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Landscape scale heterogeneity in the East Turkana ecosystem during the Okote Member (1.56–1.38 Ma)

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ABSTRACT

Placing the biological adaptations of Pleistocene hominins within a well-resolved ecological framework has been a longstanding goal of paleoanthropology. This effort, however, has been challenging due to the discontinuous nature of paleoecological data spanning many important periods in hominin evolution. Sediments from the Upper Burgi (1.98–1.87 Ma), KBS (1.87–1.56 Ma) and Okote (1.56–1.38 Ma) members of the Koobi Fora Formation at East Turkana in northern Kenya document an important time interval in the evolutionary history of the hominin genera *Homo* and *Paranthropus*. Although much attention has been paid to Upper Burgi and KBS member deposits, far less is known regarding the East Turkana paleoecosystem during Okote Member times. This study pairs spatially-resolved faunal abundance data with stable isotope geochemistry from mammalian enamel to investigate landscape-scale ecosystem variability during Okote Member times. We find that during this period 1) taxa within the East Turkana large mammal community were distributed heterogeneously across space, 2) the abundance of C_3 and C_4 vegetation varied between East Turkana subregions, and 3) the Karari subregion, an area with abundant evidence of hominin stone tool manufacture, had significantly more C_3 vegetation than regions closer to the central axis of the Turkana Basin (i.e., Ileret and Koobi Fora). These findings indicate that the East Turkana paleoecosystem during the Okote Member was highly variable across space and provided a complex adaptive landscape for Pleistocene hominins.

1. Introduction

The period between 2.0 and 1.4 million years ago (Ma) in eastern Africa documents many important events in human evolutionary history, including the morphological transition from early *Homo* (i.e., *Homo habilis*, *Homo rudolfensis*) to *Homo erectus/ergaster* (Wood, 1991; Wood and Collard, 1999; Wood and Leakey, 2011; Antón et al., 2014), the synchronic and sympatric existence of the hominin genera *Homo* and *Paranthropus* (Wood, 1991; Wood and Strait, 2004), as well as significant changes in hominin technology (Harris and Isaac, 1976; Rogers et al., 1994; Isaac and Isaac, 1997; Ludwig and Harris, 1998). Much of the evidence for these events comes from the Upper Burgi (1.98–1.87 Ma), KBS (1.87–1.56 Ma) and Okote (1.56–1.38 Ma) members of the Koobi Fora Formation at East Turkana in northern Kenya (Brown and Feibel, 1991; Brown and McDougall, 2011; Fig. 1). In addition to the hominin record from this period, non-hominin mammal fossils are particularly abundant and have featured prominently in hypotheses related to the tempo and mode of evolutionary and ecological change in eastern Africa during the Pleistocene (Vrba, 1985; Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe, 2011; Patterson et al., 2014, 2017; Bibi and Kiessling, 2015).

Nearly four decades of research into the East Turkana paleoecosystem provides a framework for testing hypotheses about

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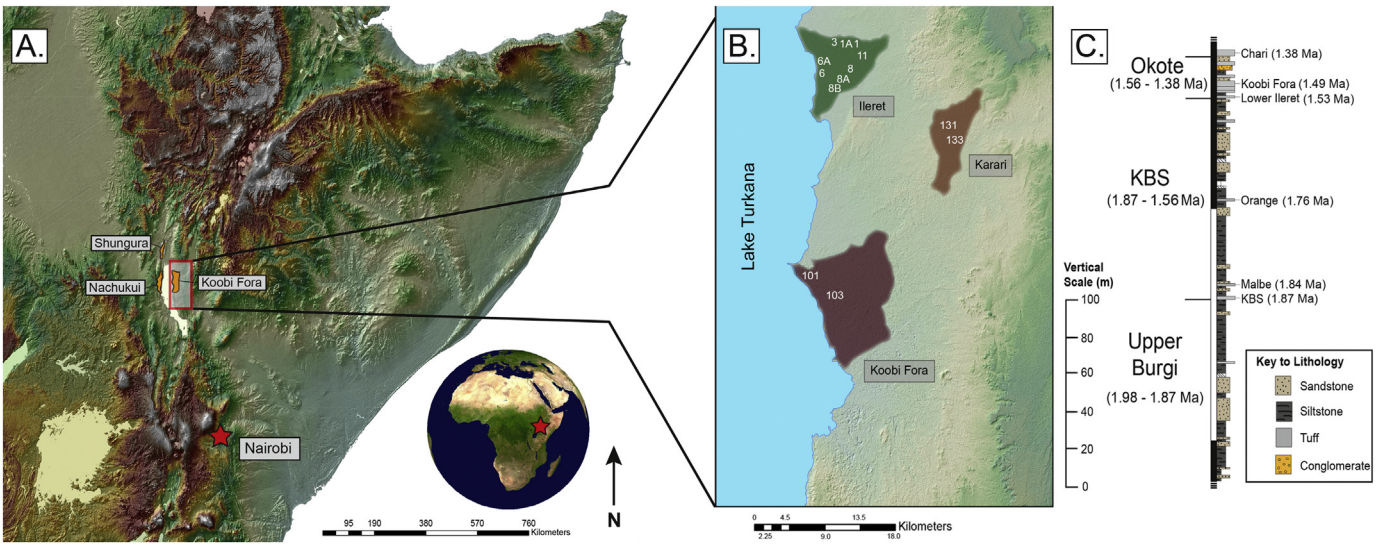

