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RESEARCH

Homo erectus technological behaviors during the Middle Pleistocene Transition: Engaji Nanyori, Oldupai Gorge

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Abstract
The Acheulean technocomplex is a milestone in the evolutionary adaptability, technological development, and dispersal of *Homo erectus*. While the earlier phases of the Acheulean have been thoroughly investigated in Eastern Africa, reliably dated assemblages in environmental context spanning the Middle Pleistocene Transition (1.2–0.8 Ma) are extremely rare at a global scale. Engaji Nanyori (Bed III, Oldupai Gorge) is one of a few sites offering a window into Acheulean behavior during this critical period of climatic crisis and aridification. We study lithic assemblages from recent excavations of an Acheulean occupational sequence dated 1.1–0.9 Ma, revealing a stable technological system that focused on flake production by relying on Oldowan-like knapping strategies while rendering infrequent the manufacture of Large Cutting Tools. We present a continental analysis of Acheulean technologies during the Middle Pleistocene transition aimed at exploring the influence of climatic, ecological, and environmental instability on adaptability. Our results underscore the numerous similarities between the technological strategies of Engaji Nanyori and those of the penecontemporary sites, illustrating the uniform character of African Acheulean assemblages regardless of their temporal, geographical or environmental settings.

Keywords Acheulean · Lithic technology · *Homo erectus* · Oldupai Gorge · Engaji Nanyori

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Introduction

The Acheulean technocomplex represents a pivotal innovation in human prehistory, marking a major step forward in hominin technological capability. Spanning more than 1.5 million years, from around 1.76 million years ago (Ma) to 200,000 years ago, the Acheulean is both the longest-lasting and most widespread technological tradition in the archaeological record (Beyene et al. 2013; Díez-Martín et al. 2015; Gallotti and Mussi 2018; Lepre et al. 2011). Moreover, the Acheulean is closely associated with *Homo erectus* and is believed to have played a crucial role in its successful dispersal across Africa (Fig. 1) and Eurasia (Lycett and von Cramon-Taubadel 2008; Lycett 2009; Mussi et al. 2023; Ollé et al. 2023; Shipton 2020, Shipton et al. 2023). Although initially described by the presence of large bifacial tools, such as handaxes and cleavers (Diez-Martín and Eren 2012; de la Torre 2016), it is now established that its emergence signals a key advance over the preceding Oldowan industry, with improvements in raw material selection and management, bifacial volumetric control, operative complexity, large flake acquisition during knapping, and higher product standardization (Cueva-Temprana et al. 2019; Duke et al. 2021; Key et al. 2020; Lombao et al. 2024; McHenry and de la Torre 2018; McPherron 2000; Sharon 2008; Stout 2011; Stout et al. 2015). However, despite its importance, several aspects of Acheulean technology remain unknown, particularly the ecological imprint on Acheulean traditions in different biomes and whether and how early hominins adapted their tool-making strategies in response to climatic, ecological, and environmental instability (Potts 2012, 2013; Potts et al. 2018).

Oldupai Gorge, one of the most important archaeological complexes in East Africa, offers a critical context for studying Acheulean technological development. The region is home to some of the earliest and largest Acheulean assemblages (Díez-Martín et al. 2015) (Fig. 1), since the pioneering work of Louis and Mary Leakey (Leakey 1936, 1951, 1967, 1971). Research into the Acheulean from Oldupai Gorge has largely focused on sites dating to 1.7 Ma − 1.3 Ma from Bed II (de la Torre 2016; de la Torre and Mora 2014). These assemblages have provided valuable insights into early Acheulean technological behavior (Arroyo and de la Torre 2018; Diez-Martín et al. 2009, 2013; 2015; 2017; 2019; 2024; Domínguez-Rodrigo et al. 2014; 2023; McHenry and de la Torre 2018; Rubio-Jara et al. 2017; Sánchez-Yustos et al. 2018; 2019; Santonja et al. 2014; 2018; de la Torre and Mora 2018a, b, 2020; de la Torre et al. 2012, 2018a, b; Torre and Mora 2018b; Uribelarrea et al. 2017, 2019) but leave a gap in the understanding of the Middle Pleistocene Transition (MPT) between 1.2 and 0.8 Ma.

The MPT represents a period notable for its pronounced climatic fluctuations and environmental changes, particularly marked aridity. At Oldupai Gorge, this is expressed in drastic fluctuations in water levels at paleolake Oldupai (Hay 1970, 1976; Kovarovic et al. 2013; Stanistreet et al. 2020a, b, c), scarce vegetation, wildfires, and limited freshwater availability. These events likely presented substantial adaptive challenges to early hominins; however, how Acheulean technology evolved—or remained stable—during this period of ecological stress is unknown, due to the scarcity of stratified sites from Bed III (1.2 Ma − 0.9 Ma) (Deino et al. 2021; Mercader et al. 2025). To date, Engaji Nanyori (JK/JK2) remains the only excavated site from Bed III that is available for the study of Acheulean behavior during a key paleoclimatic and evolutionary transition.

Engaji Nanyori is located approximately 2.5 km north of the 'junction' between the Main and Side Gorges (Fig. 1), extending from geological locality no. 14 (Hay 1976) in the east, to the part of the site first reported by Louis Leakey in 1951 and then excavated by Maxine Kleindienst (Kleindienst 1964, 1973), Mary Leakey (Leakey and Roe 1994), and our research group (Mercader et al. 2025) in the west. Detailed information on the lithological context of Oldupai Gorge, within which Engaji Nanyori is situated, is available elsewhere (a comprehensive review in Favreau 2024; Favreau et al. 2020; Hay 1976; McHenry and de la Torre 2018).

The pioneer excavations from the 1960s and 1970s yielded very large assemblages in excess of 40,000 faunal specimens and more than 20,000 lithics, along with a femur and a fragmented tibia ascribed to *Homo erectus* (Olduvai Hominid, OH34) (Day and Molleson 1976). A significant portion of the faunal legacy collections was originally deposited at the National Museums of Kenya (Pante 2013) then transported to the National Museum of Tanzania (Yravedra et al. 2020). However, the lithic legacy collection remains challenging to locate, with portions likely dispersed across various field and national museums or potentially missing altogether. The open-air museum that Mary Leakey built on the western side of Engaji Nanyori to exhibit pits and furrows, thought to represent hominin living floors for salt extraction (Leakey and Roe 1994), was then abandoned and went into ruins.

Recent archaeological and geological work (Mercader et al. 2025) revealed that north of Engaji Nanyori, a fluvial confluence formed during the MPT. Streams contributed to a complex sedimentary sequence expressed in six facies from fluvial channels approximately 1 m deep and 20 m wide with adjacent floodplain deposits, spanning three stratigraphic units—3 − 1, 3 − 2, and 3–3 (Fig. 1). Stratigraphic unit 3 − 2 contains three channel belts (A, B, C) equivalent to the deposits described in Kleindienst (1973)

