



Dietary flexibility of *Australopithecus afarensis* in the face of paleoecological change during the middle Pliocene: Faunal evidence from Hadar, Ethiopia



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ABSTRACT

One approach to understanding the context of changes in hominin paleodiets is to examine the paleodiets and paleohabitats of contemporaneous mammalian taxa. Recent carbon isotopic studies suggest that the middle Pliocene was marked by a major shift in hominin diets, characterized by a significant increase in C_4 foods in *Australopithecus*-grade species, including *Australopithecus afarensis*. To contextualize previous isotopic studies of *A. afarensis*, we employed stable isotopes to examine paleodiets of the mammalian fauna contemporaneous with *A. afarensis* at Hadar, Ethiopia. We used these data to inform our understanding of paleoenvironmental change through the deposition of the Hadar Formation. While the majority of the taxa in the Hadar fauna were C_4 grazers, most show little change in the intensity of C_4 food consumption over the 0.5 million-year interval sampled. Two taxa (equids and bovins) do show increases in C_4 consumption through the Hadar Formation and into the younger, overlying Busidima Formation. Changes in the distributions of C_4 -feeders, C_3 -feeders and mixed- C_3/C_4 -feeders in the sampled intervals are consistent with evidence of dietary reconstructions based on ecomorphology, and with habitats reconstructed using community structure analyses. Meanwhile, *A. afarensis* is one of many mammalian taxa whose C_4 consumption does not show directional change over the intervals sampled. In combination with a wide range of carbon and oxygen isotopic composition for *A. afarensis* as compared to the other large mammal taxa, these results suggest that the C_3/C_4 dietary flexibility of *A. afarensis* was relatively unusual among most of its mammalian cohort.

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1. Introduction

Recent studies of early hominin tooth enamel have challenged conventional ideas regarding the evolution of hominin diets and feeding behaviors (Cerling et al., 2011; Henry et al., 2012; Lee-Thorp et al., 2012; Cerling et al., 2013; Klein, 2013; Sponheimer et al., 2013; Wynn et al., 2013; Alemseged, 2015; Levin et al., 2015). These analyses have also raised new questions regarding interactions between early hominins and other species and their environments. In particular, they allow researchers to reexamine explanations for

the links between dentognathic configurations, food material properties and hominin dietary adaptations. Stable isotopic and other biogeochemical data from fossil tooth enamel provide direct evidence of the chemistry of the foods consumed by individual hominins and serve as proxies for foraging behavior and habitats.

The carbon isotopic composition of biological apatite in individual teeth reflects the degree to which hominins consumed C_4 - or CAM-derived foods, such as tropical grasses, sedges, and succulents commonly found in tropical savannas (Lee-Thorp et al., 1994). The oxygen isotopic composition of tooth enamel provides additional paleodietary and paleophysiological information for individual specimens, while an analysis of taxa with a range of thermophysiological adaptations and behaviors may provide additional

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paleoclimatic information (Levin et al., 2006). The recent surge of stable isotopic data from hominins also makes it clear that the middle Pliocene marked significant hominin paleodietary change, when hominins first began to exploit substantial C_4 /CAM-based foods in more open environments (Lee-Thorp et al., 2012; Cerling et al., 2013; Sponheimer et al., 2013; Wynn et al., 2013; Alemseged, 2015; Levin et al., 2015). The timing of this C_4 dietary expansion, combined with other middle Pliocene discoveries, including possible hominin tool use and manufacture (McPherron et al., 2010; Harmand et al., 2015) and potentially increased diversity of hominin taxonomic diversity (Wood and Boyle, 2016), have heightened interest in the ecological, dietary, and behavioral patterns of hominins in the middle Pliocene (~3.8–3.0 Ma).

Abundant fossils from the middle Pliocene Hadar Formation in Ethiopia's lower Awash Valley provide a unique opportunity to address the paleoecological context of hominin evolution during this key time period. The Hadar Formation has produced the majority of the *Australopithecus afarensis* hypodigm (Kimbel and Deleuzene, 2009). Recent stable isotopic analyses of *A. afarensis* dental enamel (Wynn et al., 2013), as well as material from other hominins (Levin et al., 2015), showed that the earliest perceptible transition to significant consumption of C_4 /CAM-derived food resources began in the middle Pliocene in *Australopithecus*-grade hominins (Sponheimer et al., 2013; Levin et al., 2015). The analyzed specimens of *A. afarensis* (from ca. 3.45–3.0 Ma), distributed throughout well-dated strata of the Hadar Formation, while highly variable, show no evidence of a temporal change in the overall proportion of C_4 -derived foods despite faunal and other evidence for paleoenvironmental shifts across this time period (Wynn et al., 2013). Thus, the long-term stability of C_4 /CAM food consumption by *A. afarensis* was marked by a high degree of intraspecific variation in the degree to which these foods were used. This variation spans the range between C_3 -specialists such as *Giraffa* and C_4 -specialists such as Alcelaphini, indicating that *A. afarensis* occupies a position within the isotopic dietary spectrum of the Hadar mammalian community that is distinct from most other taxa (Wynn et al., 2013).