Figure 1. A) East Turkana (Red Box), the Nachukui and Shungura formations in the context of eastern Africa; B) The Ileret, Karari Ridge and Koobi Fora subregions, and Collecting Areas (indicated by white numerals) from which the carbon isotope dataset is derived; C) Stratigraphic section of Upper Burgi, KBS and Okote deposits (modified from Brown and McDougall, 2011). Paleomagnetic polarity is indicated in the thin column to the left of the lithologic section. Normal intervals shown in white; reversed intervals shown in black. Names to the right of the lithologic column refer to selected tuffs with dates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

landscape-scale ecosystem variability during the Pleistocene. Between 2.0 and 1.4 Ma, the East Turkana record samples primarily lake margin and riverine environments. Early in this sequence (~2 Ma), a large lake (Lorenyang) occupied most of the Turkana Basin. After this phase, the lake retreated and by 1.5 Ma the region was composed of river systems draining into what remained of Lake Lorenyang (Brown and Feibel, 1991; Isaac and Behrensmeyer, 1997; Quinn et al., 2007; Behrensmeyer et al., 2016). The isotopic signature of paleosol carbonates from East Turkana during this period indicates that grassland-dominated ecosystems increased, but at a subregional scale, and that vegetative communities were heterogeneous (Quinn et al., 2007).

Ecosystem dynamism between 2.0 and 1.4 Ma presented a complex landscape context for the East Turkana mammal community, including hominins. This period in the Turkana Basin documents several macroevolutionary changes. These include the appearance of several bovid and suid grazing taxa, the replacement of *Theropithecus brumpti* by the more terrestrial *Theropithecus oswaldi*, and the disappearance of large colobine monkeys and the genus *Paranthropus* from the record (Harris, 1991; Bobe, 2006, 2011; Jablonski and Leakey, 2008). When the stable carbon isotope values from mammalian enamel dating to this period at East Turkana are compared with samples from modern eastern African ecosystems (see Cerling et al., 2015), they indicate an elevated prevalence of mixed-feeding taxa. The stable isotope record from this period also indicates that members of the genus *Homo* show a 20% increase in the ingestion of C_4 resources (i.e., warm growing season grasses and sedges, or the animals that eat these resources), a pattern that is not present in *Paranthropus*, which ingested a high proportion of C_4 resources throughout this period in the Turkana Basin (Cerling et al., 2013a). The archaeological record from East Turkana between 2.0 and 1.4 Ma indicates 1) the first evidence of aquatic resource exploitation by hominins in eastern Africa (Braun et al., 2010), 2) stone tool assemblages associated with the later portion of this sequence occur in greater diversity of depositional environments than early in the sequence (Rogers et al., 1994), and 3) hominin toolmakers selectively transported raw materials to regions distal to their sources on the landscape (Braun et al., 2008). These data indicate that the period between 2.0 and 1.4 Ma at East Turkana was marked by shifting relationships between environmental change, mammal community dynamics and hominin behavior.

Fossil assemblages relevant to understanding the East Turkana paleoecosystem between 2.0 and 1.4 Ma are largely limited to material from the Upper Burgi and KBS members (Fig. 1C). Earlier work on Okote sedimentology and vertebrate taphonomy (Behrensmeyer and Laporte, 1982; Behrensmeyer, 1985) suggested possible differences in faunal representation across subregions, but intensive paleoecological study of Okote faunas has only recently been undertaken. Renewed focus on this interval provides important new evidence relating to hypotheses about hominin evolutionary history, ecology and behavior in eastern Africa. The objectives of this study are to use new and existing data from the Okote Member to 1) investigate any variation in the distribution of large mammals across the East Turkana paleolandscape, 2) use stable isotope geochemistry to characterize any spatial variation in large mammal diet and paleovegetation, and 3) explore the dietary ecology of the mammals consumed by hominins as resources during this period.

2. Background

2.1. Geographic and geological context

Okote Member sediments at East Turkana are bounded temporally by the Okote and Chari Tuffs dated to 1.56 and 1.38 Ma, respectively (McDougall and Brown, 2006; Brown and McDougall, 2011; Fig. 2). This sediment package is temporally contemporaneous with parts of the Kaitio and Natoo members of the Nachukui Formation at West Turkana and members J and K of the Shungura Formation in southern Ethiopia (Brown and McDougall, 2011). Well-dated and widespread tephra correlations between these three regions have made it possible to compare spatial variation in contemporaneous paleoecosystems during the Plio-Pleistocene. Previous authors have suggested regional variability at a larger scale, with more arid conditions in the Koobi Fora and Nachukui formations relative to that of the Shungura (Bobe and Leakey, 2009; Levin et al., 2011), as well as substantial differences in humidity and

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