Phylogeny of early *Australopithecus*: new fossil evidence from the Woranso-Mille (central Afar, Ethiopia)

Yohannes Haile-Selassie*

Department of Physical Anthropology, The Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, OH 44106, USA

The earliest evidence of *Australopithecus* goes back to *ca* 4.2 Ma with the first recorded appearance of *Australopithecus* ‘*anamensis*’ at Kanapoi, Kenya. *Australopithecus afarensis* is well documented between 3.6 and 3.0 Ma mainly from deposits at Laetoli (Tanzania) and Hadar (Ethiopia). The phylogenetic relationship of these two ‘species’ is hypothesized as ancestor–descendant. However, the lack of fossil evidence from the time between 3.6 and 3.9 Ma has been one of its weakest points. Recent fieldwork in the Woranso-Mille study area in the Afar region of Ethiopia has yielded fossil hominids dated between 3.6 and 3.8 Ma. These new fossils play a significant role in testing the proposed relationship between *Au. anamensis* and *Au. afarensis*. The Woranso-Mille hominids (3.6–3.8 Ma) show a mosaic of primitive, predominantly *Au. anamensis*-like, and some derived (*Au. afarensis*-like) dentognathic features. Furthermore, they show that, as currently known, there are no discrete and functionally significant anatomical differences between *Au. anamensis* and *Au. afarensis*. Based on the currently available evidence, it appears that there is no compelling evidence to falsify the hypothesis of ‘chronospecies pair’ or ancestor–descendant relationship between *Au. anamensis* and *Au. afarensis*. Most importantly, however, the temporally and morphologically intermediate Woranso-Mille hominids indicate that the species names *Au. afarensis* and *Au. anamensis* do not refer to two real species, but rather to earlier and later representatives of a single phylogenetically evolving lineage. However, if retaining these two names is necessary for communication purposes, the Woranso-Mille hominids are best referred to as *Au. anamensis* based on new dentognathic evidence.

Keywords: *Australopithecus afarensis*; *Australopithecus* ‘*anamensis*’; phylogeny; Woranso-Mille; Ethiopia

1. INTRODUCTION

The genus *Australopithecus* was named in the first quarter of the twentieth century (Dart 1925) and includes at least seven species from South Africa, Tanzania, Kenya, Ethiopia, and Chad (Dart 1925; Broom 1938; Leakey 1959; Arambourg & Coppens 1968; Johanson *et al.* 1978; Brunet *et al.* 1995; Asfaw *et al.* 1999). Some workers assign three of these species (*Australopithecus boisei*, *Australopithecus aethiopicus* and *Australopithecus robustus*) to a different genus, *Paranthropus* (Broom 1938), based largely on morphological specializations related to trophic parameters (Clarke 1977; Grine 1986, 1988; Wood & Ellis 1986; Wood & Chamberlain 1987; Turner & Wood 1993). Some palaeontologists have even moved the type species of the genus, *Australopithecus africanus* into *Paranthropus* (e.g. Cela-Conde & Altaba 2002; see also Cela-Conde & Ayala 2007), leaving *Australopithecus* with only three species. Whether *Australopithecus* is a paraphyletic (Strait *et al.* 1997) or monophyletic (Tobias 1967) genus, most researchers

agree that one of its species gave rise to the genus *Homo*, possibly *Australopithecus garhi* from the Middle Awash region of Ethiopia (Asfaw *et al.* 1999; but see Strait & Grine 2004).

