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Bovoid ecomorphology and hominin paleoenvironments of the Shungura Formation, lower Omo River Valley, Ethiopia



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ABSTRACT

The Shungura Formation in the lower Omo River Valley, southern Ethiopia, has yielded an important paleontological and archeological record from the Pliocene and Pleistocene of eastern Africa. Fossils are common throughout the sequence and provide evidence of paleoenvironments and environmental change through time. This study developed discriminant function ecomorphology models that linked astragalus morphology to broadly defined habitat categories (open, light cover, heavy cover, forest, and wetlands) using modern bovids of known ecology. These models used seven variables suitable for use on fragmentary fossils and had overall classification success rates of >82%. Four hundred and one fossils were analyzed from Shungura Formation members B through G (3.4–1.9 million years ago). Analysis by member documented the full range of ecomorph categories, demonstrating that a wide range of habitats existed along the axis of the paleo-Omo River. Heavy cover ecomorphs, reflecting habitats such as woodland and heavy bushland, were the most common in the fossil sample. The trend of increasing open cover habitats from Members C through F suggested by other paleoenvironmental proxies was documented by the increase in open habitat ecomorphs during this interval. However, finer grained analysis demonstrated considerable variability in ecomorph frequencies over time, suggesting that substantial short-term variability is masked when grouping samples by member. The hominin genera *Australopithecus*, *Homo*, and *Paranthropus* are associated with a range of ecomorphs, indicating that all three genera were living in temporally variable and heterogeneous landscapes. *Australopithecus* finds were predominantly associated with lower frequencies of open habitat ecomorphs, and high frequencies of heavy cover ecomorphs, perhaps indicating a more woodland focus for this genus.

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1. Introduction

The habitat preferences of fauna found at paleontological and archeological sites can be used to infer the paleoenvironments that

existed at particular places and times and assist in reconstructing hominin habitat preferences by inference. We reconstructed habitat availability during the deposition of the Omo Shungura Formation using ecomorphology of fossil antelope (Mammalia: Bovidae) astragali. The ecomorphological approach relies on the links between morphology and environment or substrate, rather than relying on taxonomic uniformitarianism in habitat preference. It also allows an abundance-based environmental reconstruction, whereas many synecological methods used to predict environments rely on the presence or absence of particular taxa (e.g., Andrews et al., 1979; Reed, 1997; Louys et al., 2015).

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Previous work has demonstrated that bovid astragali can be classified successfully into habitat preference categories by analysis of morphologies associated with particular habitat preferences (DeGusta and Vrba, 2003; Plummer et al., 2008; Barr, 2014). This method can be used to analyze fossil bovid astragali with known stratigraphic provenance. Relative abundance of fossil astragali assigned to different habitat preferences (relative ecomorph abundance) can, subject to taphonomic analysis, be used as a proxy for the relative abundance of the types of preferred vegetation cover, allowing us to infer their prevalence regionally during the stratigraphic interval of deposition (Kappelman, 1988; Plummer and Bishop, 1994; Kappelman et al., 1997; Kovarovic and Andrews, 2007; Bishop et al., 2011).

We examined the relative frequency of ecomorphs indicating habitat preference in Members B through G (3.4–1.9 million years ago (Ma)) of the Shungura Formation. Ecomorph abundance was calculated at different stratigraphic and temporal scales to examine the extent to which these abundances fluctuated through time. This provided an independent line of paleoenvironmental evidence to compare with other indicators of Shungura Formation habitat presence and relative availability.

1.1. Geological and paleoenvironmental background of the Shungura Formation

The Omo-Turkana Basin includes the Lake Turkana Basin in northern Kenya as well as the lower Omo River Valley in southern Ethiopia (Fig. 1). Systematic investigation of the lower Omo Valley deposits was undertaken by the International Omo Research Expedition, established in 1966, by separate French, American and Kenyan teams, although the Kenyan team quickly changed its focus to Koobi Fora. The region is known for its rich Pliocene and Pleistocene paleontological and archeological records. Three major geological formations, the Shungura, Usno, and Mursi, were recognized in the stratigraphic sequence, and these have yielded over 50,000 fossils, including 220 hominin specimens (Alemseged, 2003). The Shungura Formation has an aggregate thickness of 766 m of sediment divided into 12 members: from oldest to youngest Basal, A, B, C, D, E, F, G, H, J, K, and L (Fig. 1). It covers a time span from 3.6 to 1.16 Ma (Alemseged, 2003) and each member begins with a volcanic tuff bearing the same letter as the member. Further lithological subdivisions within each member, termed units, are numbered from bottom to top of each member. For example, the fourteenth unit from the base of Member G is designated Unit G-14.