Although additional direct biogeochemical evidence from hominin teeth is needed to understand hominin dietary evolution better, a more complete picture of the ecological context and evolutionary drivers of patterns in early hominin diets can be derived from associated floras and faunas (Bobé et al., 2007; Potts, 2012; Behrensmeyer and Reed, 2013; Sponheimer et al., 2013). While fossil faunas preserved with hominins are often studied using a variety of non-isotopic approaches (Bobé et al., 2007; Reed, 2008; Behrensmeyer and Reed, 2013), one of several productive approaches has been to couple isotopic analysis of hominins with similar data from associated mammalian faunas (White et al., 2009; Bedaso et al., 2013; Levin et al., 2015). In particular, new approaches using the isotopic composition of micromammals may provide more detailed information on vegetation structure and composition (Leichliter et al., 2016). In this paper, we provide stable isotopic data from the Hadar mammalian fauna to provide a broader and more comprehensive context for the interpretation of the diet and ecology of *A. afarensis*. In particular, we examine whether the lack of change in C_4 food consumption in *A. afarensis* through half a million years of environmental fluctuation is reflected in the broader Hadar mammalian faunal community. Specifically, we compare the isotopic signature of *A. afarensis* to the cohort of large mammalian fauna in general and to those that survived the last known appearance of *A. afarensis* and continued into the Busidima Formation. We also use these data in an exploration of new approaches to the integrated study of paleoecological and paleoenvironmental change, combining stable isotopic information with other data from of mammalian fauna.

2. Background

2.1. Geology

The Pliocene Hadar Formation within the Hadar area is composed of nearly 155 m of fluvio-lacustrine sediments. It is divided into four members (Basal [BM], Sidi Hakoma [SH], Denen Dora [DD], and Kada Hadar [KH]) separated by laterally widespread tephra horizons with radiometric ages. These members are further subdivided by other lithostratigraphic markers, primarily sand bodies, into submembers (e.g., DD-1, -2, -3) that serve as the stratigraphic collecting and analytical units for the fauna (Fig. 1; Campisano and Feibel, 2008). The sediments of the Hadar Formation represent different components of a large-scale fluvio-lacustrine basin that varied significantly in extent during deposition of the sediments. Fluvial and deltaic deposition predominated within the fossiliferous Hadar collecting area. The extensive sand bodies preserved at different stratigraphic levels within the Hadar sequence were deposited by the fluvial system upstream of the stable lacustrine depocenter, located east and northeast of Hadar. At least seven lacustrine transgressive episodes are represented in the Hadar record, occurring in almost all submembers (Fig. 1; Campisano and Feibel, 2008). The most significant and persistent lacustrine episodes occur within the Basal Member, mostly exposed at the nearby Dikika site (Wynn et al., 2008), and in the uppermost Sidi Hakoma to lowermost Denen Dora Members (SH-4 to DD-1 submembers).

A regional angular unconformity separates the Hadar Formation from the overlying Busidima Formation (Quade et al., 2008; Wynn et al., 2008). In contrast to the Hadar Formation, the Busidima Formation at Hadar is dominated by cut-and-fill channel conglomerates and silt-dominated paleosols representing a high-energy fluvial system. Laterally discontinuous exposures and a lack of suitable material for dating has complicated the construction of a high-resolution chronostratigraphic framework for much of the Busidima Formation (Campisano, 2012). The Busidima specimens analyzed in this study range in age from ~2.7 to 0.8 Ma, with the majority of them likely falling between ~2.4 and 1.3 Ma (~BKT-3 to AST-3 levels). Because the age range of fossils analyzed from the Busidima Formation is wide and poorly constrained, and the fauna is not as rich as in the Hadar Formation, these samples were combined into a single stratigraphic bin and used as an "out-group" to the Hadar Formation fauna, which was analyzed at sub-member resolution.

The majority of the vertebrate fossils from Hadar are associated with fluvial and deltaic sands and silts, particularly channel and overbank deposits. However, the large mammal specimens analyzed in this study are intensively sampled from a subset of the depositional environments represented (SH-1, DD-2, and KH-2 submembers, ~3.40, ~3.23 and ~3.05 Ma respectively), with relatively few specimens from other submembers. The depositional environment of the SH-1 and DD-2 fossiliferous horizons represent distributary channel and overbank deposits across an exposed delta plain, while those of the KH-2 represent channel and overbank deposits of a major meandering fluvial system (Campisano and Feibel, 2008). While the sampling strategy provides reasonably robust data on the large mammal communities for these intervals, the samples analyzed represent only a few windows in time rather than a continuous sequence across the range of depositional environments found in the Hadar Formation. Hence, while these data may be useful in testing for long-term dietary trends, it is not possible to distinguish any cyclical patterns of environmental or ecological change occurring on shorter time scales, such as Milankovitch periodicity.

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