ANTHROPOLOGY

A Tool for All Seasons

Laser ablation carbon isotope analysis of robust-australopithecine teeth provides insights into seasonal variations in ancestral diets, while minimizing damage to precious fossils.

Stanley H. Ambrose

Seasonal variations in temperature, rainfall, and food availability drive many animals to hibernate or migrate. Animals that are tethered to their home ranges and remain active in all seasons may need flexible adaptive strategies for survival, especially in arid African savannas, where seasonal and annual rainfall can vary widely. About 2.4 to 1.4 million years ago, our earliest stone tool–making ancestors, *Homo habilis* and *H. erectus*, shared African savannas with their close relatives, commonly referred to as "robust" australopithecines or *Paranthropus* species (*1*). How variable were their environments? How much did their diets overlap in different seasons? And how did these two bipedal hominins manage to coexist for 1 million years?

Enhanced online at www.sciencemag.org/cgi/content/full/314/5801/930

On page 980 of this issue, Sponheimer *et al.* (*2*) document the seasonal variation in diet and climate of four robust australopithecines from Swartkrans Cave in South Africa. The authors use laser ablation of tooth enamel—a method that causes minimal damage to the precious fossils—followed by advanced methods of isotope analysis. They are literally blazing a new trail to answers to fundamental questions about early hominin paleoecology and evolution.

With their huge molar teeth and massive jaw muscles, robust australopithecines are considered dietary specialists that fed mainly on small, hard, tough, fibrous plant foods (see the figure). Their extinction between 1.0 and 1.4 million years ago is often attributed to their low-nutrient, high-fiber diets. However, systematic assessments of the cranial and dental anatomy (*1*) and dental microwear (*3*) suggest that their diets were less specialized than previously thought and more similar to those of their ancestors and hominin competitors.

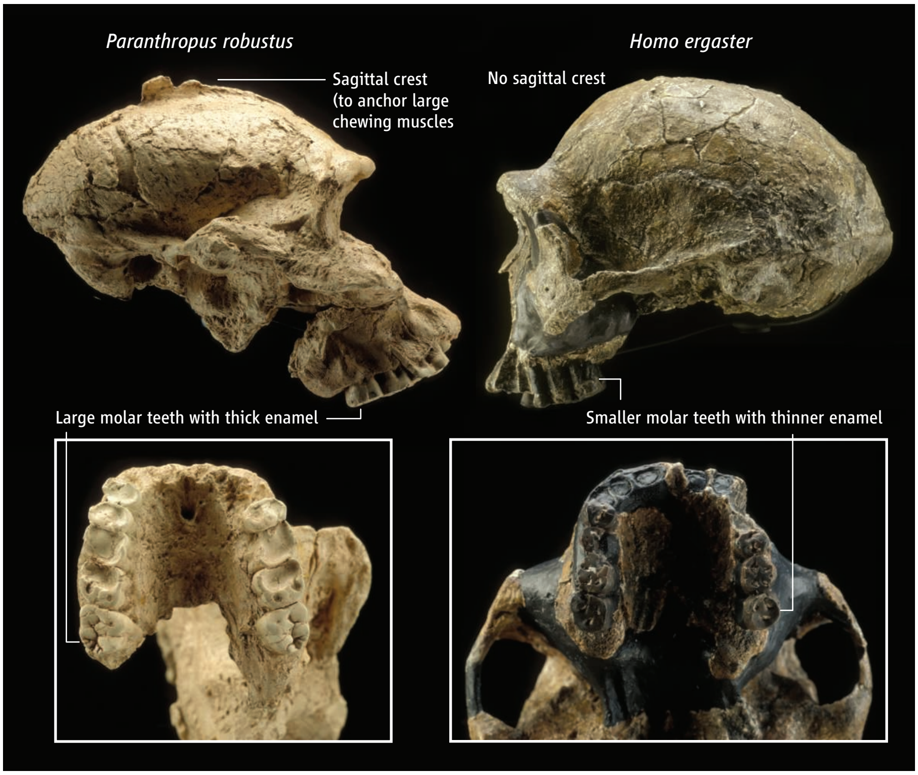
Dietary niche separation between closely related species is usually greatest when resources are scarce. For example, chimpanzees and lowland gorillas that live in the same area eat similar amounts of fruit for most of the year, but during the leanest season, gorillas rely entirely on herbaceous vegetation (*4*). The powerful teeth and jaws of *Paranthropus* (see the figure) may have been essential for survival only when they resorted to tough "fallback" foods to mitigate competition with *Homo*.

