

Asa Issie, Aramis and the origin of *Australopithecus*

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The origin of *Australopithecus*, the genus widely interpreted as ancestral to *Homo*, is a central problem in human evolutionary studies. *Australopithecus* species differ markedly from extant African apes and candidate ancestral hominids such as *Ardipithecus*, *Orrorin* and *Sahelanthropus*. The earliest described *Australopithecus* species is *Au. anamensis*, the probable chronospecies ancestor of *Au. afarensis*. Here we describe newly discovered fossils from the Middle Awash study area that extend the known *Au. anamensis* range into northeastern Ethiopia. The new fossils are from chronometrically controlled stratigraphic sequences and date to about 4.1–4.2 million years ago. They include diagnostic craniodental remains, the largest hominid canine yet recovered, and the earliest *Australopithecus* femur. These new fossils are sampled from a woodland context. Temporal and anatomical intermediacy between *Ar. ramidus* and *Au. afarensis* suggest a relatively rapid shift from *Ardipithecus* to *Australopithecus* in this region of Africa, involving either replacement or accelerated phyletic evolution.

The last quarter-century of research into hominid evolution in Africa greatly extended knowledge of early *Australopithecus*. Discoveries at Hadar and Laetoli during the 1970s led to the recognition of *Au. afarensis*, described as a geographically and ecologically widespread, bipedal, megadont, small-brained hominid species lineage. Until recently, the origins of *Australopithecus* were obscured by a sparse fossil record¹.

In 1994, the smaller-toothed, more primitive hominid *Ar. ramidus* was described from Aramis, Ethiopia² (hominid refers to the human clade subsequent to divergence from our common ancestor with chimpanzees^{3,4}). These finds were followed in rapid succession by the description of *Au. anamensis* from Kenya^{5–8} and the naming of three Late Miocene taxa (*Ardipithecus kadabba*, Ethiopia, ~5.5–5.8 million years (Myr) ago^{3,9}; *Orrorin tugenensis*, Kenya, ~5.7–6.0 Myr ago^{10,11}; and *Sahelanthropus tchadensis*, Chad, ~6–7 Myr ago¹²). Relative to extant and extinct apes, these taxa display derived craniodental and post-cranial characters suggesting that they are all cladistically hominid. Their phylogenetic relationships and locomotor capabilities are under active study and debate^{13,14}.

In contrast, the time-successive species *Au. anamensis* and *Au. afarensis* are widely interpreted as sampling an evolving lineage^{4–8}. All known *Au. anamensis* specimens date to between ~3.9 and ~4.2 Myr ago. The earliest definitive *Au. afarensis* is at Laetoli,

~3.6 Myr ago¹⁵. This younger chronospecies is known by partial skeletons, well-preserved skulls and even attributed footprints. In contrast, *Au. anamensis* was heretofore documented only from the Turkana basin, and represented there by a relatively small sample⁸.

We report here on newly recovered Pliocene fossils from the Middle Awash study area, Afar rift, Ethiopia. The Adgantole Member of the Sagantole Formation¹⁶ has yielded a hominid maxilla. Contemporary sediments exposed approximately 10 km to the west have yielded an additional 30 hominid specimens representing a minimum of eight individuals (Figs 1–3; see also Supplementary Table 1). Dated to ~4.12 Myr ago and attributed to *Au. anamensis*, these remains extend the known range of this taxon by about 1,000 km to the northeast and extend the anatomical representation of early *Australopithecus*.

Geology, geochronology and palaeoenvironment

The Central Awash Complex of the Middle Awash study area includes the well-dated >300-m-thick Sagantole Formation¹⁶. Vertebrate fossil assemblages containing *Ar. ramidus* are known from nearby Lower Aramis Member strata of this formation, dated by ⁴⁰Ar–³⁹Ar to 4.416 ± 0.031 and 4.419 ± 0.068 Myr ago (previous ⁴⁰Ar–³⁹Ar ages¹⁶ are recalculated herein to reflect a revised age for the Fish Canyon sanidine standard¹⁷). Aramis locality 14 is located stratigraphically

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~80 m above the *Ar. ramidus*-bearing interval, in the overlying Adgantole Member. It has yielded a single hominid maxilla. The Asa Issie area (ASI) lies ~10 km west of Aramis locality 14, separated from the Central Awash Complex by a major northwest–southeast trending fault (Fig. 1). Three localities in this area (ASI-VP-2 and ASI-VP-5, and HAN-VP-1 at Hana Hari) have yielded additional hominid fossils from sediments contemporaneous with the Sagantole Formation's Adgantole Member.

The age estimate of ~4.1–4.2 Myr ago for Aramis 14 and ASI-VP-2 and ASI-VP-5 (see Methods) is confirmed by the presence of

biochronologically sensitive taxa. Compared to Aramis Member precursors, *Anancus*, aff. *Hippopotamus*, *Nyanzachoerus jaegeri* and *Kuseracolobus*¹⁸ are all more evolutionarily derived and consistent with an age younger than 4.4 Myr (Gàala tuff)¹⁶ but older than 3.9 Myr ago (Moiti tuff)¹⁶.

