# Hominins living on the sedge

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The evolution of $C_4$ photosynthesis was a signal shift in the history of life on Earth, including at least 50 independent origins in 19 families of higher plants (1). Today, $C_4$ plants account for a quarter of the primary productivity on the planet despite representing a small fraction (~3%) of the estimated 250,000 land plant species (2). Most $C_4$ plants are grasses (family Poaceae, 4,500 species), followed by sedges (family Cyperaceae, 1,500 species) and dicots (1,200 species). A few $C_4$ plant species contribute significantly to the human diet, either directly as domesticated cereals (e.g., maize, sorghum, millet) and additives (e.g., cane sugar, corn syrup) or indirectly via animals raised on $C_4$ crops and pastures. As a result, human tissues can have high $\delta^{13}C$ values because $C_4$ plants and their consumers are enriched in $^{13}C$ (3). In recent years, this telltale signature of a $C_4$-based diet has also been found in a wide range of hominin species (4), a finding that has both informed and fueled debate. Now, paleoanthropologists must contend with a unique and surprising finding.

In PNAS, Lee-Thorp et al. (5) report carbon isotope data from the tooth enamel of *Australopithecus bahrelghazali*, a hominin species that lived in the Chad Basin ca. 3.5 million years ago. Their findings, which indicate an early dependence on $C_4$ biomass (~55–80% of the diet by linear extrapolation), are fascinating because they raise challenging questions concerning the diet of this species. The magnitude of $^{13}C$ enrichment, which, among australopithecines, is eclipsed only by *Paranthropus boisei* (6), suggests that the carbon in their diet was derived mainly from $C_4$ plants rather than the tissues of $C_4$ grazing animals (5). This inference led the authors to focus on sedges, a graminoid plant that is perhaps more promising than grass as a food source for hominins. Indeed, the thickly enameled, low-cusped (bunodont) teeth of *A. bahrelghazali* and *P. boisei* would appear to be functionally incompatible with a diet of grass blades (7). Could sedges, then, bring consilience to the $C_4$ conundrum?


**Fig. 1.** The appearance of $C_4$ sedges is quite variable. (*A*) Many savanna species, such as *Cyperus cristatus*, resemble grass. The corms of *C. cristatus* and *Cyperus blysmoides* account for about 15% of the diet of baboons in Laikipia, Kenya [e.g., Barton et al. (17)]. (*B*) The corm of *Cyperus fulgens* is consumed widely across southern Africa. Because the outer tunic (*C*) is often gritty with quartz particles (*Inset*; SEM), it is usually removed before ingestion (*D*) (photographs courtesy of Ben-Erik Van Wyk, University of Johannesburg, Auckland Park, South Africa). (Scale bar: *Inset* in *C*, 200 μm.) (*E*) Painting in the Tomb of Rekhmire (Theban Tomb 100) illustrating the volumetric measurement of *C. esculentus* corms, ca. 1504 to 1425 B.C. (photograph ©2001 Francis Dzikowski, Brooklyn, NY).

## $C_4$ Conundrum

Grine et al. (8) put it well when they wrote, "Dietary signals derived from microwear and isotope chemistry are sometimes at odds with inferences from biomechanical approaches, a potentially disquieting conundrum that is particularly evident for several [hominin] species." In an attempt to reconcile these discrepancies, termed the $C_4$ conundrum (9), Lee-Thorp et al. (5) call attention to *Cyperus papyrus*, a familiar $C_4$ sedge with "chewy and pleasant tasting" pith (10). A diet premised on pith is expected to require laborious loading of the jaws and teeth, a behavior that could have favored the evolution of massive chewing muscles, such as those of *P. boisei* (6). Pith is also soft and unabrasive, traits that correspond to the molar microwear of *P. boisei* (11). However, chimpanzees turn to papyrus pith only *in extremis* (12), probably because it is exceedingly fibrous and almost devoid of protein (13). In theory, few primates could survive on a diet of 55–80% papyrus pith. A puzzling exception is the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*), a rare primate from Madagascar that specializes on hydrophilic species in the Poaceae and Cyperaceae families (>95% of the diet); in fact, the pith of the papyrus-like *Cyperus madagascariensis* alone accounts for about 65% of its diet (14).

Another type of $^{13}C$-enriched plant tissue lies underground (15), and Lee-Thorp et al. (5) call attention to the potential importance of corms in the genus *Cyperus* (Fig. 1*A*). Corms are starch storage organs that feature in the diets of many baboons (16–21) and some human populations (22) (Fig. 1*B*). In fact, the corms of *Cyperus esculentus*, a $C_4$ species (23), were once widely cultivated as a food crop in ancient Egypt (Fig. 1*E*), perhaps because only 150–200 g of corm tissue per day can satisfy human lipid requirements (24). The high quality of *Cyperus* corms and their role in the diets of humans and savanna-dwelling baboons suggest that $C_4$ corms could have been a significant contributor to the elevated $\delta^{13}C$ values of *A. bahrelghazali* and *P. boisei*.

A problem with this hypothesis is that corms are gritty (21), and microwear data argue against such a diet. It is plausible that the exogenous grit on corms exerted a strong selective pressure on hominin manual dexterity, which, in turn, was preadaptive for tool use. Corms have an outer

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peel, or tunic (Fig. 1*C*), that humans can remove to avoid grit and minimize tooth wear (Fig. 1*D*). Thick mats of discarded corm tunics at some Middle and Later Stone Age sites in South Africa (25) are a testament to our aversion to grit and the ecological value of corms as a food source. For *P. boisei*, the regular but imperfect peeling of $C_4$ corms might explain the paradox of how it can have deeply chipped teeth (26) and yet, at the same time, a microwear signature that stands at odds with its robust craniodental morphology (7, 8).