It was only 30 years ago that *Australopithecus afarensis* was recognized as the ‘oldest indisputable evidence of the family Hominidae’ at 3.6 Ma (Johanson *et al.* 1978; see Kimbel & Delezenne 2009 for detailed review). However, at the end of the twentieth and beginning of the twenty-first centuries, a number of new hominid taxa were recovered, some of which are twice as old (the family Hominidae is here defined following Haile-Selassie 2001 and Haile-Selassie *et al.* 2004). During the 1990s, the discovery of *Ardipithecus ramidus* (1994, Ethiopia, 4.4 Ma; White *et al.* 1994, 1995; Semaw *et al.* 2005) was followed by *Australopithecus* ‘*anamensis*’ (1995, Kenya, 3.9–4.2 Ma; Leakey *et al.* 1995, 1998; Ward *et al.* 1999, 2001). More recent fieldwork in Ethiopia, Kenya and Chad have pushed the record further into the Late Miocene with the discovery of *Ardipithecus kadabba* (Haile-Selassie 2001; Haile-Selassie *et al.* 2004, 2009), *Orrorin tugenensis* (Senut *et al.* 2001; Pickford *et al.* 2002) and *Sahelanthropus tchadensis* (Chad, 6–7 Ma; Brunet *et al.* 2002, 2005). The phylogenetic relationships among these earlier hominids remain a point of

* yhailese@cmnh.org

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contention (see Haile-Selassie *et al.* 2004, 2009, for details), and Pliocene hominid fossils are poorly sampled from the 3.6–3.9 and 4.4–5.2 Ma time intervals.

The hominid-bearing Woranso-Mille palaeontological study area (WORMIL) has been explored since its discovery in 2004 (Haile-Selassie *et al.* 2007). The fossiliferous deposits in the north and northwestern parts of the study area sample the period between 3.4 and 3.8 Ma (Deino *et al.* 2010), a time frame poorly known in the hominid fossil record (Kimbel *et al.* 2006). These ages were determined using $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric dating method (Deino *et al.* 2010). The study area has thus far yielded about 90 fossil hominid specimens, mostly from the time period between 3.6 and 3.8 Ma. Additional hominid specimens were collected from slightly younger (3.4–3.6 Ma) deposits. Most of these specimens represent isolated teeth and partial jaws, although they also include a 3.58 Ma partial skeleton of *Au. afarensis* (Haile-Selassie *et al.* 2010a) and additional fragmentary postcranial remains. Moreover, a total of 4300 fossil specimens of diverse vertebrate taxa have been collected thus far, representing more than 25 mammalian genera and a number of new species.

Here, a brief summary of early *Australopithecus* to which the WORMIL hominids belong is presented, followed by a brief description of the new hominids and their phylogenetic relationships. Finally, a discussion is presented on the evolutionary tempo and mode of early *Australopithecus* and the proposed ancestor–descendant relationship between *Au. anamensis* and *Au. afarensis* in light of the new fossil evidence from Woranso-Mille.

2. EARLY AUSTRALOPITHECUS

The origin of the genus *Australopithecus* remained elusive until new discoveries from the Early Pliocene in eastern Africa began to shed some light (White *et al.* 2006). Based on the currently available fossil evidence, *Au. anamensis* is the earliest species of the genus. It is documented from deposits in Kenya and Ethiopia, dated between 4.2 and 3.9 Ma (Leakey *et al.* 1995, 1998; Ward *et al.* 2001; White *et al.* 2006).

The integrity and amount of variation in *Au. afarensis* have been rigorously debated since its naming in the 1970s (Johanson *et al.* 1978, 1982; Johanson & White 1979; White *et al.* 1981, 1993, 2000; Kimbel *et al.* 1985, 2004; White 1985; Kimbel & White 1988; Lockwood *et al.* 2000; Reno *et al.* 2003, 2005; Plavkan *et al.* 2005, among others). Some argued that the species hypodigm pooled from two asynchronous and geographically disparate areas, Laetoli (Tanzania; Leakey 1987; Leakey *et al.* 1987) and Hadar (Ethiopia), represents more than one species (Leakey & Walker 1980; Olson 1981, 1985; Senut & Tardieu 1985; Zihlman 1985). However, the discovery of more specimens at Hadar since the early 1990s and detailed analyses of the pooled hypodigm have demonstrated that the amount of variation in *Au. afarensis* does not significantly exceed what is observed in a single species of extant taxa (Kimbel *et al.* 1985, 2004; Kimbel & White 1988; Lockwood *et al.* 2000; White *et al.* 2000).

