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Early *Homo erectus* lived at high altitudes and produced both Oldowan and Acheulean tools

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In Africa, the scarcity of hominin remains found in direct association with stone tools has hindered attempts to link *Homo habilis* and *Homo erectus* with particular lithic industries. The infant mandible discovered in level E at Garba IV (Melka Kunture) on the highlands of Ethiopia is critical to this issue due to its direct association with an Oldowan lithic industry. Here, we use synchrotron imaging to examine the internal morphology of the unerupted permanent dentition and confirm its identification as *Homo erectus*. Additionally, we utilize new palaeomagnetic ages to show that (i) the mandible in level E is ca. 2 million-years-old, and represents one of the earliest *Homo erectus* fossils, and (ii) that overlying level D, ca. 1.95 million-years-old, contains the earliest known Acheulean assemblage.

The Melka Kunture complex consists of a cluster of prehistoric sites that extends over tens of km² in the Upper Awash, on the Ethiopian plateau at 22000 m above sea level (asl) (Fig. 1A). At this high altitude, the Pleistocene climate would have been cooler and wetter than at the lower elevations of the Rift Valley where most fossil evidence for early species of *Homo* derives. The paleovegetation belonged to the Afromontane complex, ranging from forest to grassland and bushland (1), and the plant species were distinct from those of the African savanna, which developed at lower elevations in drier and warmer environments. The degree of topographic relief of the region meant that the highlands were relatively isolated, leading to the appearance of endemic mammal sub-species (2). In 1981, an infant mandible was discovered in level E of the Garba IV site, though which species of

hominin it represents has been a subject of debate (3). In this study we review the geochronological context of the Garba deposits, characterize the Oldowan and Acheulean lithic assemblages, present the palaeoecological context of the site based on analysis of the faunal assemblage and palynology, and re-assess the taxonomic affinity of the mandible. Our aim is to determine when, how, and which hominin species was first able to adjust to the high-altitude environment of the highlands of Melka Kunture during the Early Pleistocene and the associated transition from the Oldowan to the Acheulean techno- complex. Broadening our knowledge of the environment at the time and not limiting it to the savanna and to lower altitudes is relevant to understand how *Homo erectus* was able to expand outside Africa. to expand outside Africa.

