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Late Miocene hominids from the Middle Awash, Ethiopia

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Molecular studies suggest that the lineages leading to humans and chimpanzees diverged approximately 6.5–5.5 million years (Myr) ago, in the Late Miocene[1-3]. Hominid fossils from this interval, however, are fragmentary and of uncertain phylogenetic status, age, or both[4-6]. Here I report new hominid specimens from the Middle Awash area of Ethiopia that date to 5.2–5.8 Myr and are associated with a wooded palaeoenvironment[7]. These Late Miocene fossils are assigned to the hominid genus *Ardipithecus* and represent the earliest definitive evidence of the hominid clade. Derived dental characters are shared exclusively with all younger hominids. This indicates that the fossils probably represent a hominid taxon that postdated the divergence of lineages leading to modern chimpanzees and humans. However, the persistence of primitive dental and postcranial characters in these new fossils indicates that *Ardipithecus* was phylogenetically close to the common ancestor of chimpanzees and humans. These new findings raise additional questions about the claimed hominid status of *Orrorin tugenensis*[8], recently described from Kenya and dated to ~6 Myr[9].

The western margin of the Middle Awash contains predominantly Late Miocene sediments mostly pre-dating the Kuseralee Member at the base of the Sagantole Formation of the Central Awash Complex (CAC)[10]. Palaeontological work since 1992 has yielded abundant vertebrate fossils, including hominids that date to 5.2–5.8 Myr (Table 1). Environmental indicators suggest a wooded habitat[7]. To date, 11 hominid specimens (Fig. 1) have been recovered at five localities since the first (a partial mandible) was recovered from Alayla in 1997. They represent at least five individuals and

seem to represent a single taxon, a new subspecies of *Ardipithecus* (see Methods).

The first specimen recovered was the subspecific holotype, ALA-VP-2/10, a right mandible with M_3. (Note that subscripts indicate lower teeth, superscripts upper teeth.) Four isolated left lower teeth (I_2, L_C, P_4 and M_2) are associated by spatial proximity, colour, perimortem root fracture and wear. The left I_2 is metrically and morphologically comparable to known later hominid incisors and distinctively narrower than the lateral incisors of chimpanzees (*Pan troglodytes*). The P_4 has a well developed talonid and a Tome's root rather than the single roots reported for Aramis *A. ramidus*[11].

The associated lower canine is worn apically and distally. Its mesial crown shoulder is elevated relative to the condition usually seen in modern female apes. A distinct marginal ridge is formed on the mesial lingual face. Its distal face has an exposed dentine strip from apex to distal tubercle. The large distal tubercle is shared with Aramis homologues, but the posterior orientation of the wear facet is also shared by apes with a honing canine–premolar complex. However, the distal tubercle in apes is usually worn diagonally as the upper canine extends in full occlusion below the cervico-enamel junction of the lower canine. The distal tubercle in *Ardipithecus* is worn horizontally. The functional implication of this distinction is a possible absence of a fully functional honing canine–premolar complex in *Ardipithecus.*

The M_3 shows small occlusal wear facets on the buccal slopes of the spiky metaconid and entoconid. The buccal cusps are highly worn, with a deep, cupped, coalesced dentine exposure centred at the protoconid. The M_3 of ARA-VP-1/128 (*A. ramidus*) shows a different wear pattern in which both protoconid and metaconid exhibit small apical perforations in the enamel. All later hominids have cusps that are more rounded before wear. The ALA-VP-2/10 and ARA-VP-1/128 lower third molars are similar in mesiodistal dimension. However, ALA-VP-2/10 is absolutely smaller than the known ranges of *A. anamensis* ($n = 5$) and *A. afarensis* ($n = 14$), and absolutely larger than homologues in a sample of 20 common chimpanzees. The M_2 displays a buccal occlusal half deeply excavated by wear, with a large, oval, cupped dentine exposure spanning the protoconid and hypoconid and a separate deep, round exposure at the hypoconulid position. As with the M_3, this wear pattern is different from that of later hominids owing to the extreme wear differential between the lingual and buccal cusps.

