1 **Paleoecological reconstruction of Hominin-bearing Middle Pliocene**
2 **localities at Woranso-Mille, Ethiopia**

3 Sabrina C. Curran^{a,*} and Yohannes Haile-Selassie^b

4 ^a Department of Sociology and Anthropology, Ohio University, Bentley
5 Annex 162, Athens, OH, 45701, U.S.A.

6 ^b Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland,
7 OH, 44106, U.S.A.

8

9 *Corresponding author:

10 *E-mail address:* currans@ohio.edu (S.C. Curran)

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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 aepycerotins, 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.

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 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 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).

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 3.4–2.9 Ma at Hadar, Ethiopia (Carpisano, 2007; Carpisano 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, 2011; Andrews and Bamford, 2008) 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, 2011; Su and Harrison, 2008). *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 cercopithecoid 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.

Woranso-Mille geology

The geological sequence at ARI and MSD consists of ca. 30 m thick mainly sedimentary deposits intercalated with a number of distinctive tuffs that are present in both areas. The sedimentary units are mostly composed of siltstone, sandstone, clay stone, tuffaceous sandstone, and in some areas channel deposits (Haile-Selassie et al., 2010). At the base of the sequence at ARI is a basaltic flow radioisotopically dated to 3.82 ± 0.18 Ma (Deino et al., 2010). Above the basaltic flow is a major marker tuff, a 3 m thick pumice lapillistone tuff known as the Mille Tuff (Saylor et al., 2016). This tuff is radioisotopically dated to 3.76 ± 0.02 Ma (Deino et al., 2010) and provides the maximum age for the fossils from all localities at ARI and MSD. Another prominent marker tuff is the Kilaytoli Tuff. This tuff overlies the fossiliferous horizons at both ARI and MSD. It is radioisotopically dated to 3.57 ± 0.014 Ma (Deino et al., 2010; Saylor et al., 2016). Therefore, the Mille Tuff and the Kilaytoli Tuff yield the maximum and minimum age, respectively, for the fossils at both ARI and MSD.

Materials and methods

All taphonomic and paleoecological interpretations presented in this paper are based on curated materials. Included in this study were specimens from six vertebrate paleontology (VP) fossil localities within the ARI and MSD collection areas of the

WORMIL paleontological site (Fig. 1). These collection areas, located 1.5 km apart from each other, consist of multiple fossil localities. For this study, specimens from ARI-VP-1, ARI-VP-3, and ARI-VP-4 are combined and referred to as “ARI” and specimens from MSD-VP-2, MSD-VP-3, and MSD-VP-4 will be combined and called “MSD.” These collection areas are approximately the same age, though some localities at MSD are slightly older. Most specimens included here were collected between 2004 and 2013 and are housed in the Paleoanthropology Laboratory of the National Museum of Ethiopia (NME), Addis Ababa, Ethiopia.

Faunal assemblages from ARI ($n = 1263$) and MSD ($n = 516$) are rich and represent diverse taxa (see the Supplementary Online Material [SOM] Table 1), though one unusual aspect is the extremely high frequency of primates, which are in excess of 40% for localities with more than 100 specimens. The vast majority of the primate specimens are attributable to Cercopithecidae and most (90%) of the specimens that can be identified to species level belong to *Theropithecus oswaldi* cf. *darti* (Frost et al., 2014). Primates are more common at ARI (54% of the total assemblage) than at MSD (44%). Hominins are present at both collection areas and make up 1–3% of the total fauna from each locality. For both localities, bovids are the second most common taxon, 23% at MSD and 15% at ARI. The only other taxon that has higher than 10% representation within the two faunal assemblages is Suidae with 12% at ARI and 14% at MSD. All other mammalian taxa are represented in much lower frequencies (SOM Table 1).

175 *Taphonomic methods*

176 Mammalian number of identified specimens present (NISP; Table 1) counts and
177 skeletal element data were calculated from the Woranso-Mille specimen catalog and,
178 thus, differ from the counts for other analyses (since not every single specimen is
179 included in the latter counts). Because the level of taxonomic identification varies greatly,
180 results are reported by families for the assemblages. For skeletal element data,
181 comparisons were made between the collection areas and then collection area data were
182 broken down into two types of sub-assemblages. Dental elements are very hard and, thus,
183 preserve extremely well. It is common for them to be the most frequent element type in
184 an assemblage. Dental elements make up 68.7% of the entire fossil assemblage at ARI
185 and 66% at MSD). Thus, dental elements were removed for some of the analyses to
186 compare differences amongst postcrania without element counts being deflated by the
187 disproportionately high dental element counts. Fisher's Exact Test (FET), which is
188 similar to a chi-square test (χ^2) but applicable to datasets where a cell may have fewer
189 than five specimens (Hammer and Harper, 2006), was conducted (in SAS) to test the
190 hypothesis that there was no statistical difference between ARI and MSD in the skeletal
191 element representations, both in the whole dataset and the postcrania-only dataset.

192 As specimens of Cercopithecidae dominate the ARI and MSD assemblages
193 (Haile-Selassie et al., 2010; Frost et al., 2014), to test if there was a difference between
194 the skeletal element representation of the Cercopithecidae and other taxa,
195 cercopithecidonly and non-cercopithecid sub-assemblages were created. Since the
196 collection protocol was to collect everything identifiable as a primate, it was
197 hypothesized that Cercopithecidae will be better represented by all skeletal elements than

non-primates. These differences are expected for both ARI and MSD (i.e., there should be no difference between the sub-assemblages from the two localities).

To analyze surface modifications and break morphology (after Villa and Mahieu, 1991) all ARI and MSD specimens housed in the National Museum of Ethiopia were examined under strong, low-angled light from a gooseneck microscope light (Nikon C-fid bifurcated illuminator) with a 10x hand-lens. Specimens with evident taphonomic alteration were further examined with a Nikon SMZ645 stereomicroscope. Specimens were inspected for any anomalous surface alteration, including abiotic (pitting, adhering matrix, bone surface erosion or dissolution, smoothing, sediment splitting, and general deterioration [= chipping, denting, flaking, cracking]) and biotic alterations (root/fungi/insect etching, digestion, notches, [antemortem] pathology, tooth pits, peeling), and modifications that can be caused by either (“scores” = preparation marks, cutmarks, and tooth scores).

Again, each locality was broken into cercopithecoid and non-cercopithecoid sub-assemblages to examine if the monkeys had a similar taphonomic history (represented by bone and dental surface modifications) as the rest of the assemblage. It is expected that surface modifications of Cercopithecidae postcrania (but not dentition) will be different from the rest of the postcranial assemblage and that surface modifications will not be different for the two localities. To test these expectations, pairwise *t*-tests were conducted in SAS, and a Bonferroni correction applied, bringing the *p*-value for statistical significance to $p < 0.0042$. A significant *p*-value ($p < 0.0042$) indicates that the two locations are different.

221 *Paleoecological reconstruction methods*

222 We employed a multi-proxy approach (including analyses based on taxonomic
223 profiles, community structure, mesowear of ungulate dentition, and ecomorphological
224 analyses of bovid postcrania, coupled with soil and enamel isotopic data) to reconstruct
225 the habitats that would have been available to the WORMIL hominins. The use of
226 multiple proxies, with each proxy providing information about a specific aspect of
227 palaeoecology or the palaeoenvironment, has the potential to illuminate the inherent
228 complexity of past environments and the adaptations of animals to those environments
229 (Kingston, 2007). The proxies sample different temporal and spatial scales: taxonomic
230 methods, ecomorphology, and community analysis represent processes that occurred over
231 large amounts of time and across relatively large geographic areas, whereas the scales
232 represented by mesowear of individual animals can be considered to represent much
233 shorter and more localized scales.