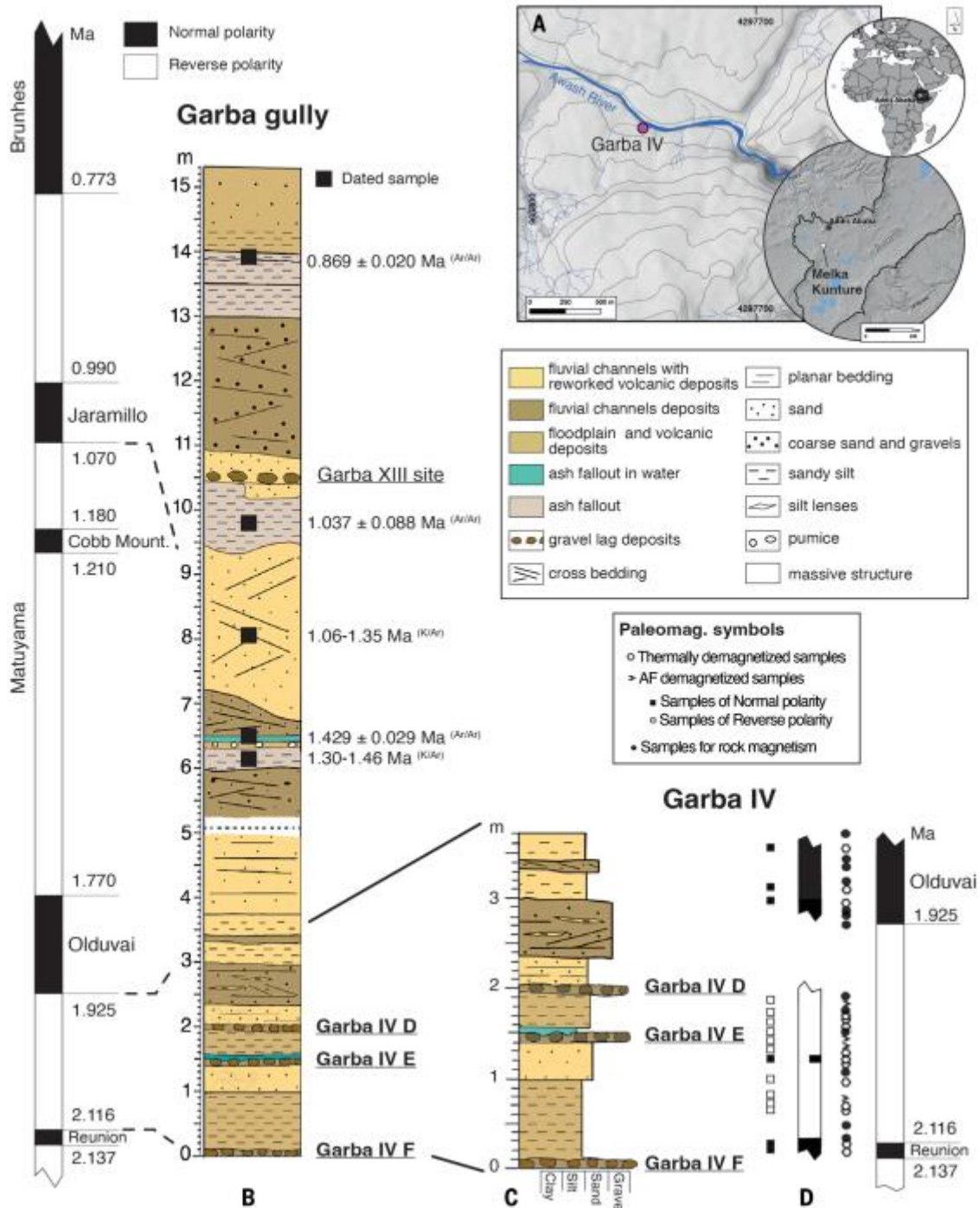


Fig. 1. Location, magnetostratigraphy, and chronostratigraphy of Garba IV. (A) Location map of the Garba IV site (Melka Kunture, Upper Awash, Ethiopia). (B) The stratigraphy of the Garba gully, with both Garba IV and Garba XIII, a middle Acheulean site

(42). Geomagnetic polarity timescale is from (43), $^{40}\text{Ar}/^{39}\text{Ar}$ dates are from (5), and K/Ar dates are from (44). (C and D) The stratigraphy of Garba IV and the paleomagnetic sequence of samples with normal (small black squares) and reverse polarity (small white squares) (6) (fig. S3).

Stratigraphy and chronology

The sedimentary sequence of the multi-layered Garba IV site records hominin activity on lag deposits close to shallow ponds and pools that are situated within a floodplain affected by the migrating paleo-Awash channel and associated flood events, and also influenced by the deposition of volcanic ashes. The site is at the mouth of a small gully, the Garba gully, incised by a seasonal tributary of the Awash River (fig. S1). We refer here to three main archaeological levels at the base of the stratigraphic sequence of the gully (Fig. 1B and figs. S1 to S3): levels F and E with faunal and hominin remains, and an Oldowan lithic industry; and level D with faunal remains and an Early Acheulean industry. $^{40}\text{Ar}/^{39}\text{Ar}$ and preliminary magnetostratigraphic analyses had previously dated these levels to shortly before and shortly after 1.7 ± 0.2 million-years ago (Ma) (4, 5), but the age was not well constrained. A new magnetostratigraphic study has recently established the age of the levels (6). In this sequence both the Olduvai/Matuyama boundary (1.925 million years), and the Matuyama/Reunion boundary (2.116 million years) are identified, which provide a maximum and a minimum age for the three archaeological layers. The Olduvai/Matuyama boundary was observed above level D. Using an estimated depositional rate and a model of sediment accumulation, the specific ages have been calculated as: level F = 2.02 (—0.095; +0.096) Ma; level E = 2.00 (—0.0075; +0.1) Ma; level D = 1.95 (-0.025; +0.1) Ma (6) (Fig. 1, C and D). These much older dates for levels D-F have significant implications for the interpretation of the archaeology and the hominin fossil found at the site.