Further analysis of *Au. afarensis* mandibles and teeth also indicated that there was a directional trend toward an increase in mandibular size through time, but not in the size of the teeth, contributing to the larger range of variation seen in the species (Lockwood *et al.* 2000; see also Kimbel *et al.* 2004). The postcranial anatomy of *Au. afarensis* is inferred to indicate obligate bipedality (for example, Lovejoy 1975, 1978; White 1980a,b; Latimer 1983, 1991; Latimer & Lovejoy 1989; Kramer 1999), although some argued that it was partly arboreal (for example, Stern & Susman 1981, 1983, 1991; Jungers & Stern 1983; Stern 2000). The Laetoli footprints, however, yield incontrovertible evidence that *Au. afarensis* was fully bipedal (for example, White & Suwa 1987).

3. THE WORANSO-MILLE FOSSIL HOMINIDS

A total of 55 hominid dentognathic (mostly isolated teeth) and fragmentary postcranial elements have been recovered from the Am-Ado (AMA), Aralee Issie (ARI), Mesgid Dora (MSD) and Makah Mera (MKM) collection areas of the WORMIL study area (figure 1). Their age has been chronometrically constrained to between 3.57 and 3.82 Ma (Deino *et al.* 2009). The associated faunal assemblage is dominated largely by cercopithecids, tragelaphines and aepycerotines, among others, indicating a more closed habitat with riverine gallery forest and abundant water.

(a) Mandibles

Two mandibular fragments were recovered from the MSD collection area. MSD-VP-5/16 is a well-preserved left mandible with M_{1-2} , anteriorly broken at the I_2 level. It was found during the 2006 field season from Mesgid Dora locality 5. Posteriorly, the preserved corpus extends as far as slightly posterior to the M_3 level. The preserved corpus base is intact. The entire ascending ramus is missing. MSD-VP-5/50 is a left mandible with P_3 – M_3 found during the 2009 field season from Mesgid Dora locality 5. This specimen is anteriorly broken lateral to the midline. Posteriorly, part of the ascending ramus is preserved although some parts of its base below the ascending ramus are missing (figure 2).

MSD-VP-5/16 probably belongs to a female individual largely owing to its small corpus size that is comparable to A.L. 128-23 (White & Johanson 1982). However, the molars (M_{1-2}) in MSD-VP-5/16 are larger relative to the corpus dimensions. *Australopithecus afarensis*-like mandibular features of MSD-VP-5/16 include corpus robusticity (corpus breadth at mid- M_1 /corpus height at mid- $M_1 \times 100$) of 62.5, the presence of a lateral corpus hollow, and a more vertical mandibular symphysis, as judged from the preserved part of the anterior corpus (Haile-Selassie *et al.* 2010b). The mandible's greatest anterior breadth, however, is at the canine level, more like *Au. anamensis* (Leakey *et al.* 1995; Ward *et al.* 1999; see Haile-Selassie *et al.* 2010b for details).

The anterior corpus of MSD-VP-5/50 is morphologically more similar to *Au. anamensis* mandibles

Figure 1. (a) Satellite imagery showing the location of hominid collection areas in the Woranso-Mille palaeontological site. (b) Stratigraphic sections showing the provenance and age of fossiliferous horizons.

than to those of *Au. afarensis* (figure 3). The corpus of MSD-VP-5/50 is very deep and transversely narrow at the M_1 and other molar levels. Its breadth at M_1 (20.7 mm) is within the range seen in *Au. afarensis* (Kimbel *et al.* 2004) and *Au. anamensis* (Ward *et al.* 2001), whereas its height at the same position (44.6 mm) and its robusticity index (46.6) are slightly outside the range documented for both groups. *Australopithecus anamensis* mandibles have a mean robusticity index (53.6, $n = 3$; Ward *et al.* 2001) slightly lower than that of *Au. afarensis* (57.5, $n = 19$; Kimbel *et al.* 2004). A.L. 277-1 approaches MSD-VP-5/50 in terms of its robusticity index (48.4; Kimbel *et al.* 2004) although the latter is absolutely deeper and wider.

