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Source: *Annual Review of Ecology and Systematics*, Vol. 31 (2000), pp. 33-59
Published by: Annual Reviews
Stable URL: http://www.jstor.org/stable/221724
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Annu. Rev. Ecol. Syst. 2000. 31:33–59

CENOZOIC MAMMALIAN HERBIVORES FROM THE AMERICAS: Reconstructing Ancient Diets and Terrestrial Communities

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Key Words browsers, grazers, isotopes, teeth, morphology, paleoclimate

■ **Abstract** Herbivory first evolved in terrestrial mammals during the late Cretaceous, ~100 million years ago (Mya). Of the ~35 ordinal-level clades of extinct or extant eutherian mammals from the New World, ~24 have been adapted to herbivory in one form or another. Dental adaptations for specialized terrestrial browsing are first recognized during the early Cenozoic (Paleocene-Eocene). Mammalian herbivores adapted for grazing did not become widespread in the New World until the middle Cenozoic; it seems that this adaptation and the spread of grasslands occurred during the late Oligocene (30 Mya) in South America ~10 million years earlier than in North America (20 Mya). Carbon isotopic evidence from fossil herbivore teeth indicates that C3 plants predominated until the late Miocene (~8 Mya). Thereafter, C3 and C4 terrestrial communities diversified. Late Pleistocene extinctions ~10,000 years ago decimated the diversity of mammalian herbivores, particularly those of larger body size.

INTRODUCTION

As primary consumers of plant biomass, herbivores represent the majority of diversity in ancient mammalian radiations. The fossil record of mammalian herbivores in North and South America is relatively well represented over the past 65 million years (My). During this time there have been considerable changes in climate and plant diversity that affected the structure and distribution of mammalian herbivore communities. In the past several decades, some important factors have influenced our understanding of, and our ability to reconstruct, ancient mammalian herbivore communities. Paleontological discoveries continuously improve our knowledge of the fossil record and oftentimes fill in critical gaps. New techniques, such as analyses of stable isotopes and enamel microwear, have advanced our ability to make paleodietary interpretations. Continuous refinements in dating techniques allow a better understanding of the time sequence of mammalian herbivore community evolution.

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The fossil record reveals a time dimension not available to modern ecologists. Paleontologists can track discrete communities through millions of years during which basic community structure is preserved but new taxa originate and fill ecological niches vacated by taxa that became extinct. This is called a chronofauna, a term originally proposed by Olson (64, 65).

This paper reviews the fossil record of terrestrial mammalian herbivore communities over the past 65 my, the Cenozoic Era in North and South America. Whenever possible, emphasis is placed on recent discoveries and new techniques that enhance understanding of this subject. The Cenozoic was a time of great global change, and it is somewhat artificial to devote this review to the New World, when parallel faunal changes occurred in the Old World. However, this focus is determined by the available space; the interested reader can also consult previous reviews on this general subject (31, 36, 94, 95).

BACKGROUND AND METHODS

In 1873, the Russian paleontologist Kowalevsky published a classic paper (38) describing fossil horses from Europe. He asserted that the evolution of horses with short-crowned teeth to those with high-crowned teeth during the Miocene indicated a corresponding change in diet from browsing to grazing. Since that time, the tooth crown height of fossil herbivores has been used to interpret the diets of ancient mammals (Figure 1). Within the past few decades, other techniques have added independent evidence to an understanding of ancient herbivore diets. Complementing gross tooth morphology, studies of skull morphology, and enamel microwear, stable carbon isotopes now can be used to reconstruct Cenozoic herbivore communities.

Morphology

Modern herbivorous mammals with short-crowned (brachyodont) teeth, e.g., the tapir (*Tapirus*) or deer (*Odocoileus*), are generally adapted to feeding on soft, leafy vegetation and hence are browsers. In contrast, modern herbivorous mammals with high-crowned teeth, e.g., the zebra (*Equus*) and bison (*Bison*), are generally grazers. High-crowned is defined as unworn premolar or molar teeth in which the height exceeds the occlusal length of the tooth (Figure 2*A*). High-crowned teeth are either of finite growth, like those of horses, or ever-growing (hypselodont) during the animal's lifetime, like those of some grazing rodents. The adaptive significance of high-crowned teeth is, in most cases, related to the abundance of phytoliths in grasses. Phytoliths are microscopic bodies of silica (SiO_2, the same compound as glass) within grasses that tend to wear teeth down and are an adaptation of the plant against herbivory (59). There are, however, some exceptions to this general short-crowned browser/high-crowned grazer pattern. For example, short-crowned llamas (*Lama*) are principally grazers (29, 52), whereas some extinct high-crowned

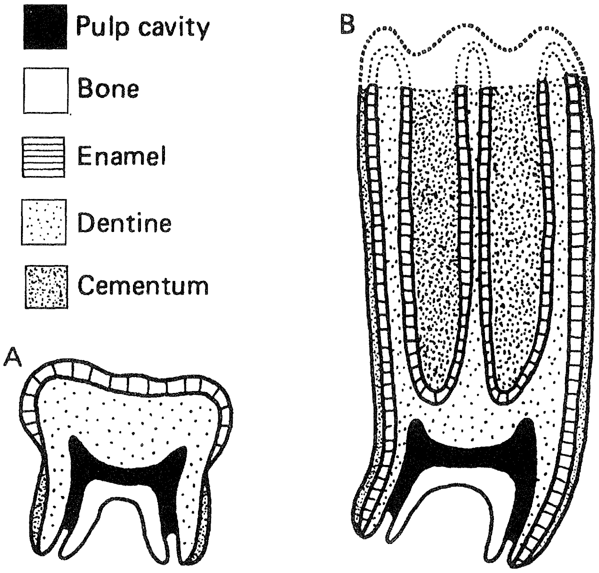

Figure 1 Comparison of short-crowned (brachyodont) human tooth (*a*) versus high-crowned horse tooth (*b*) showing expansion of the crown relative to the root area. From Ref. 33 and reproduced with permission of Cambridge University Press.

horses were principally browsers (53). Nevertheless, tooth morphology serves as a general model to interpret extinct herbivore diets.

There also is a correlation between high-crowned teeth and open-country habitats. Thus, some high-crowned herbivores may incorporate considerable amounts of grit into their diets from dust on the plant foods that they eat close to the land surface (29). Terrestrial grazers are generally considered to include animals that feed predominantly (>90%) on grasses (29), although a species is also a grazer if it crops plants other than grasses (e.g., forbs) that form the low ground cover in some biomes.

Certain cranial characters are also highly correlated to diet in extant herbivorous mammals. For example, the muzzle shape and incisor width of modern ungulates distinguish browsers from grazers (Figure 2). Grazers tend to have more transversely straight muzzles and incisors of generally similar size, which together form a functional cropping mechanism to procure grass and other plants near the ground surface. In contrast, browsers have more rounded muzzles and differentiated incisors, which together form a cropping mechanism for selective feeding from trees and shrubs (32, 84). These differences are also apparent in fossil herbivores, e.g., Oligocene notoungulates in South America (78) and Miocene sympatric horse species in North America (47). Other characters, like the depth of the jaw, development of the bony masseter prominence on the cheek, and position of the orbit, also indicate browsing versus grazing diets (85).