Archaeology

Level E at Garba IV (now dated to ca. 2.00 Ma) was first tested in 1981 and 34 m² were eventually exposed (fig. S4 and figs. S8 to S10), with an additional exposure of 12 m² of underlying level F (now dated to ca. 2.02 Ma) (fig. S4 and figs. S8 to S10). Both yielded abundant Oldowan tools (7) and the associated mandible represents one of the only hominin remains directly associated with artefacts in the Early Pleistocene (table S1). It was excavated in level E, a sealed level within a well-established stratigraphic sequence (Fig. 1, C and D; fig. S2; and figs. S9 to S11). The artefacts were mostly produced on obsidian cobbles and pebbles preferentially selected from the rocks available in the local alluvial deposits (Fig. 2A and figs. S12 to S13). Many of these are small flakes, mostly 20-50 mm in length, with ca.30% retouched and transformed into small pointed tools (Fig. 2A, 3 to 5, and fig. S13).

In overlying level D, excavated since 1973 to some 75 m² and redated to ca. 1.95 Ma, the ca. 7000 lithic tools (table S1) differ from those of the underlying Oldowan assemblage due to the production of large flakes (i.e., >100 mm in maximal length or width). There are true handaxes, cleavers and other types of Large Cutting Tools (LCTs), such as massive scrapers or knives shaped on large flakes (Fig. 2B, 6 to 12, and figs. S15 to S19). The large flakes and LCTs constitute ca. 1% of the analyzed assemblage (large flakes = 41 and LCTs = 23) but are relevant to understanding the technological shift from the underlying Oldowan assemblage (8). The features of the assemblage, including the production of large flakes and LCTs, identify it as Early Acheulean. Thus, Garba IV documents a rapid change between Oldowan and Acheulean lithic production over a period of 50,000-100,000 years in this unique high-altitude paleoenvironment.

