Origin and evolution of the grazing guild
in New World terrestrial mammals

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Grasslands extend over about 25% of the world’s land surface and exist in a wide variety of environmental, physiographic and climatic regimes (Fig. 1). Grassland biomes typically occur in regions with mean annual temperatures between 0–20°C and between 250–1000 mm of annual precipitation. Various names have been given to the different kinds of grasslands, including tropical savanna, temperate tall and mixed-grass prairies, shrub steppe, desert grasslands, high-latitude cold steppes and arid short-grass steppes, and montane grass communities. All grasslands are characterized by open country, mostly consisting of a low perennial ground cover formed by the family Poaceae (also called Gramineae), and also broadleaf herbs (forbs), and sometimes scattered low shrubs and other woody plants. As a result of their wide distribution and high primary productivity (c. 2 x 10^9 tons yr^-1), secondarily only to forests¹, grasslands provide a major food resource for a diverse assemblage of terrestrial herbivores that in the modern world constitute the ‘terrestrial grazing guild’ (Fig. 2). Although terrestrial ecosystems containing plant foods and corresponding herbivores have existed for almost 300 million years (My³), grasslands and grazers are relatively recent arrivals on the global ecological landscape. “Grazers” are defined in various ways, but in the present context they are consumers that feed primarily or exclusively (~90%) on grasses or other low herbs and forbs characteristically associated with grassland biomes. They are referred to here as the ‘grazing guild’ in the modern context and grazing ‘paleoguilds’ in ancient grassland ecosystems.

This article reviews the paleontological evidence for the origin and evolution of the grazing guild in terrestrial mammals. The primary focus is on the American prairie and grassland ecosystems of the Cenozoic. Although the generations of grazers are not preserved, their ecological interactions are. All species of ungulates have been identified by comparing the bone structures and other skeletal elements of the species to those of similar species of extinct and modern species. The evidence is that the grazers evolved from the Cretaceous planktonic foraminifera and were present in the New World by the Pleistocene Epoch.

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insects in the case of the terrestrial grazing guild. However, the fossil record of insects, much less grazing insects, is relatively poorly known, and therefore we have little knowledge about this component of the grazing guild. Therefore, we must turn to mammals, which have been the dominant (in terms of overall consumer biomass) constituents of the terrestrial grazing guild, to understand the coevolution of grassland biomes and grazers.

**Grassland/grazing coevolution: a paleontological and isotopic perspective**

In a classic monograph published in 1873, the Russian paleontologist Vladimir Kowalevsky\(^6\) believed that the evolution of high-crowned teeth and elongated limbs in fossil horses was an adaptive response to the spread of grasslands during the Miocene. This idea has since been accepted as the model to explain a time of major global change in ancient terrestrial ecosystems, which George Gaylord Simpson\(^6\) called the ‘Great Transformation’. Based on modern herbivorous mammals that serve as ecological analogs for extinct taxa, we can generally infer ancient diets and habitats from overall tooth morphology (Fig. 3).

In general, mammalian herbivores with short-crowned (brachyodont) teeth are predominantly browsers, living in closed-canopied forests or woodlands and feeding upon leaves and fruits of trees and shrubs. At the other end of the spectrum, mammalian herbivores with high-crowned or ever-growing (respectively, hypsodont and hypercynodont) teeth are predominantly grazers, living in more open biomes and feeding predominantly upon abrasive grasses. This is an oversimplified explanation, of which some herbivorous taxa are exceptions (e.g. llamas and the hippopotamus, both relatively short-crowned, are primarily grazers) and other factors may be involved such as the amount of ‘contaminant grit’ in the diet, but it is an almost universally accepted model for the feeding ecology of ancient herbivorous mammals. The biological explanation for the ‘need’ to grow elongated cheek teeth in most grazing mammals is as a coevolutionary response to the presence of silica phytoliths (microscopic, elongated and highly abrasive SiO\(_2\) fibers), which are pervasive in grasses and seem to function primarily as an anti-herbivory strategy. Thus, in a macroevolutionary and physiological sense, the ‘cost’ of becoming a grazer is the extra energy required to grow high-crowned teeth.

