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ANTHROPOLOGY

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 because of its direct association with an Oldowan lithic industry. Here, we used synchrotron imaging to examine the internal morphology of the unerupted permanent dentition and confirmed its identification as *H. erectus*. Additionally, we used revised paleomagnetic ages to show that (i) the mandible in level E is ~2 million years old and represents one of the earliest *H. erectus* fossils and that (ii) overlying level D, ~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 square kilometers in the Upper Awash, on the Ethiopian plateau at ≥2000 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, from 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 subspecies (*2*). In 1981, an infant mandible was discovered in level E of the Garba IV site, although 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 paleoecological context of the site on the basis of analysis of the faunal assemblage and palynology, and reassess 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 technocomplex. Broadening our knowledge of the environment at the time and not limiting it to the savanna and to lower altitudes is relevant to understanding how *H. erectus* was able to expand beyond Africa.

Stratigraphy and chronology

The sedimentary sequence of the multilayered 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}Ar/^{39}Ar and preliminary magnetostratigraphic analyses had previously dated these levels to shortly before and shortly after 1.7 million ± 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 Ma) and the Matuyama/Reunion boundary (2.116 Ma) 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 follows: level F, 2.02 (−0.095; +0.096) Ma; level E, 2.00 (−0.0075; +0.1) Ma; and level D, 1.95 (−0.025; +0.1) Ma (*6*) (Fig. 1, C and D). These much older dates for levels D to F have considerable implications for the interpretation of the archaeology and the hominin fossil found at the site.

Archaeology

Level E at Garba IV (now dated to ~2.00 Ma) was first tested in 1981, and 34 m^2 were eventually exposed (fig. S4 and figs. S8 to S10), with an additional exposure of 12 m^2 of underlying level F (now dated to ~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 and S13). Many of these artefacts are made from small flakes, mostly 20 to 50 mm in length, with ~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 m^2 and redated to ~1.95 Ma, the ~7000 lithic tools (table S1) differ from those of the underlying Oldowan assemblage owing to the production of large flakes (>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

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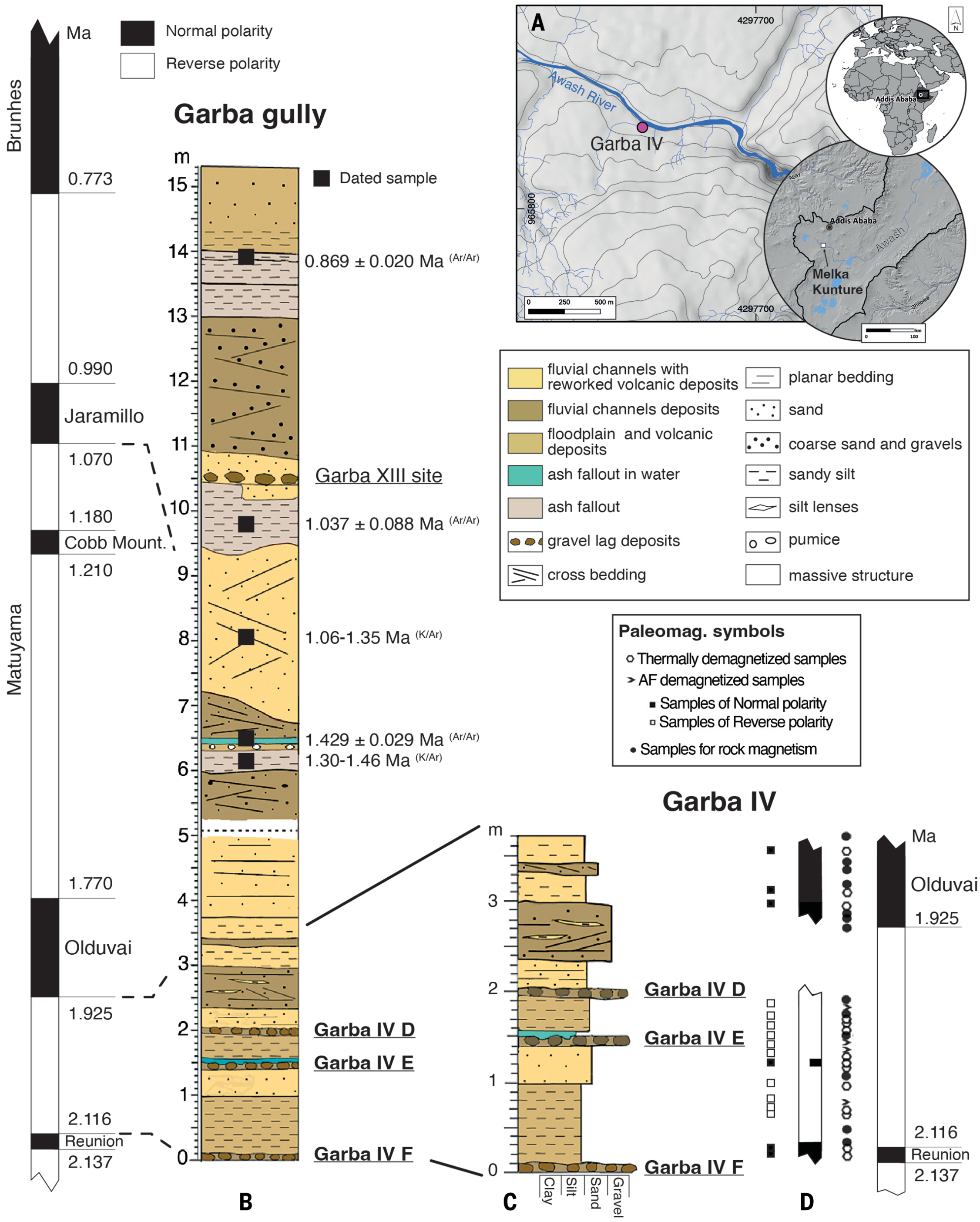