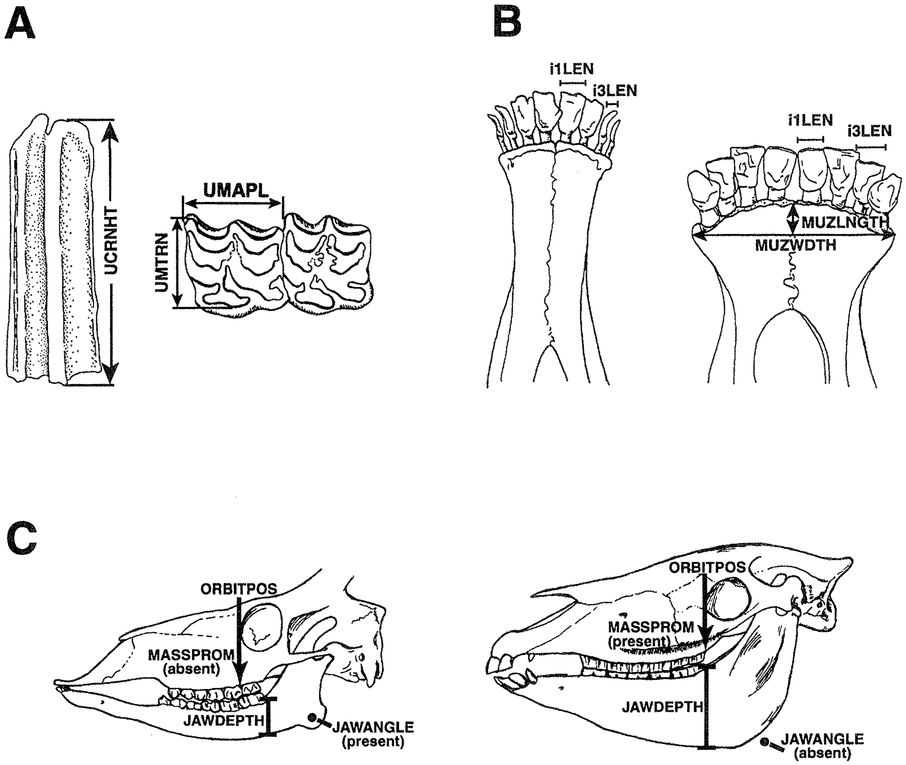

Figure 2 Dental and skull characters used to assess browsing versus grazing. (A) crown height, or hypsodonty index (HI) is the ratio of unworn crown height (UCRNHT) to molar anteroposterior length (UMAPL); in this case the HI is ~2.6, indicating a grazer. (B) Relative incisor lengths (i1LEN and i3LEN) and muzzle width (MUZWDTH) indicate a browser (narrow, left) or a grazer (broad, right). (C) The position of the orbit (ORBITPOS), presence or absence of the masseter prominence (MASSPROM), and depth and posterior angle of the jaw (JAWDEPTH, JAWANGLE) indicate a browser (left) or a grazer (right). Modified from Ref. 52 and reproduced with permission of the Paleontological Society.

The mastication of various foodstuffs imparts distinctive microscopic wear patterns to the tooth enamel of modern herbivorous mammals with known diets (83, 86). Using modern analogs, extinct herbivore diets can be interpreted using dental microwear. These enamel-microwear patterns can be quantified by determining the proportion of scratches versus pits on the enamel occlusal surface. Thus the enamel of a browser like the black-fronted duiker (*Cephalophus niger*) will have a large number of pits, which are caused by percussing leaves, in contrast to a grazer like the bison (*Bison bison*), which has many scratches caused by chewing abrasive grasses (Figure 3).

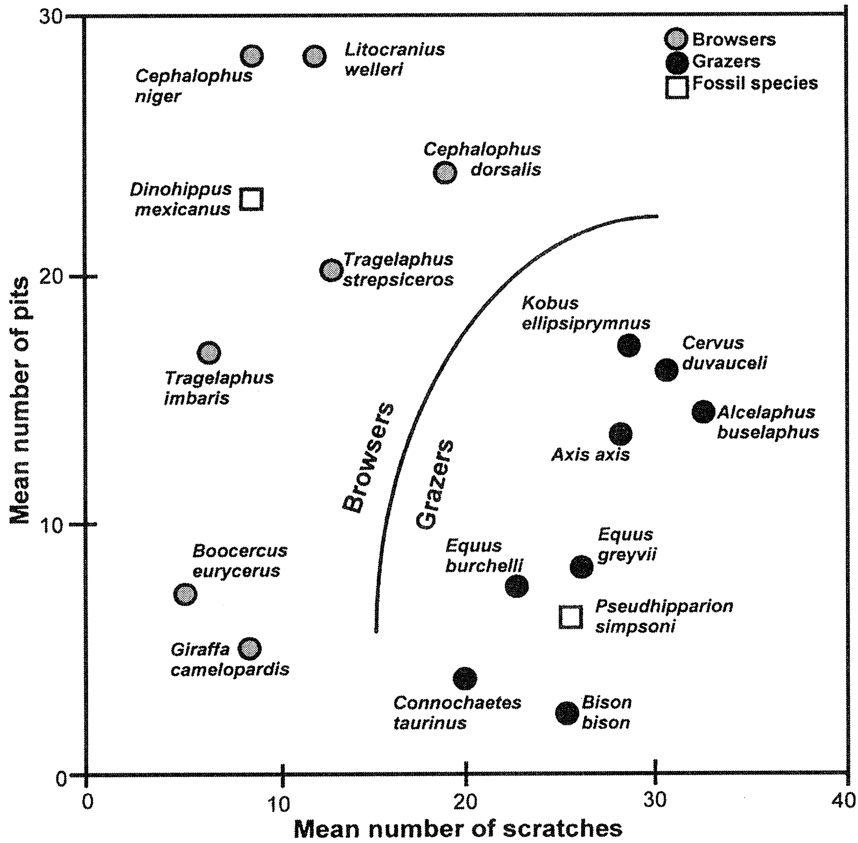

Figure 3 Enamel microwear studies the proportion of pits versus scratches per unit area (in this case 0.5 mm^2) for modern mammalian herbivores with known diets. Browsers have a high proportion of pits, whereas grazers have a high proportion of scratches. These modern analogs are used as a model to interpret the diets of fossil mammalian herbivores. Of the late Miocene fossil horses depicted here, *Dinohippus mexicanus* is a browser and *Pseudhipparion simpsoni* is a grazer. Modified from Ref. 53 and reproduced with permission of the AAAS.

Carbon Isotopes

Stable carbon isotopes have recently been used to interpret the diets and ecology of fossil mammals. For extinct herbivores, analysis of tooth enamel carbonate indicates whether the animal was feeding on C3 plants, C4 grasses, or a mixture of these foodstuffs (e.g., 37, 41, 52, 74). This technique can be used to discriminate diets because plants photosynthesize carbon by two principal pathways. The dominant photosynthetic pathway for terrestrial plants is the Calvin cycle, in which carbon is first incorporated into 3-carbon compounds, hence the term C3. About 85% of terrestrial plant biomass, including trees, most shrubs, forbs, and high-latitude or high-elevation grasses, use the Calvin cycle. In contrast, about 10% of terrestrial plant biomass photosynthesizes carbon using the Hatch-Slack cycle, in which carbon is first incorporated into 4-carbon compounds, hence C4. (The third photosynthetic pathway, CAM, or Crassulacean acid metabolism, is used by a small fraction of terrestrial plant biomass such as succulents. It is of minor relevance in the current study.) Present-day tropical and temperate grasses are predominantly C4, and they are adapted to more highly seasonal and arid climates than are C3 plants (17, 18). Not only do C3 and C4 photosynthetic pathways incorporate carbon into different compounds, they also fractionate the stable isotopes of carbon (^{12}C and ^{13}C) in different proportions. The ratio of ^{13}C/^{12}C is conventionally expressed as

$$\delta^{13}\text{C(in parts per mil, ‰)} = (\text{R}_{\text{sample}}/(\text{R}_{\text{standard}} - 1) \times 1000,$$

where R = ^{13}C/^{12}C. All measurements of an unknown (such as fossil-tooth enamel) are compared to the standard PDB (a Cretaceous marine mollusk PeeDee belemnite, which has a δ^{13}C of 0 ‰). C3 plants characteristically have δ^{13}C values ranging from −34 ‰ to −23 ‰, with a mean of −27 ‰; C4 plants characteristically have δ^{13}C values ranging from −17 ‰ to −9 ‰, with a mean of −13 ‰ (3, 16, 19). When mammals eat plants, the δ^{13}C is enriched in their skeletal tissues, so the δ^{13}C of tooth enamel is ~12–14 ‰ more positive than the corresponding plant foods (8, 37; Figure 4).

The use of carbon isotopes for dietary and community reconstructions of mammalian herbivores is best suited to the late Cenozoic, after the diversification of C3 and C4 plant communities ~8 Mya. Prior to this time, most of the dietary reconstructions presented below rely principally on morphological interpretations.