The Aramis locality 14 maxilla was unaccompanied by substantial associated faunal remains. In contrast, the hominids from ASI-VP-2 and ASI-VP-5 are stratigraphically and spatially tightly associated with over 500 vertebrate fossils for which assemblage composition and relative abundance provide strong, high-fidelity palaeoenvironmental

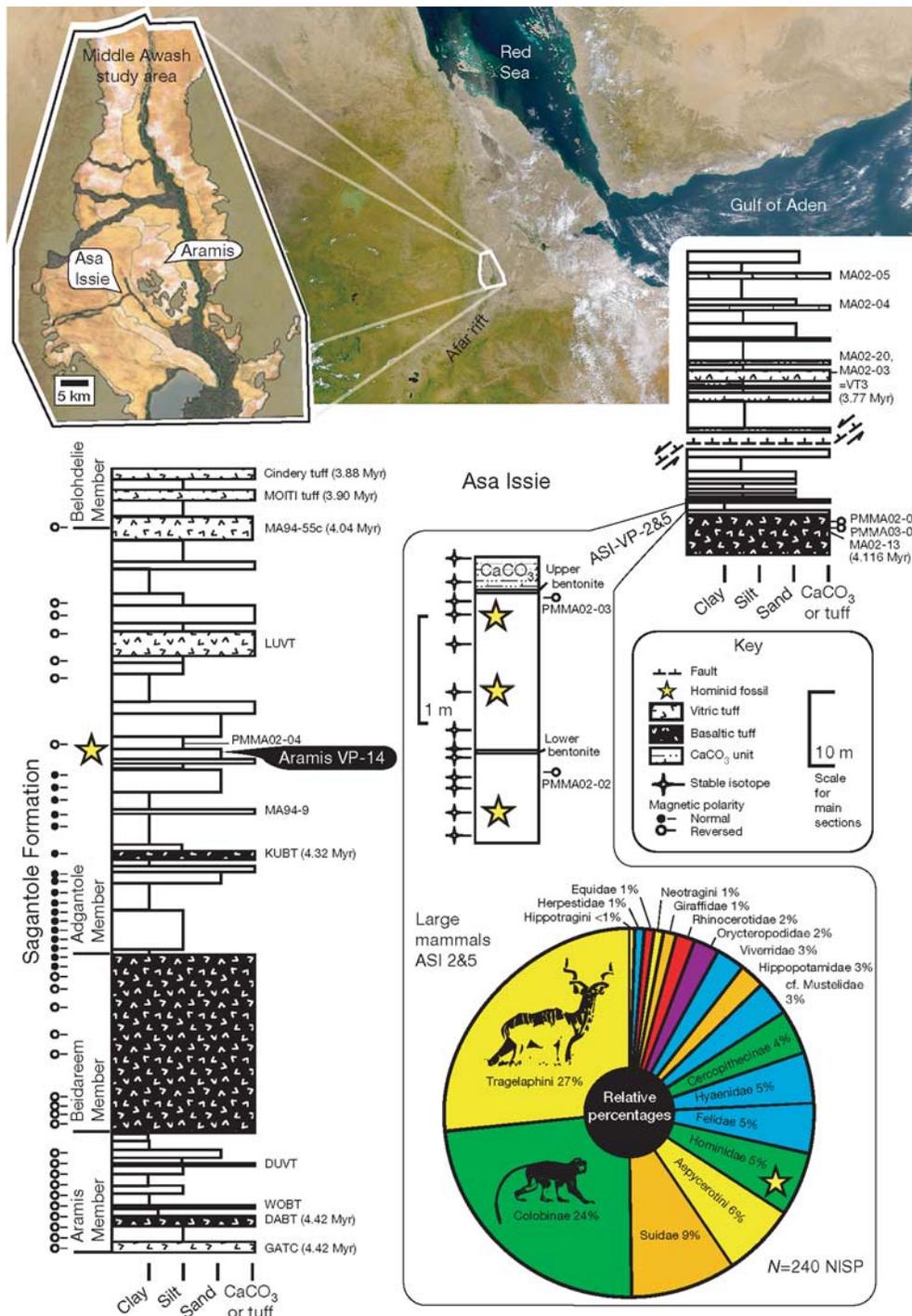


Figure 1 | Geography, stratigraphy, chronology and faunal background for the Asa Issie hominids. The chart at the bottom right shows relative abundance of the taxa indicated, based on NISP values reported in

Supplementary Table 3. DABT, Daam Aatu basaltic tuff; DUVT, Dummu vitric tuff; GATC, Gàala tuff complex; LUVT, Lubaka vitric tuff; PMMA, Middle Awash palaeomagnetic sample; WOBT, Wodara basaltic tuff.

signals. Isotopic analysis of palaeosols interbedded with these vertebrate fossils (Fig. 1) provides average carbonate root cast and nodule $\delta^{13}\text{C}_{\text{PDB}}$ and $\delta^{18}\text{O}_{\text{SMOW}}$ values (where PDB is Pee Dee belemnite and SMOW is standard mean ocean water) that reflect humid, grassy, woodland savannah environments ($\sim 25\text{--}35\%$ C_4 grass; Supplementary Table 2 and Supplementary Fig. 1). This is isotopically intermediate between the generally more closed, cooler and/or humid woodland habitats of earlier Mio-Pliocene and open, warmer and drier later Pliocene and early Pleistocene wooded grassland environments represented by eastern African Rift Valley palaeosol carbonate records^{19–23}.