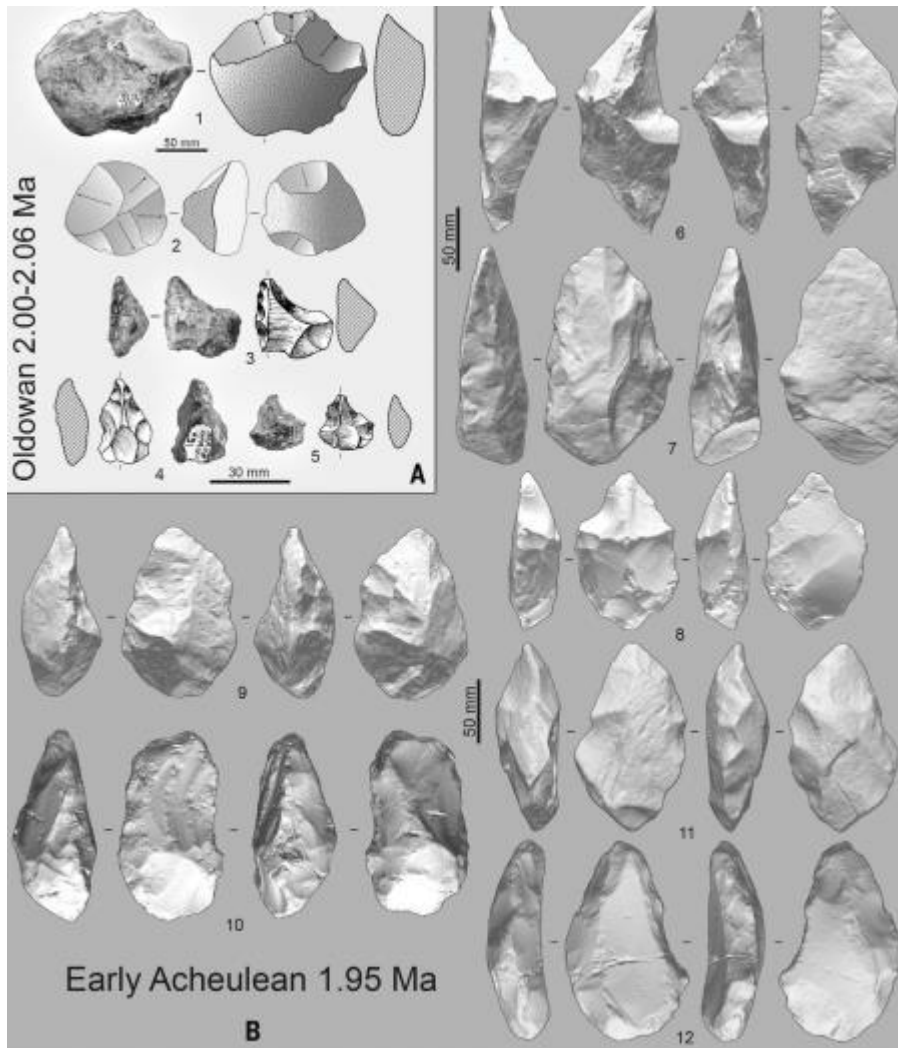


Fig. 2. Garba IV artifacts.

(A) Levels E and F (2.00 Ma to 2.06 Ma), Oldowan. Images show obsidian cores (1 and 2) and obsidian pointed tools (3 to 5). (B) Level D (1.95 Ma), Early Acheulean. Images show large retouched flakes shaped on basalt or obsidian (6 to 8) and handaxes shaped on lava, basalt, or obsidian flakes (9 to 12).

Paleoecology

The vegetation of the Garba IV site belonged to the Dry evergreen Afromontane forest and grassland complex, which currently develops on the mountains of East Africa above 1800 m asl (9, 10). Around 1.8 Ma or possibly earlier, the palynology indicates bushy woodlands alternating with patches of grassland in the area of Melka Kunture (1). A more open vegetation and a mountain grassland followed, which further expanded during the deposition of level D at Garba IV. This Afromontane vegetation develops under a mountain climate with large diurnal temperature ranges, resulting in plant species that are distinct from those of the lowland savanna or woodland.

The mammalian faunal remains of levels E and F are highly fragmented, and species-level identifications are rare. The fossil sample from level D is larger (table S3), but the three assemblages cannot be ecologically distinguished. A rare occurrence in level E is the extinct civet *Pseudocivetta ingens*, also known from several eastern African sites between c. 2.4 and 1.5 Ma. *Theropithecus*, a genus quite rare at Melka Kunture, is represented by a single specimen from level D. In this layer, the ungulate fauna is dominated by large hippos and grazing bovids, of which almost 90% are alcelaphins and antilopins, unambiguously pointing to an open environment and consistent with the relatively high frequency of equids (2). Also consistent with an open environment are measurements of $^{13}\text{C}/^{12}\text{C}$ isotopic ratios of dental enamel carbonates

carried on hippopotamus (n=11), bovid (n=1) and equid (n=1) teeth from layer D. The results show that hippos, bovids and equids consumed C1 plants, suggesting C4 high-elevation grasslands (11) (fig. S20).

The bovid material from levels E-F cannot be identified beyond generic rank, while level D alcelaphins (*Connochaetes* and *Damaliscus*) are close to those known from contemporaneous East African lower elevation sites, up to 1500 m asl, but are distinct at least at sub-specific level. Thus, the fauna record testifies to some endemism (2, 12) of the Ethiopian highlands, a factor to be considered when dealing with hominin evolution and subsistence in this paleoenvironment.