TERRESTRIAL HERBIVORE PHYLOGENY, ORIGINS, AND DISTRIBUTION

Herbivory is a widespread adaptation in the history of mammals. Of the ~35 ordinal-level clades of extinct and extant mammals from the New World, two thirds contain herbivorous species and half are exclusively herbivores (33; Figure 5). These clades include such diverse specializations as folivores, frugivores, granivores, succulent feeders, mixed-plant feeders, and grazers.

During the late Triassic through early Cretaceous (225 to 120 Mya), all mammals were small-bodied (<5 kg) and lacked the distinctive dental adaptations that indicate plant-eating. Although some of these primitive mammals probably were omnivores, with some percentage of plants in their diets, it is difficult to make meaningful dietary interpretations of most Mesozoic mammals (12).

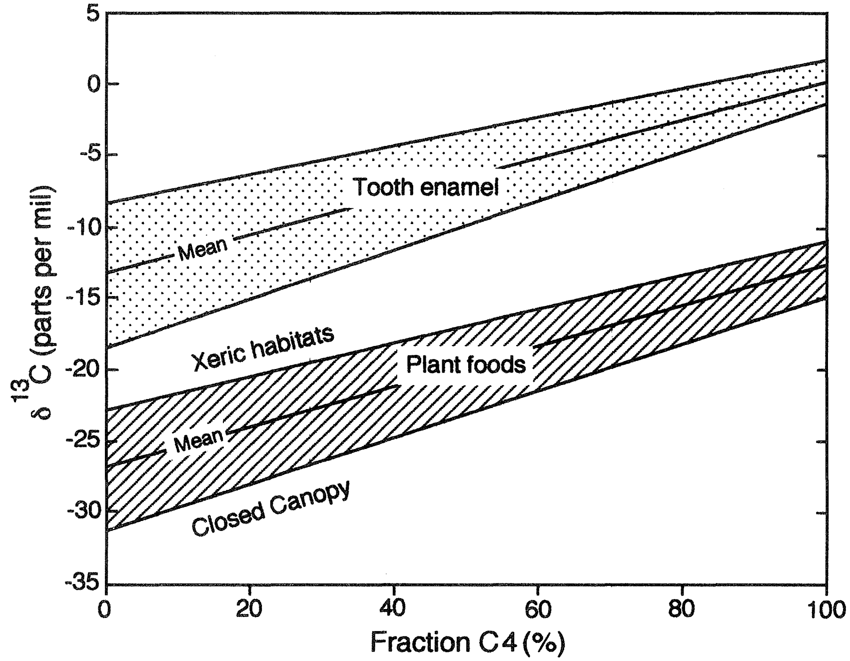

Figure 4 Carbon isotopic values, expressed in δ^{13} C_{PDB} of end-member C3 plants (left side, bottom = 0% C4) and C4 grasses (right side, bottom = 100% C4) as compared to $\delta^{13}C$ values of tooth enamel of C3 feeders (left side, top) versus C4 grazers (right side, top). Relative to plant foods, tooth enamel carbonate is enriched by about 12–14 ‰ (8, 37).

Eutherian dental evolution is marked by a key innovation during the early Cretaceous, ~100 Mya, the tribosphenic tooth (4, 69). Prior to this time, mammalian teeth were relatively simple and probably were principally sectorial (adapted for cutting), with a lesser crushing or grinding function. The tribosphenic tooth is characterized by an internal principal cusp, the protocone, in the uppers, which occludes with a talonid basin in the lowers. The evolution of the protocone and talonid basin, the function of which has been likened to that of a mortar and pestle, resulted in a morphologically complex tooth with increased surface area for mastication.

Some of the eutherian mammal clades that later developed highly specialized adaptations for herbivory originated during the late Cretaceous, 100 to 65 Mya. In North America during the late Cretaceous, some eutherian "ungulate" and condylarth clades had dentitions that were apparently adapted for masticating fibrous plant foods of low nutritive value and/or seeds and nuts of higher energy (1). The fossil record of Mesozoic mammals in South America is relatively fragmentary (11, 13), although some notable recent discoveries have been made (68). Given the overall paucity of well-preserved material, little can be said about the dental

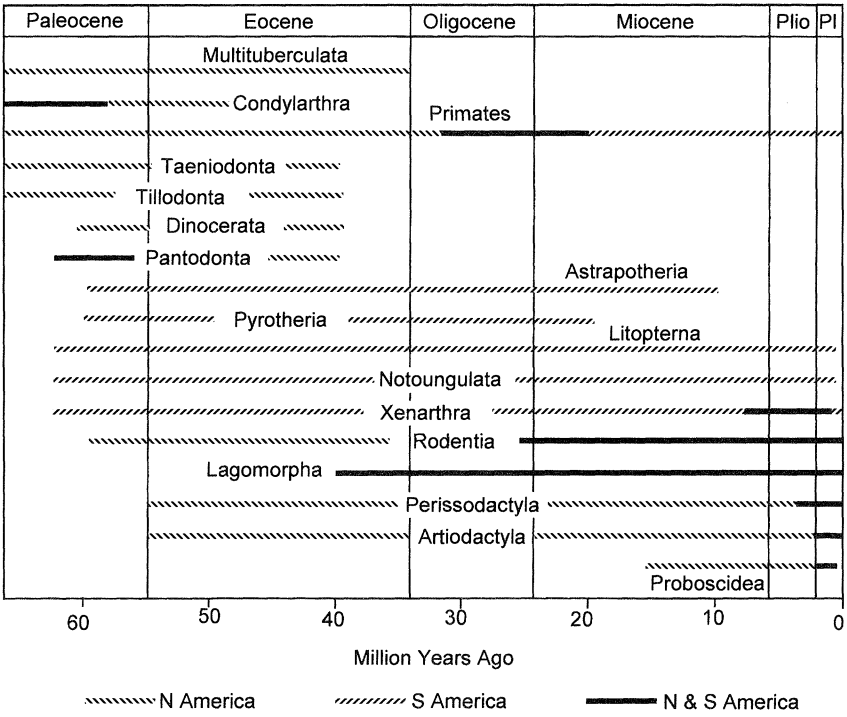

Figure 5 Geological distribution of the major ordinal-level groups of terrestrial mammalian herbivores from the Cenozoic of the Americas. Other groups with a low percentage of herbivores (Marsupialia, Chiroptera) or of low diversity that are not discussed in text (Xenungulata) are not shown here. Compiled from numerous sources, e.g. Refs. 11, 34, 67, 68.

function and diet of South American Mesozoic mammals. Nevertheless, in the New World (i.e., mostly North America), we have evidence of the primitive mammal clades that later developed specialized herbivorous adaptations.

EARLY TERTIARY MAMMALIAN HERBIVORES AND CLIMATE

The first half of the Cenozoic, represented by the Paleocene and Eocene epochs (65 to 34 Mya), represents a time of major global change. Stable isotopic evidence from both marine and terrestrial sequences at the Paleocene/Eocene boundary (~55 Mya), indicates there was a relatively abrupt global warming event resulting in much warmer "hothouse" conditions during the Eocene (37, 71). The mean annual temperature in low and middle latitudes during the early Eocene is estimated to have been between 25°C and 30°C (Figure 6), ~15°C to 20°C warmer

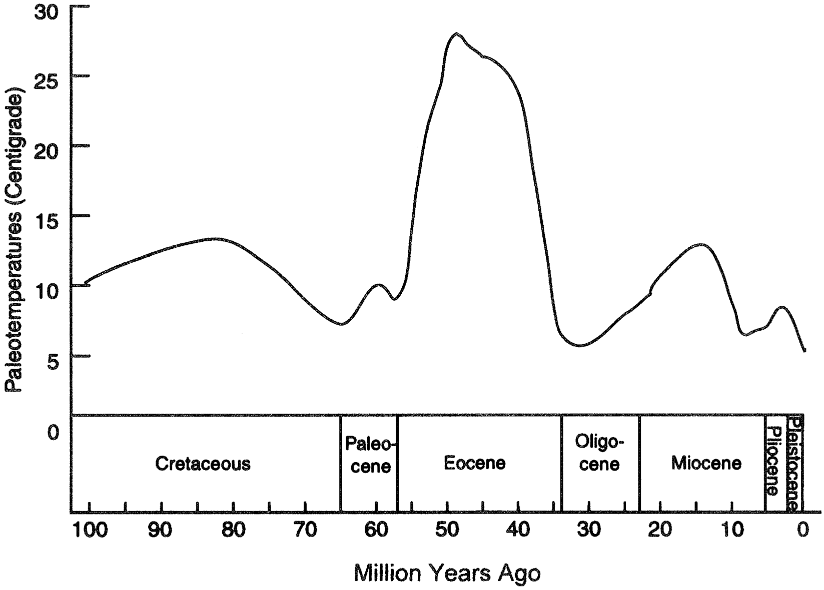

Figure 6 Change in mean annual temperature over the past 100 My as reconstructed from deep-sea oxygen isotope and paleobotanical data. From Ref. 63 and reproduced with permission of the Missouri Botanical Garden.