The ASI-VP-2 and ASI-VP-5 sediments are interpreted as having accumulated on a flood plain distal to the main channel. Silts and clays with interbedded nodular palaeosol horizons yielded a fragmented vertebrate fauna with no evidence of fluvial and/or out-of-habitat transport²⁴. Sedimentology and the combined faunal assemblage indicate strong similarity in taphonomic history with the vertebrate assemblage at the older *Ar. ramidus* ARA-VP-1 and ARA-VP-6 localities (heavy carnivore ravaging followed by rapid burial with little or no transport)².

The ASI-VP-2 and ASI-VP-5 faunal assemblage is notable for the rarity or absence of aquatic elements (fish, crocodile, hippopotamus, waterfowl, freshwater gastropods). Rather, the assemblage appears to have been primarily terrestrially emplaced. Primates and bovids predominate, with the former most abundant (221 and 113, respectively, of 540 total identifiable specimens; Fig. 1). Colobine primates outnumber cercopithecines by 57:9. Alcelaphine and reduncine bovids are absent, and *Tragelaphus* outnumbers all other bovids assignable to tribe at a ratio of 64:18 identifiable dental specimens. The avifauna and micromammalian fauna yield taxonomic profiles, abundance values and surface modifications that closely parallel

those of the *Ar. ramidus*-associated fauna from Aramis, with *Atherurus*, *Oenomys* and *Taphozous* (the forest species) reflective of heavily wooded habitats. From these faunal associations it is evident that the Asa Issie hominids were closely and regularly associated with a narrow range of habitats varying from closed to grassy woodlands. This is similar to the habitat inferred for *Ar. ramidus* at nearby Aramis ~ 0.2 Myr earlier.

Hominid fossils

Specimen ARA-VP-14/1 is a left maxilla with fragmentary crowns of I^2 and $\text{M}^2\text{--}\text{M}^3$, broken canine, premolar and molar roots, and adjacent palatal and lateral maxillary surface. The right maxilla contains the broken P^4 root and damaged molar crowns. Tooth wear is advanced, with the incisor crown worn to root and a large, deep M^3 protocone dentine exposure. The palate is very shallow anteriorly on the left. Its roof is distorted superiorly on the right. The canine jugum would have formed the margin of the pyriform aperture. The specimen is slightly smaller but anatomically similar in preserved parts to the KNM-KP (Kenya National Museums, Kanapoi site) 29283 *Au. anamensis* paratype (Fig. 2). The canine root is relatively vertically implanted as in KNM-KP 29283 and some *Au. afarensis*. Tooth rows are straight but dental arcade shape can only be approximated.

Associated dental rows ASI-VP-2/2 and ASI-VP-2/334 are from separate individuals. They definitively place the Asa Issie sample within expected ranges of *Au. anamensis* variation. Molar crown dimensions are at or slightly above (ASI-VP-2/334) the upper end of the known *Au. anamensis* range. Combined with the slightly smaller ARA-VP-14/1 dentition, these Middle Awash post-canine teeth are distinctly larger than *Ar. ramidus* but broadly equivalent to both *Au. anamensis* and *Au. afarensis* counterparts.