234

235 Taxonomic methods Within bovids, there is a general relationship between tribe and
236 habitat preference (Vrba, 1980; Greenacre and Vrba, 1984). Bovids in tribes such as
237 Bovini and Cephalophini prefer more closed habitats, while others such as Antilopini and
238 Alcelaphini prefer habitats that have little wooded coverage (Greenacre and Vrba, 1984).
239 Aepycerotins are relatively eurytopic and are most commonly found in edge or ecotonal
240 (woodland-grassland) regions. At a tribal level, the Hippotragini and Tragelaphini are
241 somewhat less useful as habitat indicators, since they have members that use both open
242 and closed habitats (Greenacre and Vrba, 1984). Tragelaphins are associated with various

types of habitats, though the Woranso-Mille tragelaphins have relatively enriched $\delta^{13}\text{C}$ values, which indicate they consumed some C_4 vegetation (Levin et al., 2015).

The WORMIL Bovidae from ARI and MSD were analyzed by tribal affiliation. Proportions of bovid tribes (by NISP) for each locality (Table 1) were examined for significant differences using a FET. A significant p -value (≤ 0.05) indicates that the proportions of bovid tribes from the two collection areas are different (not drawn from the same population).

The Suidae from WORMIL (Table 1; Haile-Selassie and Simpson, 2013; Reda, 2011) have relatively robust generic and specific assignments and proportions can thus be compared at a specific level using a FET.

Community analysis Community analysis is used to examine the patterning of ecological adaptations in organisms found in different habitat types. By setting up a comparative database of organisms with known adaptations, the relative differences by habitats in proportions of those adaptations can be used as a basis for comparison with fossil sites (Andrews et al. 1979). Reed (1998) examined 27 modern mammalian communities in Africa and assigned locomotor and trophic categories to all species weighing more than 4 kilograms (kg). Locomotion categories include arboreal [A], aquatic [AQ], terrestrial [T], terrestrial/arboreal combination [TA], and fossorial [F]. Trophic categories are carnivore [C], meat and bone [CB], meat and insects [CI], omnivore [OM], fresh-grass grazer [FG], grazer [G], browser [B], fruit and leaves [FL], graze and browse mixed feeder [MF], and roots [R]). Together, the relative percentages of these ecovariables (locomotor and trophic type) in a community provide insight into the type and density of vegetative cover

at a location. To examine how the community of mammals collected from the ARI and MSD collection areas compares to modern mammalian communities (from Reed 1998), percentages of these ecovariables were calculated for ARI and MSD specimens. Each fossil taxon greater than 4 kg in body mass was assigned to a dietary and locomotor category based on ecomorphological analyses conducted here (see below) and the results of dental enamel isotopic analysis (Levin et al., 2015), supplemented by published literature (Taylor, 1970, 1976; Taylor and Hannam, 1987; Petter et al., 1991; Krentz, 1993; Reed, 1998, 2008; Harris and Cerling, 2002; Leakey and Harris, 2003; Sorkin, 2006; Skinner, 2006; Lewis and Werdelin, 2007; Kingston and Harrison, 2007; Bekele et al., 2008; Su et al., 2009; Sutor et al., 2010; Geissler, 2013; Cerling et al., 2013a; Werdelin et al., 2014a, b).

Percentages of ecovariables from extant communities (derived from Reed, 1988) and the percentages of those ecovariables in the ARI and MSD assemblages were then arcsine transformed due to the bimodal distribution of percentage data (Su and Harrison, 2007), and analyzed (in SAS) using correspondence analysis and cluster analysis (Unweighted Pair Group Method with Arithmetic Mean [UPGMA]). UPGMA was conducted on 1) all localities (extant communities and fossil collection areas) as individual data points and 2) on the means of each habitat type to examine to which habitat type and to which extant community each fossil collection area was most similar. To explore the association between ecovariables and localities in multivariate space, a correspondence analysis (CA) was conducted. Reed's (2008) analysis showed that five of the ecovariables (A, T, FL, G, MF) showed significant differences in six pairwise habitat

comparisons and, thus, these were the main variables included in the analysis for this study.

Mesowear analysis of ungulates Due to mechanical action from a combination of mastication of hard particles (abrasion) and dental attrition, the enamel surface of a tooth is worn over the life of an animal. It has been shown that wear occurs in a behavior-specific manner that can be used to reconstruct the diet of animals (Fortelius and Solounias, 2000; Rivals et al., 2010). Grazing animals tend to have low and flat cusps while browsers have high and sharp cusps (Fortelius, 1985, Janis, 1986). The scoring system (Fortelius and Solounias, 2000; Rivals et al., 2007) used here includes two morphological categories and their assigned codes of cusp relief (low = 1 and high = 2) and three cusp shapes and their codes (sharp = 1, round = 2, blunt = 3). These codes were then used to create a score that included both relief and shape (see Table 2). All ARI and MSD fossil ungulate molars without heavy wear (ARI $n = 86$, MSD $n = 50$) were scored using the methods and data from Fortelius and Solounias (2000) and Rivals (2007). Counts of specimens for each mesowear score were calculated and plotted by taxon for each collection location.

Ecomorphology of Bovidae postcrania Ecological functional morphology (ecomorphology) is an examination of an animal's functional morphology as it relates to ecologically mediated behavior, such as food acquisition or locomotion. Morphology has been shown to vary with locomotor and, specifically, predator-escape behaviors (Kappelman, 1988; Plummer and Bishop, 1994; Kovarovic and Andrews, 2007; Curran,

2012, Barr, 2014). Density of vegetation, topographic relief, and firmness of the substrate in a habitat place constraints on the type of locomotion possible in that habitat. For example, a fast gallop works well in open grasslands, but is not possible in a dense forest, where rapid changes in direction are necessary to avoid obstacles such as trees. Since morphology varies in a predictable way with locomotion and locomotion varies with habitat, skeletal morphology can be used as a proxy for locomotion in different habitats. To test this hypothesis for bovid astragali and phalanges, a series of measurements were collected by DeGusta and Vrba (2003 and 2005, respectively) on a comparative dataset of extant African bovids. Astragali of extant bovids were reclassified into their known habitat type with 66.7% accuracy using the cross-validation method (DeGusta & Vrba, 2003) while second and third phalanges reclassified with 70% and 64% accuracy, respectively (DeGusta & Vrba, 2005). DeGusta & Vrba (2003, 2005) made their astragalus and phalanx measurements available and these data were used as the training set for classifying WORMIL fossil bovid astragalus and phalanx specimens into habitat types using Canonical Variates Analysis (CVA) in SAS. Permutation tests (after McNulty et al., 2006) were conducted for each skeletal element on the centroids of each habitat type to test for statistically significant difference. All measurements on ARI and MSD astragalus and phalanx specimens were taken by SC and can be found in the SOM Tables 2-4.

While the ultimate goal of this study is to classify fossil specimens into one of these habitat types, CVA is somewhat restrictive, as each specimen must be placed into a single habitat type. Following DeGusta & Vrba (2003, 2005), four habitat types were used here (Forest, Heavy Cover, Light Cover, and Open). In reality, however, habitats

exist along a continuum from forests to grasslands and many animals utilize a range of habitats. In an attempt to reconcile this, a Habitat Score (following Scott and Maga, 2005) was created for each skeletal feature. A subsample of the most open-adapted and the most forest-adapted extant taxa were used to make a single discriminant function to separate the two groups. This algorithm was used to score all the other specimens (here, reduced to the means for each species) along that axis (= Habitat Score). Since the distal phalanx is the place of direct contact between the bovid and the substrate, its morphology is a reflection of how dry or pliant the substrate is (Köhler, 1993; Curran, 2012). Instead of using open- and forest-adapted specimens as the training sample for the Habitat Score for the distal phalanx, specimens of modern taxa used to create the algorithm were from taxa that move across either wet/pliable or dry/hard substrates.

Klein et al. (2010) found that size is a confounding factor on bovid skeletal shape, as it is for most studies of morphology (Falsetti et al., 1993; Jungers et al., 1995). To address the issue of size in the linear datasets, raw data were divided by the geometric mean (= Mosimann shape variables [MSV]; Mosimann, 1970) and all analyses were rerun on the transformed datasets. Data were then analyzed by element (astragalus and intermediate and distal phalanges) with CVA. Regressions were conducted on all raw variables against both body weight and geometric mean, and on the MSV and body weight to evaluate the correlation between shape (measurements) and size.