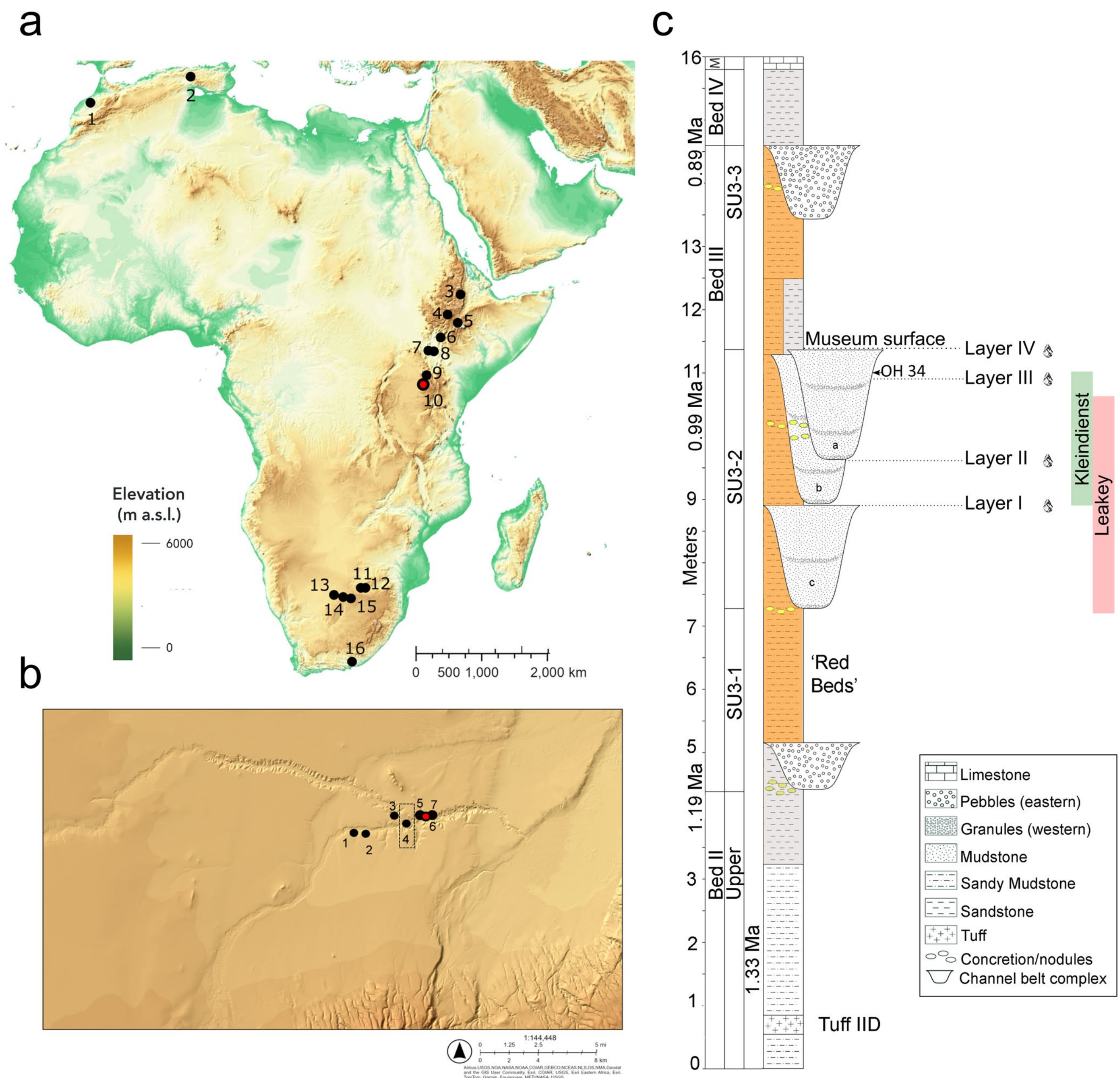

Fig. 1 **A**: Map of African Acheulean sites > 1 Ma. (1) Casablanca; (2) Ain Hanech, Tighenif; (3) Gona; (4) Melka Kunture; (5) Melka Wakena; (6) Konso Gardula; (7) West Turkana; (8) Koobi Fora; (9) Peninj; (10) Oldupai; 11. Sterkfontein, 12. Swartkrans; 13. Wonderwerk; 14. Canteen Kopje; 15. Vaal River; 16. Sundays River Penhill Farm. Red dot indicates the location of Oldupai Gorge. **B**: Map of Oldupai Gorge and sites from Beds II-III: (1) BK; (2) SHK; (3) FLK-W; (4) HWK; (5) TK; (6) EN; (7) EF-HR. Red dot indicates the location of Engaji Nanyori. Discontinuous rectangle indicates the position of the junction between the Main and Side Gorges. **C**: Lito-stratigraphic column of Engaji Nanyori, detailing the position of Beds II, III & IV, stratigraphic units, channel belts and archaeological layers. Column designed by Dr. Paul Durkin, ours modified from Mercader et al. 2025. Coordinates for sites' areas in maps **A** & **B** are in Supplementary Tables 1–2. Map and coordinates sources: https://elevation.arcgis.com/arcgis/rest/services/WorldElevation/TopoBathy/ImageServer Source: Airbus, USGS, NGA, NASA, NOAA, CGIAR, GEBCO, NLS, OS, NMA, Geodatastyrelsen, GSA, GSI and the GIS User Community

and Leakey and Roe (1994). The earliest, channel belt C, corresponds to Leakey's "lower coarse grey sand," comprising vertically and laterally amalgamated deposits. Channel belt B contains iron-stained gravel layers (Leakey's "fine-grained ferruginous sand"). Channel belt A, the most recent, consists mainly of cross-stratified gravelly sandstones that fine upward, with these finer deposits containing the *Homo erectus* fossils, located 0.5 m below Leakey's siltstones with "pits and furrows". New dating of Tuff IID establishes an age of 1.19 ± 0.06/0.07 Ma for the base of Bed III, while placing *Homo erectus* in the middle of Bed III (stratigraphic unit 3−2) at 0.99 ± 0.06/0.07 Ma (Mercader et al. 2025).

Our excavation within the perimeter of the former Leakey museum revealed four artifact-bearing layers: I-IV, all within stratigraphic unit 3−2. Layers I, II and III were deposited in sandy-to-gravelly point bars, abandoned channels, and subaqueous dunes, with an active channel dimension measuring 1 m deep and 20 m wide. These are high energy contexts yielding reworked artifacts and fossils, such as those excavated by Kleindienst (1973) and Leakey (Leakey and Roe 1994). We have recently shown that layer IV is the primary source of all cultural materials in situ (Mercader et al. 2025), in a low energy context, representing the original habitat preferred by hominins: the sinuous pond-like environments developed laterally to the stream by abandoned river channels following their avulsion.

We examine here approximately 2,000 newly excavated artifacts from Engaji Nanyori, securely dated to between 1.1 and 0.9 million years ago, offering a unique view into Acheulean technologies under the hyper arid environmental conditions of the MPT. By situating this site within a broader comparative framework of African Acheulean contexts, we further assess the influence of environmental variability on technological adaptation. Our findings contribute to understanding early examples of hominin adaptability and highlight the role of Acheulean technology in human evolution.

Materials and Methods

Stone Tool Analysis

The total number of lithics studied here is 1911 (Table 1), all retrieved during the 2022 fieldwork season from the museum trench at Engaji Nanyori. On raw materials, we determined morphology, Munsell color, grain size, texture, gloss, transparency, mineral composition, impurities, foliation and post-depositional alterations (Soto et al. 2020a, b). Macroscopic classification of raw materials was established through comparisons with a reference collection created and curated by the Stone Tools, Diet and Sociality project in the Tropical Archaeology Lab (TAL; Earth Sciences 811, University of Calgary), determining broad lithological groups (i.e. quartzite, basalt). Raw material sourcing methods and results have been detailed in associated publications (Favreau 2024; Favreau et al. 2020; Mercader et al. 2025; Soto et al. 2020a, b).