Of the 34 Orders of fossil and modern mammals, about two-thirds (24) contain species adapted to herbivory, and 13 are exclusively herbivorous\(^6\). Many of these Orders have representatives that evolved high-crowned teeth, interpreted to be a grazing adaptation. Although there were a few extinct mammal groups that were high-crowned during the early Cenozoic, by far the greatest diversification of high-crowned mammals has occurred during the second half of the Cenozoic, during the past 30–35 My.

Within the past decade, the use of stable isotopes has rapidly gained acceptance as a new technique that, when used in conjunction with fossil morphology, provides a powerful tool to reconstruct ancient ecologies. Of relevance here, stable carbon isotopes (\(^{13}\)C and \(^{12}\)C; ratio expressed as \(\delta^{13}\)C) preserved in the unaltered tooth enamel of fossil herbivores can be used to reconstruct paleodiet and inter

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**Fig. 1.** Grasslands of the world, including grasslands and savannas. Modified from Ref. 2.

**Fig. 2.** Examples of modern grazing terrestrial mammals of the world. Some grazing mammals, such as bison, are highly specialized ‘hypergrazers’, whereas others, such as the Asian elephant, feed on grass but can also have a more varied diet given available resources. (a) Cape buffalo (Syncerus caffer) Order Artiodactyla. Photo by John Anderson. (b) Asian elephant (Elephas maximus) Order Proboscidea. Photo by J.F. Eisenberg. (c) Grey’s zebra (Equus grevyi) Order Perissodactyla. Photo by D.C. Gordon. (d) Hippopotamus (Hippopotamus amphibius) Order Artiodactyla. Photo by John Anderson. (e) Llama (Lama glama) Order Artiodactyla. Photo by J.F. Eisenberg. (f) Bison (Bison bison) Order Artiodactyla. Photo by John Anderson.
photosynthetic pathways of local plant communities and local paleoenvironmental conditions. C₃-plants, including trees, shrubs and high-elevation and high-latitude (cool-growing season) grasses, which comprise roughly 85% of terrestrial plant biomass, photosynthesize C₃ using the Calvin cycle. When C₃-plant carbon is ingested by the mammalian herbivore, the tooth enamel has δ¹³C values that are less than −10‰ (Fig. 4). C₄-plants, which include most of the grasses and grassland biomes of the world today in tropical and temperate climates, represent about 10% of the terrestrial plant biomass, and have tooth enamel δ¹³C values of ≈ −2‰ (Refs 11-14).

This isotopic difference in δ¹³C values provides powerful discrimination of feeding ecology in its own right as well as refining hypotheses about ancient herbivory based on morphology: using both morphological and isotopic characters, we can distinguish C₁ browsers, C₃ grazers, C₄ browsers and C₄ grazers, which form theoretical end points in a continuum of interpreted feeding ecology (Fig. 4). C₃ browsers (low-crowned with relatively negative δ¹³C values) and C₄ grazers (high-crowned with relatively positive δ¹³C values) dominate in modern ecosystems. C₄ grazers, which are rare in modern ecosystems (found mostly in high-latitude or montane settings), were common in a diverse array of ancient ecosystems before about 7 million years ago (Mya). C₃ browse is almost non-existent in nature and no C₄ browsers have been identified from the fossil record.

The North American Miocene: the Great Transformation and the Cenozoic chronofauna

The first half of the Cenozoic fossil record in North America includes relatively few taxa with high-crowned dentitions (Fig. 5). The extinct Orders Tilodontia and Tandontia and families of Lagomorpha (Leporidae) and Rodentia (Castoridae, Geomyidae, Heteromyidae) are all either hypsodont or hypselodont, and the explanation for these feeding adaptations is not clear. Although these occurrences of high-crowned teeth suggest a grazing adaptation, and the earliest fossil grasses in North America are known from the c.55 Mya old late Paleocene/early Eocene of Tennessee (USA)°, grasslands apparently did not become as extensive terrestrial biomes during the early Cenozoic. Other explanations for the presence of high-crowned teeth during this time include ‘contaminant grit’ in the diet of herbivores feeding near the ground surface°.15