It has been demonstrated that phylogenetic relatedness between taxa has a significant effect on the morphology of bovid astragali (Barr, 2014; Barr and Scott, 2014). To test for this in the astragalus and phalanx data used here, a phylogenetic generalized least squares (PGLS) was conducted on both raw measurements (as

published by DeGusta and Vrba, 2003, 2005) and the size-adjusted (MSV) measurements for each skeletal element. Phylogenetic trees for the Bovidae were downloaded from 10Ktrees.nunn-lab.org (Arnold and Nunn, 2010) and PGLS was run with the caper package (version 0.5.2; Orme et al, 2013) in R. For each variable, the analysis returns a lambda value (Pagel's λ) that when close to 1 indicates the trait is following Brownian motion and is not different from that predicted by phylogenetic relatedness (though this does not preclude the presence of a functional signal), while lambda values closer to 0 indicate a divergence from this pattern (Freckleton et al., 2002).

Two taxa included in the DeGusta & Vrba (2005) comparative bovid dataset were excluded from the analyses performed here. *Tragelaphus oryx* (eland) is frequently not included in ecomorphological studies (Kappelman, 1988; DeGusta and Vrba, 2003, 2005) due to its very large body size and was likewise removed from all analyses in this study, except in the exploration of extant bovid body weight distribution. *Tragelaphus spekii* (sitatunga) is a swamp-dwelling bovid with extremely specialized hooves that are long, thin, and able to be splayed to decrease the risk of sinking into swampy substrates (Köhler, 1993). Due to its highly specialized distal phalanx morphology, *T. spekii* was removed only from the distal phalanx analysis.

Results and preliminary discussion

Taphonomic analysis

As with most paleontological sites, the ARI and MSD assemblages were dominated by dental specimens (68.7% of the NISP at ARI and 66% at MSD), followed by horn-cores and small, dense bones (tarsals and phalanges) and some long bones, especially the femora and tibiae (see SOM Table 5). Fisher's Exact Tests demonstrated that the assemblages from ARI and MSD differed both with ($p = 0.268$) and without ($p = 0.2873$) dentition. At ARI, there was a further difference in skeletal element representation between cercopithecoid and non-cercopithecoid sub-assemblages (FET $p = 0.9999$), while no such distinction existed at MSD ($p = 0.0041$). At ARI, long bones were more frequent for cercopithecoids than other taxa, while phalanges and astragali were more common for other taxa (especially bovids). This likely represents both preservational and collection bias. Phalanges and astragali of artiodactyls are very dense and useful for reconstructing past habitats (DeGusta and Vrba, 2003, 2005; Kovarovic and Andrews, 2007; Plummer et al., 2008; Curran 2012) and, thus, have not only a higher likelihood of preservation, but also collection. The higher frequency of cercopithecoid long bones is likely due to the higher likelihood of their collection (a *Theropithecus* radial midshaft would be collected, while an *Aepyceros* radial midshaft may not be).

Most breaks in the ARI and MSD assemblages were post-depositional in nature (irregular or straight breaks with $\sim 90^\circ$ break edges). Specimens with curved breaks, which indicate that the skeletal elements were broken while the bone was fresh, were rare in the assemblages (ARI = 21 and MSD = 5), as were breaks with crenulated edges, which indicate carnivore chewing (only ten from ARI and three from MSD).

Surface modifications associated with abiotic factors (pitting, adhering matrix, bone surface erosion or dissolution, smoothing, chipping, denting, flaking, cracking,

sediment splitting, weathering) occurred much more frequently on the ARI and MSD specimens than did those associated with biotic actors (root/fungi/insect etching, digestion, notches, [antemortem] pathology, tooth pits, peeling, and scores); see Figure 2 for examples of these modifications. By far, the most common surface modification on both the ARI and MSD specimens was that of small pits/holes across the surface of a specimen (Fig. 3). Specimens that have been exposed to surface conditions for longer were more heavily pitted (Haile-Selassie, pers. obs.). It is possible that contact with a low pH substrate (Barron et al., 2003; Dawes, 2003) and/or precipitation caused the surface pitting, since specimens become affected by pitting mainly after they are exposed to the surface. Pitting was far more frequent on dental (enamel) surfaces (72.9% of the total dental assemblage [ARI + MSD] versus 29.4% of the total postcranial assemblage; see SOM Table 6). Surface modifications that indicate carnivore activity were extremely uncommon; there were only 15 tooth scores from ARI specimens and nine from MSD specimens, and only 17 tooth pits from ARI and two from MSD.

Surface modifications were not significantly different between cercopithecoid postcranial remains and the rest of the faunal postcranial assemblage from the ARI collection area ($p = 0.9999$), however, there was a statistically significant difference at MSD ($p = 0.0045$). The MSD cercopithecoid postcranial sub-assemblage had the highest frequency of scores of all of the sub-assemblages, though they are still relatively infrequent (6.87% of the post-cranial assemblage surface modifications). The high frequency of scores is likely related to the higher frequency of long bones in the curated materials, since modifications related to carnivore activity (scores, pits) occur frequently on long bone shafts (Blumenshine, 1995; Parkinson et al., 2014).

The hypothesis that the cercopithecoid and non-cercopithecoid dental datasets would be the same was not supported ($p = 0.0076$). This seems to be mainly driven by the MSD subset ($p = 0.002$), since the ARI cercopithecoid and non-cercopithecoid dental subsets were not statistically different ($p = 0.04$). In the MSD dental elements, cercopithecoid specimens were more pitted, while the non-cercopithecoid specimens showed more signs of general deterioration. Finally, while the postcranial taphonomic surface alterations were statistically the same from ARI and MSD ($p = 0.455$), the dental assemblages were not ($p = 0.0013$). Again, this is likely due to the MSD dental subset. In sum, the overall taphonomic alterations from ARI and MSD were similar, though ARI dental specimens had more pitting, and the cercopithecoid taphonomic alterations at ARI, but not MSD, were different from the rest of the faunal assemblage.

Aralee Issie is much more fossiliferous than MSD, which may be due to favorable local depositional conditions that promoted fossilization. However, neither assemblage showed evidence of a specific accumulator, such as fluvial deposition (very few polished or smoothed specimens) or intense carnivore activity (very few tooth scores and pits).

Paleoecological reconstruction

Taxonomic analysis There was no difference in the proportions of the bovid tribes from each of the collection areas, ARI and MSD according to the FET ($p = 0.0889$, a non-significant result, indicating they were drawn from the same statistical population; Fig. 4a). Aepycerotini is the most frequently occurring tribe at both locations (50% of identified bovid specimens from both collection areas), and Tragelaphini is the second-

most frequent, though the proportional representation at ARI is higher (31.9% versus 12.8%).

The proportions of suid species did not differ between the two collection areas (FET $p > 0.9999$; Fig. 4b). Of the four Suidae species from ARI and MSD, three are shared between the areas, while one (*Cainochoerus* sp., a small suid, somewhat similar to peccaries (Harris and Leakey, 2003)) is so far found only at ARI (Table 1).

Nyanzachoerus jaegeri and *Notochoerus euilus* are both more frequent at MSD (Table 1).

Nyanzachoerus jaegeri was a mixed feeder, although specimens from Kanapoi, Kenya, tended more toward eating grasses (Bishop, 2011). Its descendent, *Not. euilus*, was found to have a diet of grazing to mixed feeding (Bishop, 2011; Levin et al., 2015), though its postcranial ecomorphology indicated that it locomoted in closed habitats (Bishop, 1999).

Kolpochoerus millensis, a newly identified species (Haile-Selassie and Simpson, 2013) that is morphologically intermediate between the earlier *Kolpochoerus deheinzellini* (Brunet and White, 2002) and the younger *Kolpochoerus afarensis* (Cooke, 1978), is the only suine at both locations, although it is better represented at ARI (67.1% of the identified Suidae specimens) than at MSD (48.5%). It was likely a mixed feeder (Bishop, 2011).

