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Paleodietary reconstruction using stable isotopes and abundance analysis of bovids from the Shungura Formation of South Omo, Ethiopia

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ABSTRACT

Preservation of the stable carbon isotopic composition of fossil tooth enamel enables us to estimate the relative proportion of C_3 versus C_4 vegetation in an animal's diet, which, combined with analysis of faunal abundance, may provide complementary methods of paleoenvironmental reconstruction. To this end, we analyzed stable carbon isotopic composition ($\delta^{13}C$ values) of tooth enamel from four bovid tribes (Tragelaphini, Aepycerotini, Reduncini, and Alcelaphini) derived from six members of the Shungura Formation (Members B, C, D, F, G, and L; ages from ca. 2.90–1.05 Ma (millions of years ago) in the Lower Omo Valley of southwestern Ethiopia. The bovids show a wide range of $\delta^{13}C$ values within taxa and stratigraphic members, as well as temporal changes in the feeding strategies of taxa analyzed throughout the middle to late Pliocene and early Pleistocene. Such variation suggests that the use of actualistic approaches for paleoenvironmental reconstruction may not always be warranted. Alcelaphini was the only taxon analyzed that retained a consistent dietary preference throughout the sequence, with entirely C_4-dominated diets. Reduncini had a mixed C_3/C_4 to C_4-dominated diet prior to 2.4 Ma, after which this taxon shifted to a largely C_4-dominated diet. Aepycerotini generally showed a mixed C_3/C_4 diet, with a period of increased C_4 diet from 2.5 to 2.3 Ma. Tragelaphini showed a range of mixed C_3/C_4 diets, with a median value that was briefly nearer the C_4 end member from 2.9 to 2.4 Ma but was otherwise towards the C_3 end member. These isotopic results, combined with relative abundance data for these bovids, imply that the environment of the Lower Omo Valley consisted of a mosaic of closed woodlands, with riverine forests and open grasslands. However, our data also signify that the overall environment gradually became more open, and that C_4 grasses became more dominant. Finally, these results help document the range and extent of environments and potential diets that were available to the four hominin species encountered in the Shungura sequence.

1. Introduction

Detailed records of paleoenvironment, paleoclimate, and paleohabitats, as well as temporal changes in these conditions, are crucial to appreciate the role of environmental change in faunal and human evolution, diversification, extinction, and migration patterns (Dart, 1925; Vrba, 1985, 1988, 1995; Coppens, 1994; Spencer, 1996; Behrensmeyer et al., 1997; Reed, 1997; Potts, 1998; Bobe et al., 2002; Wynn, 2004; Alemseged et al., 2007; Kingston, 2007). The occurrence (e.g., Vrba, 1985) and abundance (e.g., Reed, 2008) of fossil mammalian taxa, particularly bovids, are often used as paleoecological and paleoenvironmental indicators (Harris, 1991; Vrba, 1995; Spencer, 1996; Bobe and Eck, 2001). Meanwhile, stable isotope analysis of mammalian tissues can be a quantitative indicator of an organism's diet and is an efficient tool in differentiating between grazing and browsing paleodiets (DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Wang and Cerling, 1994; Koch, 1998; Kohn and Cerling, 2002). Rarely, however, have these two lines of evidence been integrated to reconstruct vegetation structure or other paleoenvironmental variables of interest to paleoanthropologists (Sponheimer and Lee-Thorp, 2003).

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The Plio-Pleistocene Shungura Formation in the Lower Omo Basin of southwestern Ethiopia is one of the most historic and prolific hominin-bearing sites in Africa. The formation comprises about 800 m of composite fluvial, lacustrine, and deltaic sediments, and is unique in that it represents a relatively long and continuous sedimentary sequence, with strata that are divided into 12 members (Basal, A, B, C, D, E, F, G, H, J, K, and L) on the basis of widespread volcanic ash at the base of each member. Radiometric dates from K/Ar and $^{40}Ar/^{39}Ar$ indicate that the formation covers a relatively wide time span, from 3.6 to 1.05 Ma (millions of years ago) (Feibel et al., 1989; McDougall and Brown, 2008; McDougall et al., 2012).