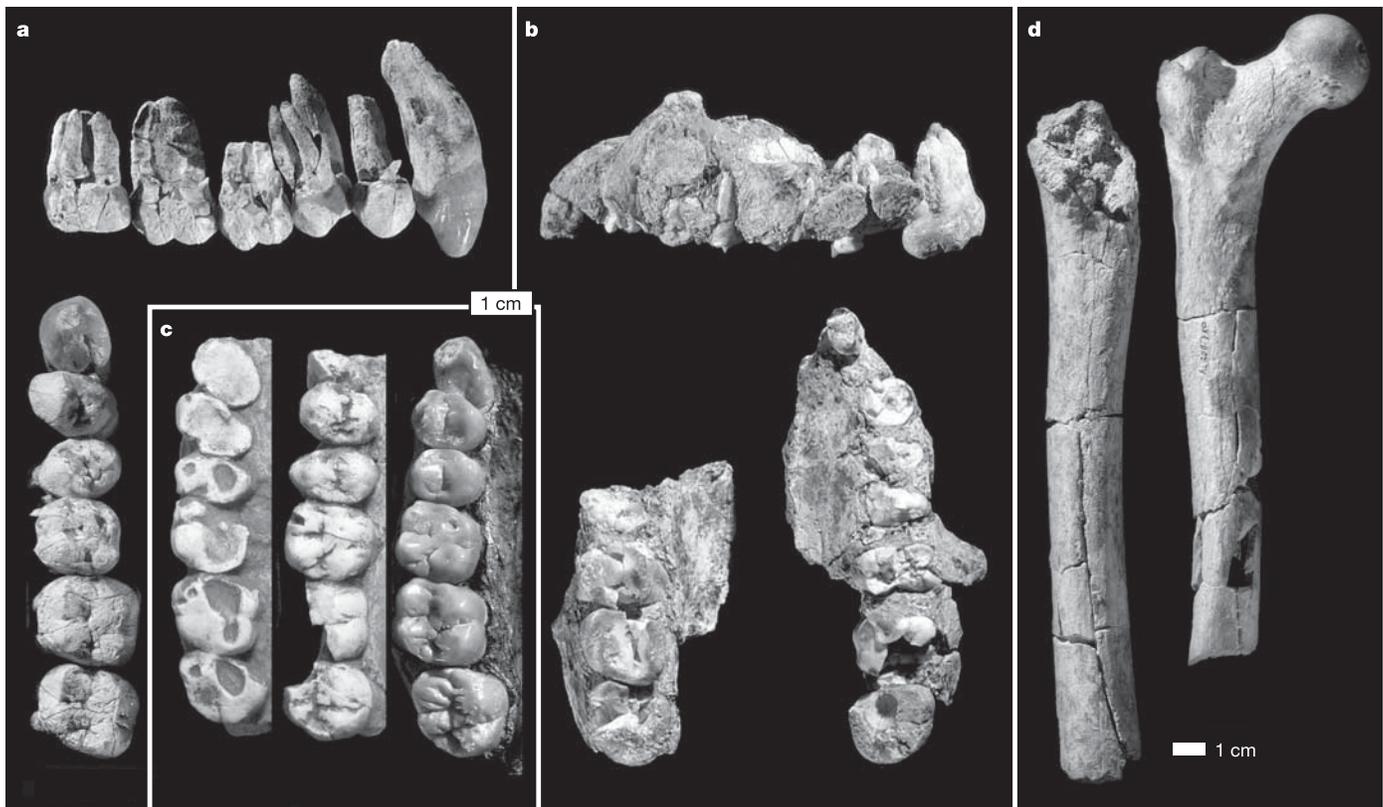


Figure 2 | Aramis and Asa Issie fossil hominids. **a**, ASI-VP-2/334 right maxillary dentition. **b**, ARA-VP-14/1 maxilla with dentition. Alignment of right and left maxillary arcades is approximate. **c**, *Au. anamensis* (KNM-KP 29283 and KNM-ER 30745, left and middle, respectively; casts, reversed)

and *Au. afarensis* (A.L. 200-1, right) dentitions. **d**, Comparison of the ASI-VP-5/154 right femoral shaft with the smaller but otherwise morphologically similar left proximal femur of A.L. 288-1 (Lucy; *Au. afarensis*).

Both ASI-VP-2/2 and ASI-VP-2/334 preserve the diagnostically important upper canines. In absolute crown dimensions, these are large, at or above the known *Au. anamensis* and *Au. afarensis* ranges of variation; isolated canine ASI-VP-2/367 is smaller. The three canines encompass the known Kenyan *Au. anamensis* size range. Asa Issie canine size relative to molar size is comparable to or slightly greater than the two known examples of *Au. anamensis* (KNM-KP 29283, KNM-KP 30498) and intermediate between the *Ar. ramidus*

and *Au. afarensis* conditions (Supplementary Discussion 1). Canine shape (mesiodistal versus buccolingual dimensions) is also intermediate between *Ar. ramidus* and known *Au. anamensis* conditions, tending towards the more mesiodistally elongate morphology considered to be distinctive of *Au. anamensis* but not *Au. afarensis* (Fig. 3; see also Supplementary Fig. 2)⁸. Another feature that we interpret to be of evolutionary significance is the development of the upper canine's mesiolingual ridge. The known Kenyan *Au. anamensis* upper