The plant fossil record indicates that grasslands first became a major part of the North American terrestrial landscape during the early Miocene c.20-25 Mya°. During this time, and after, we see dramatic evidence of a diversification of many high-crowned herbivores and otherwise (based on δ¹³C isotope evidence°°) presumed grazing herbivores, including several families of rodents (the bizarre horned Mylagaulidae, Geomyidae, Heteromyidae), proboscideans (Gomphotheriidae, Elephantidae), perissodactyls (Rhinocerotidae and Equidae) and artiodactyls (primarily Camelidae, Antilocapridae and Pleistocene Old World immigrant Bovidae; see Figs 5 and 6).

The maximum diversity of grazing herbivores in North American ecosystems occurred in the middle Miocene, during the so-called ‘Cenozoic chronofauna’°°. During this time relatively high-productivity savanna grassland biomes were fairly common. A modern analog for this ancient ecosystem is the Serengeti of Africa. The classic museum and textbook story of the ‘heyday’ of horses during the Cenozoic chronofauna has been extensively dealt with elsewhere°° and is not elaborated here. With regard to other taxa, one of the most striking and persuasive examples of grazing, only recently appreciated, occurred in the extinct rhinoceroses Teleoceras (Fig. 6), a widespread member of this chronofauna. In addition to its high-crowned dentition, our knowledge of its grazing habits comes from spectacular remains of fossil grass parts (anthoecia) preserved in the enamel infoldings of its teeth°°. Although the horses of the

![Fig. 3. Cross-sections of (a) low-crowned (human) and (b) high-crowned (horse) molar teeth showing development of the various dental tissues and elongated crown in the horse. Reproduced, with permission, from Ref. 10.](image)

![Fig. 4. Plot of carbon isotopic values (δ¹³C) versus tooth crown height to show how these two data sets can be used to discriminate C₃ and C₄ grazers, C₃ browser, mixed and/or CAM feeder and C₄ browser. (Although a C₃ browser is theoretically possible in this matrix, C₃ browse is very rare in nature. Given the intermediate δ¹³C values for CAM plants, this matrix cannot discriminate between a specialized succulent browser versus a generalized mixed feeder. Hypodometry index (HI) is the ratio of unworn/little-worn molar crown height to the anteroposterior molar length. Low-crowned (brachydont) herbivores have a tooth in which the HI is <1, high-crowned (hypsodont or hypselodont) herbivores have an HI that is >1. Maximum observed HIs are usually <3.](image)
Clarendonian chrono fauna were undoubtedly more diverse and numerically more abundant than Teleoceras, rhinoceroses were at least as important in terms of overall grazing ungulate biomass.

Some extinct artiodactyls are exceptions to the crown-height rule because although many of them had relatively short-crowned teeth, for other reasons (e.g., associated paleobotanical evidence and local paleohabitat reconstructions) they are thought to have been grazers. These grazers 'compensated' for their lack of high-crowned dentitions by evolving a more durable tooth that was less prone to rapid wear. Definitive evidence for the grazing adaptations of artiodactyls comes from recently acquired C isotope data, for example, llamas in North America were facultative grazers at least since the late Miocene and until they became extinct.

In North America, the horses declined dramatically in their diversity from 12 to 15 contemporaneous species about 12 Mya, to two or three contemporaneous species during the past 4 My, and ending in the extinction of equids in North America about 10,000 years ago. The family Rhincerotidae became extinct in North America about 5 Mya. These patterns of decreased diversity and extinction almost certainly relate to global climate change.

During the Pliocene and Pleistocene, the grazing guild in North America was occupied by some rodent groups (e.g., members of the Heteromyidae and Cricetidae), proboscideans, and a less diverse equid fauna. During the Pliocene and early Pleistocene, the 'hypergrazer' niche was occupied by horses, primarily Equus. Hypergrazers are the most highly specialized grass-feeders within the grazing guild. Recent evidence suggests that during the late Pleistocene, roughly over the past 500,000 years, the Eurasian immigrant Bison replaced Equus in the hyper-grazer niche.