How can stable-isotope variations in teeth provide insight into seasonality in diet and climate? The answer lies in the different $^{13}C/^{12}C$ ratios of different types of plants (*5*). Tropical grasses (and a few herbaceous broadleaf plants) fix atmospheric CO_2 using the C_4 photosynthetic pathway; these plants have high $^{13}C/^{12}C$ ratios. Conversely, most broadleaf plants, including trees, shrubs, and herbs, use the C_3 pathway and have low $^{13}C/^{12}C$ ratios. The isotope ratio of the diet controls that of the consumer, such that grazing (grass-eating) and browsing (broadleaf-eating) herbivores—and the carnivores that prey on them—preserve the isotopic difference at the base of the food web. The carbon-isotope ratios of mixed feeders reflect the proportions of C_3 and C_4 plants in their diets.

Oxygen-isotope ratios can also shed light on diet and climate. The $^{18}O/^{16}O$ ratio of surface water increases with temperature and evaporation and with low humidity. This "enrichment" is amplified in leaf water, which often satisfies most of the water requirements of browsing herbivores.

Tooth enamel exhibits 6- to 12-day growth layers, whose edges are marked by tiny ridges (perikymata) at the tooth surfaces (*6*). Perikymata counts show that formation times of larger mammal crowns usually exceed 1 year. Although time averaging during a few months of enamel maturation mutes short-term variations in the isotopic composition of growth increments, enamel preserves an excellent record of seasonal chemical and isotopic variations (*7*).

Oxygen- and carbon-isotope ratios of tooth



Diet and morphology. Robust australopithecines, like this *Paranthropus robustus* skull from Swartkrans Cave (**left**, specimen SK-46), were well adapted to eating tough fibrous plant foods in southern African savannas. Its bony sagittal crest anchored powerful chewing muscles, and the thick enamel of its massive molar teeth preserves an isotopic record of seasonal variations in diet and climate. *Paranthropus* shared the savanna with early *Homo* species, possibly *H. ergaster* (**right**, specimen ER-3733, from Kenya), whose smaller jaw muscles and smaller molar teeth reflect a softer diet that probably included more ripe fruit and meat.

CREDIT: THE HUMAN ORIGINS PROGRAM/SMITHSONIAN INSTITUTION

The author is in the Department of Anthropology, University of Illinois, Urbana, IL 61801, USA. E-mail: ambrose@uiuc.edu

Published by AAAS

enamel can be analyzed by conventional mass spectrometry with samples as small as 500 μg. However, seasonality analysis requires drilling a series of deep, ~1-mm-wide grooves parallel to the mineralization/growth plane. The geometry of mineralization does not closely follow that of the incremental growth structures (*7*). Deep drilling may crosscut enamel formed at different times, which could decrease the chronological resolution of seasonal isotopic variation. Moreover, museum curators are often reluctant to allow researchers to drill deep grooves into rare hominin teeth.

In contrast to conventional methods, the laser ablation technique used by Sponheimer *et al.* barely penetrates the enamel surface of an area of less than 0.5 mm^2 and is thus nearly nondestructive (*2*). Laser ablation also avoids the problem of time averaging in large drilled grooves. Moreover, perikymata can be counted, providing a good estimate of the minimum time interval sampled and of the duration of tooth formation.

The *Paranthropus* teeth studied by Sponheimer *et al.* show interesting patterns of seasonal variation in diet and climate. All have the isotopic composition of mixed feeders, and two show at least ~40% variation in the proportions of C_3- and C_4-based resources over 1 year. One individual had a predominantly C_3-based diet and foraged in a cooler, more humid environment; it may have formed its tooth in a very wet year. The others ate more C_4-based foods in a warmer, drier environment. Their average carbon-isotope ratios are similar to those of adaptively versatile savanna baboons (*2*). Analyses of seasonal variation in teeth of modern and fossil baboons and of other hominin species are necessary to evaluate dietary specialization in *Paranthropus* and niche overlap with other hominin species.

High-resolution isotopic records of seasonal variation can provide important insights into the characteristics of annual climate variation during periods of climatic and evolutionary change. For example, the transition from the warm Eocene to the cold Oligocene, 34 million years ago, is marked by a massive wave of marine animal extinctions. Most climatic proxies indicate a drop in ocean temperatures by ~1°C. However, oxygen isotopes from fish otoliths have revealed a substantial increase in the amplitude of intra-annual temperature change, including a decrease in winter temperatures by ~4°C (*8*).