Fossil bovids are abundant and comprise the majority of faunal collections in the Shungura Formation, as is the case for most African Plio-Pleistocene fossiliferous sites. The fossil faunal and floral assemblages, as well as the geological context of the Shungura Formation, have been extensively studied, and paleoenvironmental interpretations have been made using diverse approaches (Coppens, 1978; Bonnefille and Dechamps, 1983; Haesaerts et al., 1983; Wesselman, 1995; Reed, 1997; Bobe and Eck, 2001; Alemseged, 2003; Cooke, 2007). With the exception of recent work by Bibi et al. (2013) however, isotopic data from the abundant Shungura bovids remain limited. In this paper, we investigate potential changes in the diets of bovids across the different members of the Shungura Formation. We use stable carbon isotopes to reconstruct grazing vs. browsing diets for the four most abundant bovid tribes (i.e., Tragelaphini, Aepycerotini, Reduncini, and Alcelaphini) from six members of the Shungura Formation, Member B (3.44–2.90 Ma), Member C (2.90–2.53 Ma), Member D (2.53–2.40 Ma), Member F (2.32–2.27 Ma), Member G (2.27–1.91 Ma), and Member L (1.38–1.05 Ma), whose stratigraphic ages are based on $^{40}Ar/^{39}Ar$ dates from McDougall et al. (2012). Results from stable isotopic study are then combined with faunal abundance analysis to infer changes in the paleoenvironmental conditions that prevailed throughout the Shungura sequence.

2. Materials and methods

2.1. Sample selection and preparation

Samples for isotopic study were selected from dental remains collected during field seasons in the late 1960s and early 1970s by both American and French teams of the International Omo Research Expedition (IORE), who worked in the northern and southern parts of the Shungura Formation, respectively. The fossil collections are well documented and are currently housed in the National Museum of Ethiopia in Addis Ababa. All teeth sampled were identified to the tribe level: Tragelaphini, Aepycerotini, Reduncini, and Alcelaphini, while aepycerotine and tragelaphine teeth were further identified to the species level (*Aepyceros shungurae* and *Tragelaphus nakuae*, respectively). A total of 173 samples of these four bovid taxa were selected for the analysis (Table 1). Taxonomically diagnostic isolated molars, and in a few cases dental rows with broken surfaces, were selected for sampling. Taxonomic assignments of the specimens were based on previous work, and were confirmed by one of the authors. The surface of each tooth was cleaned with a diamond-tipped drill to remove adhering sediments, secondary carbonates, and surface alterations. Approximately 15–20 mg of powdered enamel was extracted by scraping the surface of each tooth along the growth axis with the 0.5 mm diamond-tipped drill, cleaning the drill tip between each sampling.

2.2. Sample treatment and analysis

The extracted powder enamel sample was treated in 3% H_2O_2 (hydrogen peroxide) for 30 min to remove any organic matter,

Table 1
Stable carbon isotope composition ($\delta^{13}C$ values) of tooth enamel from the Shungura Formation.