Fig. 1. Location, magnetostratigraphy, and chronostratigraphy of Garba IV. (**A**) Location map of the Garba IV site (Melka Kunture, Upper Awash, Ethiopia). (**B**) The stratigraphy of the Garba gully, with both Garba IV and Garba XIII, a middle Acheulean site (*42*). Geomagnetic polarity timescale is from (*43*), $^{40}Ar/^{39}Ar$ 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).

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LCTs constitute ~1% of the analyzed assemblage (large flakes, 41; 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 thousand to 100 thousand years (kyr) in this distinctive high-altitude paleoenvironment.

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*). The palynology indicates the presence of bushy woodlands alternating with patches of grassland in the area of Melka Kunture at around 1.8 Ma or possibly earlier. (*1*). A more open vegetation and a mountain grassland followed, which further expanded during the deposition of level D at Garba IV.

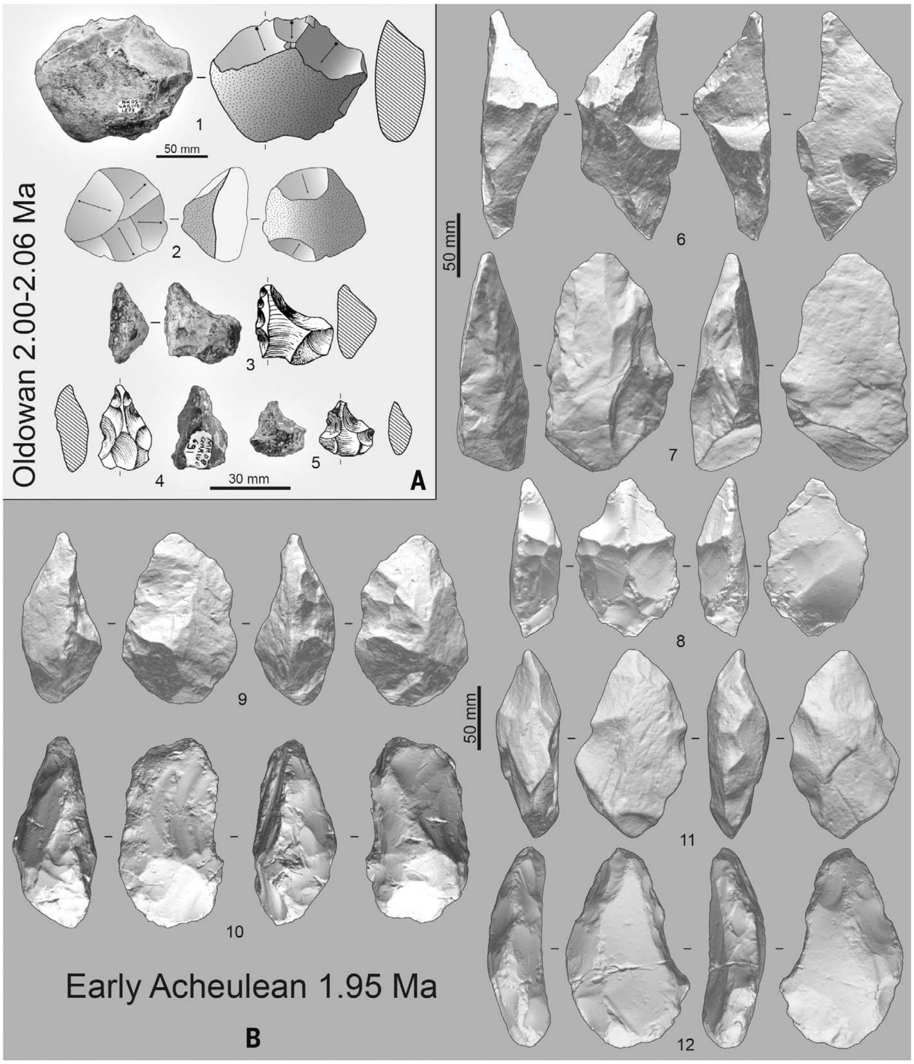

Fig. 2. Garba IV artifacts. (**A**) Levels E and F (2.00 Ma to 2.06 Ma), Oldowan. Images show obsidian cores (1 and 2) and obsidian pointed tools (3 to 5). (**B**) Level D (1.95 Ma), Early Acheulean. Images show large retouched flakes shaped on basalt or obsidian (6 to 8) and handaxes shaped on lava,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

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 ~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; this unambiguously points to an open environment and is consistent with the relatively high frequency of equids (*2*). Also consistent with an open environment are measurements of $^{13}C/^{12}C$ isotopic ratios of dental-enamel carbonates carried on hippopotamus (n = 11), bovid (n = 1), and equid (n = 1) teeth from level D. The results show that hippos, bovids, and equids consumed C_4 plants, suggesting the presence of C_4 high-elevation grasslands (*11*) (fig. S20).

The bovid material from levels E and F cannot be identified beyond generic rank, whereas 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 the subspecific level. Thus, the fauna record testifies to some endemicity (*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 described as struck by a rare genetic disorder affecting its enamel (*amelogenesis imperfecta*) (*14*), this was recently refuted with synchrotron imaging, and features previously interpreted as pathological were instead shown to result from taphonomic processes (*15*). On the basis of medical computed tomography (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 CT to produce high-resolution images of the enamel and dentine surfaces of the unerupted permanent dentition (*15*) because these have been shown to maximize the taxonomic information in hominin teeth (*16*–*18*). We conducted a three-dimensional 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.

The enamel-dentine junction shape of the permanent third premolar exhibits morphological affinities with *H. erectus* that are 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 that of *Australopithecus* and later *Homo* and plots closest to KNM-ER 992. The shape 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 [because the tooth is not crown complete (*15*), the cervix could not be used], and the GAR IVE specimen shows similarities to 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 that of *H. erectus* specimens such as KNM-ER 820 (fig. S22). The relative tooth-crown size of the premolars (i.e., having premolars that are similar in crown size) and first molar is also similar to that of *H. erectus* (Fig. 4C). It is currently difficult to make