Taxonomy of the Garba IVE mandible

Previous analyses of the external and internal morphology of the MK 81 GAR IVE 0043 (abridged name Garba IVE) mandible (Fig. 3) have identified affinities with various early Homo species such as *H. habilis*, *H. rudolfensis*, *H. ergaster* and *H. erectus* (13). Although GAR IVE had been published as affected by a rare genetic disorder affecting its enamel (amelogenesis imperfecta) (14), this was recently refuted using synchrotron imaging, and features previously interpreted as pathological were rather shown to result from taphonomic processes (15). Based on medical CT scans, Zanolli et al. (3) expanded on previous assessments to examine the sequence of dental development, tooth crown tissue proportions, tooth size in the unerupted permanent dentition, and corpus cortical bone thickness. Their conclusion was that the Garba IVE specimen shared affinities with *H. habilis/rudolfensis* and *H. erectus sensu lato*. We used synchrotron computed tomography to produce high-resolution images of the enamel and dentine surfaces of the unerupted permanent dentition (15) as these have been shown to maximize the taxonomic information in hominin teeth (16-18). We conducted a 3D landmark-based geometric morphometric analyses of the enamel- dentine junction of the third and fourth premolar and first molar. We were also able to compare the unerupted permanent dentition of Garba IVE against an expanded comparative sample that crucially includes specimens of *H. habilis* from both Tanzania and Kenya.

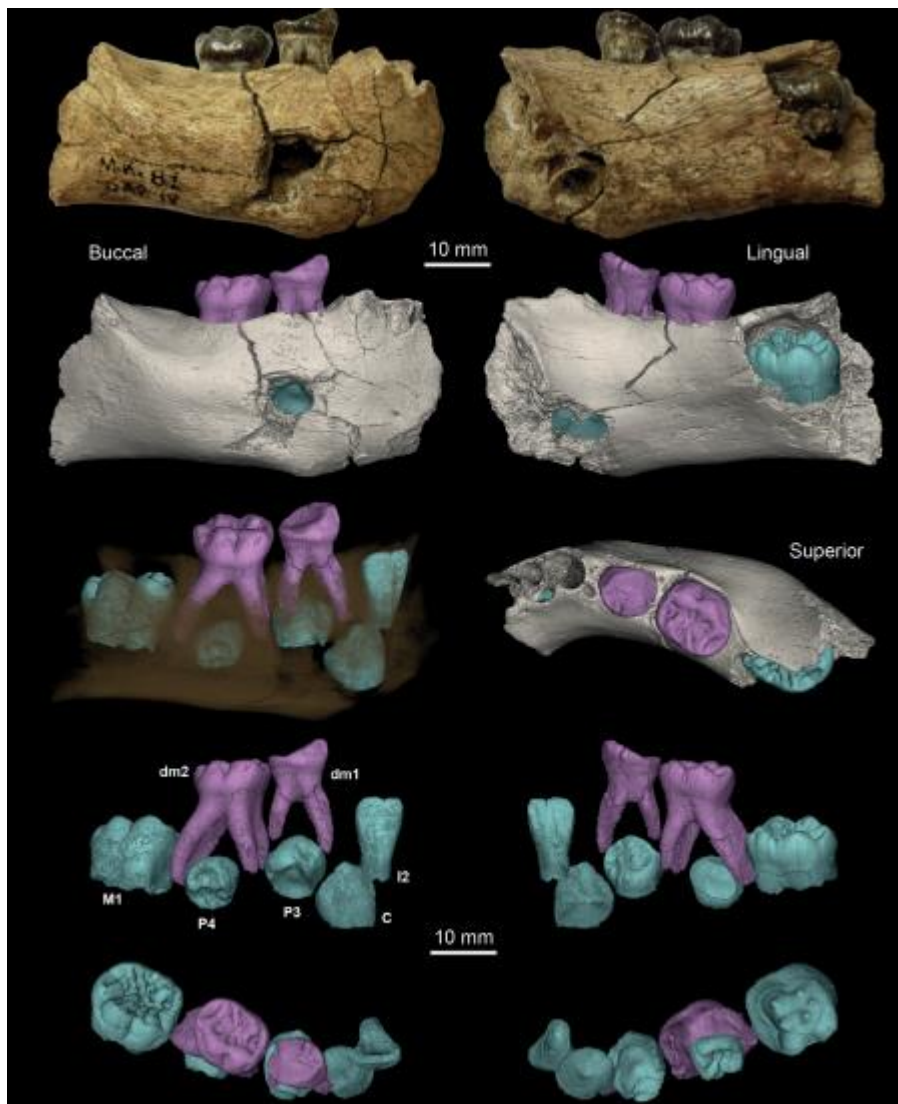


Fig. 3. The GAR IVE mandible.