When analyzing the stone tool assemblage, we followed a standardized nomenclature to allow for cross-assemblage comparability, identifying 10 techno-typological categories (Cueva-Temprana et al. 2022; de la Torre and Mora 2018b):

(1) *Cores*: Blanks modified through specific knapping systems and/or techniques designed for flake detachment, characterized by removal scars on their exploitation surfaces and impact marks on their percussion surfaces. (2) *Core fragments*: Blanks displaying removals on their exploitation surfaces along with one or more fractures, preventing definitive identification of the knapping system or technique employed. (3) *Large Cutting Tools (LCTs)*: Large blanks shaped through one or more knapping and/or retouching techniques, leading to mass and volume reduction aimed at specific configurations. This category encompasses artifacts linked to the emergence of the Acheulean technocomplex, including bifaces, cleavers, and picks, as well as modified or unmodified flakes exceeding 100 mm in length. (4) *Retouched flakes*: Knapping products subjected to post-extraction modification following defined shaping patterns. (5) *Complete flakes*: Knapping products retaining both dorsal and ventral surfaces, a percussion platform, and lacking fractures, with a technological length exceeding 20 mm. Within this category, debris are included– artifacts sharing the same technical attributes as complete flakes but measuring less than 20 mm in technological length. (6) *Fragmented flakes*: Knapping products exhibiting one or more fractures while still preserving both dorsal and ventral surfaces, as well as a percussion platform. (7) *Flake fragments*: Knapping products retaining dorsal and ventral surfaces but lacking a percussion platform due to prior fracturing. (8) *Manuports*: Unmodified natural blanks introduced into an anthropic context. (9) *Percussion material*: Blanks displaying substantial evidence of use on their surfaces, indicative of pounding activities. (10) *Undetermined shatter*: Irregular lithic fragments within the assemblage lacking sufficient diagnostic technological attributes.

Stone tools were analyzed according to established technological criteria (Andrefsky 2008; Laplace 1972), with no size-based exclusion applied to the assemblage. Each artifact's weight was recorded in grams, and rounding was assessed using a scale ranging from 0 to 3, where 0 represents fresh specimens, 1 indicates partial rounding (50%), and 3 signifies fully rounded artifacts. Fractures were documented based on technological measurements, while patina and concretion were classified on a similar 0-to-3 scale, where 0 represents the absence of patina or concretion, 1 indicates partial presence (50%), and 3 signifies full patina or concretion.

The classifications of complete flakes, retouched flakes and fragmented flakes, followed the following criteria: (1) Platform cortex (non-cortical, cortical), (2) Platform morphology (plain, lineal, point-shaped, facetted), (3) Number of platform facets, if present, (4) Platform measurements (length and width), (5) Platform angle (angle between the platform and the ventral surface), (6) Bulb type (pronounced or diffuse), (7) Ventral surface delineation (straight, concave, convex, sinuous), (8) Termination (step, hinge, feather, overshoot), (9) Cortex presence (non-cortical, non-cortical dominant over cortical, cortical dominant over non-cortical, complete cortex), (10) Cortex location, 11) Dorsal surface number of scars, 12) Arrangement of scars regarding technological orientation (longitudinal, transversal, diagonal, centripetal, etc.), 13) edge mm (full sum).

Retouched flakes were analyzed adapting the criteria of Laplace's analytic typology (Laplace 1972): (1) Perimeter configuration (%), (2) Retouch orientation (regarding the platform), (3) Retouch mode (simple, abrupt, plain), (4) Retouch amplitude (regarding the edge), (5) Retouch depth (regarding the surface), (6) Retouch direction (direct, inverse, alternate, alternating), Retouch continuity (continuous, discontinuous, notch, denticulate), (7) Edge delineation (straight, concave, convex, sinuous), (8) Retouched mm (complete sum). In accordance with Laplace's analytic typology, each retouched artifact was assigned a primary type code, which was subsequently translated into broader public nomenclature to enhance accessibility and facilitate immediate comprehension.

For cores, we studied (1) Faciality: unifacial, bifacial, multifacial, (2) Cortex: non-cortical, non-cortical dominant, cortical dominant, cortical, (3) Qualitative reduction stage (tested, initial, medium, exhausted), (4) Hierarchical surface organization, (5) Product predetermination, (6) Rotation (when possible): bifacial alternating, bifacial alternate, bifacial continuous, bifacial hierarchical, (7) Extraction negatives: unipolar, bipolar, multipolar, centripetal, (8) Angular relationship between percussion platform and removal surface, (9) Perimeter %: 1 C (0–25%), 2 C (25–50%), 3 C (50–75%), 4 C (75–100%).

Knapping methods in core exploitation were also defined: (1) Multipolar multifacial: core whose volumetric management involves a minimum of four surfaces exploited in at least four different directions. (2) Unifacial unipolar longitudinal: A single surface was exploited according to unidirectional schemes. (3) Bifacial orthogonal: knapping of two opposed surfaces unidirectionally. (4) Bifacial centripetal: exploitation of two surfaces separated by a horizontal plane, each with a minimum of three removals following a centripetal scheme. (5) Unifacial centripetal: exploitation of one surface with a minimum of three removals following a directional scheme towards the center of the surface. (6) Bipolar-on-anvil: technique in which the positioning of the blank is on anvil. (7) Unifacial bipolar opposed: one single surface was exploited following an opposed bidirectional scheme.

Descriptive data representation and statistical analysis (Tables 1 and 2; Fig. 2) was conducted using *Excel 2019* and *PAST V.4.03* software (Hammer et al. 2008). Figures of stone tool artifacts (Figs. 3, 4, 5 and 6) including technical schemes on cores and LCTs were designed using Inkscape vector free software.

Comparison with African Acheulean Sites

To contextualize the Engaji Nanyori assemblage within the broader Acheulean landscape and examine whether Acheulean assemblages reflect technological evolution over time, regional trends, or environmentally driven adaptability, we conducted a comparative analysis with several African assemblages older than 1 Ma. This dataset includes approximately 40 assemblages spanning roughly 750,000 years across diverse environmental settings in Northern, Southern, and Eastern Africa, allowing us to assess whether assemblages exhibit significant variation based on chronology or geographic context. Paleoenvironmental data was incorporated to determine whether assemblage similarities correlate with comparable environmental conditions. Additionally, an Oldowan assemblage (HWK-EE) was included as a control, given its attribution to a distinct technocomplex while remaining penecontemporaneous with many Acheulean sites at Oldupai Gorge.

Our comparison was driven by three directional hypotheses: (1) Acheulean technology exhibits a stable, uniform character across African regions and environmental contexts, as variability among assemblages normally reflects differences in artifact proportions but not manufacturing processes. (2) The observed differences in assemblage composition may primarily reflect functional adaptations rather than environmental or cultural distinctions. (3) Flake production strategies are homologous in both Oldowan and Acheulean technology.

We selected ten techno-typological categories commonly used on published African Oldowan and Acheulean datasets: (1) percussion material, (2) complete & fragmented flakes, (3) retouched flakes, (4) LCTs & LCT fragments, (5) cores, (6) unifacial/chopper cores, (7) bifacial centripetal cores, (8) bifacial orthogonal cores, (9) multifacial cores/polyhedrons, (10) bipolar-on-anvil cores. The selection of broad variables was aimed at facilitating data gathering and maximize inter-assemblage comparability, as the widespread use of varying nomenclature and criteria to describe identical artifact types has rendered comparisons among sites extremely challenging in the past.

Data tabulation was derived from existing literature (Table 2, caption) and structured into three formats. Standard numerical values were applied when technological descriptions aligned with our own classification criteria. Non-applicable values (N/A) indicate either unavailable data or instances of incompatible nomenclature. Values marked in bold represent conservative estimates or minimum counts, as the available descriptions only partially align with our technological categories. Finally, all tabulated data were normalized for Principal Component Analysis (PCA) using the Z-score formula. PCA was performed using *PAST V.4.03* software and *RStudio* v4.0.2.