A periodontal abscess affects the P_4/M_1 area, and consequent lateral corpus swelling resulted in only slight hollowing from P_4 to posterior M_1. The submandibular fossa is shallow anteriorly. The circular, anterosuperiorly opening mental foramen is positioned at or mesial to P_4 at approximately midcorpus. The preserved corpus is comparable in absolute size to AL 288-1 (*Australopithecus afarensis*) but is less robust at the M_2 and M_3 levels than AL 288-1 or KNM-LT 329 (the Lothagam mandible).

ASK-VP-3/160 is a left P^3 crown at an early wear stage. The root is entirely missing. The occlusal crown morphology is similar to Aramis homologues, but the mesial fovea is shallower. In mesial aspect, the mesial marginal ridge of ASK-VP-3/160 is below mid-crown level. Its lingual extension bears an occlusal facet suggesting a prominent P_3 protoconid. It lacks the strong mesiobuccal crown extension commonly seen in *Pan* P^3 teeth.

STD-VP-2/61 is a narrow, pointed, unworn lower right canine with three strong horizontal buccal hypoplastic lines. The distal tubercle is less prominent than on ALA-VP-2/10. The mesial crown shoulder is lower (at midcrown) than the contemporary Alayla lower canine. One morphological feature that this canine shares with chimpanzees rather than later hominids is the flattening of the mesiolingual face with an absence of a distinct marginal ridge defined by a vertical mesiolingual groove. The weak development of later hominid lower canine traits on STD-VP-2/61, as well as the tall, narrow apex, makes this the most primitive hominid canine yet found.

STD-VP-2/62 is a fully erupted and minimally worn LM^3. The protocone apex bears a small wear facet. Occlusal outline is a buccolingually elongated rectangle with the distal half slightly buccolingually shorter than the mesial. With all four cusps well defined, this molar does not show the noticeable distal tapering usually seen in later hominids, and the occlusal surface is less crenulated than in chimpanzees. The mesial fovea is shallow and not as broad as in chimpanzees. The specimen is similar in size to the reported Aramis M^3 (ref. 11).

STD-VP-2/63 is LM^1 with both protocone and paracone exhibiting deeply pitted dentine exposures. It is absolutely smaller than known *A. afarensis* M^1 teeth. It is differentiated from chimpanzee M^1 teeth by the absence of strong occlusal crenulation.

The teeth of these Late Miocene *Ardipithecus* specimens show a mosaic of primitive and derived morphological features. Studies of enamel thickness are underway, but the available broken and little-worn teeth suggest that molar enamel thicknesses in the STD and ALA hominids were comparable to, or slightly greater than, those of the younger Aramis samples of *A. ramidus*. The presence of four distinct cusps and the absence of the distal tapering of the M^3 are primitive features shared with most Miocene hominoids. The lower canines are of particular interest. The development of the distal tubercle on these new *Ardipithecus* lower canines and the observed variation in the position of the mesial crown shoulder and expression of the mesial marginal ridge are best interpreted as representing early manifestations of the evolution of an incisiform canine, a definitive feature of later hominids.

ALA-VP-2/11 is the distal half of an intermediate hand phalanx. Dorsal shaft curvature is minimal. The concave palmar surface is marked by deep, bilateral fossae for the *m. flexor digitorum superficialis*. It is larger than but morphologically similar to most *A. afarensis* intermediate hand phalanges. Head diameter is larger than the largest *A. afarensis* intermediate hand phalanx (AL 333x-46) and comparison indicates that it was very probably longer than the longest *A. afarensis* homologue. DID-VP-1/80 is the distal half of a proximal hand phalanx. Ridges for the *m. flexor retinaculum* are not as developed as in most *A. afarensis* specimens. The overall degree of curvature of DID-VP-1/80 is similar to that of *A. afarensis*.