The inferomedial sweep of the corpus contour at the C-P₄ level seen in MSD-VP-5/50 is comparable to *Au. anamensis* mandibles (figure 3). This lateral corpus profile has been described as uniquely characteristic of *Au. anamensis* mandibles such as

KNM-KP 29281, KNM-KP 29287, KNM-KP 31713, and KNM-ER 20432 from Kanapoi and Allia Bay (Ward *et al.* 2001; Kimbel *et al.* 2006). *Australopithecus afarensis* mandibles are different in having an almost vertical contour descending as far as the corpus base. However, LH 4 is an exception to this general characteristic of most *Au. afarensis* mandibles, showing a slight inferomedial sweep at the C-P₃ level (Kimbel *et al.* 2006). The ascending ramus root of MSD-VP-5/50 is positioned more posteriorly (mid- M_2) with most of the M_3 buccal face visible laterally. However, the canine does not appear to be aligned in the longitudinal axis of the postcanine tooth row, although it is seen in the other, much smaller mandible (MSD-VP-5/16). In *Au. afarensis* mandibles, the ascending ramus root is usually at M_1 . The overall morphology of MSD-VP-5/50, particularly the anterior lateral corpus profile, is intermediate between Kanapoi mandibles and LH 4 and serves, together with KNM-ER 20432, as a

Figure 2. Occlusal, medial and lateral views of mandibular specimens from Woranso-Mille dated at 3.7–3.8 Ma. (a) MSD-VP-5/16, left mandible with M_{1-2} . (b) MSD-VP-5/50, left mandible with P_3 – M_3 . Note the size variation between the two mandibles and the deep corpus in (b). Scale bar, 5 cm.

Figure 3. Cross sections of *Au. anamensis* and *Au. afarensis* mandibular corpora at distal P_3 . (a) KNM-KP 29281; (b) KNM-ER 20432; (c) MSD-VP-5/50; (d) A.L. 400-1a (right side reversed); (e) A.L. 277-1 and (f) A.L. 417-1a. Modified from Kimbel *et al.* (2006). Cross-section of MSD-VP-5/50 was acquired following the methods described by Kimbel *et al.* (2006). Scale bar, 2 cm.

good transition from Kanapoi to Laetoli/Hadar lateral mandibular corpus profiles (figure 3).

These WORMIL mandibles show a mosaic of features shared with both *Au. anamensis* and *Au. afarensis*. Some of

the mandibular features shared with *Au. anamensis* are the maximum anterior symphyseal breadth being at the canine (for example, MSD-VP-5/16; Ward *et al.* 1999) and the more posterior position of the ascending ramus

Figure 4. Dental remains from Woranso-Mille. (a) Occlusal (top row) and mesial (bottom row) views of ARI-VP-3/80g (LM²), ARI-VP-1/90 (LM³), ARI-VP-3/80d (LM₂) and ARI-VP-1/462 (LM₁). These molars show the lingual slope on upper and buccal slope on lower molars like *Au. anamensis*. (b) MSD-VP-5/50, ARI-VP-3/80a and ARI-VP-2/95, P₃s from the Woranso-Mille showing variation in P₃ occlusal crown morphology. (c) Comparison of lower deciduous canine root length relative to crown height. KNM-KP 34 725 (*Au. anamensis*), ARI-VP-1/190 (Woranso-Mille) and A.L. 333-35 (*Au. afarensis*). Like *Au. anamensis*, the Woranso-Mille specimen has longer root relative to the crown height compared with *Au. afarensis*. Image of the *Au. anamensis* specimen was obtained from Carol Ward and A.L. 333-35 was made from cast.

root (MSD-VP-5/50, see figure 2; Haile-Selassie *et al.* 2010b), which is also shared with the earlier *Ar. ramidus* (Suwa *et al.* 2009; White *et al.* 2009). The mandibular features shared with *Au. afarensis* include the presence of an incipient lateral corpus hollow (for example, MSD-VP-5/16), usually described as characteristic of this species. Judged from the preserved parts of MSD-VP-5/16, the mandibular symphysis does not show the more posteroinferiorly retreating condition seen in *Au. anamensis* (Ward *et al.* 2001; Kimbel *et al.* 2006). However, MSD-VP-5/50 shows a more receding symphysis as seen from the transverse cross-section at the P₃ level.

