



# Ecomorphological analysis of bovid mandibles from Laetoli Tanzania using 3D geometric morphometrics: Implications for hominin paleoenvironmental reconstruction



Frances L. Forrest<sup>a,\*</sup>, Thomas W. Plummer<sup>b,c,e</sup>, Ryan L. Raaum<sup>b,d,e</sup>

<sup>a</sup> Sackler Educational Laboratory for Comparative Genomics and Human Origins, American Museum of Natural History, New York, NY, USA

<sup>b</sup> Department of Anthropology, The Graduate Center, City University of New York, New York, NY, USA

<sup>c</sup> Department of Anthropology, Queens College, City University of New York, Flushing, New York, USA

<sup>d</sup> Department of Anthropology, Lehman College, City University of New York, Bronx, New York, USA

<sup>e</sup> New York Consortium in Evolutionary Primatology, New York, NY, USA

## ARTICLE INFO

### Article history:

Received 26 October 2014

Accepted 23 September 2017

### Keywords:

*Australopithecus afarensis*

Paleoecology

Chewing mechanics

Dietary adaptations

Functional morphology

## ABSTRACT

The current study describes a new method of mandibular ecological morphology (ecomorphology). Three-dimensional geometric morphometrics (3D GM) was used to quantify mandibular shape variation between extant bovids with different feeding preferences. Landmark data were subjected to generalized Procrustes analysis (GPA), principal components analysis (PCA), and discriminant function analysis (DFA). The PCA resulted in a continuum from grazers to browsers along PC1 and DFA classified 88% or more of the modern specimens to the correct feeding category. The protocol was reduced to a subset of landmarks on the mandibular corpus in order to make it applicable to incomplete fossils. The reduced landmark set resulted in greater overlap between feeding categories but maintained the same continuum as the complete landmark model. The DFA resubstitution and jackknife analyses resulted in classification success rates of 85% and 80%, respectively. The reduced landmark model was applied to fossil mandibles from the Upper Laetoli Beds (~4.3–3.5 Ma) and Upper Ndolanya Beds (~2.7–2.6 Ma) at Laetoli, Tanzania in order to assess antelope diet, and indirectly evaluate paleo-vegetation structure. The majority of the fossils were classified by the DFA as browsers or mixed feeders preferring browse. Our results indicate a continuous presence of wooded habitats and are congruent with recent environmental studies at Laetoli indicating a mosaic woodland-bushland-grassland savanna ecosystem.

© 2017 Elsevier Ltd. All rights reserved.

## 1. Introduction

The site of Laetoli in Northern Tanzania has been important in reconstructing early hominin behavioral ecology, especially for *Australopithecus afarensis*. The locality is most well-known for a 3.6 Ma trail of preserved hominin footprints attributed to this species (Leakey and Hay, 1979). Several fossil hominin species have been recovered at Laetoli, including over 30 identified specimens (NISP) assigned to *A. afarensis* (including the type specimen, LH 4) from the Upper Laetoli Beds (3.8–3.5 Ma; Kohl-Larsen, 1943; Leakey et al., 1976; White, 1977; Johanson et al., 1978; Leakey, 1987; Harrison, 2011b), a single mandible from the upper Ndolanya Beds (2.7–2.6) attributed to *Paranthropus aethiopicus*

(Harrison, 2002), and several specimens attributed to the genus *Homo* from the Pleistocene Ngaloba Beds (Leakey et al., 1976; Magori and Day, 1983). The associated faunal sample at Laetoli is diverse, spans several poorly represented time intervals, and has figured prominently in discussions of early hominin paleoecology (Leakey and Harris, 1987; Harrison, 2011a).

The sample of *A. afarensis* fossils from Laetoli is second only to that from the site of Hadar in Ethiopia (3.42–2.94 Ma), which has yielded approximately 90% of all hominin fossils attributed to the species (>370 NISP; Johanson et al., 1982; Johanson, 2004; Kimbel et al., 2004; Kimbel and Delezene, 2009; Ward et al., 2011, 2012). Recent studies of *A. afarensis* from Hadar suggest that this taxon was able to survive in a variety of habitats (Bonnefille et al., 2004; Reed, 2008; Wynn et al., 2013). Community structure analysis at Hadar indicates a landscape dominated by woodland and shrubland with permanent water sources (Reed, 1997, 2008) and

\* Corresponding author.