ASK-VP-3/78 is a left distal humerus fragment preserving some of the trochlea, the base of the medial epicondyle, the olecranon fossa and part of the distal shaft. The medial aspect of the proximal edge of the trochlear joint surface shows post-mortem subchondral erosion and minor arthritic lipping. The specimen is slightly smaller than ARA-VP-7/2 (*A. ramidus ramidus*)[11] and absolutely larger than small *A. afarensis* specimens such as AL 288-1m and AL 322-1. Radial and coronoid fossae are separated by a prominent ridge (but not by a 'Hershkovitz' tubercle). ASK-VP-3/78 is similar to ARA-VP-7/2 in having a relatively sharp lateral trochlear crest (as in most modern apes and some *A. afarensis*). The olecranon fossa of ASK-VP-3/78 differs from later hominids, which have more elliptical and shallower fossae.

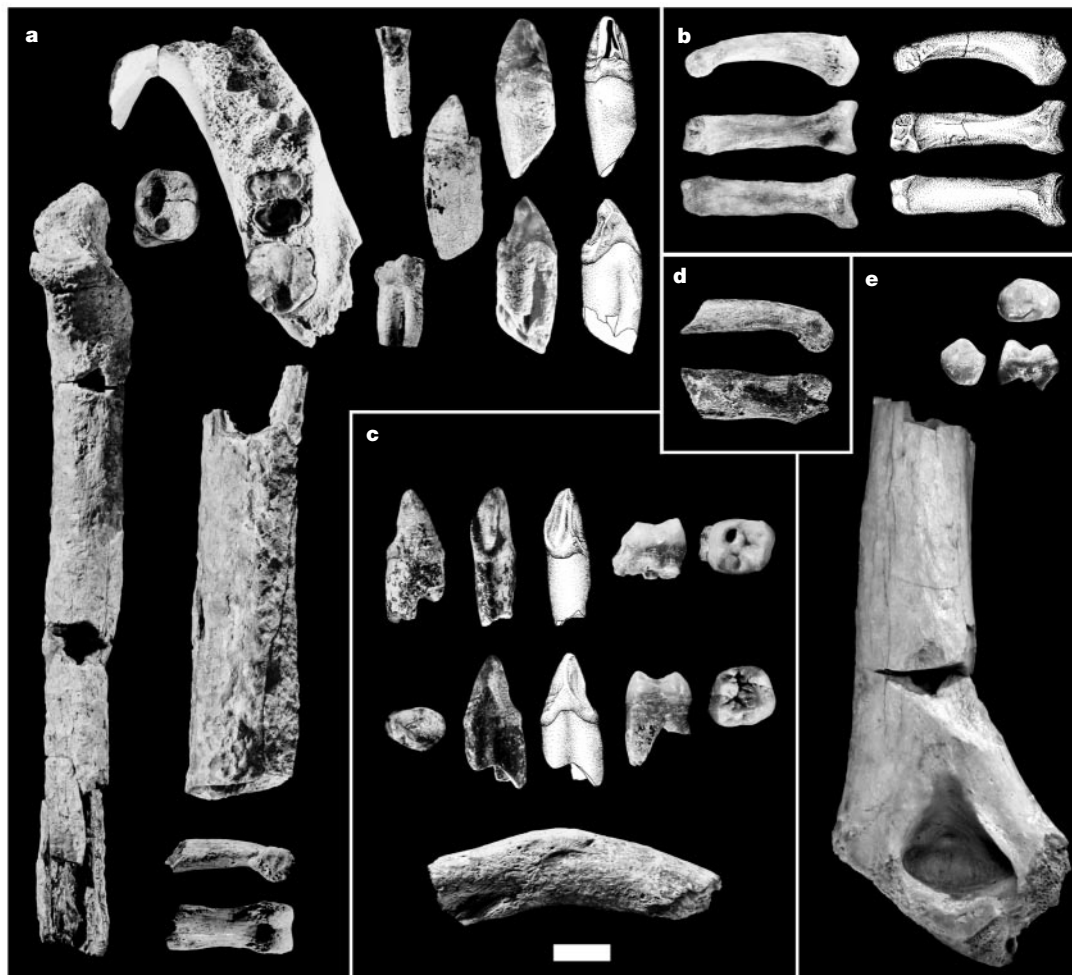ALA-VP-2/101 is an associated humeral mid-shaft and proximal