(b) Dentition

In terms of the dentition, the upper and lower molars have occlusally tapering lingual and buccal faces, respectively, a trait documented in *Au. anamensis* (Ward *et al.* 2001). As in *Au. anamensis*, the upper molars, particularly M²⁻³, taper distally (figure 4a). The deciduous lower canine (ARI-VP-1/190) is similar in its crown morphology to *Au. afarensis* specimens such as A.L. 333-35, LH 2, and DIK-1-1 from Hadar, Laetoli and Dikika, respectively (White 1977, 1980a,b; Johanson *et al.* 1982; Alemseged *et al.* 2006). However, ARI-VP-1/190 has a relatively much longer root and less lingual relief as seen in *Au. anamensis* (figure 4c). The known P₃s from WORMIL show both *Au. afarensis*-like (ARI-VP-2/95) and *Au. anamensis*-like (ARI-VP-3/80, MSD-VP-5/50) occlusal morphology and document variation in the morphology of the P₃ (figure 4b). The P₃ occlusal morphology of MSD-VP-5/50 is more similar to KNM-ER 20 432 from Allia Bay than to KNM-KP 27 286 from Kanapoi in its mesiodistally elongated crown and asymmetry, clearly defined mesial marginal ridge, and larger posterior fovea. The lingual cusp is also hardly developed.

Enamel thickness, as measured on naturally fractured WORMIL teeth, is also within the range seen for both hypodigms. The postcranial elements are not as informative owing to their fragmentary nature. The dentognathic morphological observations,

however, indicate that the WORMIL specimens are morphologically intermediate between *Au. anamensis* and *Au. afarensis*.

4. PHYLOGENETIC RELATIONSHIPS

Ardipithecus ramidus from the Middle Awash and Gona study areas in Ethiopia, dated between 4.3 and 4.6 Ma (WoldeGabriel *et al.* 1994; Semaw *et al.* 2005), is considered to be the possible ancestor of *Au. anamensis* although other possibilities cannot be ruled out (White *et al.* 2006, 2009). Recent studies on a larger sample of *Ar. ramidus* material, including a partial skeleton, from the Middle Awash show that *Ar. ramidus* and *Au. anamensis* occupied different 'adaptive plateaus' (White *et al.* 2009). Although further investigation is imperative to understand the full implication of these adaptive differences, the ancestor–descendant relationship between these two species remains one of the alternatives given the currently available fossil evidence.

The temporal distribution and apparent, but limited, morphological differences between the hypodigms currently divided into *Au. afarensis* and *Au. anamensis* justified the retention of both species names as a chronospecies pair (Leakey *et al.* 1995, 1998; Ward *et al.* 2001; Kimbel *et al.* 2006; White *et al.* 2006). However, the discovery of the WORMIL specimens dated at 3.7–3.8 Ma minimizes the differences between the inferred chronospecies pair and suggests that it represents a single lineage and should probably be referred to by a single species name in order to avoid taxonomic confusion. *Australopithecus anamensis* is interpreted to have been an obligate biped (Leakey *et al.* 1995, 1998; Ward *et al.* 2001), unlike *Ar. ramidus*, which was a facultative biped with substantial arboreal adaptation (Lovejoy *et al.* 2009). *Australopithecus anamensis* shares a number of derived dental characters and locomotor adaptations with *Au. afarensis*, and both are grouped in the same 'adaptive plateau' (White *et al.* 2009). The presence of temporal and spatial discontinuity in their fossil record, rather than observed morphological

differences, was probably one of the apparent reasons to distinguish them at the species level. The discovery of the WORMIL hominids not only fills some part of the spatial and temporal discontinuity, but also reduces the inferred anatomical differences between the two populations.