E-mail address: [FForrest@amnh.org](mailto:FForrest@amnh.org) (F.L. Forrest).

palynological analysis suggests that environmental conditions at Hadar fluctuated between closed woodland and wet/dry grasslands throughout the hominin bearing sequence (Bonnefille et al., 1987, 2004). Compared to Hadar, Laetoli appears to have been a more open and arid environment with only seasonal water sources, presenting less ideal conditions for *A. afarensis*. The relative rarity of hominin fossils at Laetoli compared with Hadar likely reflects this distinction (Su and Harrison, 2008). Taxonomic distinction between bovids at Hadar and Laetoli further emphasize the ecological differences between these two localities. Aepycerotini, Bovini, Reduncini, and Tragelaphini make up over 75% of the bovid community across the Hadar submembers (Bohe et al., 2007; Reed, 2008). Today these tribes typically inhabit densely wooded, mesic habitats. In contrast, approximately 88% of the bovids at Laetoli are identified as Alcelaphini, Antilopini, Hippotragini, or Neotragini, indicating drier bushland, shrubland, and grassland (Su, 2005; Su and Harrison, 2007). *Madoqua*, which is particularly abundant in the Laetoli fossil record, typically prefers bush and thorn scrub (Gentry, 1987; Kingdon, 1997). The fact that *A. afarensis* was present at both Laetoli and Hadar demonstrates that this species was able to inhabit ecosystems with a diverse array of habitats, and supports the notion that *A. afarensis* was eurytopic and flexible in its foraging behavior. Ecological flexibility in *A. afarensis* is also indicated by the less well studied sites of Dikika, Ethiopia, and Lomekwi, Kenya (Alemseged et al., 2005, 2006; McPherron et al., 2010; Cerling et al., 2011; Bedaso et al., 2013; Harmand et al., 2015).

Many important events in human evolution, such as bipedalism, tool use, and encephalization, have been attributed to the spreading of increasingly open habitats across Africa, and Laetoli has played a prominent role in these discussions. For example, the original savanna hypothesis attributes the appearance of the hominin lineage and the development of bipedal locomotion to a sudden environmental transition from closed forest to open grassland and paleoenvironmental reconstructions of arid grassland habitats at Laetoli have been cited in support of this hypothesis (Dart, 1925; Howell and Bourliere, 1963; Jolly, 1970; Wolpoff, 1980; Johanson et al., 1982; Vrba, 1995; deMenocal, 2004; Domínguez-Rodrigo, 2014). Nevertheless, the notion of such an abrupt environmental shift contrasts strongly with the growing body of evidence suggesting persistence and continued importance of woodland habitats for early Pliocene hominins at Laetoli and elsewhere (Kingston et al., 1994; WoldeGabriel et al., 1994, 2001, 2009; White et al., 1994, 2006, 2009; Leakey et al., 1995; Wynn, 2000; Pickford and Senut, 2001; Vignaud et al., 2002; Leakey and Harris, 2003).

Initially, the Upper Laetoli Beds were interpreted as arid to semi-arid grassland, similar to today's Serengeti, with scattered tree cover and possible patches of acacia woodland (Hay, 1981, 1987; Bonnefille and Riollet, 1987; Gentry, 1987; Harris, 1987; Leakey and Harris, 1987; Meylan, 1987; Watson, 1987; Leakey, 1987; Louys et al., 2015). However, more recent paleoenvironmental studies reveal a more densely wooded environment than previously considered. Studies of the vegetation (Andrews and Bamford, 2008), gastropods (Pickford, 1995; Peters et al., 2008), birds (Harrison, 2005), large mammals (Kovarovic, 2004; Su, 2005; Andrews, 2006; Kovarovic and Andrews, 2007; Su and Harrison, 2007), and stable isotopes (Kingston and Harrison, 2005, 2007) corroborate the presence of wooded habitats and more mesic conditions and indicate a transition to a semi-arid bushland habitat only during the later Pliocene (Cerling, 1992; Kovarovic et al., 2002). The prevalence of arboreal primates and frugivorous mammals suggest a more heavily wooded environment than is present in the region today (Walker, 1987; Reed, 1997), while the high frequency of terrestrial and grazing taxa make it unlikely that the ecosystem was exclusively wooded (Su and Harrison, 2007). The carnivore guild shows a similar degree of taxonomic diversity to that of

