evolution because C_4 grass foodstuffs would therefore have accelerated tooth wear relative to C_3 grasses. In the context of late Cenozoic mammalian herbivores, this antiherbivory adaptation of C_4 grasses that spread after approx 7 million years ago in terrestrial ecosystems could have affected grazing mammals by increasing the rate of tooth wear. This potentially would have "upped the ante" in the

coevolutionary arms race between the plant foods and the mammalian grazing species that consumed the foods.

13.6 How Were the Cenozoic Mammalian Herbivores Affected?

Decreased atmospheric CO_2 and the corresponding increase in C_4 plants resulted in lower productivity ecosystems, lower digestibility food resources available to terrestrial mammalian herbivores, and significantly increased rates of tooth wear. These parameters can now be examined in a context of patterns of mammalian herbivore morphology and macroevolution observed from the fossil record over the past 20 million years, that is, the part of the Cenozoic that seems to have been most affected by changes in threshold levels of atmospheric CO_2.

Lower productivity grassland biomes produce less biomass (Lauenroth 1979; Dyer et al. 1982; McNaughton et al. 1989) and consequently can support less overall species diversity up the food chain. It has been clearly demonstrated that after the peak diversity of the Clarendonian Chronofauna in North America (Webb 1977, 1984; Janis, Damuth, and Theodor 2000), overall herbivore diversity dropped steadily from the Miocene through the late Pleistocene. This is evidenced by the fact by approx 2 million years ago, terrestrial herbivore diversity in North America was about one-third of what it previously had been at 15 million years ago (Janis, Damuth, and Theodor 2000). The potential explanation for this decline in diversity is complex and involves several different phases. The first phase involved the reduction of browsing herbivore diversity during the late middle Miocene (~15–12 Ma) when the forested and woodland biomes decreased as grasslands spread. Thereafter, however, herbivore diversity continued to decline, as is exemplified by Equidae (see Fig. 13.8). This drop in diversity has mostly been explained by a global climate change resulting in increased aridity, seasonality, and cooling in lower productivity grassland ecosystems (Webb 1977, 1984; Webb and Opdyke 1995; Janis 1993). In the context of this discussion, decline in atmospheric CO_2 also potentially contributed to this drop in diversity.

Undoubtedly, the quality of food resources eaten by mammalian herbivores affected evolution. Species that transition from higher- to lower-quality plant foods require a different kind of digestive physiology. Feeding on lower-quality forage tends to be correlated to increased retention time in the gut, which yields more time for extracting nutrition from the plant foodstuffs. This is seen in larger perissodactyls, such as horses and grazing rhinos, and large ruminant artiodactyls, for example, bison (Janis 1976). Retention time of food in the gut of mammalian herbivores is proportional to body size, so it has been suggested that one of the contributing factors for the increased body size (Fig. 13.9) seen in some clades (e.g., horses)was the change to lower digestibility plant foods, such as would be seen by a change from feeding on C_3 to C_4 grasses (McNaughton 1991; Owen-Smith 1988; Janis, Damuth, and Theodor 2000).

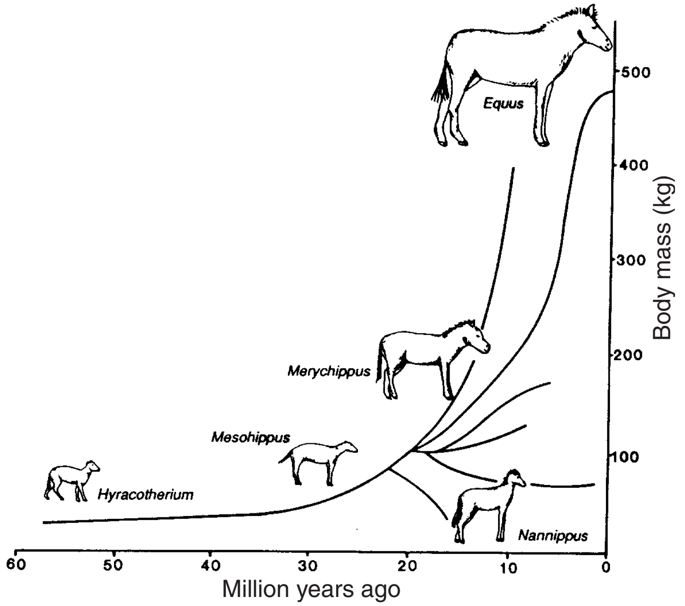

Figure 13.9. Body size evolution in horses. The first half of equid evolution is characterized by relative stasis, whereas the second half is characterized by diversification of body size since the late Miocene. The clade with *Equus* has included some of the largest extinct species, some with estimated body masses between 450 and 500 kg. From MacFadden (1992) and reproduced with permission of Cambridge University Press.

