



Paleoecological reconstruction of hominin-bearing middle Pliocene localities at Woranso-Mille, Ethiopia



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ABSTRACT

Woranso-Mille is a paleoanthropological site in Ethiopia sampling an important and under-represented time period in human evolution (3.8–3.6 million years ago). Specimens of cf. *Australopithecus anamensis*, *Australopithecus afarensis*, and the recently named *Australopithecus deyiremeda* have been recovered from this site. Using multiple habitat proxies, this study provides a paleoecological reconstruction of two fossiliferous collection areas from Woranso-Mille, Aralee Issie (ARI) and Mesgid Dora (MSD). Previous reconstructions based on faunal assemblages have pointed, due to the presence of aepycterotins, alcelaphins, and proboscideans, to the existence of open habitats as well as more closed ones, based on the occurrence of cercopithecids, giraffids, and tragelaphins. Results from community structure analysis (proportions of locomotor and dietary adaptations) at ARI and MSD indicated a predominance of open habitats, such as shrublands. Mesowear analysis revealed that ungulates of all dietary types (grazers, leaf and fruit browsers, and mixed feeders) were present in nearly equal proportions. Ecomorphological analyses using linear measurements of the astragalus and phalanges indicated that bovids utilizing locomotor behaviors associated with all habitat types were present, though the intermediate-cover habitat bovids were best represented in the sample (Heavy cover at ARI and Light cover at MSD). Together, these results suggest that the ARI and MSD localities were heterogeneous habitats (mosaics), likely with densely vegetated areas along a paleo-river and more open regions (woodlands, grasslands) available away from the river.

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1. Introduction

The Aralee Issie (ARI) and Mesgid Dora (MSD) collection areas of Woranso-Mille (WORMIL), located in the central Afar region of Ethiopia (Fig. 1), sample an important time interval (3.8–3.6 million years ago [Ma]; Deino et al., 2010) for elucidating early hominin habitat, for testing the hypothesized ancestor–descendent relationship between *Australopithecus anamensis* and *Australopithecus afarensis* (Haile-Selassie, 2010; Haile-Selassie et al., 2010), and for addressing the question of middle Pliocene hominin diversity (Haile-Selassie et al., in press). In relation to the hypothesized ancestor–descendant relationship between *Au. anamensis* and *Au. afarensis*, the 3.8–3.6 Ma hominins from WORMIL show a mosaic of dental morphological features shared with both *Au. anamensis* and *Au. afarensis*, making their assignment to either taxon extremely

difficult (Haile-Selassie, 2010; Haile-Selassie et al., 2010). However, understanding their paleoecological context is important in order to understand the range of habitats occupied by these chronospecies.

Taphonomic analyses of the ARI and MSD collection areas may be biased due to the collection strategy. Only some of the fossil material is currently collected at ARI and MSD. Very large specimens (elephant, hippopotamus) and very abundant taxa (crocodile and fish) are noted but not collected. Only mammalian specimens identifiable to skeletal element and/or taxon were collected from the field (as detailed in Haile-Selassie et al., 2007). As such, few long bone shaft fragments were collected, introducing bias into the assemblages (Eck, 2007; Thompson et al., 2015). However, based on the fossil material collected thus far, and brief observations in the field, the analyses do not reveal any one specific accumulator, though abiotic factors affected the collected specimens more heavily than did biotic factors, suggesting attritional and time-averaged deposits. The ARI and MSD faunal assemblages appear to be different from other penecontemporaneous eastern African

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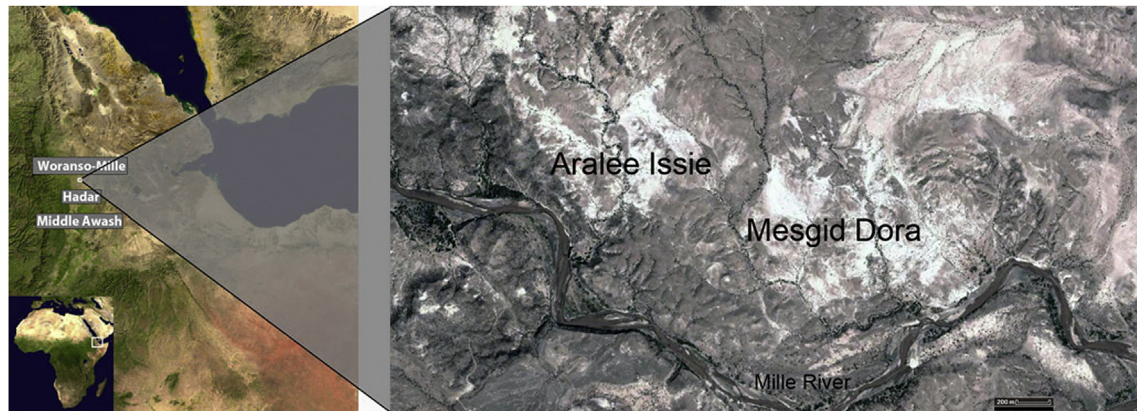


Figure 1. Map of the Woranso-Mille research area in Ethiopia. Aralee Issie (ARI) and Mesgid Dora (MSD) are noted.

sites, particularly in the unusual abundance of cercopithecids (Frost et al., 2014). Hominin fossils are also much more abundant at the ARI and MSD collection areas of WORMIL (Haile-Selassie et al., 2010) compared to the only other contemporaneous site, Laetoli (Su, 2011). This poses an interesting question about why there is such a difference in the relative abundance of hominins at these two sites. As a first step to address this question, this study uses a multiproxy approach in order to reconstruct the paleoenvironment(s) in which the WORMIL hominins lived.

