COMMENTARY

Four million years of African herbivory

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The vast African continent is an ecological stage with ever-changing scenery and casts of characters that included human ancestors. The mammals that came and went upon this stage have been enlisted to help answer a compelling question relevant to our own evolutionary story: How do land animals respond to long-term environmental change? The paper by Cerling et al. (1) is a milestone in this quest. It synthesizes a huge amount of information on stable carbon isotopes to reconstruct the dietary history of three major herbivore groups over the last 4.3 million y. The study focuses on Kenya's Turkana Basin, a prime source of vertebrate fossils and geological information relating to human evolution. Results from the fossil record are interpreted using an even larger sample of isotopic data from modern eastern and central Africa ecosystems, making this study a unique comparison of past and present herbivore adaptations on a changing continent.

The power of carbon isotopes is that they can record what an individual animal ate during its lifetime via differing ratios of ^{12}C and ^{13}C in their tissues, providing information on trophic links between primary producers and consumers. This insight on ancient diets is possible because of a rapidly expanding collaboration between geochemists, ecologists, and paleobiologists. Although organic molecules are not well preserved in most vertebrate fossils, decades of research have established that the original biochemical signal is retained in the $\delta^{13}C$ values of preserved tooth enamel. The method presented in this paper focuses on Artiodactyla (Cetartiodactyla), Perissodactyla, and Proboscidea (APP) and classifies modern and fossil herbivores in these groups using $\delta^{13}C$ ratios that signal a diet of grass (C_4), dicots (C_3), or a mix of the two, expressed as a ratio of grazers: mixed feeders:browsers (G:M:B). This ratio is examined through time in the Turkana Basin and compared with G:M:B for the same groups in modern Central and East Africa.

Before discussing the implications of the paper by Cerling et al. (1), it is worth considering how stable isotopes record animal diet at different scales. The $\delta^{13}C$ ratios represent an individual's diet during the time of tooth formation. If the individual is a selective C_3 or C_4 feeder, the enamel records this faithfully; if it eats a mix of leaves and grass, then the isotopic ratio falls in an intermediate range. The $\delta^{13}C$ data points are compiled by taxonomic group and averaged over space (modern ecosystems) or time (fossil-bearing intervals, ~10^5 y in this case) to represent larger-scale patterns of G:M:B. The number of isotopic values per time interval from the 919 Turkana Basin fossil teeth is variable but provides a sound basis for inferring general dietary trends. Taxa previously established as dedicated browsers or grazers (2, 3) have consistent C_3 or C_4 isotopic values. There is no known diagenetic process that would mimic these patterns. The $\delta^{13}C$ data thus provide a highly credible macroscale view of herbivore diets over more than 4 million y as well as across tropical Africa today.

Stable isotope research is opening up new possibilities for ecologists, isotope geochemists, and paleontologists to collaborate in reconstructing an ancient Africa.

Carbon Isotopes Reveal Nonanalog Herbivore Diets

The importance of this research lies not only in novel interpretations based on massive data compilation and analysis, but also in the ecological and evolutionary questions that emerge from these findings. The authors demonstrate that (*i*) dietary ecology represented by the target groups was different in the past, with more mixed feeders followed by more nonruminant grazers than occur in African ecosystems today, (*ii*) some herbivore lineages shifted their diet over time whereas others did not, and (*iii*) the diversity of APP taxa was higher in the Turkana Basin of the late Pliocene–Pleistocene than in present-day mammal faunas. These findings record major shifts in the African herbivore community and provide direct evidence for ecological change operating over large temporal and spatial scales.

Ecosystem structure is defined in this paper as the proportions of C_3 browsers, C_3+C_4 mixed diets, and C_4 grazers. The authors convincingly show that there were many C_3+C_4 mixed feeders in the Turkana Basin between 4.3 and 2.3 Ma, a pattern that persisted for 2 million y. What does this imply about the vegetation? Herbivores as primary consumers depend on plant productivity, and more C_3+C_4 feeders should indicate abundant mixes of browse (i.e., dicots) and grass that provided opportunities for mixed feeding strategies. This suggests a vegetation structure different from any today and raises the question of what could have generated habitats with mixed C_3 and C_4 vegetation but reduced them later (2.3–1.0 Ma) and in modern ecosystems.

Causes of past and present ecological difference could relate to physical (including climatic) factors. The Turkana Basin's fossil record is derived from fluvial, deltaic, and lake margin environments in a low-altitude rift setting. Over the past 4 million y, the basin has alternated between riverine and lacustrine deposition, modulated by drainage from the Ethiopian highlands (4). Temperatures in the past were similar to those today (5), but rainfall was generally higher (6). The 30 modern tropical ecosystems represented in this study range from mountane to lowland and wet to dry, but none matches the Turkana Basin in terms of scale and physiographic complexity. Physical conditions in this basin between 4.3 and 1.0 Ma could have promoted unique habitats with nonanalog combinations of grass, bush, and trees. This is consistent with soil carbonate $\delta^{13}C$, which records woodland and wooded grassland vegetation trending toward increased C_4 through time but no pure C_4 grasslands (6). Of course, biological processes interact with physical ones to determine ecosystem structure, and diverse mammalian herbivores, especially larger-bodied APP species, would have helped shape and sustain mixed C_3–C_4 habitats of the Turkana Basin. After 2.3 Ma,

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climate-driven grassland expansion could have increased competition among mixed feeders, leading to greater segregation of C_3 and C_4 vegetation and driving C_3+C_4 herbivores extinction or greater specialization as browsers or grazers.