than today. This was the most significant global warming event during the Cenozoic, and it had a profound effect on the terrestrial biota. For example, in the well-sampled Paleocene/Eocene sequence in northern Wyoming, plant macrofossil diversity doubled (25 to 50 recognizable species) between 55 and 53 Mya (100; Figure 7). Thus, the fossil record indicates a dramatic shift from Paleocene mesic woodlands to Eocene subtropical vegetation throughout much of North America. The presence of cold-intolerant turtles, tortoises, crocodylians, and primates throughout North America, including at extreme northern latitudes (e.g., in the Canadian Arctic at 80° N; 24), indicates global expansion of subtropical and some temperate belts during this time (71). Although grasses originated during the early Cenozoic (the oldest reported fossil grass is from the Paleocene/Eocene of Tennessee, 14), there were no extensive grasslands then as there are today.

By the Paleocene, faunal interchange between the Americas, as represented by the pan-American groups Condylarthra and Pantodonta, had ended. Herbivore diversification thereafter until the late Cenozoic was represented by separate adaptive radiations of endemic groups in South and North America. The isolation of South America during most of the Cenozoic gives us a unique opportunity to compare radiations of mammalian herbivores that originated from different clades and to observe parallel evolution of adaptations. Similarly, the reconnection of the

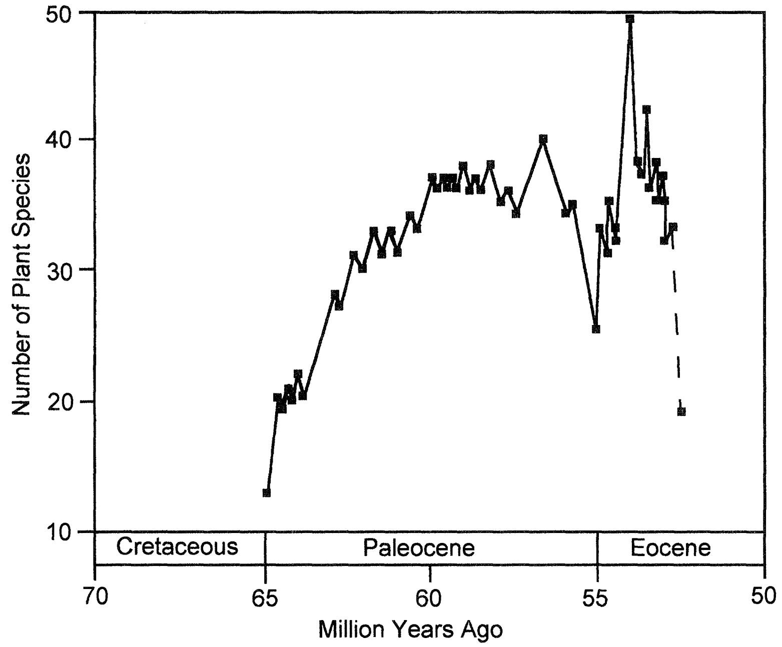

Figure 7 Fossil plant diversity across the Paleocene-Eocene boundary. Notice the doubling in the early Paleocene and subsequent drop from 40 to 25 species within about 2 My (from 57 to 55 Mya). From Ref. 100 and reproduced with permission of Elsevier.

Americas at the end of the Cenozoic had a profound impact on the native biotas. These "natural evolutionary experiments" are discussed below.

Morphological evidence from both North and South American mammalian faunas during the Paleocene and Eocene reveals considerable body size diversification (particularly increase; 11) and dental specializations. Dental morphology of numerous clades indicates a complex tooth apparently specialized for herbivory, including increased tooth area for mastication of plant foodstuffs. In the smaller range of body sizes (<5 kg), the abundance of forested biomes during this time yielded a correspondingly diverse array of arboreally adapted herbivores, including folivores, frugivores, and granivores (71).

In the New World, many of the modern groups of terrestrial herbivores originated and/or radiated during this time. The orders include Xenarthra (edentates), Lagomorph, Rodentia, Perissodactyla, and Artiodactyla (Figure 5). Now-extinct orders of New World terrestrial herbivorous mammals alive at that time included the Tillodontia, Taeniodontia, Condylarthra, Dinocerata, Astrapotheria, Pyrotheria, Pantodonta, and non-therian Multituberculata. With a few exceptions, all of these Paleocene and Eocene herbivores had relatively brachyodont dentitions, indicating a principally browsing diet. They exploited the niches created in open, nonarboreal, habitats. Taeniodonts and tillodonts from North America were high-crowned exceptions. Their diets have been reconstructed as having contained a considerable proportion of underground roots and tubers. They probably contended with grit on their foods, which explains the hypsodont teeth (42, 43).

The earliest horse *Hyracotherium* ("eohippus"; family Equidae) is known from the early Eocene of Holarctica. Because of its widespread abundance, and its importance near the base of both the equid and perissodactyl diversifications, *Hyracotherium* is an instructive example of an early Cenozoic mammalian herbivore. Traditionally, because of its short-crowned dentition, *Hyracotherium* was considered a forest-dwelling browser (e.g., 62, 80, 81). However, an extraordinary population of 24 individuals from a single quarry in Colorado is interpreted to represent an open-country form, which fed in early savanna-like, woodland mosaics (22). But instead of grass, this horse may have fed on soft ground vegetation, including herbaceous dicots and dry-adapted ferns, as well as some low shrubs (e.g. hackberry—*Celtis*). Fossilized brain endocasts of *Hyracotherium* indicate a relatively advanced neocortex, suggesting increased tactile sensitivity of the lips for selective feeding (75). Dental microwear studies of *Hyracotherium* show mostly pits, indicating a mixed-browsing diet, the animals having fed primarily on fruits, bushes, seeds, ferns, and other leaves (5). The mean δ^{13}C of *Hyracotherium* teeth is -12.5 ‰, indicating a diet of C3 plants (91).

The early diversification of the orders Perissodactyla and Artiodactyla occurred during the Eocene. By the Oligocene, ~34 to 30 Mya, more advanced artiodactyls diversified, particularly within the ruminants. It has been suggested that ruminant digestion provided a competitive advantage relative to hind-gut perissodactyl fermentation. Perissodactyls remained of modest diversity while the artiodactyls increased dramatically in diversity later during the Cenozoic, and some workers (81) have suggested a causal interdependence between these two orders. It seems, however, that this is an oversimplification and actually climatic and vegetative changes during this time are also causative factors in the relative diversities of the Perissodactyla and Artiodactyla (10, 30).

In South America, the fossil record of herbivorous mammals is predominantly represented by brachyodont forms, indicating principally browsing (70). An exception, the Archaeohyracidae, a family of small-bodied notoungulates, had ever-growing teeth. This may have been an early (Eocene) shift to grazing (82), an adaptation that greatly expanded during the later Cenozoic. Another group, the polydolopid marsupials, was rodent-like, an adaptation also seen in the multituberculates in North America during the Paleocene and Eocene (31, 67, 68).