Figure 1 Fossil hominid remains from the Late Miocene Middle Awash deposits. **a**, ALA-VP-2/10, mandible and all associated teeth; ALA-VP-2/120, ulna and humerus shaft; ALA-VP-2/11, hand phalanx . **b**, AME-VP-1/71, lateral, plantar and dorsal views of foot phalanx. **c**, STD-VP-2, teeth and partial clavicle. **d**, DID-VP-1/80, hand phalanx. **e**, ASK-VP-3/160, occlusal, mesial and buccal views; ASK-VP-3/78, posterior view. All images are at the same scale. Scale bar, 1 cm. Line drawings by L. Gudz.

Table 1 Fossil specimens of *Ardipithecus ramidus kadabba*

Specimen no.	Year collected	Element	Discoverer	Dental dimensions (mm)
AME-VP-1/71	1999	Proximal foot phalanx	L. Hlusko	
ALA-VP-2/10	1997–99	Right mandible with M_3 and associated teeth	Y. Haile-Selassie	RM_3 (13.3)MD; LI_2 6.3MD, 8.3LL; L_C 11.2MD, 7.8LL, (13.1+)CH; LP_4 (8.1)MD, 10.0BL; LM_2 (12.7)MD, 11.8BL
ALA-VP-2/11	1997	Intermediate hand phalanx fragment	S. Eshete	
ALA-VP-2/101	1999	Left humerus and ulna	T. White	
ASK-VP-3/78	1998	Left distal humerus	Y. Haile-Selassie	
ASK-VP-3/160	2001	LP^3	Group	7.6MD, 11.3BL
DID-VP-1/80	1998	Proximal hand phalanx fragment	Y. Haile-Selassie	
STD-VP-2/61	1998	R_C	M. Humed	10.8MD, 7.8LL, 14.3CH
STD-VP-2/62	1998	LM^3	Y. Haile-Selassie	10.9MD, 12.2BL
STD-VP-2/63	1999	LM^1	Group	(10.6)MD, 12.1BL
STD-VP-2/893	1998	Left clavicle fragment	Y. Haile-Selassie	

Numbers in parentheses are estimates. BL, buccolingual; LL, labiolingual; MD, mesiodistal; CH, crown height.

ulna. The humeral mid-shaft is smaller than that of ARA-VP-7/2 and matches the smallest *A. afarensis*. The ulna is more complete. Most of its shaft is preserved but abraded. The coronoid and olecranon processes and the radial facet are damaged. The insertion area for the *brachialis* muscle is neither excavated nor medially or laterally well marked. Despite being incomplete, the ulnar shaft appears more curved than is typical of most later hominids.

The chronologically younger (5.2 Myr) AME-VP-1/71 is a complete left fourth proximal foot phalanx with a maximum length of 31.9 mm. It is close in maximum length to AL 333-71 (32.5 mm) (ref. 12). In lateral view, the shaft shows strong plantar curvature also comparable to AL 333-71. The distal half of the shaft is dorsoventrally compressed, whereas the proximal half is mediolaterally compressed with a prominent constriction above the base. AME-VP-1/71 shows a mosaic of features shared with both apes and *A. afarensis.* The proximal pedal phalanges of *A. afarensis* are unique in combining both strong phalangeal curvature (similar to apes) with a dorsally canted proximal joint surface (similar to later hominids)[13]. The dorsal orientation of this surface in AME-VP-1/71 may therefore constitute important evidence of a unique pedal morphology in this specimen similar to that in Hadar.

STD-VP-2/893 is the lateral half of a left clavicle lacking the acromial extremity. The deltoid muscle attachment is well marked on the superior surface. The shaft cortex is thick, with an oval cross-section immediately medial to the deltoid attachment. The conoid tubercle is a mediolaterally elongate, roughened surface comparable in overall robustness to AL 333x-9 and absolutely more robust than in chimpanzees.