**South American grazers and precocious hypsodonty**

Mammalian herbivores with high-crowned teeth first appear in South American land-mammal faunas during the early Tertiary about 50 Mya, but do not become pervasive until the middle Tertiary about 35 Mya (Fig. 5). At that time, hypsodont and/or hypsodontid herbivores were represented by the noto-ungulate (noto- southern: ungulate, hufed mammal)

**Fig. 5.** Time chart showing the distribution and taxonomic composition of the predominant grazing mammals in North and South America. Interpretation of grazing feeding ecology is inferred from either the presence of high-crowned or ever-growing teeth in the clade, or evidence from carbon isotopes, as discussed in the text. The grazing adaptation in edentates (Ed) and Pilomery (Li) is questionable. Only the portion of a particular clade's range with high-crowned taxa is included here. For example, fossil horses are known in North America beginning in the Eocene, but only become high-crowned in the middle Miocene, the latter of which is shown here. Symbols: vertical dashed line, North America; shaded line, South America; black line, North and South America. Abbreviations: Ta, Taeniocodontid; Ti, Tildontid; La, Lagomormph; Pro, Proboesidae; Peris, Perissodactyla; Artiod, Artiodactyla. Compiled from Refs. 15-17.
Tertiary South American notoungulates seems to represent adaptive coevolution. It has been suggested that grasses probably became a dominant part of the ecological landscape earlier than the continent in North America. Like North America later during the middle Miocene (c. 20 Mya), the C isotopic evidence from tooth enamel (and ancient soils) indicates that the original grasses in the South American ecosystems used the Calvin, or C cycle. During the late Cenozoic, notoungulates such as toxodonts occupied the hypergrowing niches until about 3 Mya when the dry-land bridge in Panama resulted in the 'Great American Interchange'. After that time, the hypergrowing niches were mostly occupied by the horse (Equus), llama (Lama) and proboscideans such as Castoroides. The widespread Pleistocene rhino-like notoungulate Toxodon, although having hypselodont teeth and a linear grazing-like incisor arcade, seems (based on isotopic evidence) to have been a mixed-feeder.

Late Miocene global carbon shift, modern terrestrial ecosystems and grazing guild patterns

Before the late Miocene about 7 Mya, C isotopic evidence indicates that most terrestrial ecosystems of the world were primarily C-based with little evidence for C photosynthesis. It follows, therefore, that members of the grazing guild between 20 and 7 Mya evolved the grazing adaptation in a regime of C grasses. From 7 Mya, there seems to have been a significant decrease in levels of atmospheric CO2, increasing aridity, and more-pronounced seasonality, worldwide. After this late Miocene global C shift, C photosynthesis became favored as an adaptive strategy, resulting in the origins of C grasses, which dominate modern temperate and tropical grassland biomes.

Several general patterns are apparent from a study of Cenozoic grazing mammal guilds from the New World. The earlier (by about 10 My) evolution of the South American grazing guild is almost certainly a result of the earlier spread of C grassland biomes on that continent. Despite having evolved from fundamentally different placental groups, grazing mammals, whether they existed in North or South America (or elsewhere for that matter), are characterized by high-crowned teeth, which apparently are a coevolutionary strategy for feeding on abrasive grasses. Regardless of their low diversity within the present-day mammalian grazing guild.

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References


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Fig. 6. Extinct grazing morphotypes from the New World. (a) Horned rodent (Epipalaeotherium) from Miocene of North America. From Ref. 23, with permission. (b) Notoungulate (Toxodon) from the Pleistocene of South America. Illustration by Laurie Walz. (c) Proboscidean (Rhinoceros) from the late Miocene and early Pliocene of North America. From Ref. 24, with permission. (d) Exquisitely preserved remains of the Miocene notoungulate Xenos (Teleoceras) from Ashfall Fossil Beds, NE, USA. Reproduced courtesy of the University of Nebraska State Museum. (e) Pleistocene horse (Equus), widespread in Eurasia, Africa and the New World. Reproduced courtesy of the American Museum of Natural History. (f) Pleistocene llama (Lama) from the Pleisto- cene of Bolivia. Illustration by Laurie Walz.
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