Results

Assemblage Composition and Raw Material Distribution

1911 artifacts were newly excavated in the museum area from Engaji Nanyori throughout four archaeological layers: I (n = 730, lowermost), II (n = 268), III (n = 342), and IV (n = 571, uppermost). A comprehensive description of raw material distribution and techno-typological groups is presented in Table 1; Fig. 2, with representative artifacts from layers I-IV shown in Figs. 3, 4, 5 and 6.

Layer I (Fig. 3) comprises the largest assemblage, with >95% of stone tools made on quartzite and some on lava and sandstone. The assemblage weighs 22.4 kg, of which quartzite contributes 14.5 kg. In layer II (Fig. 4), the assemblage amounts to 6.1 kg, exhibiting identical quartzite and phonolite proportions with a slightly higher frequency of basalt use (4.1%). A similar raw material distribution pattern is present in layer III (Fig. 5), where artifacts were made mainly on quartzite (94.1%). However, this layer presents– albeit in small proportions– the highest raw material variety identified at the site, with evidence of phonolites, basalts, granitoids and sandstones. The total weight of the layer III assemblage amounts to 9.5 kg, of which 7.7 is quartzite. Finally, layer IV (Fig. 6) contains the second largest assemblage of the sequence, with a raw material distribution continued to be predominated by quartzite (85.6%), followed by the highest proportion of phonolite use at the site (n = 53, 9.3%) and a marginal presence of other rocks. The total weight of the assemblage is ~14 kg, from which 9.5 kg are quartzite and 1 kg are phonolite.

In summary, the complete Engaji Nanyori assemblage is overwhelmingly dominated by quartzite, which constitutes approximately 95% of all artifacts across all layers (Fig. 2), with lower proportions of basalt and phonolite and marginal contributions of other rocks such as sandstones and granitoids. Only slight variations in raw material proportions occur between layers, indicating stable access to quartzite over time.

Reduction Strategies

Knapping strategies are well represented at Engaji Nanyori through a sample of cores (n = 101, 5% of the complete

Table 1 Summary description of the Engaji Nanyori 2022 stone tool assemblage based on techno-typological categories (cores, core fragments, LCTs, etc.) identified by archaeological layers and raw material types(Q, quartzite; B, basalt; P, phonolite; G, granitoid; S, sandstone).

	Layer I						Layer II						Layer III						Layer IV					
	Q	B	P	G	S	Total	Q	B	P	G	S	Total	Q	B	P	G	S	Total	Q	B	P	G	S	Total
Cores	34	1	0	0	0	**35**	11	1	0	0	0	**12**	15	1	1	1	0	**18**	29	4	3	0	0	**36**
Core fragments	7	0	0	0	0	**7**	1	0	0	0	0	**1**	6	0	0	0	0	**6**	5	0	0	0	0	**5**
LCTs	1	0	0	0	0	**1**	0	0	0	0	0	**0**	1	0	0	0	0	**1**	0	2	0	0	0	**2**
Retouched flakes	3	0	0	0	0	**3**	1	0	0	0	0	**1**	5	1	0	0	0	**6**	12	5	4	0	0	**21**
Complete Flakes	443	6	7	0	0	**456**	165	0	1	0	0	**166**	189	1	6	0	0	**196**	285	8	37	0	1	**331**
Flake fragments	174	1	0	0	1	**176**	60	0	0	0	0	**60**	73	1	1	0	0	**75**	106	1	4	0	0	**111**
Fragmented flakes	17	0	0	0	0	**17**	11	0	1	0	0	**12**	22	0	1	0	0	**23**	31	0	3	0	0	**34**
Percussion material	2	5	0	0	0	**7**	0	7	0	0	0	**7**	1	3	0	1	1	**6**	4	3	0	0	1	**8**
Manuports	2	10	0	0	2	**14**	0	3	0	0	0	**3**	0	1	0	0	0	**1**	1	3	1	0	0	**5**
Shatter	13	0	1	0	0	**14**	6	0	0	0	0	**6**	10	0	1	0	0	**11**	16	1	1	0	0	**18**
Total	**696**	**23**	**8**	**0**	**3**	**730**	**255**	**11**	**2**	**0**	**0**	**268**	**322**	**7**	**10**	**2**	**1**	**342**	**489**	**27**	**53**	**0**	**2**	**571**

Table 2 Comparison among representative Late Oldowan/Acheulean African sites older than 1 ma. based on generic techno-typological categories. Values highlighted in bold indicate a minimum number for comparison. N/A categories indicate lacking information and/or impossibility to reliably translate to our categories

Country	Area	Site	Environment	Age (Ma.)	Percussion material	Complete & fragmented flakes	Retouched flakes Total	LCTs & LCT fragments	Cores Total	Unifacial / Chopper cores	Bifacial centripetal cores	Bifacial orthogonal cores	Multifacial cores/ Polyhedrons	Bipolar-on-anvil cores
Tanzania	Oldupai	FLK-W	Woodland-grassland mosaics	~1.75	120	429	27	26	213	35	7	16	37	33
Tanzania	Oldupai	HWK-EE	Woodland-grassland mosaics	~1.7	349	4449	157	0	925	213	65	208	60	83
Tanzania	Oldupai	BK	Woodland-grassland mosaics	~1.6–1.3	4	86	6	0	12	1	4	0	7	23
Tanzania	Oldupai	SHK	Woodland-grassland mosaics	~1.6–1.3	173	536	79	2	243	67	9	46	84	3
Tanzania	Oldupai	EF-HR	Woodland-grassland mosaics	~1.5	50	1570	57	117	144	32	10	33	12	12
Tanzania	Oldupai	TK – LF	Woodland-grassland mosaics	~1.5–1.3	74	1421	56	83	268	50	27	0	59	44
Tanzania	Oldupai	TK – SF	Woodland-grassland mosaics	~1.5–1.3	38	341	9	48	91	11	11	0	13	41
Tanzania	Oldupai	EN 2022	Xerophytic shrublands	~1.1–0.9	27	1654	31	4	101	21	23	26	12	10
Tanzania	Oldupai	EN Leakey	Xerophytic shrublands	~1.1–0.9	48	3201	51	25	79	2	10	**0**	39	0
Tanzania	Oldupai	EN Kleindienst	Xerophytic shrublands	~1.1–0.9	66	12181	351	38	390	N/A	N/A	N/A	N/A	N/A
Tanzania	Oldupai	Engaji Nanyori Total	Xerophytic shrublands	~1.1–0.9	141	17036	433	67	570	**23**	**33**	**26**	**51**	**10**
Tanzania	Peninj	ST. Complex	Woodland-grassland mosaics	~1.6–1.4	9	76	28	0	29	7	9	2	7	0
Tanzania	Peninj	EN1 Noolchalai	Woodland-Grassland Mosaics	~1.5–1.4	7	162	22	154	59	9	2	7	11	0
Tanzania	Peninj	Es2 - Lepolosi	Woodland-grassland mosaics	~1.5–1.4	26	238	18	139	60	11	2	10	18	0
Kenya	West Turkana	Kokiselei 4	Grassland	~1.76	N/A	N/A	N/A	28	N/A	N/A	N/A	N/A	N/A	N/A
Kenya	Koobi Fora	FxJj63	Woodland-grassland Mosaics	~1.4	0	584	3	17	6	3	2	0	1	0
Kenya	Koobi Fora	FxJj37	Woodland-grassland mosaics	~1.4	22	333	8	11	41	10	14	3	14	0
Ethiopia	Gona	OGS-12	Woodland-grassland mosaics	~1.6–1.5	**1**	**31**	**4**	**3**	**5**	**5**	0	0	0	0
Ethiopia	Gadeb	8F	Afromontane grassland mosaics	~1.4–0.7	17	62	34	6	29	8	0	4	2	0
Ethiopia	Konso Gardula	KGA6-A1C	Woodland-grassland mosaics	~1.75	N/A	N/A	N/A	28	N/A	N/A	N/A	N/A	N/A	N/A