The Middle Awash fossils described above share some dental characters exclusively with later hominids, and do so to the exclusion of all fossil and extant apes. These characters include lower canines with developed distal tubercles and expressed mesial marginal ridges. In addition, the proximal foot phalanx from Amba, dated at 5.2 Myr, is derived relative to all known apes and is consistent with an early form of terrestrial bipedality. Because of this combination of characters, the Middle Awash fossils described here are classified as cladistically hominid. They are currently distinguishable from the later *A. ramidus* at the subspecies level by more primitive dental characters consistent with their antiquity (see Methods). However, larger samples may reveal additional evidence that will require elevation of this subspecies to species rank.

Another candidate for hominid ancestry is the recently described *Orrorin tugenensis*[8]. The authors report thick molar enamel and suggest that *Ardipithecus* and African apes are commonly derived in having 'thin' enamel. However, enamel thickness is a complex character and intraspecifically variable, and its within-tooth three-dimensional patterning is characteristically expressed both serially and taxonomically. Therefore, the simplistic dichotomous characterization of enamel as either 'thick' or 'thin' on the basis of

unspecified measurements of naturally broken sections (as was done in the *Orrorin* report[8]) is problematic.

The upper canine morphology of *O. tugenensis* is quite primitive, as it lacks the derived, elevated crown shoulders shared by *Ardipithecus* and all other hominids. Furthermore, the locomotor anatomy of *Orrorin* remains uncertain at this time because its description lacked comment on characters directly diagnostic of bipedality, such as the presence of an obturator externus groove[14] or an asymmetrical distribution of cortex in the femoral neck[15]. Given its antiquity and characters, as currently described, there is nothing to preclude *Orrorin* from representing the last common ancestor, and thereby antedating the cladogenesis of hominids. It is equally plausible that it represents a previously unknown African hominoid with no living descendants, or an exclusive precursor of chimpanzees, gorillas or humans.

The phylogeny proffered in the description of the *Orrorin* fossils interprets *Ardipithecus* as a chimpanzee ancestor[8]. The authors state that this view is consistent with early hominids evolving east of the African rift system and chimpanzees and gorillas evolving to the west. But how could a putative chimpanzee ancestor found east of the rift (*A. ramidus* according to ref. 8) be consistent with such a model? It is vastly more likely that *Ardipithecus* is not a member of the chimpanzee clade, because of the many derived characters it shares with later hominids[11]. It is also clear that more information will be needed to resolve the role of *Orrorin* in hominoid phylogeny.

Likewise, the phylogenetic and taxonomic status of the Middle Awash fossils described here will require review as hypodigms increase. They appear to represent a hominid situated temporally and anatomically close to the last common ancestor of chimpanzees and humans. These Late Miocene fossils are followed temporally in the Middle Awash by a 5-Myr succession of increasingly derived hominid taxa, including *Ardipithecus ramidus*, *Australopithecus afarensis*, *Australopithecus garhi* and species of *Homo*. □

Methods
Description

Primates Linnaeus, 1758
Anthropoidea Mivart, 1864
Hominoidea Gray, 1825
Hominidae Gray, 1825
Ardipithecus White, Suwa and Asfaw, 1995
Ardipithecus ramidus (White, Suwa and Asfaw, 1994)
Ardipithecus ramidus kadabba subsp. nov.

Etymology. The subspecific name, kadabba, is taken from the Afar language. It means basal family ancestor.

Holotype. ALA-VP-2/10 (Fig. 1) is a right mandibular corpus with M_3, left I_2, C, P_4, M_2 and M_3 root fragment. Holotype and referred material are housed at the National Museum of Ethiopia, Addis Ababa. Holotype from Alayla Vertebrate Paleontology Locality Two (ALA-VP 2); differentially corrected GPS coordinates 10° 16.483′ N and 40° 15.313′ E; elevation 690 m.