EOCENE GREENHOUSE TO OLIGOCENE ICEHOUSE

For almost a century paleontologists have recognized a major change in Eocene to Oligocene mammalian faunas from Europe, termed the Grand Coupure ("big cut") (71, 73). A series of climatic events (including the Grand Coupure) occurred during a period of ~7 My from ~39 to 32 Mya (71, 73). Climatic reconstructions indicate significant global change from the peak Eocene "greenhouse" conditions to early Oligocene colder "icehouse" conditions. Temperatures are estimated to have dropped ~20°C from 50 to 35 Mya (Figure 6). Profound faunal and floral changes, including extinctions, originations, and geographic range shifts, during the late Eocene and into the early Oligocene occurred in such diverse groups as plant macrofossils, marine microfossils, marine invertebrates, amphibians, reptiles, and land mammals. Recent analysis of the ecology across the Eocene/Oligocene boundary indicates a change from principally warm, humid forest types during the Eocene to more zonal climates during the Oligocene that included arid, colder, and more open savanna-like habitats (71, 73).

The shift from greenhouse to icehouse conditions coincided with sweeping changes in New World herbivore communities. Archaic groups such as the condylarths, primitive primates, tillodonts, taeniodonts, and uintatheres (Dinocerata) became extinct by the end of the Eocene. As global climate shifted toward more glacial conditions, sea levels dropped, providing opportunities for intercontinental dispersal routes, such as the Bering land bridge connecting Holarctica. Immigrant herbivores from the Old World that first appeared during the Eocene in North America include lagomorphs, rhinoceroses, and several clades of artiodactyls (e.g., camels). With the possible exception of the lagomorphs, the other groups of mammalian herbivores had short-crowned teeth and were presumably browsers (31).

Some of the best early Tertiary mammal faunas of South American endemic groups are known from classic early and middle Eocene localities in Argentina, ~53 to 45 Mya (21). These faunas include xenarthrans, notoungulates, and litopterns, which together represent the majority of the herbivore diversity on that continent at that time (several other ordinal-level groups that also existed in South America during this time are either poorly represented by fossils or were of low diversity and enigmatic phylogenetic relationship). Before the late Eocene, 80% of the herbivorous mammals were short-crowned and thus are interpreted to have been browsers, and 10% were either partially or fully high-crowned and thus are interpreted either to have been early grazers or to have fed on gritty foods (67, 70). Fossil phytoliths first become common in the late Eocene of South America, suggesting the spread of early grassland biomes (27, 87). As we will see below, the adaptive radiation of high-crowned grazers and presumed spread of grasslands occurred at different times in North and South America.

PRECOCIOUS HYPSODONTY AND GRAZERS IN SOUTH AMERICA

Patterson & Pascual (70, also 67) noticed a fundamental change in dental morphology and presumed diets of middle Cenozoic mammalian herbivores in South America. The early and middle Eocene (45 Mya) herbivores are principally short-crowned, presumed to be browsers. In younger faunas of late Eocene/early Oligocene "Tinguirican" (~35 Mya; 101) and late Oligocene/early Miocene

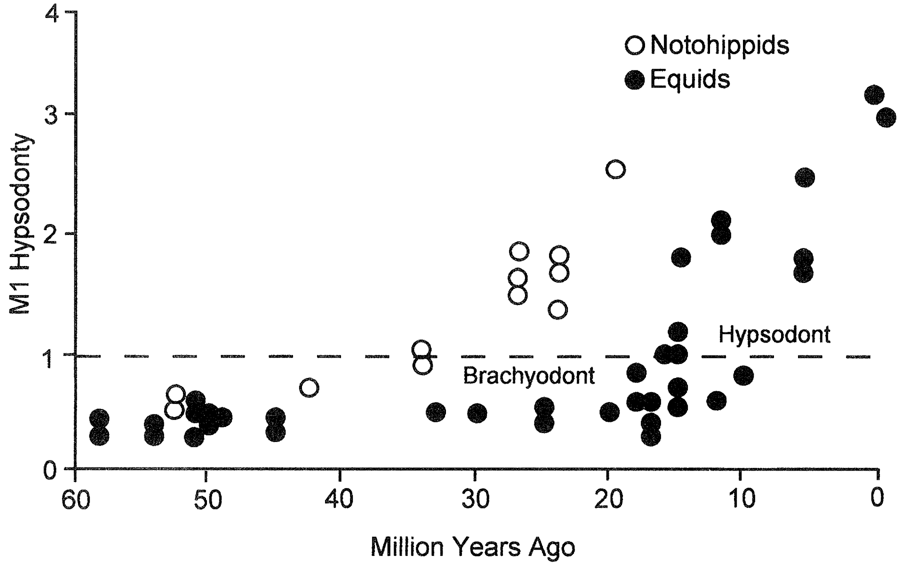

Figure 8 Advent of "precociously hypsodont" South American notohippid notoungulates at ~25 to 30 Mya compared to hypsodonty in North American horses at ~15 to 20 Mya. Modified from Ref. 78 and reproduced with permission of the Society of Vertebrate Paleontology.

Deseadan (~30 to 20 Mya) ages, the dominant small- to medium-sized herbivores are represented by the Notoungulata, which include a striking diversity of high-crowned forms—with hypsodonty indices between 1.5 and 2 (Figure 8). The teeth are characteristically evergrowing (hypselodont).

The abundance of South American mammals with high-crowned teeth (70) in the middle Tertiary has been suggested to indicate the advent of grassland communities, but this advanced morphology occurs as much as 15 My earlier in South America than in North America. This asynchrony has led to the concept of "precocious hypsodonty" (70) for South American notoungulates relative to, for example, horses (family Equidae) in North America (Figure 8). Carbon isotopic evidence from both short- and high-crowned herbivores from Deseadan localities in Argentina and Bolivia uniformly yields δ^{13}C values more negative than ~−10 ‰ (50, 54), indicating that these presumed grazers were feeding on C3 grasses. This indicates a major difference from modern terrestrial grasslands, which are predominantly C4. There are both climatic and physiological explanations for this difference, as is discussed below.

The deseadan Salla Beds of Bolivia, which contain precociously hypsodont herbivores, have been precisely dated between 28 and 25 Mya (35). The Salla fauna includes a diversity of short-crowned herbivores (*Pyrotherium*, astrapotheres, litopterns), small- to medium-sized high-crowned notoungulates, early caviomorph rodents, and the primate *Branisella*. Modern primates occur in rain forests, so by analogy it might be suggested that Salla was tropical. However, given the

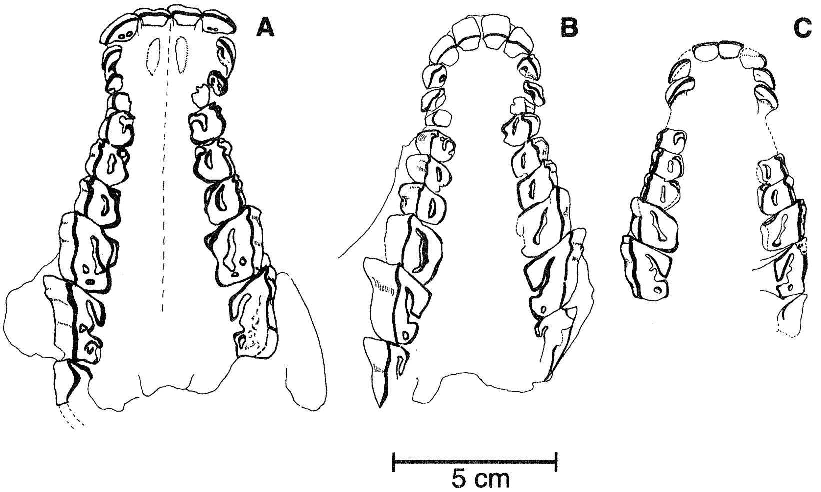

Figure 9 Ventral views of upper dentitions of notoungulates from the late Oligocene of Salla, Bolivia, showing differences in incisor series. In *Pascualihippus* (*a*), the incisor series is transversely linear, indicating a grazer. In *Eurygenium* (*b*) and *Rhynchippus* (*c*), the incisor series is rounded, indicating a browser, or more selective feeder. From Ref. 78 and reproduced with permission of the Society of Vertebrate Paleontology.

preponderance of high-crowned herbivores, and based on associated evidence from the sediments, Salla was reconstructed as a relatively arid grassland habitat (46). The Salla fauna contains three notoungulates, *Pascualihippus*, *Eurygenium*, and *Rhynchippus*, all of which have high-crowned teeth (HIs of 1.5, 1.8, and 1.4, respectively; also see Figure 2*a*), but they have different incisor morphologies. *Pascualihippus* has a broad, transversely linear incisor series, indicating a grazer (Figure 9*A*). In contrast, *Eurygenium* and *Rhynchippus* have rounded muzzles (Figure 9*B*,*C*), which otherwise might suggest a browser (84). The incisor morphology of *Eurygenium* and *Rhynchippus* suggest browsing, whereas their high-crowned teeth suggest grazing. How then does high-crowned dental morphology fit with the rounded incisor series? *Eurygenium* and *Rhynchippus* are both interpreted as selective feeders, and thus with niches more specialized than that of *Pascualihippus* (78). *Eurygenium* and *Rhynchippus*, although of similar incisor and cheek tooth morphologies, differed in size, which apparently facilitated their niche separations within the same community, perhaps corresponding to "Hutchinsonian ratios" (26, 77).