Community analysis In the correspondence analysis, the modern communities were spread out along a continuum from open to forest on the first dimension (Fig. 5). Reed (2008) states that the distribution along dimension 1 (x-axis) can be conceptualized as a seasonality gradient. Communities associated with environments that have more seasonal rainfall scored negatively on dimension 1 (see Fig. 5), while communities with high

annual rains without seasonal differences scored more positively. Both WORMIL localities plotted closest to modern communities that have seasonal rainfall, with ARI falling closest to those regions with shrubland habitats and MSD plotting closest to regions with grassland habitats, supporting the hypothesis that MSD was slightly more open than ARI. These associations were further supported with the UPGMA cluster analysis, with ARI closely affiliated with shrublands (Fig. 6a), and MSD, although not closely affiliated with any single habitat type, being closest to the ([Desert + Grassland] + [Shrubland + ARI]) group. When UPGMA was performed with the modern localities instead of the means of each habitat type, MSD was closely linked to the Serengeti Plains community, which together formed a cluster relative to all other habitat types (including the other grasslands) except forests (Fig. 6b). That is, MSD and the Serengeti Plains were more similar to each other than either is to any other location and they are differentiated from the rest of the locations (extant and fossil).

Mesowear analysis of ungulates There was no single dominant mesowear score for specimens in the ARI assemblage. Instead, the distribution of mean mesowear scores indicated that there were taxa with very flat occlusal surfaces (= grazers; *Eurygnathohippus* spp.) along with taxa that had high dental relief and sharp cusps (= browsers; Tragelaphini, Giraffidae; see Fig. 7 and Table 2).

The MSD assemblage was dominated by specimens with low mesowear scores (52% for score 0 and 26% for score 1), which indicates a significant presence of browsing taxa in the dental assemblage. There were several instances where bovid specimens belonging to the same tribes had different mean mesowear scores between the

ARI and MSD assemblages (Fig. 7). For the antilopini specimens, this is likely due to small sample sizes for the taxon (ARI $n = 3$, MSD $n = 1$), but this does not explain the difference in the aepycerotini specimens (ARI $n = 27$, MSD $n = 20$). On average, aepycerotins from ARI have a higher grazing signal (mesowear mean score = 1.41) than do specimens from MSD (mesowear mean score = 0.30). Aepycerotins with low mesowear scores may appear to be driving the analysis toward dominance by browsers, probably due to their high representation in the MSD assemblage. However, the MSD Alcelaphini, Bovini, and Tragelaphini mesowear scores are also relatively lower.

Ecomorphology of Bovidae For the astragalus, there was a significant decrease in Pagel's λ from the raw measurements, where most variables were either $\lambda = 1$ or close to it, to the MSV, where $\lambda = 0$ for many variables (Table 3). Further, all regressions of Mosimann Shape Variables (MSV) and body weight were significant minimally at $p = 0.05$ and most at $p < 0.0001$, and R^2 values dropped markedly from the raw to MSV analyses (Table 4). Clearly there is a strong phylogenetic signal in these data, however, by adjusting the raw measurements by size, much of that signal is eliminated.

The influence of size is evident when the CVA of the raw data is compared to the CVA of the MSVs (Table 4). While the first Canonical Variate (CV) of both analyses summarized just over half of the sample variation, the R^2 of the regression for body weight versus raw measurements was much higher than the R^2 for body weight versus MSV ($R^2 = 0.5528$ and 0.2739 respectively). This suggests that while there is still a relationship between size and shape in the MSVs, the relationship is weaker than for raw data. For this reason and since the MSVs have much lower phylogenetic signals, MSVs will be used in all subsequent astragalus analyses.

Permutation tests demonstrate that all habitat group centroids (using the full set of measurements from extant specimens) are significantly different from each other at $p < 0.0001$ (Table 5). However, it was not always possible to collect all eight astragalus measurements (see Table 3) on every fossil specimen due to breakage; thus, several CVAs were computed using different combinations of the variables to accommodate broken specimens. In total, seven different analyses were run with six to eight of the original variables, for which the correct reclassification rates ranged from 69.74% to 76.32% (resubstitution) and 62.43% to 66% (cross-validation); see Table 6. Since some specimens were damaged and hence lacked certain dimensions, they could only be evaluated with some of the CVAs. For example, specimen ARI-VP-1/369 lacked measurements lateral length (LL) and proximal thickness (TP) (see Table 3; DeGusta and Vrba, 2003 for definitions of variables), thus, this specimen had to be excluded from any analysis that included those measurements. Many specimens were included in seven separate CVAs, though some were only represented in a single CVA (see Table 7). The habitat assigned to each fossil specimen was the most frequent habitat assignment from all analyses. Though there were many more specimens available from ARI than MSD, the proportions of specimens assigned to the habitat types were similar between the two localities. In both collection areas, specimens assigned to the intermediate habitat categories were dominant, though there are specimens from across all four habitat types.

While the open and forest specimens were somewhat differentiated using the Habitat Score (Fig. 8b), there was still overlap and the intermediate habitat groups (Light and Heavy cover) did not fall along the continuum in order of vegetative density (Heavy and Light are reversed). The fossil specimens falling to the extreme negative end of the

scale were the very small specimens that likely belong to Neotragini (e.g., ARI-VP-1/365). The rest of the specimens fell into the intermediate zone of the habitat score and away from the Open extreme end of the habitat spectrum.

For the intermediate phalanx, Pagel's λ decreased slightly from the raw measurements to the MSVs, it still remained > 0.7 for all measurements after the adjustment, except for two (Proximal-lateral height and Proximal-medial height), which decreased markedly (Table 8). Reclassification rates for the intermediate phalanx were not improved with the use of MSVs (Table 9), suggesting that its morphology is highly related to body size (Table 10). This relationship can be seen in the distribution of specimens along the Habitat Score (Fig. 8c), which closely mirrors that of the body weight distribution (Fig. 8a). Further, habitat centroids were generally less differentiated in the permutation tests using MSVs than raw data (Table 5), though the distinctions did increase in the Forest versus Open and Light Cover versus Open pair-wise tests. Because there was little change in Pagel's λ between raw measurements and MSVs and because reclassification rates dropped significantly with the MSVs, raw measurements were used for all subsequent analyses.

There were only four intermediate phalanges complete enough to be included in this analysis, and all are from ARI (Table 11). Two of these were very strongly associated with the Heavy cover group (see Fig. 8c and posterior probabilities of group membership in Table 11). The other two phalanges were assigned one each to Forest and Light cover. In the Habitat Score analysis, the four ARI specimens were found at the end of the CV that had much overlap between all habitat types except Open.

Like the phylogenetic analysis for the astragalus (but unlike that of the intermediate phalanx), the distal phalanx raw measurements had medium (0.4–0.6) to very high (0.8–1) λ values (Table 12), and as with the astragalar analysis, Pagel's λ dropped significantly when the MSVs were used ($\lambda = 0.0$ –0.3). Thus, MSVs were used in the final analyses of the distal phalanx as a proxy for habitat.

While the elimination of *Tragelaphus oryx* and *T. spekii* from the training distal phalanx dataset resulted in higher reclassification rates than reported by DeGusta & Vrba (2003) transformation of the distal phalanx data into MSVs incurred a loss of discriminatory power due to the strong association of morphology with body size (see Table 13). Even with the loss of classificatory power, the cross-validation results for the CVA with the two taxa removed were still relatively good (61.6% mean correct reclassification with resubstitution and 58.7% with cross-validation; Table 14) and their robusticity was supported by the permutation tests (Table 5), which show all habitat group centroids to be different at $p < 0.0001$. All fossil specimens except one are assigned to the Light cover category, while the other is assigned to the Forest habitat group (Table 15). Using the Habitat Score algorithm, the extant specimens formed a continuum from more open to more closed habitats (Fig. 8d) and the fossil distribution tended to be predominantly toward the more open habitat types along this continuum.