The extinction of a number of large nonruminant grazers between 2.0 and 1.0 Ma indicates a different change in ecosystem structure. Pedogenic isotope values record the continuing presence of grasslands (6), but competition with ruminant grazers, more extreme seasonality, and changes in predation pressure could have been operating to limit resources for dedicated grazers. A missing piece to this puzzle is what happened with the continuing story of changing vegetation between 1.0 Ma and today. The authors suggest that the shift to the modern herbivore fauna was abrupt, but a million years is a long time, and faunas from this period are still poorly known in East Africa. There is tantalizing evidence for hyperhypsodont grazers (7), and it is likely that there were multiple shifts between C_3- and C_4-dominated ecosystems throughout this time, subjecting surviving lineages to ever-changing pressures for dietary flexibility or specialization.

A remarkable aspect of this study is the isotopic evidence that some APP herbivore lineages could adopt different dietary strategies over time. Readers should not miss figure S5 in Cerling et al. (1), which provides a compelling summary of stable vs. changing diets for 20 APP taxa. Previous research has shown dietary changes within lineages adapting to the Miocene expansion of C_4 vegetation (2, 8), but Cerling et al.'s (1) findings are the first to offer a detailed analysis of multiple African lineages. No longer can we assume that African large herbivore diets, at the level of tribes or genera, have remained constant over time, even when dental morphology shows little change. Bovid tribes such as tragelaphines (kudus, bongo, etc.) were thought to be browsers in the past, as they are today (1). Elephants with simpler, lower-crowned teeth were regarded as mixed feeders to browsers (*Loxodonta*) as was the brachyodont suid *Kolpochoerus*, a relative of the modern giant forest hog (9). The $\delta^{13}C$ isotope research has upended many of these assumptions by showing that the same tooth morphology can work with very different diets, even over millions of years. Dietary flexibility with respect to C_3 and C_4 forage was (and is) an important strategy for large herbivores dealing with habitat change, whether caused by climate, biological processes (e.g., competition), or accelerating human impact.

This gives us a new way to view both modern and ancient herbivore communities as an assemblage of C_3, C_4, or mixed C_3+C_4 herbivores and flexible feeders capable of major dietary shifts along the C_3–C_4 spectrum over time, presumably as an opportunistic response to changing ecological conditions. A flexible diet clearly is not the only effective survival strategy because specialist C_3 and C_4 feeders also have many long-term success stories. Perhaps it is the combination of these strategies that helped the Turkana Basin (and other) species assemblages persist in the face of ecological change. The flexible taxa include modern examples that changed from C_4 to C_3 diets during the past million years, hinting at times of significantly reduced grassland productivity or increasing dominance of grazing specialists (including numerous modern ruminants) that pushed other APP lineages toward C_3 diets or extinction.

The paper in PNAS (1) also draws attention to the lower diversity of APP taxa in modern ecosystems. Modern parks in Kenya, using the best available compilations of mammal richness (10), have 15–16 APP taxa (counting genera and tribes, as in ref. 1), whereas the total in the Turkana Basin record reaches a maximum of 20 in the time interval from 1.9–1.5 Ma. Proboscidea, equids, and giraffes show losses at the generic level, but other groups are little changed. The grazing *Elephas* was the dominant African proboscidean for millions of years but went extinct, whereas the surviving *Loxodonta* is a flexible feeder that now eats mostly C_3 plants but also can incorporate large amounts of C_4 (e.g., Amboseli National Park in ref. 1, dataset S1). This example suggests one case in which dietary flexibility may have trumped specialization.

New Interdisciplinary Perspectives From Fossil Herbivores

Ecologists who question the quality of ecological information from the fossil record should take note of this research—the wealth of new isotopic data on herbivore diets should be seriously considered in light of ongoing debates about community dynamics and assembly rules. Although these data may not tell us about population abundances, species of plants consumed, or competitive interactions at any given time or place, the paper's macroscale analysis shows that carefully constructed datasets open new windows on longer-term processes in ecology and evolution. Many questions emerge from this work that can stimulate future research. What should we make of the apparent disconnect between dental morphology and diet in some herbivore lineages? If these dentitions are not indicative of specific diets, how did natural selection shape them in the first place? How can we explain the ability of some taxa to shift their diets whereas others remain unchanged over time? What happened to the G:M:B in mammalian faunal assemblages in the last million years as humans became a more effective predator and habitat changer while the amplitude of climate cycles increased (11)?

Cerling et al. (1) also are helping to remove a conceptual roadblock in the search for clues about the ecology of our ancestors. Hominin fossils typically occur in fossil assemblages with grazers, browsers, and mixed feeders, and this is taken as evidence for mosaic habitats of C_3 and C_4 vegetation similar to modern wooded grasslands and woodlands. Based on the new evidence in this paper, we should question whether modern Africa provides adequate models for past vegetation and mammal community structure. Stable isotope research is opening up new possibilities for ecologists, isotope geochemists, and paleontologists to collaborate in reconstructing an ancient Africa with different stage sets and roles for herbivores, and perhaps even different ecological rules, than we see operating today.

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