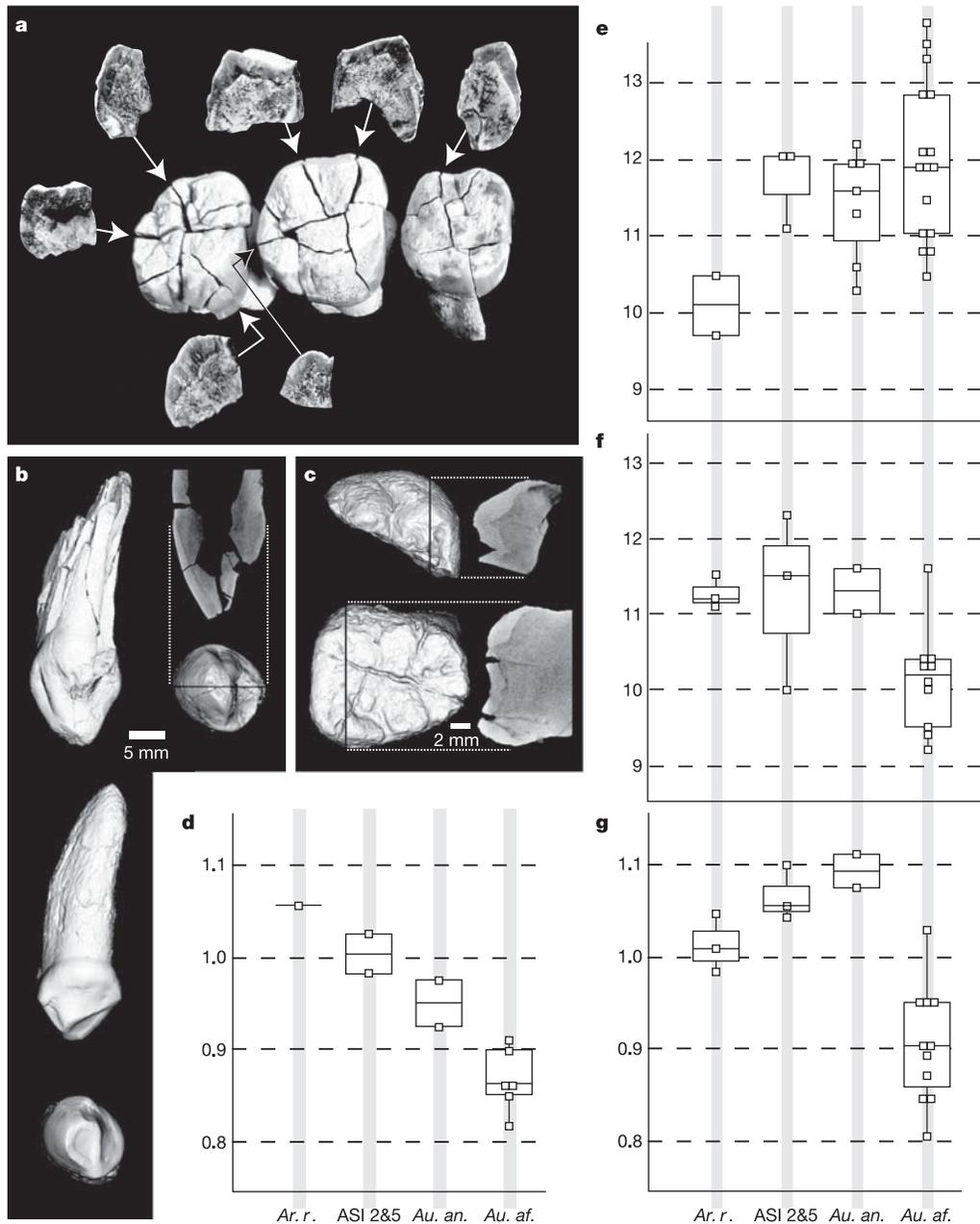


Figure 3 | Dental features of the Asa Issie hominid dentition. a, ASI-VP-2/334 maxillary molars (unglued) showing enamel thickness in natural cross-sections. **b**, ASI-VP-2/334 (top) and ASI-VP-2/2 (bottom) maxillary canines, micro-CT-based surface-rendered images and cross-section through the cusp tip. Lingual and occlusal views are shown; note the enamel thickening towards the cusp tip in micro-CT section view (maximal radial thickness is 1.54 mm; Supplementary Discussion 2). Note the mesiodistally elongate crown of ASI-VP-2/2. **c**, ASI-VP-2/146 (top) and ASI-VP-5/1 (bottom) molars, micro-CT-based surface-rendered images and cross-sections. Occlusal and section views are shown. Note the strongly concave buccal crown enamel–dentine junction contour resulting in exaggerated molar

crown flare. **d–g**, Dental metric comparisons among early hominid taxa. **d**, Relative canine size (upper canine maximum dimension divided by upper M¹ mesiodistal length). **e**, Upper M¹ mesiodistal length (in mm). **f**, Upper canine mesiodistal length (in mm). **g**, Upper canine shape (mesiodistal length divided by buccolingual breadth). Each small square represents one specimen; vertical lines are total ranges, whereas horizontal lines are medians and quartiles. *Ar. r.*, *Ar. ramidus*; ASI 2&5, and Aramis locality 14 *Au. anamensis*; *Au. an.*, Kenyan *Au. anamensis*; *Au. af.*, *Au. afarensis*. Comparative sample sizes and sources are outlined in Supplementary Discussion 1.

canines were noted to have a stronger mesiolingual ridge than *Au. afarensis* homologues⁸. *Au. afarensis* upper canines tend to have a more spatulate or incisiform lingual fossa, although expression of the mesiolingual ridge is variable. All three Asa Issie canines show a strong mesiolingual ridge as in KNM-KP 35839 (and slightly less so in KNM-KP 30498). The same ridge is even stronger in known *Ar. ramidus* examples² (ARA-VP-1/300, ARA-VP-6/1).

The upper P³ is asymmetric in shape, as in known *Au. anamensis* and some *Au. afarensis* (Laetoli) examples. The Asa Issie molars tend to be low crowned with flaring buccal and lingual crown faces. The second molar is much larger than the first in ASI-VP-2/334 and less so in the other two available specimens. The Asa Issie lower third molars exhibit a developed distal crown as is commonly the case in *Au. afarensis* and *Au. anamensis* homologues, but not in known examples of *Ar. ramidus* (for example, ARA-VP-1/128)².