The influence of body size and phylogeny Body size is known to have a large influence on morphology (Falsetti et al., 1993; Jungers et al., 1995). Klein et al. (2010) argued that size (length) is the only 'conspicuous' difference in shape among bovid metapodials and astragali and that taxonomy (or at least species identification) is more important than any

habitat-related morphology. Recent studies (Barr, 2014; Barr and Scott, 2014) demonstrated that bovid astragali are useful proxies for locomotion in different habitats, even after body size is taken into account and measurements with low phylogenetic signals are utilized. This was the approach taken in this study. It is intriguing that adjusting for size (that is, using MSVs) in both the astragalus and distal phalanx analyses greatly reduced the phylogenetic signals for those datasets, while the same was not true for the intermediate phalanx. This may be an indicator that the morphologies of the astragalus and distal phalanx are more tightly linked to locomotor adaptations, while the intermediate phalanx is more phylogenetically conservative.

It has been shown that open-adapted bovids that depend on speed as their predator-escape behavior have proximodistally short astragali with a greater angular excursion to increase speed and stride length, large joint surfaces to resist ground-reaction forces (Barr, 2014), anterioposteriorly deep distal medial condyles to increase running velocity, and a more deeply notched superior condyle to provide great joint stability (Plummer et al., 2015), though Barr (2014) found that the latter hypothesis was not supported in his study. There are clearly functional aspects related to astragalar morphology and those functional signals remain even when body size is taken into account. Thus, astragalus morphology is a good proxy for locomotion in different habitats.

The case is similar for the distal phalanx. Köhler (1993) has shown that artiodactyls that move across difficult terrain splay their distal phalanges to increase stability and traction; the hooves act as a break for slippage. Further, artiodactyls in habitats with moist substrates have thin and tapered phalanges to increase size but not

surface area of substrate contact surface (Köhler, 1993; Curran, 2012). As with the astragalus, the functional signal in the distal phalanx is stronger than the phylogenetic signal, which is why it is a good proxy for locomotion across different substrates.

The situation is quite different for the intermediate phalanx. Scott (1985) found that bovid limbs, especially the more distal elements, are elongate in cursorial bovids. Though the intermediate phalanx was not part of her study, perhaps elongation also occurs in this element in cursorial taxa. Thus, once length was removed (in the MSVs), the functional signal of the intermediate phalanx becomes minimal. In general, despite differences in length, intermediate phalanx morphology appears to be relatively conservative morphologically.

Discussion

This study provides the first multi-proxy analysis of the paleoecology of two major and well-dated vertebrate fossil collection areas, ARI and MSD, within the WORMIL paleontological site. Habitat reconstructions varied between different proxies and differed between the two collection areas. However, understanding the significance of these differences requires a closer look at what they mean within the overall context of other penecontemporaneous sites where similar proxies have been used to reconstruct paleoecology. Such inter-site comparisons bring about a discussion of the merits (and challenges) inherent in a multi-proxy analysis.

Arablee Issie (ARI)

While the five proxies used here did not provide exactly the same results for ARI, they are relatively close to each other and point to a heterogeneous paleoenvironment that was relatively open, though with closed vegetation available. In the community analysis, ARI was placed closest to modern shrublands. In shrublands, trees account for less than 10% of total vegetation and are dominated by grasses and plants more than 10 cm in height (Reed, 1998). Grazers were found to be slightly more abundant in the ARI assemblage than other dietary feeding categories in the analysis of specimen mesowear, however, the differences in representation of the various dietary types are not statistically significant. Specimens with wear associated with fruit or leaf browsing are evenly represented, each with approximately a quarter of the assemblage, though mixed feeders are slightly less frequent. *Aepyceros* appears to have been quite plastic in its dietary behavior, as has been shown in extant impalas (Sponheimer et al., 2003). Specimens attributed to *Aepyceros* demonstrate all wear stages except the highest (grazer) in fairly equal proportions. Whether the WORMIL aepycerotins actually consumed different diets (C_3 or C_4 resources) is currently unknown, though testable with future isotopic analyses. Analysis of bovid ecomorphology revealed that even though specimens from all habitat types are represented, the intermediate habitat categories were the most frequently assigned to fossil specimens. “Heavy Cover” specimens were slightly more abundant than “Light Cover” specimens.

The proxies used here indicate that ARI had a relatively open but heterogeneous environment. This reconstruction is remarkably similar to other nearly contemporaneous sites (as discussed above), which are reported to have had mosaic environments wherein open and more closed (but rarely forested) habitats are found.

655

656 *Mesgid Dora (MSD)*

657

658 When the community analysis results found here are compared to other
659 community analyses of Mid-Pliocene hominin sites, the MSD collection area from
660 Woranso-Mille appears to be very similar to the nearly contemporaneous Upper Laetoli
661 Beds (ULB) at Laetoli, Tanzania (Su, 2011). As with MSD, Su (2011) found ULB to be
662 the closest (using hierarchical clustering analysis) to the Serengeti Plains. These results
663 are somewhat surprising given the distinctive nature of the Serengeti Plains (lack of
664 mammals with arboreal and aquatic locomotion, and no browsers or frugivores). There
665 are several possible explanations for why these similarities are found. The assemblages
666 may have similar taphonomic or collection biases. The collection methods reported by Su
667 and Harrison (2008) for Laetoli are nearly identical to those used at WORMIL; that is,
668 they are surface collections of identifiable remains. This alone would not necessarily
669 produce assemblages with the same reconstructed environments because the methods
670 used at these sites are basically the same for most eastern African sites. Further, the two
671 sites have similar taphonomic histories of being time-averaged attritional depositions
672 (Musiba et al., 2010). Once again, this is likely the case for many of the eastern African
673 Pliocene sites and is unlikely to account for the similarity of the two sites to the Serengeti
674 Plains. Alternatively, the reconstructions could represent an actual ecological signal. That
675 is, both MSD and ULB were most similar to the modern Serengeti grasslands in their
676 mammal community structure. Comparison of results from other paleohabitat proxies for
677 MSD can help to resolve this.

678 Results from the mesowear analysis of MSD specimens are incongruent with the
679 community analysis; that is, the majority of specimens available for analysis had low
680 mesowear scores, indicating that they were browsers. However, mesowear analysis
681 samples a specific subset of those taxa (the ungulates) that are included in the community
682 analysis. Though the ungulates do typically account for the majority of specimens from
683 paleontological sites, community analysis is performed on presence/absence data of taxa.
684 To illustrate the importance of this distinction, consider the Aepycerotini from MSD.
685 While 89% of the aepycerotins were identified as having been browsers, their presence
686 (specifically, their dietary and locomotor ecovariates) in the community analysis is only
687 counted once. This is not to argue that one analysis is superior to another, but instead
688 brings into focus the scale of each paleohabitat proxy. Community analysis affords a
689 view of a community as a whole, while mesowear (and ecomorphology) allow us to
690 narrow the scope and focus on specific guilds of animals within that community. In the
691 case of MSD, analysis of the mesowear scores of the hoofed herbivores demonstrates that
692 they were preferentially consuming browse during their lives.

693 Narrowing the scope even further to the bovids, ecomorphology illustrates how
694 these bovids moved through their habitats. For MSD, results from analyses of the
695 astragalus and distal phalanx demonstrate that bovids using intermediate-cover habitats
696 (and especially those with lighter density) were most frequent in the assemblage. These
697 results appear to offer a middle-ground between the results of the community analysis
698 (open habitat-grasslands) and the mesowear analysis (more closed habitat-browsers
699 dominant). It is likely that the different proxies are picking up signals from slightly

different parts of the ecosystem and when used in concert, they increase our ability to recognize the complexity of these environments.

An additional aspect to consider in the interpretation of multiple proxies is the timeframe in which they operate. Communities and the morphology of the organisms within those communities evolve over relatively long periods of time, making the timeframe for community analysis and ecomorphology long. Mesowear, which is influenced by both the genotype of the organism and its behavior, can reflect much shorter time frames (the lifetime of the organism). Thus, the near congruence of community analysis and the ecomorphological analyses may reflect the adaptive genotype of the organisms in the study areas, while mesowear is more sensitive to their actual behavior. Analyses of dental enamel isotopes (formed while the organism is a juvenile) and microwear (accrued during the last few weeks of the organism's life) will help to clarify this (e.g. Louys et al., 2012).