Views showing the preserved deciduous molars (dm1 and dm2) and the germs of the permanent teeth (I2, lateral incisor; C, canine; P3 and P4, third and fourth premolar; M1, first molar). The image was modified from (15).

The enamel-dentine junction shape of the permanent third premolar exhibits morphological affinities with *H. erectus* based on similarities in crown height and the position and relative height of the metaconid (Fig. 4A). The enamel-dentine junction shape of the permanent first molar is intermediate between *Australopithecus* and later *Homo*, and plots closest to KNM-ER 992. This reflects a number of features including a relatively reduced hypoconulid, which separates *H. erectus* from *H. habilis* (Fig. 4B). The enamel-dentine junction ridge of the permanent fourth premolar is less diagnostic [since the tooth is not crown complete (15), the cervix could not be used] and the GAR IVE specimen shows similarities with both *H. habilis* and *H. erectus* (fig. S21). Both premolars show strong similarities to KNM-WT 15000 at the outer enamel surface (fig. S22). The permanent canine is not crown complete [supplementary figure S1 in (15)], but the preserved enamel morphology is similar to *H. erectus* specimens such as KNM-ER 820 (fig. S22). Relative tooth crown size of the premolars (i.e., having premolars that are similar in crown size) and first molar also resembles *H. erectus* (Fig. 4C). It is currently difficult to make comparisons with material definitively attributed to *H. rudolfensis* (e.g., KNM-ER 1482, 1801 and KNM-ER 60000) due to the limited number of specimens and the preservation/degree of attrition of many of the mandibular teeth, but we consider what is measurable of the dentition of both to be more similar to *H. habilis* than to *H. erectus*. Overall, this expanded analysis of the external and internal morphology of the Garba IVE specimen is consistent with an attribution to *H. erectus* rather than *H. habilis*.