Specimen number	Taxon	Member	$\delta^{13}C_{enamel}$ (‰)
Omo28-70-1853	*Tragelaphus nakuae*	B	−9.0
Omo28-68-2463	*Tragelaphus nakuae*	B	−4.2
Omo28-67-508	*Tragelaphus nakuae*	B	−11.6
Omo28-67-463	*Tragelaphus nakuae*	B	−1.8
L47-63	*Tragelaphus nakuae*	C	−2.5
Omo18-68-1719	*Tragelaphus nakuae*	C	−1.7
L344-4	*Tragelaphus nakuae*	C	−0.5
Omo18-68-1738	*Tragelaphus nakuae*	C	−3.7
L109-5	*Tragelaphus nakuae*	C	−3.7
L78-74b	*Tragelaphus nakuae*	C	−2.3
L18-3-68	*Tragelaphus nakuae*	C	−4.6
L188-2	*Tragelaphus nakuae*	C	−0.5
Omo71-1129	*Tragelaphus nakuae*	D	−0.1
L161-4	*Tragelaphus nakuae*	D	−8.2
L21-38b	*Tragelaphus nakuae*	D	−2.2
Omo34-73-887	*Tragelaphus nakuae*	D	−4.9
L113-2b	*Tragelaphus nakuae*	D	−2.9
L551-1	*Tragelaphus nakuae*	D	−5.9
L76-11	*Tragelaphus nakuae*	D	−0.2
L9-110	*Tragelaphus nakuae*	D	−5.8
Omo33-72-1	*Tragelaphus nakuae*	F	−6.8
Omo33-ir(1)-73-5530	*Tragelaphus nakuae*	F	−5.2
Omo33-69-1931	*Tragelaphus nakuae*	F	−5.6
Omo33-74-3933	*Tragelaphus nakuae*	F	−6.2
Omo33-69-2114	*Tragelaphus nakuae*	F	−5.1
Omo33-74-6084	*Tragelaphus nakuae*	F	−4.7
Omo33-74-3763	*Tragelaphus nakuae*	F	−4.0
Omo33-74-3977	*Tragelaphus nakuae*	F	−3.7
Omo47-68-2500	*Tragelaphus nakuae*	G	−5.3
Omo47-68-2536	*Tragelaphus nakuae*	G	−9.8
Omo47-70-2030	*Tragelaphus nakuae*	G	−6.0
Omo47-73-1050	*Tragelaphus nakuae*	G	−5.0
Omo47-71-1407	*Tragelaphus nakuae*	G	−5.1
Omo47-68-2771	*Tragelaphus nakuae*	G	−10.8
Omo47-68-1398	*Tragelaphus nakuae*	G	−5.7
Omo47-68-2755	*Tragelaphus nakuae*	G	−6.6
Omo28-LM	Reduncini	B	−0.7
Omo28-68- 2455	Reduncini	B	−1.5
Omo28-73-2000	Reduncini	B	−1.3
Omo28-67-558	Reduncini	B	−10.6
Omo28-73-521	Reduncini	B	−2.3
Omo28-68-2474	Reduncini	B	−3.9
Omo28-68-1904	Reduncini	B	−0.4
Omo28-68-1893	Reduncini	B	−4.2
Omo18-73-136	Reduncini	C	−0.1
Omo18-68-1722	Reduncini	C	2.1
Omo18-69-937	Reduncini	C	−1.9
Omo18-68-1720	Reduncini	C	−5.0
Omo18-68-2899	Reduncini	C	−0.7
Omo18-70-1804	Reduncini	C	−2.5
Omo18-68-1721	Reduncini	C	−4.9
Omo18-70-1798	Reduncini	C	−2.1
L9-113	Reduncini	D	−6.3
L161-9	Reduncini	D	−3.1
L582-1	Reduncini	D	−1.4
L225-1D	Reduncini	D	−2.8
L76-33	Reduncini	D	−0.9
Omo119-73-4348	Reduncini	D	−2.8
L9-34	Reduncini	D	−1.4
Omo10A-67-746	Reduncini	D	−5.8
Omo33-71-1893	Reduncini	F	0.1
Omo33-69-2038	Reduncini	F	−3.3
Omo33-70-2625	Reduncini	F	−1.9
Omo33-73-5655	Reduncini	F	−1.4
Omo33-70-2627	Reduncini	F	−0.5
Omo33-69-1941	Reduncini	F	−0.5
Omo33-69-1997	Reduncini	F	0.2
Omo33-69-1964	Reduncini	F	−1.9
Omo47-70-2097	Reduncini	G	−1.2
Omo47-73-1046	Reduncini	G	−0.1
Omo47-68-2507	Reduncini	G	−1.9
Omo47-68-2639	Reduncini	G	−0.1
Omo47-71-1413	Reduncini	G	−0.3