How does the evolution of body size in horses and other terrestrial grazers potentially relate to changes in atmospheric CO_2? At first glance this may seem like a stretch, but actually, an indirect mechanistic relationship can be argued, particularly for those examples of increased body size. Previous explanations for increased body size in mammalian clades have included such factors as more adaptive physiology (Eisenberg 1981), increased energy input into species (Brown 1995), more efficient defense against predators in the coevolutionary arms race (Janis 1993), and/or larger home ranges (McNab 1963) in which to forage for seasonally available plant food resources (Owen-Smith 1988). To these can be added the factor that C_4 grasses, with their lower digestibility and lower per unit volume nutritive value, could potentially favor increased body size for longer retention times in the gut to increase digestive efficiency (Owen-Smith 1988; Janis, Gordon, and Illius 1994).

Grazers that feed on more abrasive plant foods with increased phytolith content will concomitantly increase tooth wear rates. It therefore follows that those late Miocene grazing species that fed on C_4 grasses after 7 million years ago that had relatively more hypsodont teeth would be adaptively favored. Mac-

Fadden, Solounias, and Cerling (1999) studied six species of 5-million-year-old sympatric horses from the latest Miocene (late Hemphillian) of Florida. This diversity was just before a major extinction event at the Hemphillian/Blancan boundary at 4.5 million years ago. Of the six species clades that coexisted and divided up the available plant food resources prior to the end of the Hemphillian, only three survived after 4.5 million years ago. The three surviving Pilocene (Blacan) clades demonstrate a range in adaptive characteristics, most notably body size and relative tooth crown height (hypsodonty index [HI], higher index indicates increased relative crown height), as follows:

1. The "dwarf" *Nannippus* (species *aztecus* to *peninsulatus*), with body masses estimated to be approx 65 to 75 kg and HIs of approx 2.5 to 3.
2. *Cormohipparion* (single late-surviving species *emsliei*), with body mass estimated to be approx 105 kg and a relatively low HI of approx 2.
3. *Dinohippus/Equus* (*D. mexicanus* to *E. simplicidens*, to several later *Equus* species) with body masses ranging from approx 275 to 450 kg and HIs from 2.3 to >>3 (MacFadden 1987; MacFadden, Solounias, and Cerling 1999).

Of the three equid clades that persisted into the Pliocene and earliest Pleistocene, only one, *Equus*, continues through the late Pleistocene after approx 1.5 million years ago when it further diversifies into several apparently distinct species and is exceedingly abundant throughout North America, South America, Eurasia, and Africa. During the late Pleistocene *Equus* becomes geographically restricted to the Eurasian steppe after about 10,000 years ago, when this genus became extinct elsewhere throughout its previous range.

The foregoing discussion predicts that the equid clade with increased body size and relatively more hypsodont teeth would be adaptively favored in a regime of more abrasive and less nutritious C_4 grasses. This is the pattern that is observed: *Equus* was the latest surviving and most widespread of the late Cenozoic equid clades observed in the fossil record. Its adaptability stems not only from some critical adaptations that indirectly result from changes in atmospheric CO_2 and the spread of C_4 grasses, but also from the fact that *Equus* has been a generalist and can shift to a more mixed diet when other hypergrazers invade, or are dominant in, a local grassland community: for example, bison (*Bison bison*) in North America (MacFadden and Cerling 1996; Feranec and MacFadden 2000) or wildebeest (*Connochaetes taurinus*) in Africa (Owen-Smith 1988).

13.7 Summary

Changes in atmospheric CO_2 potentially had a profound, albeit indirect, effect on the evolution of terrestrial mammalian grazers during the late Cenozoic. As evidenced from fossil horses (Family Equidae), the larger-bodied and higher-crowned clade that included *Dinohippus* and *Equus* persisted through the series of extinctions that occurred since the middle Miocene. This clade survival is consistent with an adaptive strategy for feeding on more abrasive and less nutritive C_4 grasses that spread in tropical and temperate regions after the late Miocene global carbon shift approx 7 million years ago.

This observation can be further tested through future studies of molar wear rates in clades such as *Dinohippus/Equus* that fed on C_4 grasses. The prediction is that relative to other clades that fed mostly on relatively less abrasive C_3 grasses, those feeding on C_4 grasses would demonstrate increased molar wear rates. Although such a study has not yet been done with this goal in mind, it is theoretically possible given the available specimens from the fossil record.

Earth underwent a profound global change during the late Cenozoic, including the advent of the glacial stages over the past 5 million years. This "climatic deterioration" has traditionally been explained by increased aridity, seasonality, and decreased mean annual temperature, all of which undoubtedly affected the global floras and faunas. To this array of physical and climatic determinants now can be added decreased atmospheric CO_2 to a level below which C_4 photosynthesis in grasses was favored as an adaptive strategy; the change in atmospheric CO_2 ultimately affected the terrestrial mammalian grazers of the world, as exemplified by late Cenozoic horses from North America.

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