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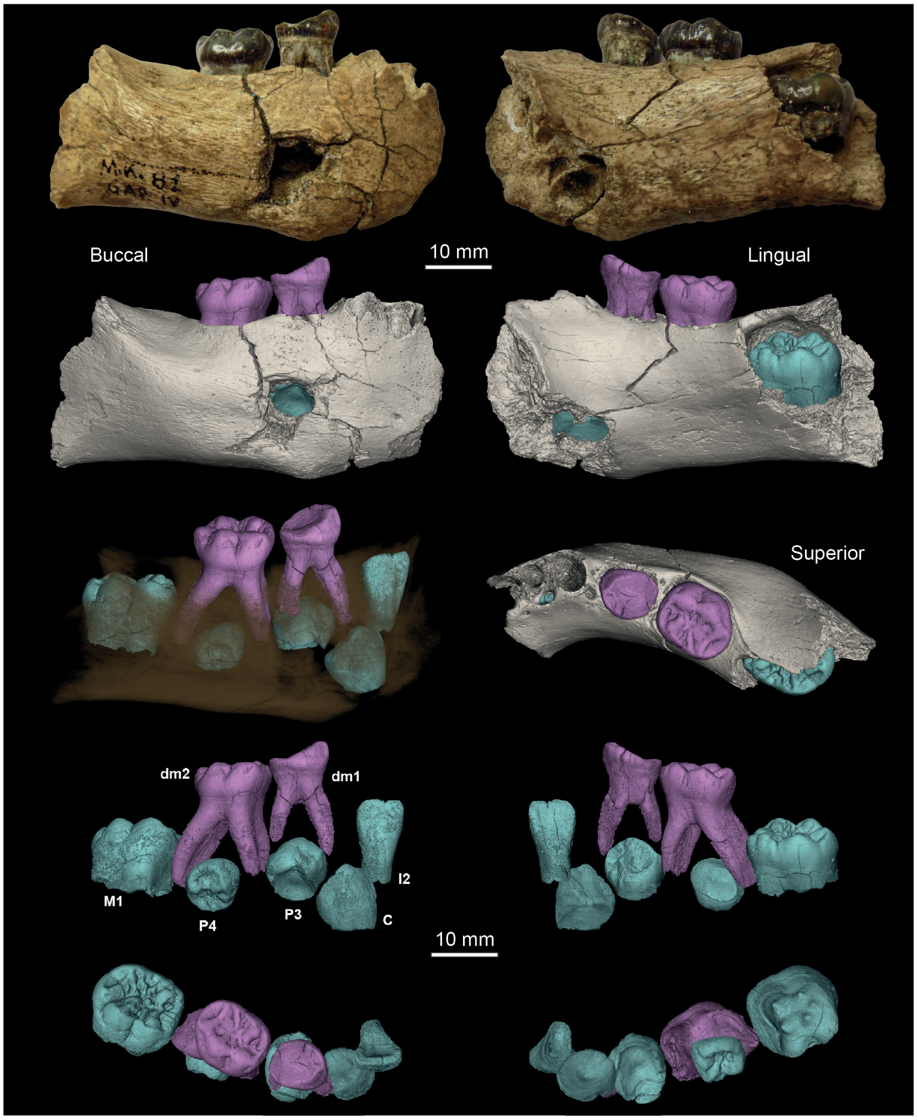

Fig. 3. The GAR IVE mandible. Views showing the preserved deciduous molars (dm1 and dm2) and the germs of the permanent teeth (I2, lateral incisor; C, canine; P3 and P4, third and fourth premolar; M1, first molar). The image was modified from (*15*).

comparisons with material definitively attributed to *H. rudolfensis* (e.g., KNM-ER 1482, 1801, and KNM-ER 60000) because of the limited number of specimens and the preservation and 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*.

Discussion

At ~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 IVF, pointing to a fully ingrained behavior that we attribute to *H. erectus* activity. The many small, pointed tools and the systematic use of obsidian make this assemblage conspicuously different from the 2.4- to 1.6-Ma Oldowan material 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 although a ~2.04-Ma neurocranium (*20*) has been classified as *H.* aff. *erectus* on the basis of affinities with the Mojokerto cranium (and we note that there is no similarly aged *Paranthropus* cranium with which it can be compared), the site is dominated by *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*), whereas 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 (up to 1500 m asl) and likely coexisted with *H. erectus*, such as at Drimolen, Olduvai, and Koobi Fora (*24*). On the basis of this 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*), although published data based on fieldwork tentatively pointed to the initial development of this technology at ~1.8 Ma (*26*–*29*). The Garba IVD data suggest that the Acheulean actually emerged 200 kyr earlier and that there is a substantial chronological gap between the emergence of the Early Acheulean at Garba IV and in the Rift Valley. Compared with 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 considerably 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 bifacially 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 ~1.66 Ma (*6*, *30*), where a very robust *Homo* humerus was found in association (*30*, *31*). As at Garba IVD, 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 ultraviolet 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 were smaller-bodied hominins such as *Australopithecus* and *H. habilis*.

