LETTER

African hominin stable isotopic data do not necessarily indicate grass consumption

A series of three papers published in the early PNAS edition of June 3, 2013 (1) evaluate the diet of numerous species of fossilized hominins who lived in Africa from 4.1 to 1.4 million y ago.

These three studies (1) have been interpreted by many in the popular press to suggest that these early hominins were regular consumers of grass and grass seeds (cereal grains), which is an incorrect assumption.

The measurement of ^{13}C and ^{12}C was made from samples of dental enamel in these extinct hominins, and $\delta^{13}C$ was calculated relative to a standard value (2). Indeed, $\delta^{13}C$ values in enamel ultimately indicate the isotopic dietary carbon source, from plants using either the C_3 (trees, shrubs, herbs, and bushes) or C_4 (grasses and sedges) photosynthetic pathways.

A number of fundamental limitations exist with $\delta^{13}C$ analysis to evaluate diet, because it cannot determine the exact species of either C_3 or C_4 plants that were consumed. Furthermore, $\delta^{13}C$ values cannot distinguish if the C_3 or C_4 signatures originated from the direct consumption of plants or from the indirect consumption of animals that consumed these plants.

The point in time (∼3.5 Mya) at which the C_4 signature begins to increase occurs simultaneously with the earliest known use (before 3.39 Mya) of stone tools to cut flesh from animal carcasses and to extract marrow from their bones (3). In addition, the gathering of small animals, invertebrates, and fish likely contributed to early hominin diet. Hence, by triangulating this archaeological information with stable carbon isotope data, it is virtually certain that $\delta^{13}C$ values present in hominin enamel were enriched partially or perhaps mainly from increasing consumption of animals that ate C_4 plants.

Other lines of evidence indicate that early African hominins were increasingly consuming more animal foods during the same time interval (3.5 Mya to 1.5 Mya) that $\delta^{13}C$ had become enriched. The "expensive tissue hypothesis" suggests a reduction in hominin gut size and metabolic activity and a concurrent increase in brain size starting ∼2.5 Mya that was resultant from increased animal food consumption with higher dietary quality (4), although this hypothesis has been recently disputed. Furthermore, grass leaves and seeds are devoid of arachidonic acid (20:4n6) and docosahexanoic acid (22:6n3), which are necessary structural fatty acids required for the synthesis of brain and neural tissues (5). The conversion of linoleic acid (18:2n6) and α-linolenic acid (18:3n3), which are found in plant foods, to arachidonic acid and docosahexanoic acid, respectively, are inefficient pathways with low product to substrate ratios. Likely candidate animal foods, which simultaneously increased the dietary quality and provided arachidonic acid and docosahexanoic acid, were scavenged de-fleshed long bones (marrow), skulls (brains), and aquatic animals. Other nutrients essential to present day *Homo sapiens* (and presumably for hominins) are vitamin B12 and iodine, which are scarce or nonexistent in plant foods, but abundant in animal flesh and organs. These foods, along with meats from grazing animals, likely represent the dominant dietary source for the increasing C_4 signature in our African ancestors.

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2 Lee-Thorp JA, Sponheimer M, Passey BH, de Ruiter DJ, Cerling TE (2010) Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. *Philos Trans R Soc Lond B Biol Sci* 365(1556):3389–3396.
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5 Broadhurst CL, et al. (2002) Brain-specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African *Homo sapiens*. *Comp Biochem Physiol B Biochem Mol Biol* 131(4):653–673.

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