Each paleoecological or paleoenvironmental proxy reconstructs different aspects of past environments, and when used in concert, multiple proxies provide a more nuanced reconstruction than any one proxy alone (Kingston, 2007). In this study, four methods are used: taxonomic approaches, community analysis, ungulate dental mesowear, and bovid ecomorphology. All four approaches are based on the mammalian fauna and reconstruct environment at the local level (as defined by Kingston, 2007).

1.1. Middle Pliocene hominin paleoenvironments

The paleoenvironments of *Au. anamensis* (Leakey et al., 1995, 1998; Ward et al., 2001) from deposits at Kanapoi and Allia Bay, Kenya, dated to between 4.2 and 3.9 Ma, have been reconstructed as mosaics containing forb-dominated edaphic grasslands and gallery woodlands at Kanapoi (Wynn, 2000) to woodlands at Allia Bay (Schoeninger et al., 2003). *Australopithecus anamensis* from Asa Issie, Middle Awash, Ethiopia (4.2–4.1 Ma) was recovered from a grassy woodland context (White et al., 2006). However, dental microwear analysis indicated that *Au. anamensis* preferred C₃ resources despite the availability of C₄ resources (Cerling et al., 2013b). Also in the Middle Awash region, Galili is reported to have been predominantly woodland with grassy patches (Kullmer et al., 2008). Though the degree of heterogeneity varies in these reconstructions, they all indicate that *Au. anamensis* is associated with habitats that are mainly woodland with some open/grassy areas.

Multiple lines of evidence indicate that *Au. afarensis*, recovered from deposits dated to between 3.4 and 2.9 Ma at Hadar, Ethiopia (Campisano, 2007; Campisano and Feibel, 2007), utilized very to moderately open habitats such as bushlands, open woodlands, and shrubland with varying regions of wetlands or edaphic grasslands through time (Reed, 2008). The paleoenvironment at Dikika, a site adjacent to Hadar and equivalent to the Basal Member of the Hadar Formation (3.8–3.3 Ma), is reconstructed as mesic woodlands with some open areas (Wynn et al., 2006). At Laetoli, Tanzania, the only site contemporaneous with ARI and MSD, the habitat reconstruction of *Au. afarensis* varies from closed woodland (Reed, 1997; Kovarovic and Andrews, 2007; Andrews and Bamford, 2008;

Kovarovic et al., 2011) or woodland with patches of forest (Andrews, 2006), to a more open, arid habitat (Harris, 1987; Louys et al., 2015). Recent studies suggest that Laetoli was mostly a mosaic of open woodland–bushland–grassland habitats with areas of closed woodland and riparian woodland along ephemeral river courses (Su and Harrison, 2008; Su, 2011). *Australopithecus afarensis* is considered to have been a eurytopic species (Reed, 2008; Behrensmeyer and Reed, 2013) with broad habitat tolerance (White et al., 2006; Kimbel and Deleuzene, 2009). Most evidence indicates that neither *Au. anamensis*, nor *Au. afarensis* was limited to any specific habitat and that they exploited a variety of available habitats (Behrensmeyer and Reed, 2013; Table 4.1). However, it is most likely that these deposits are time-averaged, which may result in a signal of more mixed habitats than actually existed. Increased precision in paleoecological proxies, and taphonomic and depositional factors are necessary to resolve issues of time-averaging (as discussed in Behrensmeyer and Reed, 2013).

Previous habitat reconstructions of the WORMIL study area based on bovid taxa dated to 3.8–3.6 Ma suggested that the region consisted of shrublands with enough variation in vegetation to support both grazers and browsers, thus indicating heterogeneous habitats, specifically characterized by the presence of gallery forests along a river with more open regions found farther out from the river (Geraads et al., 2009). The presence of gallery forests at WORMIL might be one possible explanation for why cercopithecids in both the ARI and MSD assemblages were abundant. Frost et al. (2014) found that the dominant cercopithecid was *Theropithecus oswaldi*, which utilized both arboreal and terrestrial substrates in open habitats (Elton, 2002). Sanders and Haile-Selassie (2012) state that the presence of *Elephas recki* and cf. *Loxodonta adaurora* indicates that open habitats with C₄ grasses were widely available. Geraads et al. (2009) argue that the bovid assemblage, which is dominated by *Tragelaphus* and *Aepyceros* taxa, points to a habitat with medium-closed vegetation, though with some open regions for some alcelaphin taxa. These reconstructions, based on specific taxonomic groups, indicate that Woranso-Mille, like so many of the sites discussed above, was heterogeneous in habitat types. The present study further expands our understanding of the paleohabitat(s) that would have been available to the early-middle Pliocene hominins and other primates by placing Woranso-Mille within a paleoecological context using several types of paleoecological proxies.

1.2. Woranso-Mille geology

The geological sequence at ARI and MSD consists of ca. 30 m thick mainly sedimentary deposits intercalated with a number of

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