The Shungura Formation has five major depositional phases, starting with lacustrine deposition in the first unit of the Basal Member (Bobe and Eck, 2001). Fluvial deposition predominated between the second unit of the Basal Member and Unit G-13. Lacustrine conditions returned in the third major depositional phase, from Units G-14 to G-27. The fourth phase saw the resumption of fluvial deposition from G-28 to L-6, and the final phase was lacustrine from L-7 to L-9.

The Shungura Formation is one of the best studied sequences in eastern Africa, and its paleoenvironments have been extensively researched. A variety of methods (sedimentological analysis of depositional environments, analysis of pollen and macrobotanical fossils, analyses of microfaunal and macrofaunal taxa with specific habitat preferences, changes in faunal diversity and the relative abundances of taxa over time, correspondence analysis of macromammalian faunal abundances, stable isotopic analyses of paleosol carbonates to reconstruct vegetation cover, and stable isotopic analyses of enamel to indicate diet) have been used to reconstruct its paleoenvironmental history (Bobe and Eck, 2001; Bobe et al.,

2002; Alemseged, 2003; Bobe and Behrensmeyer, 2004; Bobe, 2006; Bobe et al., 2007; Bobe and Leakey, 2009; Bobe, 2011; Levin et al., 2011). Study of fossil plants suggests that a mosaic of forest (both moist, evergreen forests with epiphytes, and drier deciduous forests with few epiphytes), woodlands, and grasslands in varying proportions characterized the paleo-Omo environs (Bonnefille and Dechamps, 1983). *Typha* pollen provides evidence of wetlands, and taxa from the Chenopodiaceae and Amaranthaceae groups provide evidence of arid conditions. The discontinuous paleobotanical and microfaunal records suggest that there was a drying trend from Member C to Member F (Bobe and Eck, 2001).

Taxon-based analysis of the bovid fossil samples suggests that there was a transition around 2.8 Ma from wet, closed environments in Member B to closed but dry environments in Member C, and a drying trend from Members D through F (Bobe and Eck, 2001). The shift from predominantly moist to drier closed environments at 2.8 Ma corresponds to an increase in species richness and a rapid change in taxonomic abundance, with a particularly large increase in the abundance of species in the tribe Tragelaphini (kudu and allies). Analyses of bovid tribes and suid and primate genera indicate an interval of relative faunal stability from 2.7 Ma to 2.5 Ma, followed by greater variability in the Omo fauna from 2.5 to 2.1 Ma (Bobe et al., 2002). After 2.5 Ma, taxa associated with secondary grasslands became more abundant than those associated with forests, and at 2.35 Ma (Member F) there was a slight increase in taxa indicative of open grasslands (Bobe and Leakey, 2009). At approximately 2.3 Ma in lower Member G, bovid diversity and abundance were exceptionally high, possibly reflecting greater environmental heterogeneity (Bobe and Eck, 2001), with evidence for an expansion of edaphic grassland (Alemseged, 2003). In upper Member G there was a major shift in depositional environment as a large lake formed in the valley. There was also an increase in open grassland-indicating taxa, although these still comprised less than 15% of the macromammalian faunal sample, suggesting that environmental heterogeneity remained pronounced (Bobe and Behrensmeyer, 2004). The faunal and isotopic records indicate that the lower Omo Valley had higher proportions of woodland and forest through time than either the eastern or western sides of the Lake Turkana Basin (Bobe and Behrensmeyer, 2004; Bobe and Leakey, 2009; Levin et al., 2011), with significant increases in grassland vegetation not occurring until after 2 Ma, in Members H through L.

1.2. Shungura Formation taphonomy and faunal change

Bobe and Eck (2001) examined faunal change in the Shungura Formation and concluded that it was a real phenomenon unlikely to have resulted from taphonomic processes. In Member B to lower Member G fluvial deposition predominated, and isolated teeth are frequently preserved. When examined by member, the relative frequencies of isolated teeth and analysis of other skeletal parts suggests that the Shungura Formation is essentially isotaphonomic, that is to say, the taphonomic biases remained uniform over time (Bobe and Eck, 2001; Bobe et al., 2002; Bobe and Behrensmeyer, 2004; Bobe and Leakey, 2009). Moreover, no significant association was found between the taxonomic and taphonomic data sets, lending further support to the idea that the two signals are independent of each other (Bobe et al., 2002). Because astragali were collected systematically, and taphonomic conditions were consistent through much of the sequence, stability or changes in the relative frequency of different ecomorphs over time provide evidence of how environments changed over time.

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