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 phyletically 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 africanaus* 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 & Delezene 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*

One contribution of 14 to a Discussion Meeting Issue ‘The first four million years of human evolution’.

This journal is © 2010 The Royal Society
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 M1,2 anteriorly broken at the I2 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 M2 level. The preserved corpus base is intact. The entire ascending ramus is missing. MSD-VP-5/50 is a left mandible with P1–M1 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 (M1–2) 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-M1/corpus height at mid-M1 × 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...
than to those of *Au. afarensis* (figure 3). The corpus of MSD-VP-5/50 is very deep and transversely narrow at the M1 and other molar levels. Its breadth at M1 (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-M2) with most of the M3 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 M1. 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...
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 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 M₁–₂. (b) MSD-VP-5/50, left mandible with P₃–M₃. 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 P₃. (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.
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 M²₋⁴, 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. PHYLGENETIC 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 ancestors–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 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 phylogenetically 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 hominin 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; Macchiarella 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 phylogenetically 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 M3’s (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 M₃ 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 fossils 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 hominin 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 hominin diversity during the middle Pliocene.

I thank the Authority for Research and Conservation of Cultural Heritage and the National Museum of Ethiopia of the Ministry of Culture and Tourism for field and laboratory permissions and facilities, the Afar Regional Government, its local administrative units, and the Afar people of Mille District, for facilitating and directly participating in my research endeavours. I thank all of the field participants who helped find the fossils and many others for discussion and access to their unpublished data. I thank Stephanie Melillo for assistance with figures and Liz Russell for photography. Finally, discussions with Bill Kimbel, Denise Su, Gen Suwa, Carol Ward and Tim White significantly improved the content of this manuscript. The WORMIL project was financially supported by National Science Foundation (NSF; grant nos 0234320, 0542037), The Leakey Foundation, Wenner-Gren Foundation, and National Geographic Society.

REFERENCES


Clarke, R. J. 1977 The cranium of the Swartkrans hominid SK 847 and its relevance to human origins. PhD disser-tation, University of the Witwatersrand, Johannesburg.