modern day carnivore communities in African savanna ecosystems and includes a high diversity of hyaenids and felids (Barry, 1987). The dominant suid species at Laetoli, *Notochoerus euilus*, has moderately hypsodont dentition suggesting a preference for drier conditions (Harris, 1987) while the presence of *Potamochoerus* suggests that wooded habitats also existed (Harris, 1987; Kingdon, 1997). Some of the smaller fauna at Laetoli, including rodents, snakes, and herpestids, indicate the presence of open arid environments (Denys, 1985, 1987; Meylan, 1987; Petter, 1987; Davies, 1987a,b), while the bush squirrel, *Paraxerus*, and giant elephant shrew, *Rhynchocyon*, are suggestive of closed woodland with dense undergrowth (Butler, 1987; Denys, 1987; Kingdon, 1997). Kaiser (2011) demonstrated that browsing was the dominant ungulate feeding strategy at Laetoli, even in some Alcelaphini that are typically obligate grazers today and ecomorphological analysis of bovid post-crania reveals that bovids preferring forest and heavy cover dominate the assemblage (Bishop et al., 2011).  $\delta^{13}\text{C}$  studies of fossil tooth enamel signify a heterogeneous environment with both  $\text{C}_3$  and  $\text{C}_4$  vegetation and a significant bushland and/or woodland component (Kingston and Harrison, 2007). Stable isotopic analysis of paleosol carbonates reveals that  $\text{C}_4$  vegetation made up less than 50% of the photosynthesized biomass at Laetoli from 9.4 to 1.8 Ma (Cerling, 1992). Phytolith studies indicate that grass cover was an important part of the Laetoli paleoenvironment but was not the dominant component of the floral community (Rossouw and Scott, 2011). While dry shrubland-grassland habitats likely contributed significantly to the ancient ecosystem at Laetoli (Su, 2005; Su and Harrison, 2007, 2008), the overall ecology likely represented a diverse woodland-shrubland-grassland savanna mosaic with closed woodland surrounding seasonal river courses (Andrews, 1989; Reed, 1997; Hicks, 1999; Musiba, 1999; Kingston and Harrison, 2001, 2002, 2007; Musiba et al., 2002; Su and Harrison, 2003; Bamford and Harrison, 2004; Harrison and Su, 2004; Harrison, 2005; Kingston and Harrison, 2005; Kovarovic et al., 2005; Su, 2005; Su and Harrison, 2005, 2007; Bishop et al., 2011).

Inconsistencies in the interpretation of the Laetoli paleoenvironment may in part be due to the fact that different methods of paleoenvironmental reconstruction sample slightly different aspects of the ecology. For example, morphological adaptations reflect adaptive responses to the environment and can be used to infer evolutionary history, sometimes even after the environment has changed dramatically. Other paleoenvironmental methods such as isotopic analysis, provide a more direct look at feeding behavior during the individual's lifetime. When explored in conjunction, these different aspects of the feeding ecology reveal important information about the overall ecological role of a species within the larger ecosystem, including patterns of dietary flexibility and habitat stability through time. The Upper Laetoli Beds provides an interesting case study for comparing paleoenvironmental methods as it appears to have formed during a time when many herbivores in East Africa had more generalized diets than their extant relatives (Cerling et al., 2015).

The current study uses bovid ecomorphology to assess the degree of vegetation cover at Laetoli during early hominin occupation. Ecomorphology allows researchers to explore the relationship between an organism's functional morphology and ecological variables such as diet (Figueirido et al., 2010, 2013; Meloro et al., 2015), preferred habitat (Meloro and Louys, 2014), substrate use (Kappelman et al., 1997), and predator avoidance strategies (Meachen-Samuels and Van Valkenburgh, 2009). Variations in feeding and locomotor adaptations result in morphological differences in skeletal structure that can be used to deduce habitat preference and reconstruct paleoenvironments. Unlike uniformitarian approaches, ecomorphology does not assume that extinct taxa inhabited the same range of habitats, or utilized the same

Download English Version:

<https://daneshyari.com/en/article/8887332>

Download Persian Version:

<https://daneshyari.com/article/8887332>

[Daneshyari.com](https://daneshyari.com)