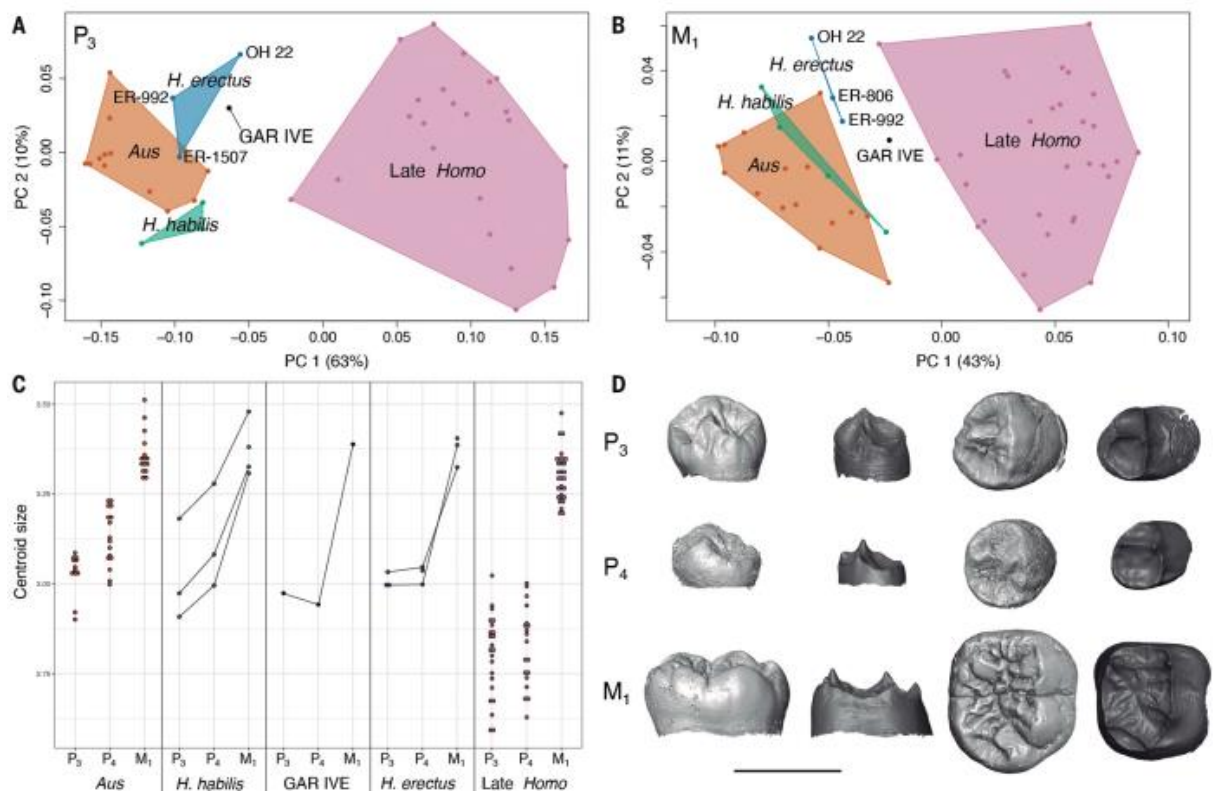


Fig. 4. Analysis of the internal tooth shape of the permanent postcanine dentition. (A) Plot of first and second principal components (PC 1 and PC 2) of mandibular third premolar enamel-dentine junction shape. (B) First and second principal components of mandibular first molar enamel-dentine junction shape. The variation explained by each principal component is shown in parentheses. In both principal components analysis (PCA) plots, GAR IVE is most closely associated with *H. erectus*. (C) Tooth-size variation (centroid size of enamel-dentine junction ridge landmarks) between the third premolar, fourth premolar, and first molar in GAR IVE and the comparative sample. (D) Surface models of the third premolar, fourth premolar, and first molar in (left) lingual and (right) occlusal view (enamel surface in light gray and enamel-dentine junction surface in dark gray).

Discussion

At ca. 2 Ma, the GAR IVE mandible is one of the earliest *H. erectus* fossils so far discovered, and the only specimen whose taxonomic identification is based on teeth, which are known to have a strong taxonomic signal (15-18). Furthermore, it is the first to be directly associated in a sealed deposit with Oldowan stone tools in Africa. The same industry is also found in underlying level Garba IV F, pointing to a fully-in- grained behavior that we attribute to *H. erectus* activity. The many small, pointed tools and the systematic use of obsidian make it conspicuously different from the 2.4-1.6 Ma Oldowan found elsewhere, and notably at sites where remains of *Homo habilis* were also discovered (table S2). Six knapped stones classified as Oldowan have been reported at Drimolen (19) and while a ca. 2.04 Ma neurocranium (20) has been classified as *H. aff. erectus* based on affinities with the Mojokerto cranium (and we note that there is no similarly aged *Paranthropus robustus* remains and thus the hominin that produced the material cannot be determined with certainty (19, 21). The innominate hip bone KNM-ER 3228 from Koobi Fora is not directly associated with stone tools (22), while at Olduvai PTK, the OH 86 proximal phalanx attributed to *Homo cf. H. erectus sensu lato* is associated with Oldowan stone tools (23), but is dated to 1.84 Ma. Hominin taxa such as *H. habilis*, *Paranthropus*, and *Australopithecus* lived at the low to middle elevation of eastern and southern Africa, i.e., up to 1500 m asl, and likely coexisted with *H. erectus*, such as at Drimolen, Olduvai, and Koobi Fora (24). Based on the current study, however, only *H. erectus* is known to have inhabited the Ethiopian highland, at or above 2000 m asl.