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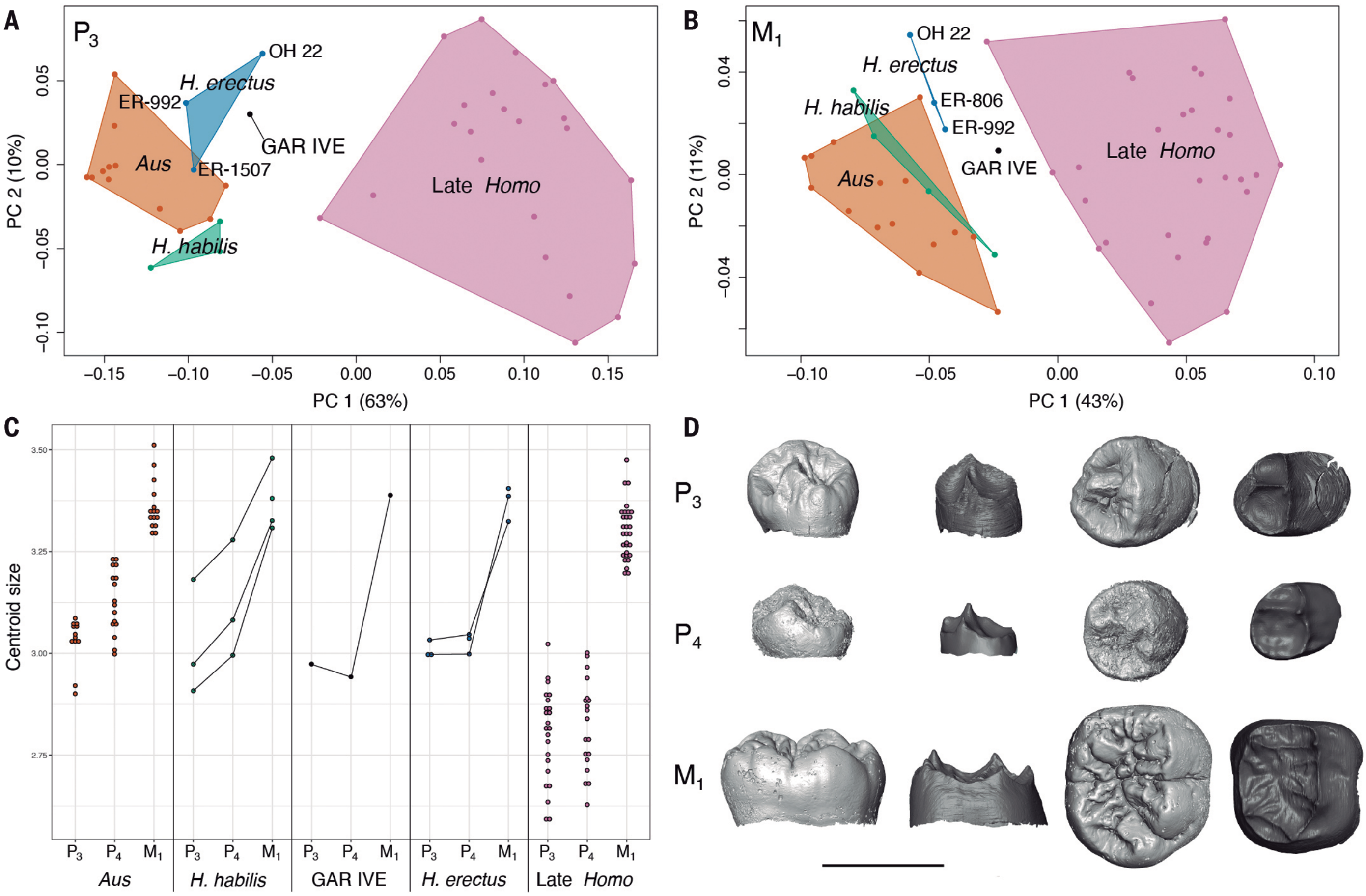

Fig. 4. Analysis of the internal tooth shape of the permanent postcanine dentition. (**A**) Plot of first and second principal components (PC 1 and PC 2) of mandibular third premolar enamel-dentine junction shape. (**B**) First and second principal components of mandibular first molar enamel-dentine 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).