The phylogenetic relationship between the two time-successive ‘species’ of *Au. anamensis* (3.9–4.2 Ma) and *Au. afarensis* (3.0–3.6 Ma) has been addressed in detail using various analytical methods (Leakey *et al.* 1995, 1998; Ward *et al.* 1999, 2001; White 2002; Kimbel *et al.* 2006; White *et al.* 2006). *Australopithecus anamensis* is suggested to have rapidly evolved from its putative ancestor *Ar. ramidus* (White *et al.* 2006). However, this remains to be more rigorously tested, particularly in light of the new revelations about *Ar. ramidus* (e.g. Lovejoy *et al.* 2009; Suwa *et al.* 2009; White *et al.* 2009). *Australopithecus anamensis* and *Au. afarensis* are considered by most workers as a chronospecies pair sampling a single phyletically evolving lineage, although other alternatives have also been entertained (Kimbel *et al.* 2006; White *et al.* 2006). Most analytical methods have, thus far, failed to falsify the proposed ancestor–descendant relationship, or unequivocally recognize them as two distinct lineages.

The Woranso-Mille hominids dated at 3.6–3.8 Ma are morphometrically intermediate between *Au. afarensis* and *Au. anamensis*. They represent the best fossil hominid sample that clearly bridges the temporal and morphological gaps between *Au. afarensis* and *Au. anamensis*, lending strong support to the suggestion that they represent a chronospecies pair (White *et al.* 2009). Therefore, every available line of evidence suggests that *Au. anamensis* represents an earlier deme of *Au. afarensis*. Their separation at a species level was clearly an artefact of the lack of adequate fossils from the time between Allia Bay (3.9 Ma) and Laetoli (3.6 Ma) than the presence of discrete and functionally significant anatomical characters distinguishing the two groups.

Cladistic analysis on four site-samples of *Au. afarensis* and *Au. anamensis* (Hadar, Laetoli, Allia Bay and Kanapoi) demonstrated that the *Au. anamensis*–*Au. afarensis* lineage is paraphyletic because the younger *Au. afarensis* sample from Hadar appears to be the sister taxon of *Au. africanus* (Kimbel *et al.* 2006, p. 145). Moreover, even *Au. afarensis* is paraphyletic since the Laetoli sample shares some dentognathic features exclusively with *Au. anamensis*. The Woranso-Mille specimens, regardless to which group they are assigned, further demonstrate the paraphyly of not only the entire *Au. afarensis*–*Au. anamensis* lineage, but also that of *Au. anamensis*. Kimbel *et al.* (2006, p. 146) suggested that the two most preferred solutions for the taxonomic conundrum related to *Au. afarensis* and *Au. anamensis* are the ‘recognition of a single evolutionary species or the maintenance of the status quo...’. The evidence from Woranso-Mille strongly supports the former as the most parsimonious solution and *Au. africanus* as the sister taxon of this species.

Haile-Selassie *et al.* (2010b) avoided specific assignment of the Woranso-Mille specimens to either group. Based on the dentognathic description and comparison, however, they showed that the Woranso-Mille hominids shared more dental characters with *Au.*

anamensis than with *Au. afarensis*. New discoveries from the 2009 field season support this observation by yielding critical information on the anterior mandibular morphology of the Woranso-Mille hominids. The transverse profile of MSD-VP-5/50 at posterior P₃ shows that the lateral mandibular corpus shape is more like those from Allia Bay and Kanapoi than like those of *Au. afarensis* (figure 3) shown by Kimbel *et al.* (2006). If the Woranso-Mille hominids dated between 3.7 and 3.8 Ma had to be assigned to one of these two arbitrary groups, they could be put into the earlier *Au. anamensis* with some confidence. The temporal range of *Au. anamensis* would then be extended to between 3.7 and 4.2 Ma. It should also be noted that *Au. anamensis* from Asa Issie is bracketed between 3.77 and 4.2 Ma (White *et al.* 2006). Although this does not result in any changes in terms of how these two groups are related to each other, it would mean that specimens such as the Belohdeli frontal (BEL-VP-1/1; Asfaw 1987), the hominid specimens from Fejej (Fleagle *et al.* 1991; Kappelman *et al.* 1996; Grine *et al.* 2006a,b), and teeth and femur fragment from Galili (Haile-Selassie & Asfaw 2000; Macchiarelli *et al.* 2004; Viola *et al.* 2008) should be recognized as *Au. anamensis*. However, this assignment would simply be based on their geological age although it gives great valence to the idea of *Au. anamensis*–*Au. afarensis* being a chronospecies pair.