Table 2 (continued)

Country	Area	Site	Environment	Age (Ma.)	Percussion material	Complete & fragmented flakes	Retouched flakes Total	LCTs & LCT fragments	Cores Total	Unifacial / Chopper cores	Bifacial centripetal cores	Bifacial orthogonal cores	Multifacial cores/ Polyhedrons	Bipolar-on-anvil cores
Ethiopia	Konso Gardula	KGA4-A2	Woodland-grassland mosaics	~1.6	N/A	N/A	N/A	71	N/A	N/A	N/A	N/A	N/A	N/A
Ethiopia	Konso Gardula	KGA10-A11	Woodland-grassland mosaics	~1.45	N/A	N/A	N/A	46	N/A	N/A	N/A	N/A	N/A	N/A
Ethiopia	Konso Gardula	KGA7-A1, A3	Woodland-grassland mosaics	~1.4	N/A	N/A	N/A	72	N/A	N/A	N/A	N/A	N/A	N/A
Ethiopia	Konso Gardula	KGA12-A1	Woodland-grassland mosaics	~1.25	N/A	N/A	N/A	110	N/A	N/A	N/A	N/A	N/A	N/A
Ethiopia	Melka Kunture	Garba IVD	Afromontane woodland-grassland mosaics	~1.6	85	3611	193	23	1816	231	171	175	516	6
Ethiopia	Melka Kunture	Gombore IB	Afromontane grassland mosaics	~1.6	532	**1191**	358	**13**	1712	**1462**	N/A	N/A	N/A	N/A
Ethiopia	Melka Kunture	Gombore Iγ	Afromontane grassland mosaics	~1.4	3	43	16	10	17	**5**	**6**	0	0	0
Ethiopia	Melka Kunture	Gombore Iδ	Afromontane grassland mosaics	~1.3	0	291	10	0	11	**3**	5	0	0	0
Ethiopia	Melka Kunture	Garba XIIIB	Afromontane grassland mosaics	~1	0	91	1	26	32	0	15	0	5	0
Ethiopia	Melka Wakena	MW2	Afromontane grassland mosaics	~1.62–1.34	54	2485	5	48	301	34	67	89	73	0
Ethiopia	Melka Wakena	MW5	Afromontane grassland mosaics	~1.62–1.34	45	**625**	22	114	82	N/A	N/A	N/A	N/A	N/A
South Africa	Canteen Kopje	Pit 6E	Grasslands	>1.5	**0**	**422**	33	33	164	**11**	**11**	**0**	11	0
South Africa	Canteen Kopje	Pit 6 C-D	Grasslands	~1.51	**0**	**1825**	105	89	348	**24**	**34**	**0**	46	0
South Africa	Canteen Kopje	Pit 6B	Grasslands	~1.2–0.7	**1**	**3766**	293	170	338	**46**	**46**	**0**	32	0
South Africa	Sterkfontein	Member 5	Woodland-grassland mosaics	~1.7–1.4	N/A	40	3	**5**	263	N/A	N/A	N/A	N/A	N/A
South Africa	Sunday Rivers	Penhill Farm	Grasslands	~1.1	**0**	2242	**306**	49	206	**60**	**56**	**0**	4	0
South Africa	Swartkrans	Member 2	Woodland-grassland mosaics	~1.5–0.96	N/A	**30**	N/A	N/A	**26**	N/A	N/A	N/A	**10**	N/A
South Africa	Vaal River	Rietputs 15−1	Grassland	~1.7	7	294	9	18	93	7	**14**	17	16	21
South Africa	Vaal River	Rietputs 15−5	Grassland	~1.3	0	612	22	145	328	88	133	0	34	0

Table 2 (continued)

Country	Area	Site	Environment	Age (Ma.)	Percussion material	Complete & fragmented flakes	Retouched flakes Total	LCTs & LCT fragments	Cores Total	Unifacial / Chopper cores	Bifacial centripetal cores	Bifacial orthogonal cores	Multifacial cores/ Polyhedrons	Bipolar-on-anvil cores
South Africa	Wonderwerk	Stratum 11	Woodland-grassland mosaics	~1.5	**0**	11	0	2	0	0	0	0	0	0
South Africa	Wonderwerk	Strata 8–10	Woodland-grassland mosaics	~1.07–0.99	**0**	127	0	45	20	N/A	N/A	N/A	N/A	N/A
Algeria	Sétif	Ain Hanech	Woodland-grassland mosaics	~1.67	0	2	1	19	3	N/A	N/A	N/A	N/A	N/A
Algeria	Mascara	Tighennif	Woodland-grassland mosaics	~1.4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Morocco	Casablanca	Thomas Quarry I	Woodland	~1.3	36	**1085**	6	234	549	124	21	108	95	39

Lithics and environment data obtained from Avery 2001; Balout and Biberson 1967; Beyene et al. 2013; 2023; Bibi et al. 2018; Bobe and Carvalho 2019; Bobe et al. 2022; Bonnefille et al. 1982; Brain et al. 1988; Briatico et al. 2023; 2024; Brink et al. 2016; Chazan 2015; Chazan et al. 2008, 2012; Clark 1993; Clark and Kurashina 1980; Diez-Martín et al. 2013; 2014; Domínguez-Rodrigo et al. 2001, 2002; Duke et al. 2021; Duval et al. 2021; de la Torre 2009; 2011; de la Torre et al. 2003; 2008; Everett 2010; Fernandez-Jalvo and Avery 2015; Frost 2014; Gallotti 2013; Gallotti and Mussi 2017; 2018; Gallotti et al. 2014; 2020; 2021; 2023; Geraads 2016; Geraads et al. 1986; 2022; Gossa and Hovers 2022; Gossa et al. 2023; Harmand 2009; Harmand et al. 2023; Harris and Isaac 1997; Horwitz and Chazan 2015; Hovers et al. 2021; Isaac and Harris 1997; Jehle 2013; Kuman 1994; 2007; Kuman and Clarke 2000; Kuman and Gibbon 2018; Kurashina 1978; 1987; Leader 2013; Leader et al. 2016; Lepre et al. 2011; Li et al. 2017; Lotter and Kuman 2018;Lotter et al. 2023; Mora et al. 2003; Piperno et al. 2004a, b; Quade et al. 2004; Raynal et al. 2010; Reynolds and Kibii 2011; Roche et al. 2003; Rogers et al. 2023; Rossouw 2016; Sahnouni 2006, 2023; Sahnouni and de Heinzelin 1998; Sahnouni et al. 2010; Semaw et al. 2018; Sistiaga et al. 2020; Stratford 2008; Suwa et al. 2020; Texier 2018; Texier et al. 2006; Toffolo 2024. Coordinates of sites' areas are in Supplementary tables 1–2