Enamel thickness was examined non-invasively either at appropriately broken natural fracture locations (ASI-VP-2/334) or by high-resolution micro-computerized-tomography (micro-CT) visualization²⁵ (Fig. 3; see also Supplementary Discussion 2). Maximum radial thickness of the lateral crown face of the two posterior molars²⁶ ranged between ≥ 1.7 mm to ≥ 2.3 mm in the 'functional-side' cusps (buccal in lowers and lingual in uppers) and ≥ 1.3 mm to 2.0 mm in the opposite-side cusps. This is comparable to known *Au. anamensis* where molar enamel thickness appears to be close to the *Au. afarensis* condition in the functional-side cusps⁸, but varies towards the thinner distribution in the opposite-side cusps. Enamel thickness measures of *Ar. ramidus* have been reported to occupy a thinner range of variation², although considerable within-species variation is currently being documented in modern human and ape control samples^{25,26}.

The ASI-VP-2 and ASI-VP-5 post-crania include a metatarsal shaft without ends, an eroded distal foot phalanx, and an intact intermediate hand phalanx. The last shows slight dorsal longitudinal curvature, accentuated distally. The proximal half of the palmar surface shows deeply excavated attachment sites for m. flexor digitorum superficialis encroaching on a prominent, raised central ridge. The specimen is morphologically similar to those from Hadar, but is longer relative to its breadth. Four vertebral fragments include

an atlas larger than its single Hadar homologue and a thoracic arch larger than any in the Hadar A.L. 288-1 specimen.

One study⁷ predicted that when found, the *Au. anamensis* femur would be similar to that of *Au. afarensis*. Specimen ASI-VP-5/154 is approximately 75% of an adult right femur shaft preserving the base of the lesser trochanter and part of the neck–shaft junction. The shaft is well preserved except for its entire distal-most portion, lost just proximal to the popliteal surface. The shaft retains surface detail but is broken into slightly offset fragments that artificially accentuate the very slight (original) anteroposterior shaft curvature (in its original condition the shaft would have been much straighter). The shaft is remarkable for its thick cortex revealed throughout its length by the broken cross-sections.

A strongly roughened, >3-cm long (superioinferiorly), posterolaterally positioned attachment for m. gluteus maximus represents the most rugose part of the bone and contrasts sharply with the otherwise minimal relief of its shaft. There is no linea aspera, but only relatively blunt outlines of the adductor attachments both medially and laterally. At the shaft's approximate midpoint, these two minimal ridges are separated by about 11 mm, a distance of considerable breadth given the probable original length of the bone. The Asa Issie femur is thereby similar to the 'minimal linea aspera' morphology of the posterolateral femur that characterizes the smaller A.L. 288-1 femur (Fig. 3). In this sense, the older Asa Issie specimen is on the presumably primitive end of the considerable range of variation in *Au. afarensis* with respect to this character.

Early *Australopithecus* environment and biogeography

Palaeoenvironmental circumstances surrounding *Au. anamensis* ~1,000 km to the south in Kenya have been described for Allia Bay as a mixed assemblage sampling aquatic, forest, grassland and bushland^{27,28}. Nearby Kanapoi conspecifics were found in another mix of environments described as dry, possibly open, wooded, or bushland conditions with a wide gallery forest in the vicinity⁵. Habitat preferences in such mixed assemblages are difficult to ascertain despite the assertion²³ that hominids "favored mosaic settings". In contrast, the Ethiopian occurrence of *Au. anamensis* described here allows its tight spatial and temporal placement in a vertebrate assemblage with

