

Thinking outside the box: A lemur's take on hominin craniodental evolution

Cerling et al. (1) and Lee-Thorp (2) presented formidable evidence against nut consumption by the so-called “Nutcracker Man,” robust australopith *Paranthropus boisei*. Unusually high $\delta^{13}\text{C}$ isotope values bear testimony, instead, to a diet rich in C_4 resources (e.g., grasses, sedges). Such isotope values are rivaled, among anthropoid primates, only by those of the extinct gelada baboon, *Theropithecus oswaldi*. There is, however, another primate with similar carbon isotope values, a fossil lemur from Madagascar, *Hadropithecus stenognathus* (Fig. 1). When, in 1970, Jolly advanced his gelada analog for *P. boisei*, he erected a similar model for *Hadropithecus* (3). Indeed, the craniodental convergences of *H. stenognathus* to *P. boisei* (4, 5) are stronger than those of gelada baboons.

In many ways, the history of research on *Hadropithecus* has paralleled that on *P. boisei*, with some researchers defending a hard-object diet (mainly C_3 plant resources) and others defending an interpretation closer to Jolly's (mainly C_4 plant resources, including grass, leaves, and grains) (5). Just as recent analyses of $\delta^{13}\text{C}$ values of *P. boisei* have largely vindicated Jolly's original interpretation (1, 2), recent analyses of $\delta^{13}\text{C}$ in *Hadropithecus* (now including 9 individuals from 4 sites in Southern and Southwestern Madagascar and spanning a temporal range from well before to after human arrival) have drawn similar conclusions (4, 5).

Lee-Thorp (2) suggested that the primary resource for *P. boisei* may have been *Cyperus papyrus*. We suspect that other resources were more central to the diet of *Hadropithecus*, and these will be explored elsewhere. However, there are important ways in which the diets of *Paranthropus* and *Hadropithecus* likely converged. Both probably consumed large quantities of “low-quality” foods (i.e., foods that were relatively high in structural carbohydrates and poor in nutrients and required heavy repetitive trituration). Such conclusions may have important implications for the evolution of the craniodental features that these species share.

Laurie R. Godfrey^{a,1}, Brooke E. Crowley^b, and Elizabeth R. Dumont^c

Departments of ^aAnthropology and ^bBiology, University of Massachusetts, Amherst, MA 01003; and ^cDepartments of Geology and Anthropology, University of Cincinnati, Cincinnati, OH 45221

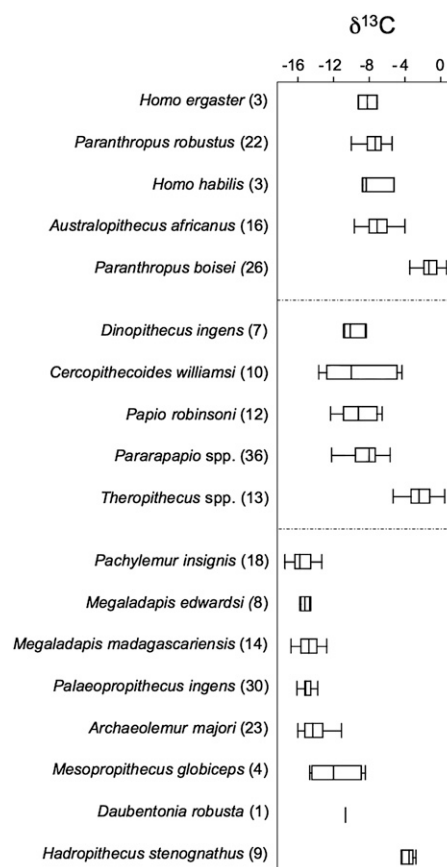


Fig. 1. Box and whisker plots of $\delta^{13}\text{C}$ values (in ‰) for fossil hominin enamel, fossil cercopithecoid enamel, and subfossil lemur bone collagen. Sample sizes are shown in parentheses. Lemur collagen $\delta^{13}\text{C}$ values were converted to their enamel equivalents by adding 5.6‰, a value derived from the mean apparent enrichment between collagen and carbonate for a broad spectrum of primates. Unpublished lemur data were collected by B.E.C.; other data were compiled from the literature.

1. Cerling TE, et al. (2011) Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Natl Acad Sci USA* 108:9337–9341.
2. Lee-Thorp J (2011) The demise of “Nutcracker Man.” *Proc Natl Acad Sci USA* 108:9319–9320.
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¹To whom correspondence should be addressed. E-mail: lgodfrey@anthro.umass.edu.

Reply to Godfrey et al.: Outside the box

We thank Godfrey et al. (1) for their comments comparing the possible diet of *Hadropithecus* with that of *Paranthropus boisei* (2, 3). We wrote: “Indeed, the only known haplorrhine primate with a similar carbon isotope composition is the extinct grass-eating baboon *Theropithecus oswaldi*,” which explicitly excluded *Hadropithecus* and other Malagasy strepsirrhine primates from the comparison as they are only very distantly related to modern apes and humans. Molecular and morphological approaches indicate that the strepsirrhine-haplorrhine divergence occurred before the Eocene (4, 5).

Although certain morphological convergences between the taxa may exist, it is far from certain that this implies similar diets. For instance, we noted that despite the craniodental similarities of closely related *P. boisei* and *Paranthropus robustus*, there is growing evidence from microwear and stable isotopes that their diets diverged. As for *Hadropithecus*, it is possible that its moderately high $\delta^{13}\text{C}$ values reflect consumption of CAM rather than C_4 plants (which we suggest dominated *P. boisei* diets), because the former are highly abundant in the unique spiny forests of Madagascar (6). *Hadropithecus*, *P. boisei*, and *T. oswaldi* may well have consumed dissimilar foods despite some similarities in their $\delta^{13}\text{C}$ values. Further refinement of the estimates of diets of these and all fossil primates will be a challenge

but will provide further constraints on our understanding of primate evolution through time. In the meantime, we prefer to eschew inferring diet for one extinct species from the inferred but unknown diet of another fossil taxon, especially one that is very distantly related and inhabited a very different environment.

Thure E. Cerling^{a,1}, Emma Mbua^b, Francis M. Kirera^b, Fredrick K. Manthi^b, Frederick E. Grine^c, Meave G. Leakey^{b,c,d}, Matt Sponheimer^e, Kevin T. Uno^a, and Julia Lee-Thorp^f

^aDepartment of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112-0111; ^bNational Museums of Kenya, Nairobi, Kenya; ^cDepartment of Anthropology, Stony Brook University, Stony Brook, NY 11794-4364; ^dTurkana Basin Institute, Nairobi, Kenya; ^eDepartment of Anthropology, University of Colorado, Boulder, CO 80309-0233; and ^fResearch Laboratory for Archaeology, University of Oxford, Oxford OX1 3QY, United Kingdom

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6. Winter K (1979) $\delta^{13}\text{C}$ values of some succulent plants from Madagascar. *Oecologia* 40: 103–112.

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¹To whom correspondence should be addressed. E-mail: thure.cerling@utah.edu.