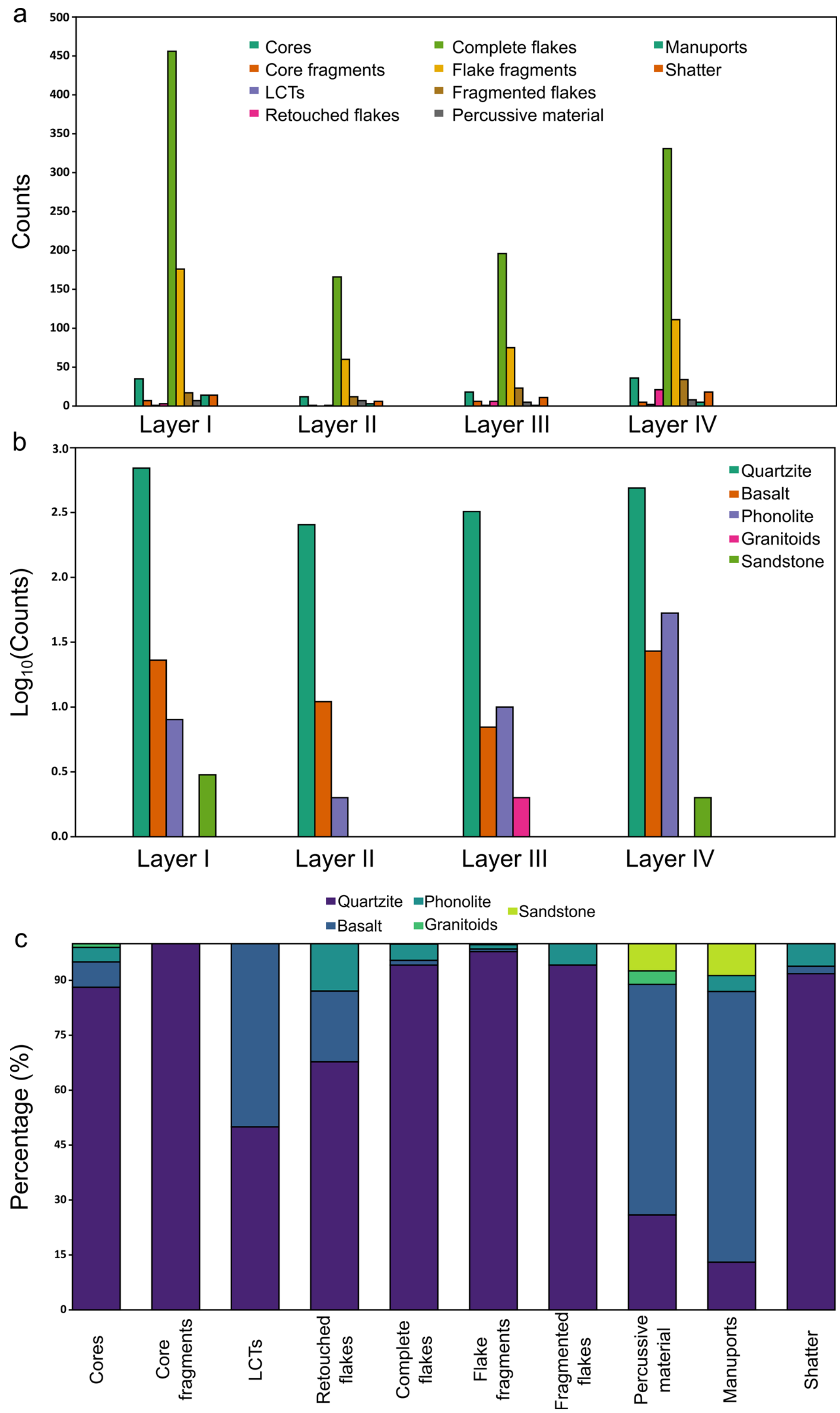

Fig. 2 **A**: Distribution of identified techno-typological categories by layer. **B**: Distribution of identified raw material per layer. **C**: Proportion of raw material per techno-typological category

assemblage) exhibiting a variety of reduction methods reflecting the use of both cobbles and flakes as original blanks (Supplementary Table 3). Data on average number of removals per knapping method, and core's metrics are in Supplementary Tables 4–7. Core fragments are also present throughout the sequence (Table 1) but lack sufficient diagnostic criteria to be associated with specific knapping methods.

In layer I, cores ($n=35$) reflect predominantly the reduction of quartzites (97.1%) through five distinct knapping methods: unifacial unipolar longitudinal ($n=6$, 17.1%), unifacial centripetal ($n=5$, 14.3%), bifacial orthogonal ($n=7$,

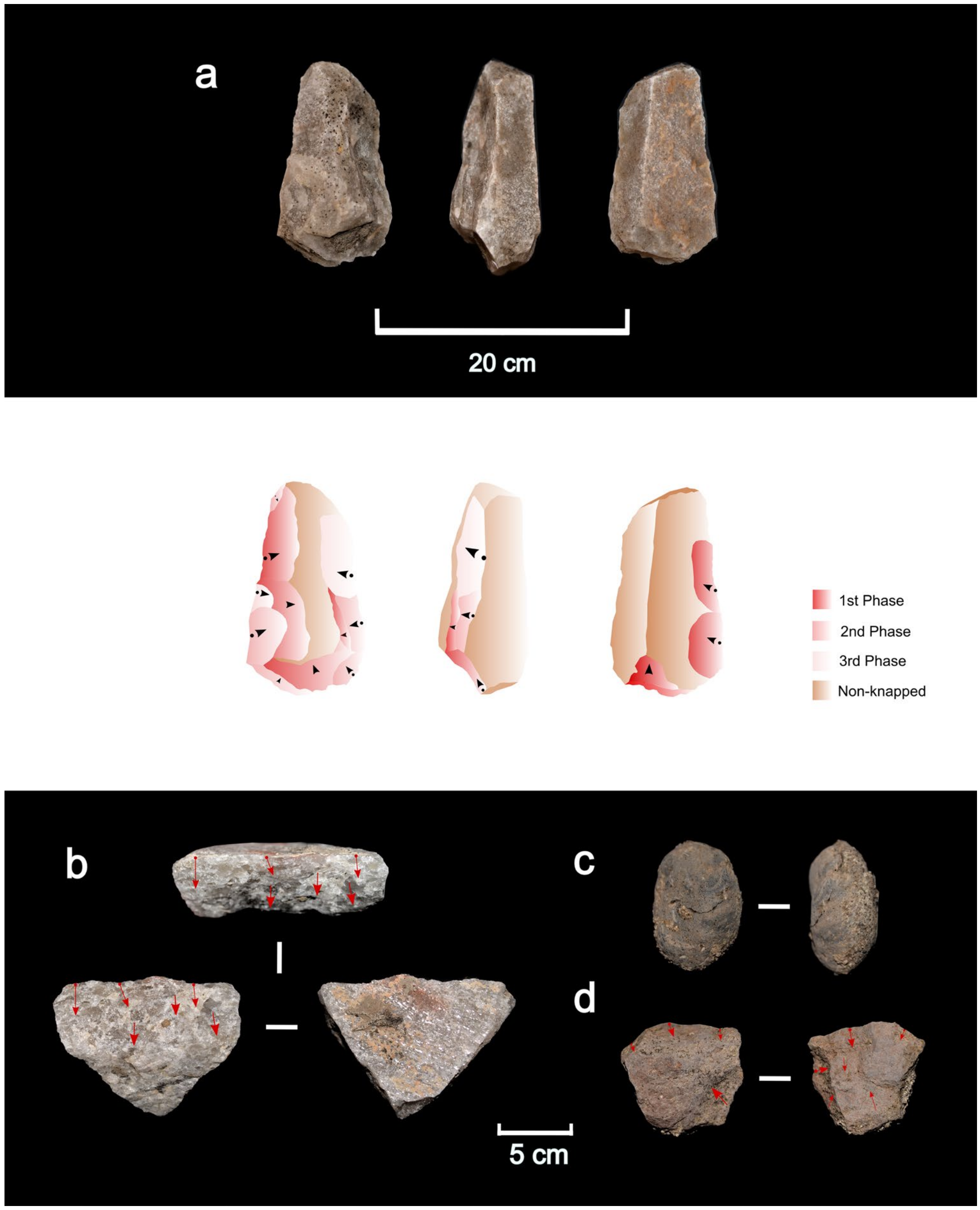

Fig. 3 Stone tool selection from layer I. **A**: Quartzite handaxe roughout. **B**: Quartzite unifacial unipolar longitudinal core. **C**: Basalt hammerstone. **D**: Basalt bifacial centripetal core

20%), bifacial centripetal (n=9, 28.6%) and multifacial multipolar (n=5, 14.3%). We have also identified uses of the bipolar-on-anvil technique (n=2, 5.7%). In both cases, these cores present two knapping phases: an initial bipolar-on-anvil reduction splits the blank, generating a surface that becomes the striking platform for a posterior unifacial unipolar longitudinal reduction phase.