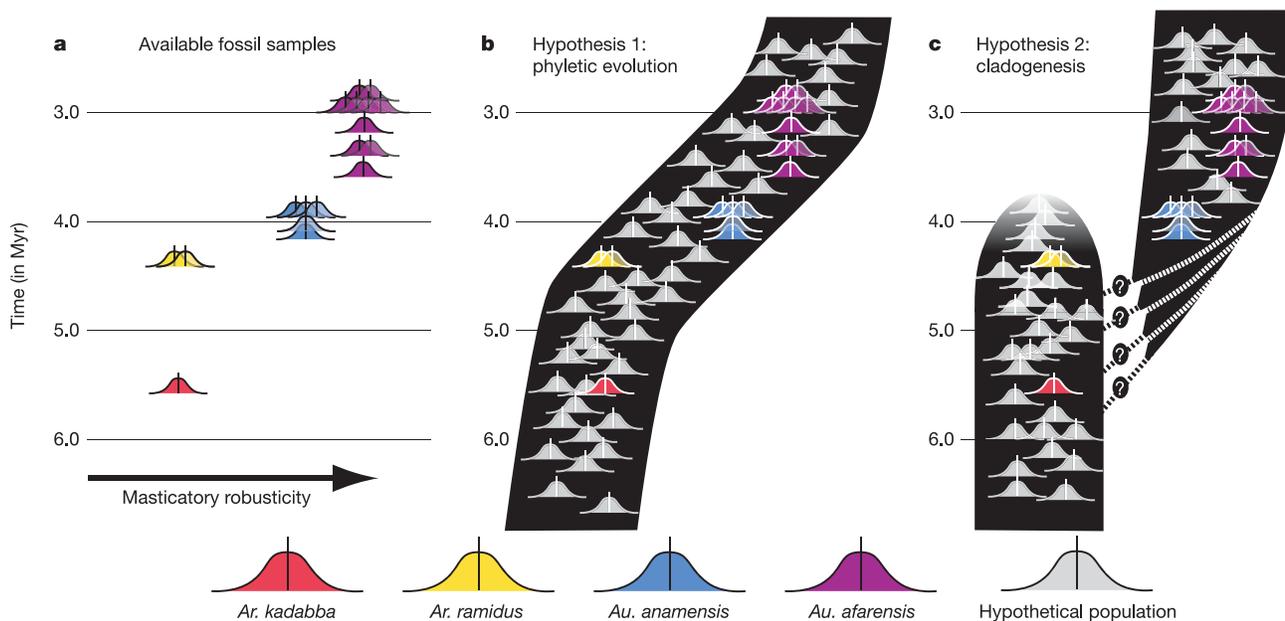


Figure 4 | Phylogenetic hypotheses. Known fossil hominid samples are depicted in colour, by site (for example, Middle Awash for *Ar. kadabba*; Aramis and Gona for *Ar. ramidus*; Kenyan, Tanzanian and Ethiopian occurrences for *Australopithecus*). Currently available samples may be

hypothesized to represent a single lineage evolving at varying rates (phyletic evolutionary origin of *Australopithecus*) or a speciation event (cladistic evolutionary origin of *Australopithecus*). Neither hypothesis can be falsified with available sample densities.

taphonomic integrity. Its relative abundance suggests that it was a regular occupant of a wooded biome that appears to have persisted in this part of the Afar during the 200,000-yr interval subsequent to *Ar. ramidus* at Aramis.

At Aramis, the lone hominoid and largest primate was *Ar. ramidus* (109 of 6,156 identified specimens so far). No trace of *Australopithecus* has been recovered in this (4.4 Myr ago) or any contemporary or older African deposit²⁹ (*contra* refs 30, 31). Furthermore, *Ardipithecus* has not been found at Asa Issie (~4.1–4.2 Myr ago) or in any other contemporary or younger fauna. Thus, *Ardipithecus* and *Australopithecus* are, so far as is known, mutually exclusive in temporal distribution. Defining the first appearance datum of *Australopithecus* is hazardous given the incompleteness of the geological record, but its first appearance in the Turkana basin at three separate sites (Kanapoi, Allia Bay and Fejej) is coincident (within age constraints) with its appearance in the Afar Rift at Aramis, Asa Issie and possibly Galili³².

Phylogenetics of early *Australopithecus*

In an assessment of fossils from Kanapoi (3.9–4.2 Myr ago), the anagenetic series *Ar. ramidus*, *Au. anamensis* and *Au. afarensis* has been hypothesized^{7,8}. The evidence reported here from the Afar Rift constitutes a strong test from a single stratigraphic succession that fails to falsify this hypothesis. Middle Awash *Au. anamensis* is anatomically intermediate in many characters between the earlier *Ar. ramidus* and the later *Au. afarensis* from the same study area (see Supplementary Discussion 3 for cladistic analysis). Twenty years ago, *Au. afarensis* was heralded as the “epitome of australopithecine primitiveness”³³ and a “locomotor missing link”³⁴, but it is decidedly derived relative to *Au. anamensis* and *Ar. ramidus*.

Two phylogenetic hypotheses concerning the origin of *Australopithecus* can be offered to account for the available data. The first hypothesis (Fig. 4) derives *Au. anamensis* phyletically from *Ar. ramidus* within a 200,000-yr interval. The second involves cladogenesis of *Au. anamensis* from an ancestor (presumably *Ardipithecus* or some close relative) even deeper in the Pliocene or Late Miocene. Under the latter hypothesis, *Ar. ramidus* would represent a relict species in an ecological refugium.

Early hominid evolutionary mode and tempo

Gould³⁵ suspected that “punctuated gradualism” was rare. In contrast, punctuated equilibrium (with speciation by “budding cladogenesis”³⁶) is thought to be more common, but demonstrating it requires the verified contemporaneity and persistence of both the ancestral and daughter species. As Gould³⁵ noted, “We can distinguish the punctuations of rapid anagenesis from those of branching speciation by invoking the eminently testable criterion of ancestral survival following the origin of a descendant species. If the ancestor survives, then the new species has arisen by branching. If the ancestor does not survive, then we must count the case either as indecisive, or as good evidence for rapid anagenesis—but, in any instance, not as evidence for punctuated equilibrium.” (p. 795).

These requirements have rarely been met among fossil hominids. For the origin of *Australopithecus*, phyletic evolution with a burst of rapid directional change during the 200,000-yr period between 4.4 and 4.2 Myr ago remains plausible given the geographic, temporal and morphological relationships of *Ar. ramidus* and *Au. anamensis* and our understanding of primate dental anatomy and development³⁷. Indeed, given the available evidence, the origin of *Australopithecus* could well turn out to be a case of “punctuated gradualism”³⁸ or “punctuated anagenesis”³⁹ rather than rectangular evolution *sensu* Stanley⁴⁰. Only the recovery of additional fossils from dated contexts will allow a more accurate and precise determination of the mode and tempo of early hominid evolution on the African continent.