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In addition, the vegetation of Melka Kunture was different from that of the savanna, although some of its 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 IVD (*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 ~2-Ma core and flake assemblages made by *H. 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*). These assemblages could be the outcome of an earlier expansion or the record of 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 establishes that Oldowan and Acheulean industries coexisted over at least 300 kyr, which revives the 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 their different paleoenvironment, are 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*. *H. erectus* was still producing core and flake assemblages but with different features than those of typical Oldowan technocomplexes. Then around 1.95 Ma, the Early Acheulean emerged with its 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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ACKNOWLEDGMENTS

We are grateful to the Authority for Research and Conservation of the Cultural Heritage (currently the Ethiopian Heritage Authority) and to the Ministry of Culture and Tourism of the Federal Republic of Ethiopia for the loan and temporary export permit of MK 81 GAR IVE 0043 (27 November 2015 to 26 January 2016) awarded to M. Mussi. For access to comparative fossil specimens (and associated CT scans), we thank the following individuals and institutions: B. Zipfel and S. Jira (Evolutionary Studies Institute, University of the Witwatersrand); E. Mbua and J. Kibii (National Museums of Kenya); A. Mabulla (National Museum of Tanzania); the Tanzania Commission for Science and Technology; M. Endalemaw and Y. Assefa (Ethiopian Authority for Research and Conservation of Cultural Heritage); W. Kimbel (Arizona State University); Z. Alemseged (University of Chicago); F. Spoor (Natural History Museum, London); J.-F. Tournepiche (Musée d'Angoulême); J.-J. Cleyet-Merle (Musée National de Préhistoire, Les Eyzies-de-Tayac); J. Radovčić (Croatian Natural History Museum); F. Groening (Senckenberg, Forschungsstation für Quartärpaläontologie); V. Merlin-Langlade (Musée d'Art et d'Archéologie du Périgord); and M. Toussaint (ASBL Archéologie Andennaise and Royal Belgian Institute of Natural Sciences). Isotopic analyses have been funded by the Biogeology Lab (University of Tübingen), and we thank P. Tung for technical support. For technical assistance, we thank F. Spoor, D. Plotzki, and H. Temming. We are grateful to P. Tafforeau and colleagues at the ESRF for accessing beamtime on the ID19 beamline and for technical assistance. This research benefited from the scientific framework of the University of Bordeaux's IdEx Investments for the Future program/GPR Human Past. **Funding:** This research has been funded by Università di Roma Sapienza grant C26S133Z4B (M.M.); Università di Roma Sapienza grant SA11715C7C936C01 (M.M.); Ministero degli Affari Esteri e della Cooperazione Internazionale grant ARC-000799 (M.M.); Ministero degli Affari Esteri e della Cooperazione Internazionale grant ARC-001666 (M.M.); European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program grant agreement 819960 (M.M.S.); Fundación Palarq (Spain) grants 2019 (J.P. and M.M.), 2020 (J.P., M.M., E.M.-Q., and S.R.-J.), and 2021 (J.P., M.M., E.M.-Q., and S.R.-J.); Leakey Foundation grant 42137 (E.M.-Q.). Deutscher Akademischer Austauschdienst (DAAD) grant 57552336 (G.B.); Università di Roma Sapienza grant 0044296 (G.B.); CNRS (A.L.C.); and postdoc Xunta de Galicia grant ED481D-2022/023 (E.M.-Q.). **Author contributions:** Conceptualization: M.M. Methodology: L.D.B. reopened the excavated area and reidentified the archaeological levels for sampling. G.B. collected the faunal teeth-enamel samples (sampling and pretreatment). Investigation: R.T.M., stratigraphy and geology; M.M.S., T.W.D., A.G., A.L.C., and J.-J.H., analysis of the dental samples; D.G., paleontology; H.B. and G.B., stable isotopes; E.M.-Q., J.P., and S.R.-J., archaeological analysis; R.B., paleobotany; and A.L.C., analysis of the synchrotron micro-CT scans. Funding acquisition: M.M., M.M.S., J.P., E.M.-Q., S.R.-J., G.B., and A.L.C. Project administration: M.M., J.P., and E.M.-Q. Supervision: M.M. Writing – original draft: M.M., with contributions from all authors. Writing – review and editing: M.M. and E.M.-Q., with contributions from all authors. **Competing interests:** The authors declare that they have no competing interests. **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 paleontological and archaeological collections from the site, are kept at the National Museum in Addis Ababa and are available for scientific research.

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science.org/doi/10.1126/science.add9115
Materials and Methods
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Submitted 15 July 2022; resubmitted 16 December 2022
Accepted 29 September 2023
10.1126/science.add9115

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