Layer II yielded a smaller sample of cores (n=12), representing quartzite exploitation (92%) through four knapping methods: unifacial unipolar longitudinal (n=5, 41.6%), bifacial orthogonal (n=2, 16.6%), bifacial centripetal (n=3, 25%) and multifacial multipolar (n=1, 8.3%). Similarly to layer I, the bipolar-on-anvil technique is present on a single core: it was used to split the original blank generating a striking surface for a subsequent unifacial unipolar longitudinal reduction. In addition, this core presents extensive pounding marks on its opposite surface.

In layer III, cores (n=18) continue to be predominantly on quartzite (83%), although we recovered instances of basalt, phonolite and granitoid material. Reduction is represented mainly by the same knapping methods: unifacial unipolar longitudinal (n=3, 16.6%), unifacial centripetal (n=1, 5.5%), bifacial orthogonal (n=6, 33.3%) and bifacial centripetal (n=4, 22.2%), although a single unifacial bipolar opposed core constitutes a novelty. Three extra cores were reduced using the bipolar-on-anvil technique; in contrast with previous examples, these do not exhibit further

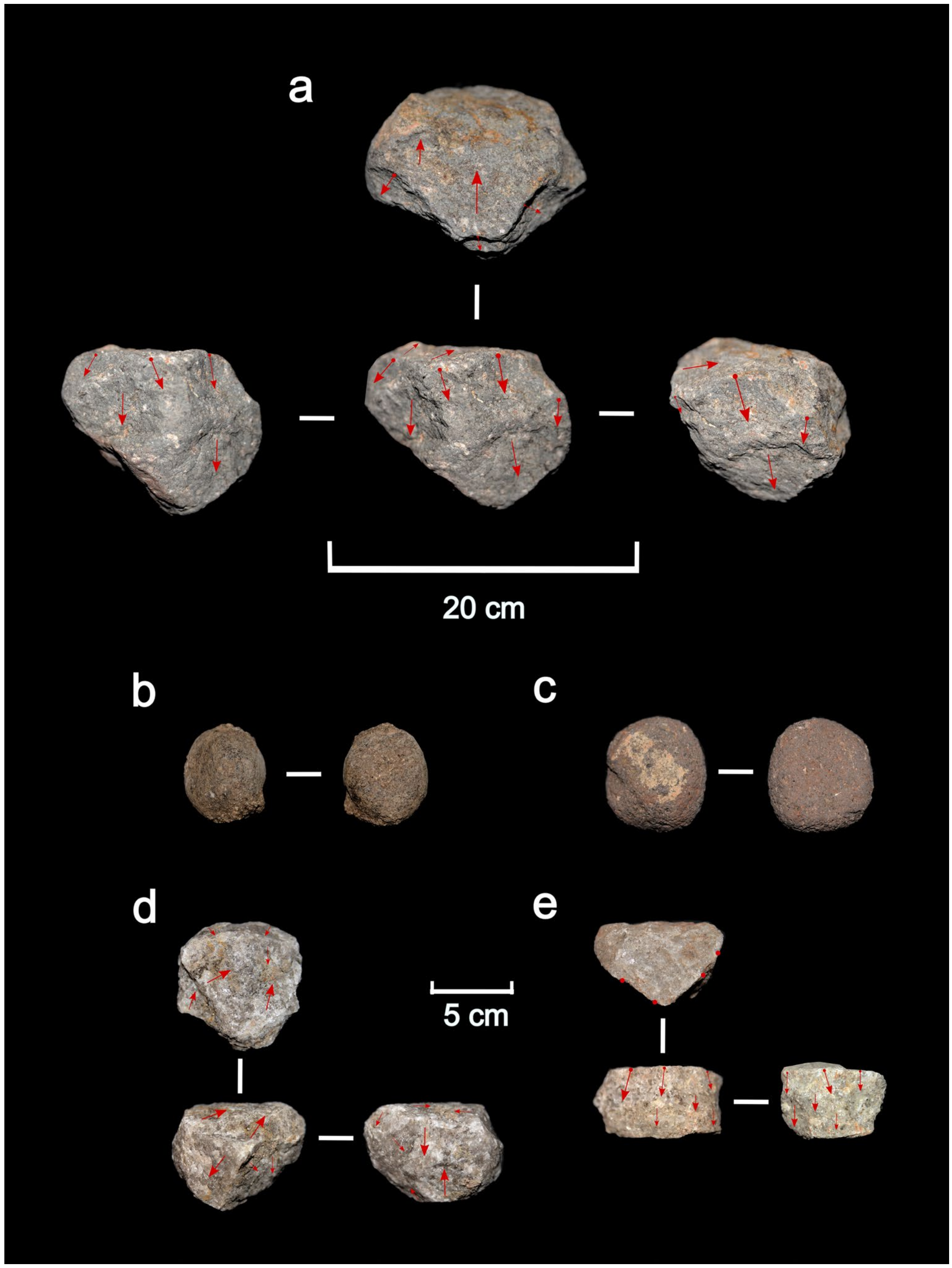

Fig. 4 Stone tool selection from layer II. **A**: Quartzite bifacial orthogonal core. **B**– **C**: Basalt hammerstones. **D**: Quartzite multifacial multipolar core. **E**: Quartzite unifacial unipolar longitudinal core

reduction through other knapping methods. Interestingly, in this layer flake blanks are only used for bifacial and/or centripetal knapping methods.

Cores (n=36) represent a relatively high proportion (6.3%) of layer IV's assemblage. Here, reduction occurs primarily using cobbles as original blanks (92%) and quartzite as the preferred raw material. Reduction strategies remain unchanged, with evidence of unifacial unipolar longitudinal (n=7, 19.4%), unifacial centripetal (n=1, 2.8%), bifacial orthogonal (n=11, 30.5%), bifacial centripetal (n=7, 19.4%) and multifacial multipolar (n=6, 16.7%) knapping methods. Bifacial centripetal cores present both alternate and alternating organization, the latter deriving in discoid-like morphologies. As in layer II, one of the cores exhibits evidence of pounding around its surface. There are also four examples of the bipolar-on-anvil technique, with an instance of previous core preparation: initial unifacial unipolar longitudinal reduction that created a flat surface allowing the ideal blank-positioning for bipolar-on-anvil percussion. This contrast with bipolar-on-anvil use on previous layers, were the use of the technique preceded other knapping methods.