In roughly equivalent 30 Mya Oligocene sediments from North America, as represented by the classic Badlands of South Dakota and Nebraska, the terrestrial mammalian herbivore community was relatively primitive in its morphological and presumed feeding adaptations. Although there was a significant diversification of the principal ungulate groups Artiodactyla and Perissodactyla in the North American Oligocene, they had uniformly short-crowned teeth with rounded incisors, indicating a browsing diet. Enamel-microwear studies of the common Oligocene horse *Mesohippus* indicate that it was a browser and fed on a varied diet of fruits, shoots, and leaves (5). Thus, in contrast to their North America counterparts, the South American mammalian herbivores were indeed precociously hypsodont.

MIOCENE SAVANNAS OF NORTH AMERICA

The extensive North American fossil record reveals major floral and faunal changes during the late Oligocene and early Miocene, ~20 to 25 Mya. Although fossil grasses occur in earlier Cenozoic sediments in North America (14), the first evidence of abundant fossil grasslands is from the early Miocene (55, 87). The adaptive radiation of hypsodont herbivorous mammals occurred during the middle Miocene, ~15 to 20 Mya. Members of the Rodentia, Proboscidea, Perissodactyla, and Artiodactyla all developed hypsodont clades. This resulted in a striking array of herbivores, including browsers, mixed feeders, and the grazing guild (48), with a diversity and community structure similar to that of the modern African savanna (94, 96). Simpson (80) called this the Great Transformation, a time when mammals invaded a new adaptive zone (81) that allowed them to exploit grassland resources. The evolutionary "cost" of becoming grazers was rapidly accelerated tooth wear caused by feeding on abrasive grasses containing phytoliths. The response in grazers was the evolution of hypsodonty. This time of fundamental morphological change (76), as groups of herbivorous mammals in North America evolved from primarily browsers to primarily grazers, resulted in the terrestrial grazing guild.

Horses (family Equidae) diversified rapidly during the Great Transformation with pronounced morphological reorganization of the skull and dentition, resulting in a total of 13 genera in late Miocene faunas (Figure 10). Evidence from

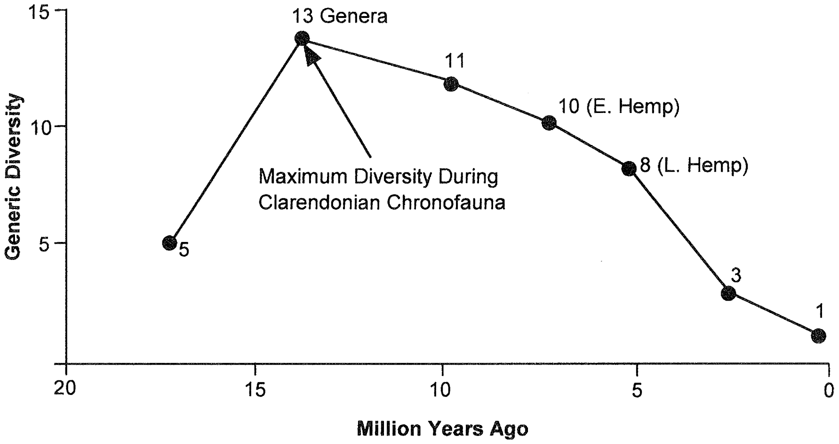

Figure 10 Generic diversity of Miocene and Pliocene horses (Equidae) from North America showing decline after about 15 Mya. Hemp = Hemphillian land-mammal age. From Ref. 47 and reproduced with permission of Cambridge University Press.

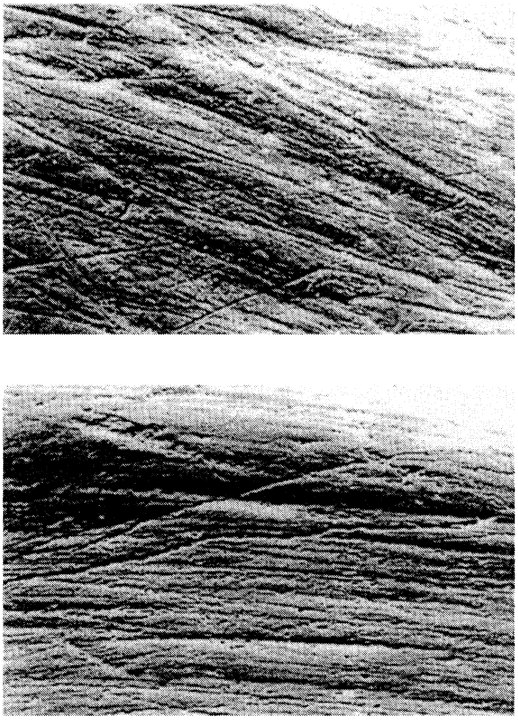

Figure 11 SEM showing enamel microwear in modern and fossil horses. Top: *Equus burchelli*, the modern Burchell's zebra, showing a predominance and density of elongated scratches characteristic of a grazer. Bottom: Late Miocene horse *Cormohipparion* from North America showing a lower density of scratches and the presence of pits; this pattern is characteristic of a mixed feeder. From Ref. 23 and reproduced with permission of the Finnish Zoological Publishing Board.

muzzle morphology and hypsodonty indicates that these coexisting horses spanned a broad range of diets (47). Enamel microwear of North American *Cormohipparion* (23; Figure 11) and Old World *Hipparion* (5) indicates that these horses fed on, respectively, a mixed diet and principally grass. (23). Evidence of grazing also comes from the transversely linear incisor morphology shape of the late Miocene equid *Calippus* (25). During the height of the Clarendonian chronofauna ~10 Mya, horses reached their peak diversity of 13 genera, declining in diversity thereafter. The Clarendonian chronofauna is a North American mammalian assemblage from ~12 to 7 Mya (92, 94, 96). The first horses to become extinct during this time were short-crowned, browsing anchitheres, presumably in response to the decline of forested communities. Thereafter, during the late Miocene, diversity dropped to eight genera by the late Hemphillian, 5 Mya (Figure 8).

Evidence of diverse herbivorous adaptations in the Clarendonian chronofauna comes from a variety of Miocene mammals. At the height of the Clarendonian chronofauna in Nebraska, mammalian herbivore taxa were represented by 87% grazers, 10% mixed feeders, and 3% browsers (96). Aepycameline camels evolved stilt-legs, elongated cervical vertebrae, and body heights approaching 6 m, thereby occupying a niche similar to modern-day giraffes (96). Gomphothere proboscideans, with elongated, flattened, and spatulate lower incisor tusks, were previously thought to have scooped up aquatic vegetation, but more recently have been reinterpreted as mixed feeders, with their incisors performing a variety of food-procuring roles (39). Definitive paleontological evidence of grazing is represented by the presence of fossil grass in the dental cavities of the late Miocene rhinoceros *Teleoceras* from the Ashfall Fossil Beds in Nebraska (90).