Were changes in patterns of seasonality important for human evolution? Highly variable, often cool and dry climate episodes characterized the end of the Miocene (5 to 7 million years ago) (*9*), when the human, chimpanzee, and gorilla lineages originated. Did greater seasonal variation play a role in their divergence? From 2.6 to 1.0 million years ago, drier, cooler climates predominated, and the lengths of the climate cycles increased from ~21,000 to ~41,000 years. *Homo* and robust australopithecines appeared around 2.5 million years ago. Foley (*10*) has proposed that their divergence and coexistence were achieved by different strategies of adaptation to increased seasonality. More pronounced glacial/interglacial cycles of ~100,000 years characterize the past million years. Potts (*11*) has proposed that the increasing amplitude of climate change through time, including greater seasonal and interannual variation, is a prime mover for the trend of increasing human adaptability.

Seasonality hypotheses for human evolution can be tested most directly by isotopic analysis of fossil teeth. Greater seasonality should result in higher variance in isotope ratios within and between teeth in a fossil assemblage. However, analysis of fossils should be preceded by compilation of a comprehensive modern comparative database of a wide range of species from different climates and environments.

Laser ablation can be a powerful and versatile technique for reconstructing seasonal and interannual variation in diet and climate, and the structure of animal communities. The results reported by Sponheimer *et al.* should persuade museum curators to permit comprehensive surveys of isotopic variations within fossil teeth.

References

1. B. Wood, D. Strait, *J. Hum. Evol.* **46**, 119 (2004).
2. M. Sponheimer *et al.*, *Science* **314**, 980 (2006).
3. R. S. Scott et al., *Nature* **436**, 693 (2005).
4. C. B. Stanford, J. B. Nkurunungi, *Int. J. Primatol.* **24**, 901 (2003).
5. T. E. Dawson, *Annu. Rev. Ecol. Syst.* **33**, 507 (2002).
6. M. C. Dean, *Proc. R. Soc. B* **273**, 2799 (2006).
7. M. Balasse, *Int. J. Osteoarch.* **13**, 3 (2003).
8. L. C. Ivany, W. P. Patterson, K. C. Lohman, *Nature* **407**, 887 (2000).
9. P. B. deMenocal, J. Bloemendal, in *Paleoclimate and Evolution, with Emphasis on Human Origins*, E. S. Vrba, Ed. (Yale Univ. Press, New Haven, CT, 1996), pp. 263–288.
10. R. Foley, *Another Unique Species* (Longman Scientific and Technical, Essex, UK, 1987).
11. R. Potts, *Yrbk. Phys. Anthropol.* **41**, 93 (1998).

10.1126/science.1135741

MICROBIOLOGY

Bacterial Bushwacking Through a Microtubule Jungle

Jean-Pierre Gorvel

The cellular cytoskeleton represents an obstacle to the movement of bacteria inside an infected cell. Certain bacteria have developed virulence factors to remove or sabotage it.

Our view of the cell's cytoplasm has come a long way. Once considered static "free space" between the nucleus and plasma membrane, it is now known to be a highly dynamic cellular entity with limited space for free movement. It is a dense, organized, tightly regulated, and dynamic network of organelles, cytoskeleton (including microtubules, actin, and intermediate filaments), and vesicles that shuttle between organelles. Yet, some pathogenic bacteria move quite efficiently through this cytoplasmic jungle, invading one cell to the next. On page 985 of this issue, Yoshida *et al.* (*1*) report that *Shigella*, the bacteria responsible for dysentary, hacks its way through microtubules by wielding a tubulin-specific protease.

The author is at Centre d'Immunologie INSERM-CNRS-Université de la Méditerranée Parc Scientifique de Luminy Case 906, 13288 Marseille Cedex 9, France.

Cytoplasm-invading pathogens such as *Shigella flexneri* (*2*), *Listeria monocytogenes* (*3*), *Mycobacterium marinum* (*4*), *Rickettsia prowasekii* (*5*), and *Burkholderia pseudomallei* (*6*) recruit and polymerize actin at one pole of the bacterium to give them a propulsive force to move through the host cell's cytoplasm and into adjacent host cells. In the course of *Shigella* infection, the outer membrane protein VirG interacts with host cell proteins CDC42 and neural Wiskott-Aldrich syndrome protein (N-WASP). This leads to the recruitment of the Arp2/3 complex at one pole of the bacterium, which stimulates the local formation of an actin tail that supplies a propulsive force and intracellular motion (*7*).

Despite this powerful propulsive device, movements of pathogenic bacteria are influenced by other cytoskeletal elements and organelles. In the case of *Listeria*, the bacterium recruits stathmin, a microtubule-sequestering protein of the host cell, presumably to destabi-