

ORIGIN AND EVOLUTION OF THE GRAZING GUILD IN TERRESTRIAL MAMMALS: MORPHOLOGICAL AND ISOTOPIC EVIDENCE

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"Grazers" are defined as animals with diets consisting predominantly (> 90 %) of grass. Mammalian grazers are characterized by the presence of high-crowned cheek teeth which appear to be a coevolutionary response to the pervasive presence of highly abrasive silica phytoliths in grasses. This paper is primarily concerned with the origin and evolution of the grazing guild in land mammals from North and South America. Based on the timing of acquisition of high-crowned teeth, the rich fossil record of extinct mammalian herbivores indicates that grazing first developed as a major feeding guild during the Miocene. Although some fossil grasses have been reported earlier in the Cenozoic, it seems that the rapid acquisition of high-crowned teeth in many clades of extinct herbivores was a coevolutionary response to the advent of widespread grassland communities during the Miocene. The grazing guild originated and evolved independently in terrestrial communities in South America (Order †Notoungulata) and North America (Orders Rodentia, Proboscidea, Artiodactyla, and Perissodactyla) prior to the formation of the Panamanian land bridge.

In addition to dental evidence pertaining to grazing, within the past decade stable carbon isotopes have rapidly gained acceptance as another tool to understand ancient herbivore diets, paleoecology, and global change. C₃ plants, consisting primarily of trees, shrubs, and some (high-latitude, montane, and cool growing season) grasses, have mean stable carbon ($\delta^{13}\text{C}_{\text{PDB}}$) isotope values of about -27 ‰. In contrast, C₄ plants, which comprise most grasslands in modern terrestrial ecosystems, have mean $\delta^{13}\text{C}$ values of about -13 ‰. These carbon isotopic ratios are fixed into the compact hydroxyapatite mineral phase of herbivore tooth enamel and they are not prone to post-mortem diagenetic alteration. With the use of both tooth morphology and carbon isotopes we can discriminate among C₃ browsers and C₄ grazers, both of which are very common in modern ecosystems, and C₃ grazers, which are rare in modern ecosystems.

This integrative approach using morphology and isotopes indicates that grasslands, and the grazing guild, probably originated slightly earlier in South America (ca. 25 myr ago) than in North America (ca. 20-15 myr ago). The carbon isotopic data indicate that the earliest spread of grasslands occurred with C₃ grasses (unlike the common C₄ grasses of today). The physiological change to predominantly C₄-dominated grassland communities occurred after the late Miocene "global carbon shift" between about 8-6 myr ago. The decline in grazing diversity after the late Miocene appears related to the lower productivity of the more widespread C₄ prairie grasslands relative to the higher productivity savanna grasslands prior to the late Miocene. The late Pleistocene megafaunal extinction resulted in a major drop in overall diversity within the grazing guild as we know it in modern terrestrial ecosystems.