Referred material. ALA-VP-2/11 (intermediate hand phalanx); ALA-VP-2/101 (left humerus and ulna); ASK-VP-3/78 (distal humerus); ASK-VP-3/160 (left P^3); DID-VP-1/80

(proximal hand phalanx fragment); STD-VP-2/61 (right lower canine); STD-VP-2/62 (LM³); STD-VP-2/63 (LM¹); STD-VP-2/893 (left clavicle fragment); AME-VP-1/71 (proximal foot phalanx).

Localities. Saitune Dora (STD-VP-2), Alayla (ALA-VP-2), Asa Koma (ASK-VP-3) and Digiba Dora (DID-VP-1) are all located along the western margin of the Middle Awash study area in the Afar depression of Ethiopia. Amba East (AME-VP-1) is in the CAC[7,10].

Horizons. The four western-margin hominid localities discussed here are within the Asa Koma Member of the Adu Asa Formation and bracketed by an overlying basaltic flow dated to 5.54 ± 0.17 Myr and an underlying basaltic tuff dated to 5.77 ± 0.08 Myr[7]. The Amba hominid is from the Kuserale Member of the Sagantole Formation of the CAC and is bracketed to 5.2–5.6 Myr[10].

Diagnosis. On the limited available evidence, a subspecies of *Ardipithecus* distinguished from Aramis *A. ramidus* (*A. ramidus ramidus*) by sharp M₃ lingual cusps that retain their prominence even in extreme crown wear; squared distal outline to M³ with four distinct cusps; shallow mesial fovea on P³; tendency for less relief on the mesiolingual crown face of the lower canines (one of two specimens); mesiolingually-to-distobuccally compressed lower canines.

Ardipithecus ramidus kadabba is distinguished from fossil and extant apes in its tendency toward incisiform lower canines, comparable to the condition of Aramis *A. ramidus*, with a developed distal tubercle and variants with high mesial crown shoulder placement and some expression of the mesial marginal ridge.

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Rapid and recent origin of species richness in the Cape flora of South Africa

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The Cape flora of South Africa grows in a continental area with many diverse and endemic species[1–4]. We need to understand the evolutionary origins and ages of such 'hotspots' to conserve them effectively[5]. In volcanic islands the timing of diversification can be precisely measured with potassium–argon dating. In contrast, the history of these continental species is based upon an incomplete fossil record and relatively imprecise isotopic palaeotemperature signatures. Here we use molecular phylogenetics and precise dating of two island species within the same clade as the continental taxa to show recent speciation in a species-rich genus characteristic of the Cape flora. The results indicate that diversification began approximately 7–8 Myr ago, coincident with extensive aridification caused by changes in ocean currents. The recent origin of endemic species diversity in the Cape flora shows that large continental bursts of speciation can occur rapidly over timescales comparable to those previously associated with oceanic island radiations[6,7].

Phylica is a genus of the buckthorn family (Rhamnaceae) with approximately 150 species, most of which occur in the Cape province, but it is also disjunctly distributed through other parts of southern Africa. Species of *Phylica* also occur on several oceanic, volcanic islands, such as St Helena[8], which enabled us to calibrate a molecular clock both within and outside this radiation. Two critical points of calibration were known, and these two bracketing dates provide mutual checks for the accuracy of the dating: (1) dispersal of one species from Mauritius to the volcanic island of Réunion, which is known to be two million years old, provided us with a calibration point for a relationship within *Phylica*; and (2) *Nesiota*, a closely related, endemic genus on St Helena (known to be 14.3 million years old), served as an external calibration point. We used DNA sequence data, from both the plastid and nuclear genome, to reconstruct the biogeographical history of *Phylica* and related genera, demonstrating that rapid species diversification in *Phylica* took place from 7–8 Myr ago, with most species appearing even more recently.

Aridification in the Cape region has been attributed to the separation of Antarctica from South America, which allowed a cold circum-Antarctic (Benguela) current to develop around 11–14 Myr ago. Such aridification may have been an important factor in initiating the transformation of the Miocene (26 Myr ago) subtropical forest to the fynbos vegetation of today[9–12]. The sparse fossil record of the Cape gives evidence of changes in the ecological dominance of genera typical of the fynbos, but it cannot provide direct evidence of increasing species richness. Previously there has

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