Despite the close geographic proximity and stratigraphic equality of the two collection areas, there is a difference in the proportions of habitat assignments between ARI and MSD (Fig. 9, Table 16). It is unclear if this difference represents an actual difference in vegetative density as one moves south and east from ARI to MSD or if the distinction is simply due to sample size differences, though this is currently under investigation.

Our analyses demonstrate that the two WORMIL fossil collection areas studied here were each characterized by individual habitat heterogeneity and most of the proxies yielded different habitat signals for both areas. For example, evidence for more closed conditions at ARI was derived from the bovid postcranial ecomorphological analyses,

while at MSD, evidence for more closed conditions was derived from more frequent browsing mesowear signals. Nevertheless, when viewed in concert, these data suggest both collection areas were generally mosaic, which was likely shaped by the presence of a paleo-river and associated gallery forest laterally giving way to more open habitats. Vegetative density would have decreased moving away from the river and into the open habitats that supported grazers and open-adapted bovids.

This reconstruction, from one of the earliest *Australopithecus afarensis* sites, helps to provide insight to the question proposed by Behrensmeyer and Reed (2013: 42), “Did this genus initially live in forests, woodlands, or other types of closed habitats, or was it adapted to a mix of open and closed habitats from its beginnings?” The results here demonstrate the presence of early *Au. afarensis* in a heterogeneous habitat, as was found for the roughly contemporaneous sites in other parts of Ethiopia, Kenya, and Tanzania (Behrensmeyer and Reed, 2013). Even though each of these reconstructions indicates a mixture of habitats, they do fall along a spectrum from more closed/mesic to more open/arid, supporting the hypothesis that *Australopithecus* was eurytopic (Behrensmeyer and Reed, 2013). But what is the nature of that eurytopy? If *Au. anamensis* and *Au. afarensis* are a chronospecies (Kimbel et al., 2006; White et al. 2006; Haile-Selassie et al., 2010), then it appears that the earlier sites from which this lineage is derived (Kanapoi, Allia Bay, Woranso-Mille, Laetoli) were more open (Louys et al., 2015), albeit still heterogeneous than the younger sites such as Hadar, where *Au. afarensis* was abundant. Further, some hominins from Woranso-Mille were incorporating significant amounts of C₄ resources into their diet, indicating an expansion of dietary breadth (Levin et al., 2015). However, other individuals still utilized C₃ resources, suggesting that the

Woranso-Mille hominins dated to between 3.8 and 3.6 Ma were exploiting resources from across the variety of habitats that were available at the site.

The unusual abundance of cercopithecids is one of the most intriguing aspects of the WORMIL faunal assemblage; Frost et al. (2014) suggest multiple hypotheses to explain this phenomenon, particularly the unique abundance of a single primate taxon (*Theropithecus oswaldi*), including the presence of some valued resource (grasses, sleeping areas) in the area of the localities, or that the region was in a favored hunting area for predators that preferred *T. oswaldi*. Our studies here indicate that the latter hypothesis is unlikely to be the case, since there are so few indications of carnivore activity in the assemblage. Presence of favored resources is much more likely, as there would have been trees available for sleeping refuges and grasses available for consumption. Evidence of heterogeneous habitats was found at both ARI and MSD, though taphonomic analyses based on the collected fossils suggest that the two collection areas may have had different depositional environments. More cercopithecids have been collected from ARI, and these specimens tend to be more complete and with more biotic bone surface modifications than the cercopithecids from MSD.

Conclusion

The Aralee Issie and Mesgid Dora Pliocene fossil collection areas of Woranso-Mille, Ethiopia, sample a critical time period (3.8 to 3.6 Ma) in the evolution of *Au. afarensis*. Based on five analyses of paleocommunity and paleohabitats, the two WORMIL collection areas can be reconstructed as being heterogeneous in nature, likely

with dense vegetation along a river, grading into more substantial open habitats moving away from the river. This reconstruction is not unlike paleohabitats reported for other *Au. afarensis* localities in eastern Africa, indicating that this species inhabited a variety of habitats.

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Figure legends

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

Figure 2. Examples of bone surface taphonomic modifications. A) Thin coat of matrix adhering to an equid metatarsal. Note that the scores on this specimen are under the matrix, indicating that they are not recent (though some may be the result of preparatory work or other recent damage). B) *Aepyceros afarensis* right mandible displaying cracks in-filled with sediment or matrix. C) Beginning stages of dissolution on a hipparion astragalus (ARI-VP-1/128). D) Deteriorated specimen (Cercopithecidae femur; MSD-VP-2/441) showing several types of modifications (dissolution, dents, chips, scores). E) Smoothing of a partial Cercopithecidae upper canine (ARI-VP-1/793). F) Comparison of trabeculae of a recently broken specimen (top, Pantherinae femur; ARI-VP-1/132) and (bottom) a specimen with ancient breaks and trabecular smoothing and adhering matrix (*Eurygnathohippus* astragalus from superior view; MSD-VP-2/165). G) A score that is likely to be ancient in nature (MSD-VP-2/225b). Note that it crosses the crack, but there is not bone pushed into the cracks. Thus, the score was created before the cracking took place. H) A bovid proximal phalanx (ARI-VP-3/174) with scores that likely occurred recently. Score “A” cuts across “B” and, therefore, “B” was created first. I) Pits (crocodile tooth marks) on both sides of a specimen found (and left) at ARI1 in 2013 (compare to Njau, 2006; Photo VIII). J) “Root-etching” on a *Homotherium* upper canine

(MSD-VP-3/55a). K) A fossil (ARI-VP-5/5, calcaneus of a rhinoceros) with (recently living) roots invading trabecular spaces. L) Insect damage on a Felidae femur (KER-VP-1/195). M) Possible termite damage on Proboscidean specimen found (and left) in the field at ARI1 (in 2013). N) Right calcaneus of a Cercopithecidae specimen (ARI-VP-1/19) showing the eroded appearance associated with digestion. O) Rodent gnawing on an equid metatarsal (ARK-VP-2/2). P) Possible peeling on two specimens. Left: ARI-VP-1/681, cercopithecoid right humerus; Right: ARI-VP-4/23, bovid left tibia with matrix adhering to the peeled surface. All scale bars = 1 cm.

Figure 3. Enamel etching progression from an unaltered state (A: Giraffidae right P^4 , ARI-VP-694a), to partially altered states (B: Tragelaphini right M_1 or M_2 , with diffuse spots of etching; C: Bovidae left M^2 , ARI-VP-1/197, with etching emanating from a discrete location), to a complete altered state (D: Giraffidae right P^4 , ARI-VP-1/690). Scale bar = 1 cm. E. Extreme pitting on metatarsal of a canid (ARI-VP-1/692) with close-up of pitting (inset). Scale bar = 1 cm.

Figure 4. A) Percentage representation of the Bovidae tribes from the two collection areas (Aralee Issie [ARI] and Mesgid Dora [MSD]) with sample sizes indicated. B) Percentage representation of the Suidae species from the two collection areas (ARI and MSD) with sample sizes indicated.

1200 Figure 5. Correspondence analysis of modern communities with ARI (asterisk) and MSD
 1201 areas (X) localities and ecovariates for the ‘significantly different mammalian
 1202 adaptations’ (SDMA: Reed, 2008).
 1203
 1204 Figure 6. A) Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster
 1205 analysis of modern community means by habitat type and the Aralee Issie (ARI) and
 1206 Mesgid Dora (MSD) localities using ecovariates for the ‘significantly different
 1207 mammalian adaptations’ (SDMA, Reed, 2008); B) UPGMA cluster analysis of individual
 1208 modern communities and the ARI and MSD localities using the SDMA ecovariates.
 1209
 1210 Figure 7. Mesowear mean scores for extant species (left side, provided by Fortelius,
 1211 Solounias, and Rivals, 2013, pers. comm.) by diet and fossil taxa (right side, ARI = black
 1212 circles, MSD = gray squares).
 1213
 1214 Figure 8. A) Distribution of body masses (weights) for bovids (species means) in the
 1215 comparative sample. Note the position of *Tragelaphus oryx*. Data and habitat
 1216 assignments from DeGusta and Vrba (2003). B) Habitat Score analysis for the analysis of
 1217 all astragalar measurements (DeGusta and Vrba, 2005), ARI specimens = black asterisks
 1218 and MSD specimen = black X. C) Habitat Score analysis for the intermediate phalanx
 1219 specimens. ARI specimens = black asterisks. D) Habitat Score of the distal phalanx, ARI
 1220 specimens = black asterisks and MSD specimen = black X. For all plots: black horizontal
 1221 line represents the median, the box encloses the 25th and 75th percentiles, and thin vertical

1222 lines (whiskers) contain specimens in the range of up to 1.5 times the distance between
1223 the quartiles.