Around 2 Ma (i.e., before the Olduvai/Matuyama boundary at 1.925 Ma), there is a shift toward the production of Acheulean tools, such as handaxes and cleavers produced on large flakes. Previously, only statistical models had suggested such an early date (25), while published databased on field- work tentatively pointed to the initial development of this technology at ca.1.8 Ma (26-29). The Garba IV D data suggest that the Acheulean actually emerged 200,000 years earlier and that there is a substantial chronological gap between the emergence of the Early Acheulean at Garba IV and in the Rift. Compared to small flake production in the Oldowan, this major step in technological and cultural development implies both the accurate search and management of larger blanks of stone, and the strength to produce significantly larger flakes. Some large flakes were then partially retouched, and others were shaped into more complex tools. Outside Melka Kunture, fully knapped handaxes, with a true bilaterally and bifacial balanced shape, are documented 1.7 Ma at FLK West (27). At Melka Kunture, the Early Acheulean was also discovered at Gombore IB, later in age at ca.1.66 Ma (6, 30), where a very robust *Homo* humerus was found in association (30, 31). As at Garba IV D, there were fully-shaped handaxes, which implies that in the earliest phases of the Acheulean the mental templates and skills of bifacial shaping were already developed.

The aridification of Africa, which started after 2.8 Ma (32, 33), could have driven hominin groups beyond previously occupied environments. A highland environment, such as that at Garba IV, at an altitude of 2000 m asl and more, exposes individuals to less oxygen, higher exposure to UV rays, more rain and cooler temperatures. Will et al. (34) have recently examined the *Homo* fossil record up to 1 Ma, and show that Bergmann's rule applies, which predicts a larger body size in colder environments. The larger-bodied and larger brained *H. erectus* was possibly better adapted to the highlands than smaller-bodied hominins such as *Australopithecus* and *H. habilis*. Additionally, the vegetation was different from that of the savanna, while some animal species testify of a degree of endemism. The hominins would have needed to acquire knowledge of these novel resources. Information on plant use is not preserved, but the nearby forests would have offered resources such as fruit, nuts, tubers, and roots. Butchery marks have been detected on hippopotamus and bovid bones from Garba IV D (35). The fossil and archaeological evidence from Garba IV indicates that *H. erectus* could cope with demanding local conditions; eventually changing their way of producing stone tools, and configuring the pieces that define the emergence of the Acheulean technocomplex, as also recorded at Gombore IB. The ca. 2 Ma core and flake assemblages made by *Homo erectus* at Melka Kunture allow us to put into a new perspective the North African and Asiatic assemblages which, later on, still include only small flakes, without any handaxes or other large tools (36-39). They could be the outcome of an earlier expansion or record an expansion from areas where *H. erectus* and the Acheulean appeared later than in the Ethiopian highlands. In Sub-Saharan Africa, the early Acheulean of Garba IVD means that Oldowan and Acheulean industries co-existed over at least 300,000 years, which revives the de- debates about who were the makers of core and flake assemblages at lower elevations. At Olduvai (Bed II) and in the Middle Awash the coexistence of different hominins producing different lithic industries has been suggested (27, 40, 41). The hominin fossil record is dominated by the discoveries made at low to middle elevations in the Rift Valley and in the cave deposits of South Africa. The fossil and archaeological remains from Melka Kunture demonstrate that the highlands of East Africa, with a different paleoenvironment, is pivotal to understanding *H. erectus* behavior. Around 2 Ma, there is evidence at Garba IV of *H. erectus* retaining behavioral characteristics close to those of *H. habilis*. It was still producing core and flake assemblages but with different features than typical Oldowan technocomplexes. Then around 1.95 Ma, the Early Acheulean emerged with archetypal bifacial tools. Between 2 and 1.9 Ma, the Melka Kunture site provides the earliest evidence of *H. erectus*, who quickly adjusted to a high-altitude environment first producing Oldowan technology and then developing Acheulean technology.

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Data and materials availability: All data supporting the findings of this study are available within the paper and its supplementary materials. Landmark data and R code used to conduct the geometric morphometric analyses used in this study are available on the Publications page of Human Fossil Record.org (<https://human-fossil-record.org/index.php?/category/595>). The hominin mandible #MK 81 GAR IVE 0043 as well as the palaeontological and archaeological collections from the site are kept at the National Museum in Addis Ababa and available for scientific research.

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SUPPLEMENTARY MATERIALS

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