Is there evidence of carbon isotopic discrimination like that seen during the transition from browsers with short-crowned teeth to grazers with high-crowned teeth during the middle Miocene? Although horses became hypsodont between 15 and 20 Mya, there is no corresponding shift of $\delta^{13}C$ in the Equidae (9, 91). Mammalian herbivores had tooth enamel carbonate $\delta^{13}C$ values characteristically less than -10% (7, 49, 50, 54, 91). Thus, mammal herbivores in the New World prior to the late Miocene lived in C3 grass biomes that were widespread throughout temperate and tropical climes, a situation very different from modern-day ecosystems.

LATE MIOCENE GLOBAL CARBON SHIFT

Prior to the late Miocene, carbon isotopic evidence from North and South America indicate that mammalian herbivores existed in a C3 world, with tooth enamel carbonate $\delta^{13}C$ values characteristically <10 ‰ (7, 49, 50, 54, 91). The dominance of C3 plants in terrestrial ecosystems throughout the early and middle Cenozoic relates to atmospheric CO_2 concentrations. C3 plants are favored in regimes of elevated levels of atmospheric CO_2, as has been modeled for most of the Cenozoic (2). During the late Miocene, however, major global change reduced atmospheric CO_2 to below a critical threshold and increased aridity and seasonality, all of which favor C4 photosynthesis (17, 18). Carbon isotopic values from fossil mammals, ancient soils, and deep-sea cores indicate a major global change ~7–8 Mya (6, 7, 40, 74). $\delta^{13}C$ values of post–late-Miocene fossil grazing mammals and grassland paleosol carbonates have $\delta^{13}C$ values around 0 ‰ indicating C4 terrestrial communities. (Figure 12).

This late Miocene global carbon shift had a profound effect on the history of Cenozoic ecosystems: It resulted in a latitudinal gradient of C3/C4 grasses, with C3 grasses predominating in colder, more polar regions, and C4 grasses predominating in temperate and tropical regions (51, 89). C4 grasses are generally found in ecosystems of lower productivity, which in turn support a lower overall biomass and diversity.

After 7 Mya, horses continued to decline in diversity. It is plausible that horses were part of the overall drop in diversity supported by lower productivity steppe-like C4 grasslands. Which equid taxa survived this extinction? Isotopic and

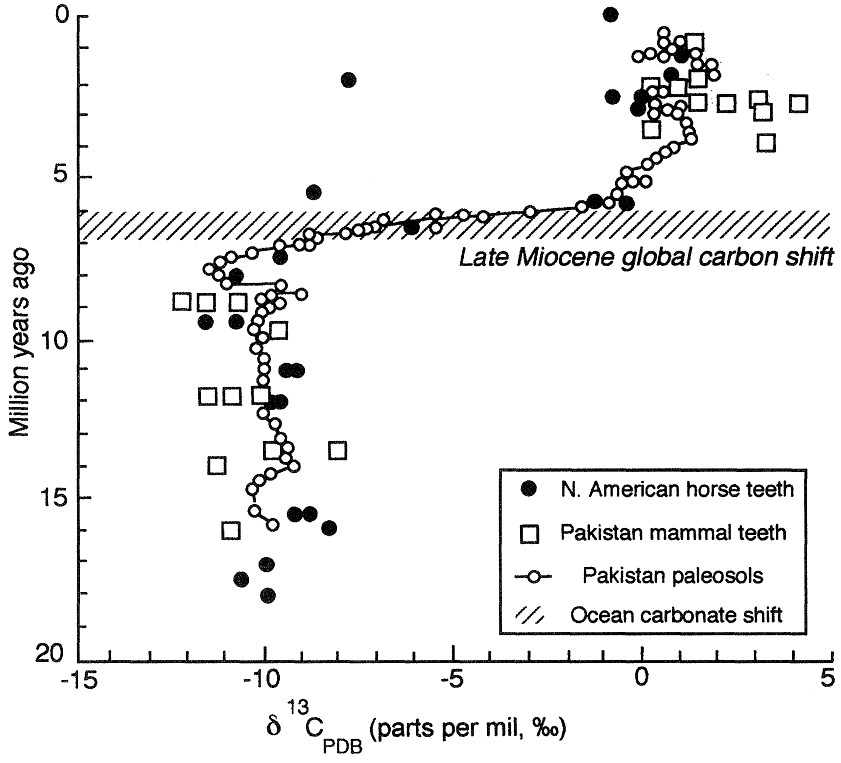

Figure 12 Isotopic evidence for the late Miocene global carbon shift between ~7 and 8 Mya. Modified from Ref. 6 and reproduced with permission of Macmillan.

microwear studies of the six coexisting high-crowned equid genera from 5-My-old sediments in Florida indicate that these horses included grazers, mixed feeders, and C3 browsers (53). Two grazing and one browsing species became extinct during the latest Miocene at 5 Mya. Other taxa of North American mammalian herbivores also experienced extinctions at 5 Mya, including the family Rhinocerotidae, and genera and species of Rodentia, Artiodactyla, and Proboscidea (96). The corresponding South American record at 5 Mya is not well known. Although C4 grasses are known to have been part of South American grazing diets (50, 54), it is difficult to determine if extinctions were above background levels at this time.

GREAT AMERICAN INTERCHANGE AND PLEISTOCENE MEGAHERBIVORES

For most of the Cenozoic, North and South America were geographically isolated from one another, and unique mammalian herbivore communities evolved on each of these continents. During the Pliocene (5 to 2 Mya), however, this faunal isolation changed with the formation of a dry-land connection by the closing of the Isthmus of Panama ~3 Mya. This closure resulted in a land-bridge dispersal corridor for the various immigrants. Paleontologists have studied this "Great American Interchange" (GAI; 88), the height of which occurred during the middle Pleistocene, ~1 Mya. The community structure and faunal equilibrium were disrupted by the addition of immigrant mammals into the resident biotas. Immigrant herbivores from North American that dispersed into South America included phyllotine rodents, mastodons, tapirs, horses, peccaries, llamas, and deer. Herbivores from South America that immigrated into North America included caviomorph rodents and the edentates, including armadillos, glyptodonts, and giant ground sloths.

It has been suggested that during times of faunal interchange, the immigrants, or "invaders," generally have a competitive advantage over the native, or resident biota, as Simpson (79, 82) asserted was the case during the GAI. Although the concept of competition is difficult to quantify and test in the fossil record, nevertheless, some general patterns of the GAI are instructive here. First, in South America (Figure 13), the native fauna of ungulate mammals consisted of 12–13 genera before the formation of the land bridge, and decreased to five and then three genera during the GAI. Correspondingly, the North American invaders

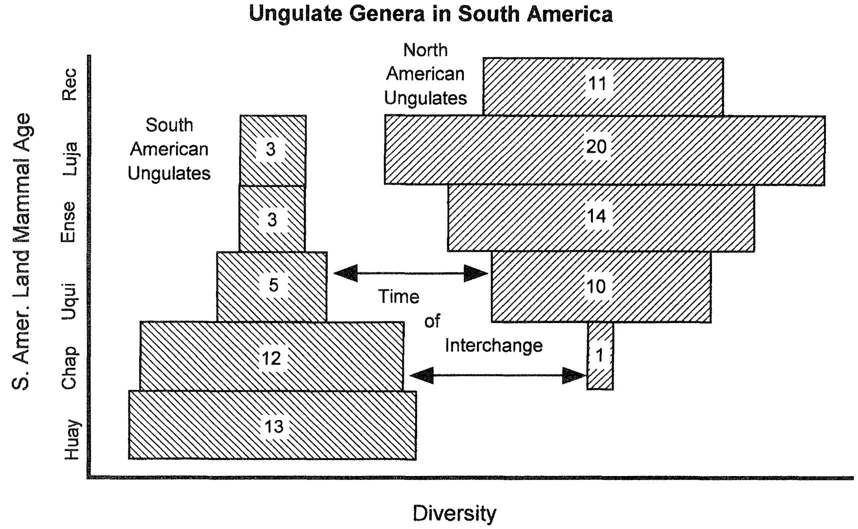

Figure 13 Turnover of ungulate genera in South America during the Plio-Pleistocene Great American Interchange. Modified from Ref. 92 and reproduced with permission of the Paleontological Society. Land-mammal abbreviations and boundaries are as follows (Ref. 21): Huay, Huayquerian, Miocene, 7 to 9 Mya; (hiatus); Chap, Chapadmalalan, Pliocene, 3.4 to 4 Mya; Uquian, Pliocene–early Pleistocene, 1.5 to 3 Mya; Ense, Ensenadan, middle Pleistocene, 0.5 to 1.5 Mya; Luja, Lujanian, late Pleistocene, 10,000 years ago to 0.5 Mya.

went from one to 10 to 14 to 20 genera before the late Pleistocene extinctions (93, 95). Second, the pattern of extinctions during the GAI is asymmetric; that is, the immigrants apparently affected the native herbivores in South America, but the reverse was not true, i.e. in North America the immigrant taxa from South America did not seem to have a competitive advantage over the native herbivores (82, 98, 99). It is tempting to suggest simple explanations (e.g. competition) for complex biological phenomena such as the GAI. Other factors, however, including climate change and loss of specialized habitats, almost certainly were related to the demise of the native herbivore faunas throughout the Americas during the Pleistocene.