1224

1225 Figure 9. Summary of proportions of fossil specimens assigned to the four habitat groups
1226 in the ecomorphological analyses.

Table 1. Sample size (Number of Identified Specimens Present, or NISP) and proportions of bovid tribes (top) and suid species (bottom) from each collection location: Aralee Issie (ARI) and Mesgid Dora (MSD).

Bovidae tribe	ARI		MSD	
	NISP	%	NISP	%
Tragelaphini	37	31.9	10	12.8
Bovini	3	2.6	8	10.3
Aepycerotini	58	50.0	39	50.0
Alcelaphini	6	5.2	10	12.8
Antilopini	7	6.0	7	9.0
Neotragini	0	0.0	1	1.0
Hippotragini	3	2.6	2	2.6
Reduncini	1	0.9	1	1.3
Cephalophini	1	0.9	0	0.0
Suidae species	ARI		MSD	
	NISP	%	NISP	%
<i>Cainochoerus</i> sp.	7	10.0	0	0.0
<i>Nyanzachoerus jaegeri</i>	4	5.7	8	24.2
<i>Notochoerus euilus</i>	12	17.1	9	27.3
<i>Kolpochoerus millensis</i>	47	67.1	16	48.5

Table 2. The mesowear scoring methods used in this study (left three columns) and the results for the Aralee Issie (ARI) and Mesgid Dora (MSD) specimens by counts and percentages. For “Relief” coding, 1 = low and 2 = high. For Shape coding, 1= sharp, 2 = round, and 3 = blunt. Summary of taxa included for ARI and MSD are provided at bottom.

Relief	Shape	Score	ARI		MSD	
			Counts	%	Counts	%
1	3	3	22	25.6	7	14.0
1	1	2.5	3	3.5	0	0
1	2	2	7	8.1	4	8.10
2	2	1	27	31.4	13	26.0
2	1	0	27	31.4	26	52.0
Taxon			ARI		MSD	
			Mean score	<i>n</i>	Mean score	<i>n</i>
Aepycerotini			1.41	27	0.30	20
Alcelaphini			1.64	7	1.00	5
Antilopini			0.33	3	2.00	1
Bovidae			0.00	4	0.67	2
Bovini			0.50	2	0.75	4
Equidae			2.72	18	2.56	9
Giraffidae			0.00	2	NA	0
Hippotragini			1.33	3	NA	0
Neotragini			NA	0	0.00	1
Reduncini			NA	0	0.00	1
Tragelaphini			0.50	20	0.38	7
Totals				86		50

Table 3. Top section: Results of Phylogenetic Generalized Least Squares (PGLS) analyses Pagel's lambda (λ) of raw astragalus measurements (left) and Mosimann Shape Variables (MSV; right).

PGLS		
Measurement	λ (Raw)	λ (MSV)
Lateral length (LL)	0.714	0
Intermediate length (LI)	1	0
Medial length (LM)	1	0
Intermediate width (WI)	1	0.366
Distal width (WD)	1	0.142
Proximal thickness (TP)	1	0.556
Intermediate thickness (TI)	0.733	0
Distal thickness (TD)	0.677	0
LI/WI	0.863	

Table 4. Regressions of the untransformed (raw) univariate astragalus data on body weight mean (BWx) and the geometric mean (GM), and the MSVs (right-hand column) on BWx for comparative bovid specimens. Bottom section: Regressions of multivariate canonical variate (CV) scores of raw and MSV data on BWx, with percent of variance summarized for each CV indicated. Measurement definitions same as Table 3 and defined in DeGusta and Vrba (2003).

Univariate Regressions						
Variable	Raw v. BWx		Raw v. GM		MSV v. BWx	
	R ²	<i>p</i> -value	R ²	<i>p</i> -value	R ²	<i>p</i> -value
LL	0.8448	<0.0001	0.9937	<0.0001	0.4031	<0.0001
LI	0.8469	<0.0001	0.9871	<0.0001	0.4036	<0.0001
LM	0.8461	<0.0001	0.9924	<0.0001	0.4087	<0.0001
WI	0.8489	<0.0001	0.9631	<0.0001	0.3293	<0.0001
WD	0.865	<0.0001	0.9887	<0.0001	0.6051	<0.0001
TP	0.8495	<0.0001	0.9773	<0.0001	0.507	<0.0001
TI	0.8417	<0.0001	0.9888	<0.0001	0.3523	<0.0001
TD	0.8143	<0.0001	0.9597	<0.0001	0.2448	<0.0001
LIWI	0.0251	0.0232	0.0387	0.0026	0.5401	<0.0001
GM	0.8488	<0.0001				
Multivariate Regressions						
Variable	On Raw data			On MSV		
	% summarized	R ²	<i>p</i> -value	% summarized	R ²	<i>p</i> -value
CV1	0.5377	0.5528	<0.0001	0.5228	0.2739	<0.0001
CV2	0.3769	0.1657	<0.0001	0.3534	0.5057	<0.0001
CV3	0.0854	0.0536	<0.0001	0.1238	0.0115	0.0302

Table 5. Results of permutations tests between habitat types for astragalus, intermediate phalanx, and distal phalanx analyses. MSVs = Mosimann shape variables, raw = untransformed raw measurements, F = forest, H = heavy cover, L = light cover, O = Open.

Element	FvH	FvL	FvO	HvL	HvO	LvO
Astragalus (MSVs)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
2nd Phalanx (raw)	<0.0001	0.3017	0.0027	<0.0001	0.1117	0.006
2nd Phalanx (MSVs)	0.0004	0.9648	0.0008	<0.0001	0.9728	<0.0001
3rd Phalanx (MSVs)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table 6. Reclassification rates for the various Canonical Variates Analyses (CVAs) conducted on astragali in this study in order to include fossil specimens that are missing data.^a

Analysis	Resubstitution					Cross-validation				
	Forest	Heavy cover	Light cover	Open	Mean	Forest	Heavy cover	Light cover	Open	Mean
All variables	58.82	87.23	62.5	71.05	69.9	52.94	82.98	58.33	69.74	66.00
w/o LL	55.88	78.72	64.58	69.74	67.23	52.94	78.72	56.25	67.11	63.76
w/o LL TD	52.94	85.11	58.33	71.05	66.86	47.06	85.11	58.33	69.74	65.06
w/o LM TD	52.94	87.23	62.5	76.32	69.75	50.00	82.98	58.33	72.37	65.92
w/o TD	55.88	85.11	58.33	69.74	67.27	52.94	80.85	58.33	68.42	65.14
w/o TD TP	55.88	85.11	64.58	73.68	69.81	44.12	82.98	62.5	69.74	64.84
w/o WD TD TP	50.00	85.11	54.17	69.74	64.76	44.12	85.11	52.08	68.42	62.43
Mean	54.62	84.80	60.71	71.62	67.94	49.16	82.68	57.74	69.36	64.73

^a Left-most column specifies which variables (from DeGusta and Vrba, 2003) were removed from each CVA. Only mean correct reclassification rates for each habitat type and the CVA's overall mean correct reclassification rate are reported here.

Table 7. Assigned habitat type for each fossil astragalus specimen based on the most frequently assigned habitat in Canonical Variates Analyses (CVAs) with differing numbers of variable to accommodate broken specimens (see text for details). (Aralee Issie = ARI, Mesgid Dora = MSD).