5. DISCUSSION

The 3.7–3.8 Ma WORMIL hominid specimens share a number of dental characters with both *Au. afarensis* and *Au. anamensis*. They are temporally and morphologically intermediate between the two groups and suggest that *Au. anamensis* and *Au. afarensis* do not warrant an evolutionarily meaningful distinction at the species level. The Woranso-Mille hominids clearly connect *Au. anamensis* and *Au. afarensis* regardless of which end of the continuum they belong to, and suggest that the recognition of two different species names for two temporally and morphologically continuous populations of a single phyletically evolving species is confusing and unwarranted. Following the currently available classification, the dental and mandibular morphological similarities of the WORMIL specimens (dated at 3.7–3.8 Ma) with *Au. anamensis* outweigh their similarity with *Au. afarensis sensu stricto* (i.e. specimens from Hadar and Laetoli). If the two names have to be retained, mainly for communication purposes as some researchers suggest, the available but limited evidence supports assignment of the WORMIL hominids to *Au. anamensis*, extending the temporal range of the latter group to 3.7 Ma.

There is considerable size range in the relatively small WORMIL upper ($n = 9$) and lower ($n = 19$) molar samples although they fall within the range of both *Au. anamensis* and *Au. afarensis*. However, they also represent some of the largest molars in the entire *Au. anamensis*/*Au. afarensis* sample, particularly the M³s (for example, ARI-VP-1/90, ARI-VP-1/215). Lockwood *et al.* (2000) observed a statistically significant temporal trend towards an increase in M³ crown size (mainly by mesiodistal elongation) in *Au. afarensis*,

although they noted that outliers (Lockwood *et al.* 2000) and small sample sizes (White 1985) from specific time periods could bias this observation. At the same time, an increase in M^3 crown area might have been the general trend in the *Au. anamensis*–*Au. afarensis* lineage, as seen in the shift from molars with sloping buccal (lowers) and lingual (uppers) faces in *Au. anamensis* to molars with more vertical lingual and buccal faces in *Au. afarensis*, which would have resulted in an increase in overall crown occlusal surface. This increase in occlusal area would have resulted in larger chewing surface, which could be linked to an increase in trophic capability in using a wide variety of resources (Teaford & Ungar 2000; Grine *et al.* 2006a,b), ranging from soft fruits and leaves to harder and brittle fallback foods (Ungar 2004; Grine *et al.* 2006b). Although *Au. afarensis* was probably better fitted (largely owing to its larger molars and thicker enamel, among others) for a variety of food items including fallback resources, dental microwear analyses on a limited number of teeth fails to show differences in the dietary preferences of *Au. afarensis* and *Au. anamensis* (Grine *et al.* 2006a,b). However, this remains to be tested with a larger sample of *Au. anamensis*.

6. CONCLUSION

Palaeontological fieldwork at a newly discovered fossiliferous area in the central Afar region of Ethiopia has yielded new hominid fossil remains dated between 3.4 and 3.8 Ma. The temporal placement of these fossils renders them crucial to test some of the outstanding human evolutionary hypotheses such as the phylogenetic relationships between *Ar. ramidus* and *Au. anamensis*, and the issue of ancestor–descendant relationship between *Au. anamensis* and *Au. afarensis*. The 3.7–3.8 Ma hominid specimens from the Woranso-Mille clearly show that they are morphologically intermediate between *Au. anamensis* and *Au. afarensis* and their dental measurements overlap with both groups, lending support to the hypothesis of *Au. anamensis*/*Au. afarensis* being a chronospecies pair representing a single lineage. Regardless of what part of this ‘pair’ the Woranso-Mille hominids are assigned to, however, they document the best example of the presence of transitional populations in a single phylogenetically evolving hominid lineage.

Slightly younger fossil hominids (3.0–3.6 Ma) not described here promise to shed some light on current debates related to early middle Pliocene hominid diversity. The Woranso-Mille palaeontological site has opened a new window into the deep human past and promises to yield more fossils relevant to answering crucial questions in human evolutionary studies, including the presence or absence of early hominid diversity during the middle Pliocene.

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