



## Invited review

## The paleoecology of the Upper Laetolil Beds, Laetoli Tanzania: A review and synthesis

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## ABSTRACT

The Upper Laetolil Beds of Laetoli, Tanzania (~3.6–3.85 Ma) has yielded a large and varied faunal assemblage, including specimens of *Australopithecus afarensis*. In contrast with contemporaneous eastern African *A. afarensis* sites in Kenya and Ethiopia, there is no indication of permanent rivers or other large bodies of water at the site, and the apparently drier environment supported a quite different faunal and floral community as reconstructed from the fossil record. Therefore, a deeper understanding of the paleoecology at Laetoli can be illuminating for questions of habitat access and use by *A. afarensis*, as well as its behavioral flexibility. This paper reviews the substantial body of evidence accumulated that allows for a detailed reconstruction of the Pliocene paleoenvironment of Laetoli. A synthesis of the different lines of evidence suggests that the Upper Laetolil Beds was a mosaic of grassland–shrubland–woodland habitats with extensive woody vegetation in the form of shrubs, thickets and bush, as well as a significant presence of dense woodland habitats along seasonal river courses and around permanent springs. The vegetation during the Pliocene at Laetoli was likely impacted by the strongly seasonal availability of water and the volcanic ash falls that periodically blanketed the area. A comparison with the paleoenvironments of other *A. afarensis* sites and a review of its inferred dietary behavior suggest that *A. afarensis* was an ecological generalist that was able to consume a wide variety of dietary resources in mosaic habitats, although their differential abundances at different sites may be indicative of specific ecological requirements that impact their success in particular environments.

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## 1. Introduction

One of the most fundamental questions in the study of mammalian paleobiology is the nature of the relationship between ecology and evolution. Climatic perturbations, environmental changes, and modifications in the dynamics and structure of the biotic community have all been proposed as potential causal factors in evolutionary change (e.g., Dart, 1925; Robinson, 1953; Howell, 1978; Hill, 1987; McKee, 1991; Stanley, 1992; Vrba, 1985, 1988, 1992, 1995a,b; Potts, 1998, 2013; Bobe and Eck, 2001; deMenocal, 2004, 2011; Bobe and Behrensmeyer, 2004; Trauth et al., 2005, 2007, 2009, 2010; Kingston, 2007; Kingston et al., 2007; Maslin and Christensen, 2007; Maslin and Trauth, 2009; Reed and Russack, 2009; Bobe and Leakey, 2009; Bonnefille, 2010; Bailey et al., 2011; Levin et al., 2011; Barboni, 2014; Macho, 2014; Maslin et al., 2014), making it necessary to document and interpret the environmental context. This is equally the case for paleoanthropology. A better understanding of the paleoecology of early hominins provides critical evidence for its context and allows us to ask questions relating to hominin habitat preferences, ecology, and paleobiology. Furthermore, with detailed studies of the associations between climatic, environmental change and evolutionary transformation it might be possible to generate hypotheses about the factors that ultimately contributed to significant events in the evolutionary history of the hominin lineage, including speciation, adaptive shifts, and extinctions.

With this in mind, this paper will review the evidence accumulated since 1998 by an international multidisciplinary team led by

TH on the paleoenvironmental context of the Upper Laetolil Beds (ULB) at Laetoli in Tanzania (dated at ~3.6–3.85 Ma), associated with the mid-Pliocene hominin *Australopithecus afarensis*. Laetoli is important not just for its paleontological productivity (see Fig. 1) – over thirty fossil hominin specimens (Table 1), the oldest known trails of hominin footprints, and a large and diverse vertebrate fauna (>20,000 specimens) – but also because of its unusual depositional setting among eastern African Plio-Pleistocene hominin-bearing sites. It is one of the few sites where fossiliferous sediments have been accumulated subaerially in the form of airfall or reworked volcanic ashes and evidence for rivers or other large, permanent bodies of water is absent. These factors have had a dramatic impact on the preservational context, taphonomy and ecology at Laetoli, making it a unique and distinctive site compared with other mid-Pliocene hominin sites in Africa. As a consequence, inferences about the paleoenvironment of the Upper Laetolil Beds are crucial to our understanding of the range and patterns of *Australopithecus afarensis* habitat use and our ability to draw inferences about its behavioral flexibility.

## 2. Brief history of research at Laetoli

Laetoli was first visited by Louis and Mary Leakey in 1935, accompanied by Peter Kent, who published a preliminary account of the geology of the area (Kent, 1941). The small collection of fossil vertebrates and terrestrial gastropods they made are housed at the Natural History Museum in London. In 1939, Ludwig and Margrethe Kohl-Larsen visited the Laetoli region as part of their



**Fig. 1.** Examples of fossil specimens recovered from Laetoli. (A) EP 2400/00, R. mandibular fragment with P<sub>3</sub>–M<sub>1</sub> of *A. afarensis*; (B) EP 1000/03, a complete egg referred to *Francolinus* sp., large species; (C) EP 332/98, partial skeleton of *Madoqua avifluminiis*; (D) hominin footprint trails discovered by Mary Leakey and her team in 1976, covered since 1997 for conservation and preservation; (E) an example of footprint trails at Locality 11 left by various animals, including dik-diks, hares and guinea fowl.

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