The Tarija fauna of southern Bolivia is a classic middle Pleistocene GAI locality. It serves as a good example from which mammalian herbivore community structure can be examined. The Tarija medium- and large-bodied herbivores comprise two dozen species within the endemic orders Edentata, Notoungulata, Litopterna, and caviomorph Rodentia and to these were added the North American immigrant orders Proboscidea, Perissodactyla, and Artiodactyla. A multivariate study of the carbon isotopes, cranial morphology, and hypsodonty of these Tarija herbivores (except for the edentates, which lack enamel for carbon isotopic analysis) revealed some interesting patterns within the herbivore community (52). Of the 13 herbivore species analyzed, three were browsers, five were mixed feeders, and five were grazers. The grazers span the largest range of body size, from *Vicugna* to the mastodon *Cuvieronius*. The larger body sizes (to the right on the first principal component axis, Figure 14) supports the idea that grazers need longer retention times for processing low-nutritive-value forage in their gut (58, 66). Within families consisting of more than one herbivore species at Tarija, there is evidence of niche differentiation. For example, of the three sympatric llamas, two are grazers (*Lama, Vicugna*) and one is a mixed feeder (*Palaeolama*), and of the horses, two species are mixed feeders (*Hippidion, Onohippidium*) and one is a pure C4 grazer (*Equus*; Figure 14).

Large-bodied herbivores (megaherbivores) have a significant impact on terrestrial communities (66). In North America, the ecological impact of megaherbivore immigrations was profound during the GAI. Sloths were consummate browsers, as has been documented by the presence of low shrub twigs and roots in the dung of the late Pleistocene sloth *Nothriotheriops* from Arizona (44). Glyptodonts have heavily infolded, high-crowned teeth, and were probably mixed feeders with a significant amount of grass in their diets. An added component of biogeographic complexity resulted from immigrations across Holarctica during the Pleistocene. Two Old World immigrant megaherbivores, in particular, played a role in the hypergrazer niche, which during the Pliocene was occupied by *Equus* (49). The mammoth, *Mammuthus*, and bison, *Bison*, dispersed into North America at respectively 1.5 and 0.5 Mya (45). Studies of the carbon isotopic values of the teeth of mammoth and bison indicate that they were principally grazers, and *Equus* was also a grazer at this time, although the horse had more of a grazing/mixed feeding component to its diet during this time (15, 20, 36).

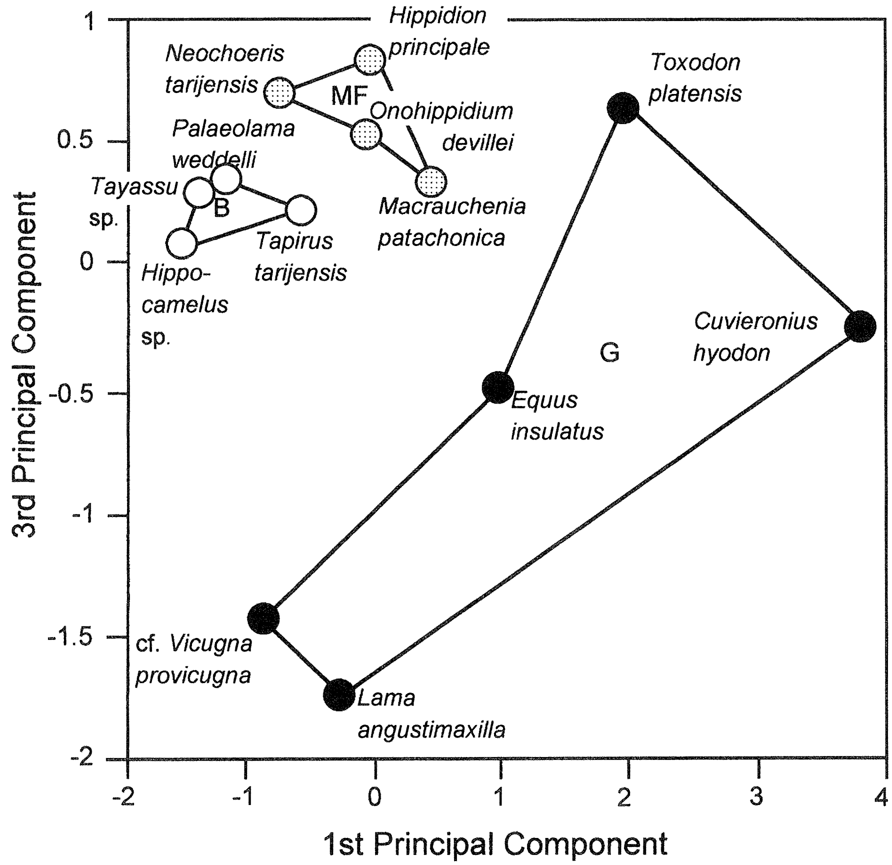

Figure 14 Principal components analysis of 13 herbivore taxa from the middle Pleistocene of Tarija, Bolivia, using carbon isotopes, molar length, muzzle width, and hypsodonty index. The grazers (G, black circles), mixed feeders (MF, shaded circles), and browsers (B, white circles) fall into discrete groups in multivariate space. From Ref. 52 and reproduced with permission of the Paleontological Society.

Only a fraction of the vast herbivore diversity that existed throughout the Americas during the Pleistocene persists today. In a very short period of time, from ~15,000 to 10,000 years ago, megaherbivores such as mammoths, mastodons, horses, sloths, glyptodonts, and giant armadillos became extinct throughout the Americas, and other taxa including llamas, tapirs, and bison have greatly reduced ranges today relative to those before 15,000 years ago (97, 99). Two principal hypotheses have explained these late Pleistocene megaherbivore extinctions. The first is climate and habitat change; the other is that humans rapidly populated the Americas, resulting in "Pleistocene overkill" of large prey species (60, 61). As with all complex natural systems, these two explanations undoubtedly both played roles as causal factors of late Pleistocene extinctions.

CONCLUDING COMMENTS

The analysis of Cenozoic herbivore communities in the Americas illustrates numerous evolutionary and ecological principles and patterns. We see the coevolution of grass and grazers, the evolution of similar adaptations (e.g., hypsodonty) in different groups on different continents, the biotic reaction to major climate perturbations, the change in diversity of browsing and grazing herbivore groups with corresponding changes in vegetation, and the extinctions resulting from climate and/or biotic factors. These examples are more clearly interpreted using a combination of morphological and isotopic techniques now available to paleontologists.

The fossil record of Cenozoic mammalian herbivores reveals both change and stability of overall community structure through time, the idea inherent in the concept of the chronofauna. The fundamental question about long-term changes in community evolution is whether biotic equilibrium and change are affected principally by external, climatic factors, or by internal factors such as species interactions and competition (28, 31, 72). Natural systems are rarely simple and, in reality, long-term changes are almost certainly structured by both climatic and biotic factors. The fossil record provides definitive and unique evidence from which we can understand the history of evolving communities of Cenozoic herbivores of the Americas.

ACKNOWLEDGMENTS

I thank RM Hunt and SD Webb for making helpful comments on this manuscript. This paper was written during support from NSF grants EAR-9506550, IBN-9528020, and EAR-9909186. This is University of Florida Contribution to Paleobiology no. 515.

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