Early hominid adaptation

Whatever the geometry of early hominid phylogeny, diagnostic

megadontia and related dentognathic morphology of *Australopithecus* herald its appearance at or before 4.2 Myr ago. Its masticatory apparatus appears better adapted to a more heavily chewed diet of tough and abrasive items^{41,42} than that of *Ardipithecus*. These phenotypic signals indicate an adaptive shift towards the exploitation of tougher and more abrasive food resources. This may signal an ‘ecological breakout’ involving niche expansion with intensified exploitation of more open African Pliocene habitats². Such habitats were evidently available even in the Late Miocene⁴³, but hominids older than *Australopithecus* apparently did not exploit them as intensively. Greater habitat and dietary specificity among the earliest hominids probably explains the difficulty of recovering them as fossils from pre-*Australopithecus* deposits, except in specific ecological circumstances.

The Asa Issie occurrence of *Au. anamensis* suggests that the habitat previously frequented by *Ardipithecus* continued to attract its more derived and probably more eurytopic descendant. Having crossed the threshold of megadontia, all *Australopithecus* subsequent to Asa Issie (the *Au. anamensis*–*Au. afarensis*–*Au. garhi* lineage; the *Au. aethiopicus*–*Au. boisei* lineage; *Au. africanus*; *Au. robustus*) continued to display hypertrophy of craniodental features, presumably evolved under natural selection involving intensified mastication. Species of the genus *Homo* violated this trend, but only subsequent to the appearance of stone tools.

The origin of *Australopithecus* between 4 and 5 Myr ago does not seem to correspond to any proxy signalling global climatic change^{44,45}. Neither is there an obvious pattern of an evolutionary pulse affecting other contemporary mammalian lineages. The triggers for the adaptive shift towards early hominid megadontia and the Pliocene origin of *Australopithecus* therefore remain elusive.

METHODS

Aramis vertebrate palaeontological locality 14 is approximately 9 m above the Kullunta basaltic tuff (KUBT) dated to 4.317 ± 0.055 Myr ago¹⁶ and about 50 m below another volcanic stratum, MA 94-55C, dated to 4.041 ± 0.060 Myr ago¹⁶. The hominid fossil maxilla ARA-VP-14/1 was found in 1994 in a palaeomagnetically reversed, orange–brown silty clay. The reversal immediately below the maxilla appears to be the base of chron C2Ar (ref. 46) at 4.21 Myr ago (recalculated; younger limit of chron is 3.61 Myr ago).

The ASI/HAN stratigraphic succession is dominated by fluvial deposits and minor interbedded bentonitic and glassy silicic and hydromagmatic basaltic tephra deposits. At the ASI-VP-2 site, the local stratigraphic sequence dips slightly to the west and is emplaced atop basalts and sediments locally representing the Gawto, Haradaso and Aramis members¹⁶.

All of the Asa Issie faunal collections and hominid remains described here are from a 2–3-m-thick zone of fluvial silty clays with root cast and pedogenic carbonates atop a widespread yellow–green altered hydromagmatic basaltic tephra (Fig. 1). Four samples spanning the 3 m of fossiliferous strata at the ASI-VP-2 locality are of reversed geomagnetic polarity, consistent with their placement in chron C2Ar. The upper portion of the underlying basaltic tephra includes a 15-cm-thick basaltic tuff that consists of fine- to medium-grained glass shards that are strongly calcite cemented and partially altered. It is a primary deposit and has homogeneous chemistry. We have dated it by ^{40}Ar – ^{39}Ar to 4.116 ± 0.074 Myr ago (MA02-13, weighted mean of the two plateau ages; integrated ages of 4.4 ± 0.4 Myr and 4.6 ± 0.2 Myr ago; Supplementary Table 4 and Supplementary Fig. 3), providing a maximum age for the fossils.

A widespread gastropod-bearing sandstone marker horizon overlies the hominid-bearing localities. In other portions of the Middle Awash study area a similar unit is capped by the Early Pliocene Cindery tuff dated by ^{40}Ar – ^{39}Ar to 3.88 ± 0.02 Myr ago^{16,47–49}. At Asa Issie this marker horizon is separated from younger deposits by a west-dipping, northwest–southeast-trending normal fault with ~30 m of displacement. This fault crosses ~100 m southwest of the ASI-VP-2 site, and the hanging wall contains a distinct 90–120-cm silicic tephra (MA00-19, MA00-20, MA00-21), the geochemical characteristics of which provide a firm correlation to the widespread 3.77-Myr VT-3/Wargolo tuff^{16,47–50}. From the cumulative evidence we conclude that the vertebrate fossils from the ASI-VP-2, ASI-VP-5 and HAN-VP-1 localities were embedded between 4.12 and 3.77 Myr ago, but much closer to the former based on stratigraphic proximity and biochronological considerations.

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