Regardless of whether *A. bahrelghazali* was consuming papyrus pith or *Cyperus* corms, or both, Lee-Thorp et al. (5) have

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thrown a spotlight on the importance of sedges in hominin evolution. A collaborative focus on the nutritional composition, isotopic ecology, and mechanical properties of sedges could prove very instructive, and researchers in the disciplines of primatology, human ecology, and paleoanthropology are well poised to collect these data. For example, an improved knowledge of sedge phytoliths, such as the one recovered from the dental calculus of *Australopithecus sediba* (27), could help to distinguish between sedge species or possibly even the type of tissue that was consumed. Congratulations to Lee-Thorp et al. (5) on a fine paper.


1. Muhaidat R, Sage RF, Dengler NG (2007) Diversity of Kranz anatomy and biochemistry in $C_4$ eudicots. *Am J Bot* 94(3):362–381.
2. Sage RF (2004) The evolution of $C_4$ photosynthesis. *New Phytol* 161(2):341–370.
3. Schoeller DA, Minagawa M, Slater R, Kaplan IR (1986) Stable isotopes of carbon, nitrogen and hydrogen in the contemporary North American human food web. *Ecol Food Nutr* 18(3):159–170.
4. Ungar PS, Sponheimer M (2011) The diets of early hominins. *Science* 334(6053):190–193.
5. Lee-Thorp J, et al. (2012) Isotopic evidence for an early shift to $C_4$ resources by Pliocene hominins in Chad. *Proc Natl Acad Sci USA* 109:20369–20372.
6. Cerling TE, et al. (2011) Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Natl Acad Sci USA* 108(23):9337–9341.
7. Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW (2008) Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol Biol* 35(3):159–175.
8. Grine FE, Sponheimer M, Ungar PS, Lee-Thorp J, Teaford MF (2012) Dental microwear and stable isotopes inform the paleoecology of extinct hominins. *Am J Phys Anthropol* 148(2):285–317.
9. Sponheimer M, Lee-Thorp JA (2003) Differential resource utilization by extant great apes and australopithecines: Towards solving the $C_4$ conundrum. *Comp Biochem Physiol A Mol Integr Physiol* 136(1):27–34.
10. van der Merwe NJ, Masao FT, Bamford MK (2008) Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *S Afr J Sci* 104(3-4):153–155.
11. Ungar PS, Grine FE, Teaford MF (2008) Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE* 3(4):e2044.
12. Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G (1996) Social ecology of Kanyawara chimpanzees: Implications for understanding the costs of great ape groups. *Great Ape Societies*, eds McGrew WC, Marchant LF, Nishida T (Cambridge Univ Press, Cambridge, UK), pp 45–57.
13. Wrangham RW, Conklin NL, Chapman CA, Hunt KD (1991) The significance of fibrous foods for Kibale Forest chimpanzees. *Philos Trans R Soc Lond B Biol Sci* 334(1270):171–178, discussion 178.
14. Mutschler T (1999) Folivory in a small-bodied lemur: The nutrition of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). *New Directions in Lemur Studies*, eds Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM (Kluwer Academic, New York), pp 221–239.
15. Yeakel JD, Bennett NC, Koch PL, Dominy NJ (2007) The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet. *Proc Biol Sci* 274 (1619):1723–1730.
16. Post DG (1982) Feeding behavior of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Int J Primatol* 3(4):403–430.
17. Barton RA, Whiten A, Byrne RW, English M (1993) Chemical composition of baboon plant foods: Implications for the interpretation of intra- and interspecific differences in diet. *Folia Primatol (Basel)* 61(1):1–20.
18. Byrne RW, Whiten A, Henzi SP, McCulloch FM (1993) Nutritional constraints on mountain baboons (*Papio ursinus*): Implications for baboon socioecology. *Behav Ecol Sociobiol* 33(4):233–246.
19. Altmann SA (1998) *Foraging for Survival: Yearling Baboons in Africa* (Univ of Chicago Press, Chicago).
20. Alberts SC, et al. (2005) Seasonality and long-term change in a savanna environment. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*, eds Brockman DK, van Schaik CP (Cambridge Univ Press, Cambridge, UK), pp 157–195.
21. Galbany J, Altmann J, Pérez-Pérez A, Alberts SC (2011) Age and individual foraging behavior predict tooth wear in Amboseli baboons. *Am J Phys Anthropol* 144(1):51–59.
22. Youngblood D (2004) Identifications and quantification of edible plant foods in the Upper (Nama) Karoo, South Africa. *Econ Bot* 58(Suppl. 1):43–65.
23. Hesla BI, Tieszen LL, Imbamba SK (1982) A systematic survey of $C_3$ and $C_4$ photosynthesis in the Cyperaceae of Kenya, East Africa. *Photosynthetica* 16(2):196–205.
24. Eteshola E, Oraedu ACI (1996) Fatty acid compositions of tigernut tubers (*Cyperus esculentus* L.), baobab seeds (*Adansonia digitata* L.), and their mixture. *J Am Oil Chem Soc* 73(2):255–257.
25. Deacon HJ (1993) Planting an idea: An archaeology of Stone Age gatherers in South Africa. *South Afr Archaeol Bull* 48(158):86–93.
26. Constantino PJ, et al. (2010) Tooth chipping can reveal the diet and bite forces of fossil hominins. *Biol Lett* 6(6):826–829.
27. Henry AG, et al. (2012) The diet of *Australopithecus sediba*. *Nature* 487(7405):90–93.