Specimen ID	Assigned habitat	# of CVAs
ARI-VP-1/112	Heavy cover	7
AR-VP-11/115	Heavy cover	7
ARI-VP-1/271	Open	7
ARI-VP-1/301A	Heavy cover	7
ARI-VP-1/339	Light cover	7
ARI-VP-1/340	Forest	7
ARI-VP-1/344	Heavy cover	1
ARI-VP-1/365	Forest	7
ARI-VP-1/365	Forest	7
ARI-VP-1/369	Light cover	4
ARI-VP-1/371	Heavy cover	7
ARI-VP-1/373	Heavy cover	7
ARI-VP-1/427	Light cover	4
ARI-VP-1/499	Heavy cover	7
ARI-VP-1/658	Heavy cover	4
ARI-VP-1/672	Open	7
ARI-VP-1/711	Heavy cover	4
ARI-VP-1/791	Heavy cover	4
ARI-VP-3/553	Light cover	7
ARI-VP-3/616	Open	7
ARI-VP-3/63	Light cover	4
ARI-VP-3/70	Open	4
MSD-VP-2/270	Heavy cover	2
MSD-VP-2/288	Light cover	1
MSD-VP-2/290	Light cover	4
MSD-VP-2/369	Heavy cover	4
MSD-VP-2/373	Open	7
MSD-VP-2/420	Forest	1

Table 8. Results of Phylogenetic Generalized Least Squares (PGLS) analyses Pagel's lambda (λ) of raw intermediate phalanx measurements (left) and Mosimann Shape Variables (MSV; right).

PGLS		
Measurement	λ (Raw)	λ (MSV)
Superior length (LS)	0.945	0.788
Inferior length (LI)	0.881	0.711
Proximal width (WP)	1.000	0.889
Distal width (WD)	1.000	1.000
Proximal-lateral height (HL)	1.000	0.081
Proximal-medial height (HM)	1.000	0.062
Distal height (HD)	1.000	0.821

Table 9. Reclassification results of the Canonical Variates Analyses (CVA) for the extant (training) specimens of the intermediate phalanx with raw data and Mosimann Shape Variables (MSV).

Analysis	Resubstitution					Cross-validation				
	Forest	Heavy cover	Light cover	Open	Mean	Forest	Heavy cover	Light cover	Open	Mean
Raw	57.14	78.95	61.11	77.05	68.56	52.38	73.68	58.33	77.05	65.36
MSV	47.62	81.58	61.11	80.33	67.66	33.33	71.05	55.56	80.33	60.07

Table 10. Regressions of the untransformed (raw) univariate intermediate phalanx data on body weight mean (BWx) and the geometric mean (GM), and the MSVs (right-hand column) on BWx for comparative bovid specimens. Bottom section: Regressions of multivariate canonical variate (CV) scores of raw and MSV data on BWx, with percent of variance summarized for each CV indicated. Measurements definitions same as Table 8 and described in DeGusta and Vrba (2005).

Univariate Regressions						
Variable	Raw v. BWx		Raw v. GM		MSV v. BWx	
	R ²	<i>p</i> -value	R ²	<i>p</i> -value	R ²	<i>p</i> -value
LS	0.6883	<0.0001	0.9277	<0.0001	0.5672	<0.0001
LI	0.676	<0.0001	0.9166	<0.0001	0.5402	<0.0001
WP	0.8565	<0.0001	0.9715	<0.0001	0.4573	<0.0001
WD	0.8112	<0.0001	0.9244	<0.0001	0.2801	<0.0001
HL	0.7746	<0.0001	0.9306	<0.0001	0.0017	0.6144
HM	0.7543	<0.0001	0.9412	<0.0001	4.60E-06	0.9791
GM	0.8219	<0.0001				
Multivariate Regressions						
Variable	On Raw data			On MSV		
	% summarized	R ²	<i>p</i> -value	% summarized	R ²	<i>p</i> -value
CV1	0.704	0.1309	<0.0001	0.7618	0.001	0.6929
CV2	0.2793	0.6888	<0.0001	0.2165	0.5936	<0.0001
CV3	0.0167	0.0012	0.6751	0.0217	0.00008	0.9127

Table 11. Posterior probabilities of group membership for the analysis of intermediate phalanx specimens.

Specimen ID	Assigned habitat	Posterior probability
ARI-VP-1/111	Heavy cover	0.8552
ARI-VP-1/117	Heavy cover	0.9964
ARI-VP-1/763	Forest	0.6266
ARI-VP-3/427	Light cover	0.5756

Table 12. Results of Phylogenetic Generalized Least Squares (PGLS) analyses Pagel's lambda (λ) of raw distal phalanx measurements (left) and Mosimann Shape Variables (MSV; right).

PGLS		
Measurement	λ (Raw)	λ (MSV)
Superior length (LS)	0.845	0.000
Inferior length (LI)	0.874	0.012
Articular facet height (HA)	0.651	0.336
Total height (HT)	0.414	0.000
Basal width (WB)	1.000	0.277

Table 13. Regressions of the untransformed (raw) univariate distal phalanx data on body weight mean (BWx) and the geometric mean (GM), and the MSVs (right-hand column) on BWx for comparative bovid specimens. Bottom section: Regressions of multivariate canonical variate (CV) scores of raw and MSV data on BWx, with percent of variance summarized for each CV indicated. Measurement definitions same as Table 12 and defined in DeGusta and Vrba (2003).

Univariate Regressions							
Variable	Raw v. BWx		Raw v. GM			MSV v. BWx	
	R ²	<i>p</i> -value		R ²	<i>p</i> -value	R ²	<i>p</i> -value
LS	0.5477	<0.0001		0.5477	<0.0001	0.0111	0.2682
LI	0.5672	<0.0001		0.5672	<0.0001	0.0093	0.3118
HA	0.7561	<0.0001		0.7561	<0.0001	0.0173	0.1669
HT	0.7431	<0.0001		0.7431	<0.0001	0.0009	0.7553
WB	0.7272	<0.0001		0.7272	<0.0001	0.0408	0.0327
GM	0.7458	<0.0001					
Multivariate Regressions							
Variable	On Raw data			On MSV			
	% summarized	R ²	<i>p</i> -value	% summarized	R ²	<i>p</i> -value	
CV1	0.5566	0.5171	<0.0001	0.6718	0.0088	0.3247	
CV2	0.3478	0.0004	0.8404	0.2788	0.0228	0.1118	
CV3	0.0956	0.1771	<0.0001	0.0494	0.0054	0.4428	

Table 14. Correct reclassification rates for resubstitution and cross-validation for the distal phalanx without *T. oryx* and *T. spekii*, on raw measurements and on the Mosimann Shape Variables (MSVs). .

	Forest	Heavy cover	Light cover	Open	Mean
Raw data					
Resubstitution	100	71.43	80.95	63.83	79.05
Cross-validation	100	64.29	66.67	57.45	72.10
MSVs					
Resubstitution	71.43	57.14	47.62	70.21	61.60
Cross-validation	64.29	57.14	47.62	65.92	58.74

Table 15. Posterior probabilities of habitat group membership for the analysis of distal phalanx raw data without the two tragelaphine taxa for Aralee Issie (ARI) and Mesid Dora (MSD).

Specimen	Habitat	Posterior
ARI-VP-3/532	Light cover	0.8903
ARI-VP-3/515	Forest	0.6534
ARI-VP-3/538	Light cover	0.4994
MSD-VP-2/229	Light cover	0.6481

Table 16. Summary of all analyses of habitat for Aralee Issie (ARI) and Mesgid Dora (MSD).

Analysis	ARI	MSD
Community analysis	Closest to Shrubland All dietary types present	Closest to Grassland All dietary types present
Mesowear analysis	Grazers most frequent	Browsers most frequent
Astragalus ecomorphology	Heavy cover best represented	Intermediate habitats dominant
Phalanx 2 ecomorphology	All except Open present	NA
Phalanx 3 ecomorphology	Forest and Light cover present	One Light cover specimen

Figure 1

Figure 1 B&W

Figure 2

Figure 2 B&W

Figure 3

Figure 3 B&W

Figure 4

Figure 4 B&W

Figure 5

Figure 5 B&W

Figure 6

Figure 6 B&W

Figure 7

Figure 8

Figure 9