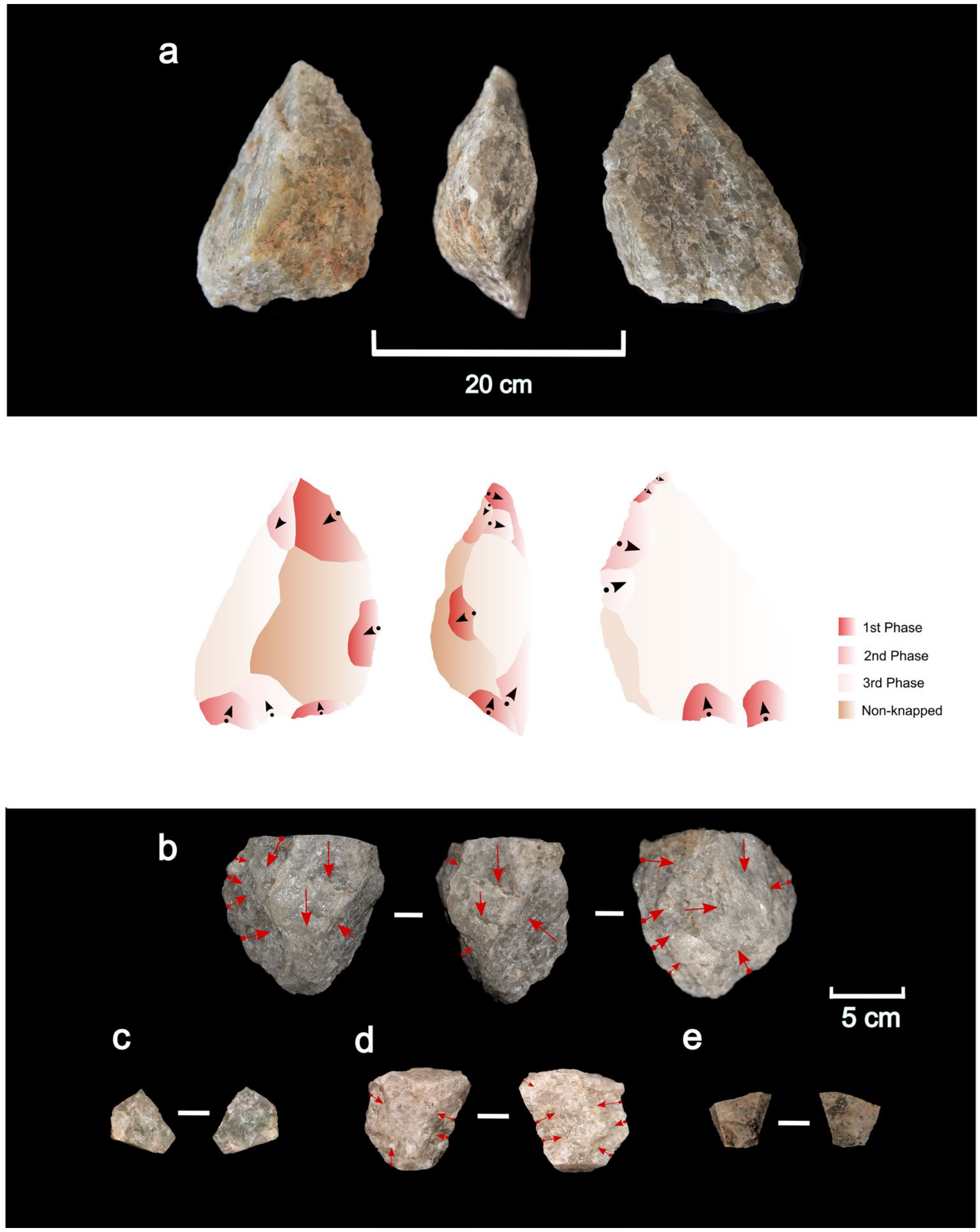

Fig. 5 Stone tool selection from layer III. **A**: Quartzite handaxe on flake. **B**: Quartzite multifacial multipolar core. **C**: Quartzite burin-like/dihedral. **D**: Quartzite bifacial centripetal core. **E**: Phonolite flake

Large Cutting Tools (LCTs)

LCTs are present, but in low quantities. Layer I yielded one LCT, a handaxe roughout, made on tabular quartzite (Fig. 3) [145 mm x 79 mm x 61 mm]. The handaxe does not exhibit a high level of configuration; although bifacially reduced, the blank's natural elongation and flat surfaces required scarce flake removal from one of its sides.

No LCTs were found in layer II. In layer III, a quartzite handaxe [185 mm x 111 mm x 71 mm] was made on a large flake blank, then it was reduced with a series of bifacial centripetal removals dedicated to thinning the partially cortical flake surface. As in layer I, there is a minor blank modification; the elongated flaked required little configuration, the removals were barely invasive, and they targeted both the tip and the base.

Finally, LCTs in layer IV amount to two: a cleaver-like artifact made on a basalt flake and basalt fragment corresponding to the base of a handaxe and amounting for approximately a third of the complete volume. The cleaver is small [85 mm x 70 mm x 34 mm] and exhibits little configuration; it naturally exhibits a double-beveled edge, one of its surfaces is cortical, and the opposite presents simple side-retouch and a slight thinning towards the base.

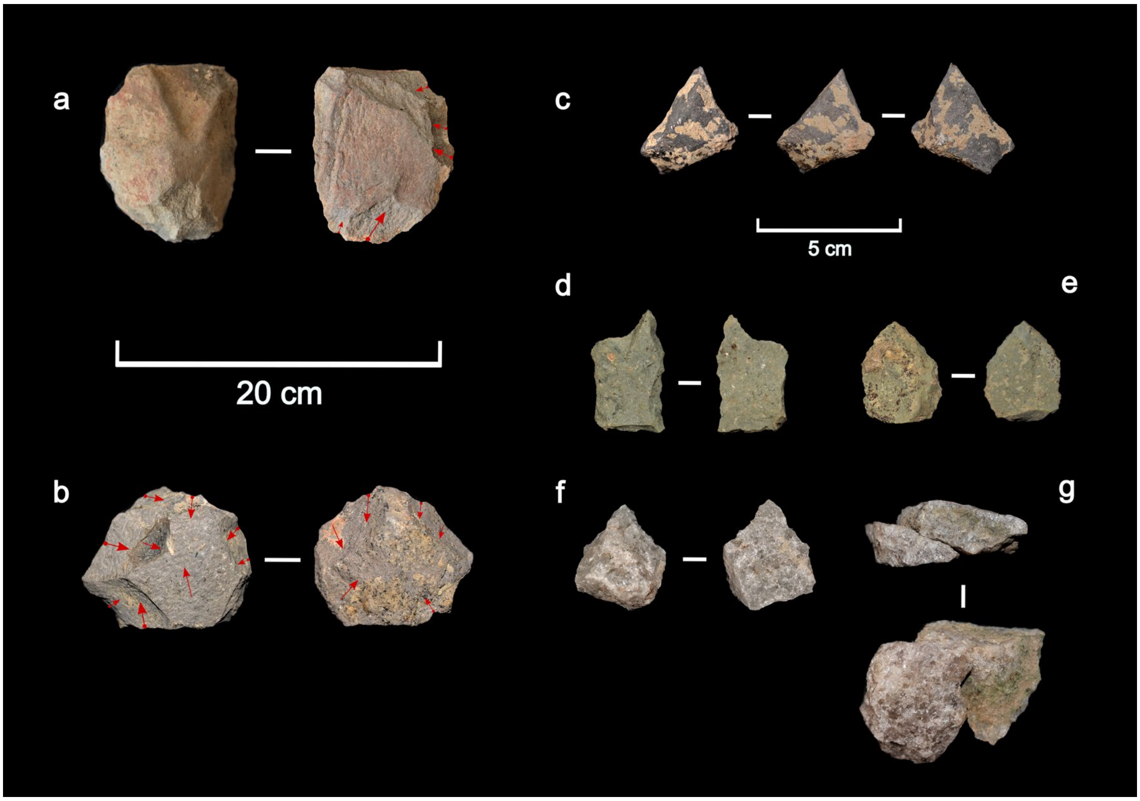

Fig. 6 Stone tool selection from layer IV. **A**: Basalt cleaver on flake. **B**: Basalt bifacial centripetal core. **C**-**F**: Burin-like/dihedral retouched flakes on basalt I, phonolite (**D**-**E**) and quartzite (**F**). **G**: Quartzite dorsal-ventral refit of two flakes

Retouched Flakes

At Engaji Nanyori, retouched flakes constitute a small proportion of the assemblage ($n=31$, 1.6%) (Table 1) and are distributed unevenly across the layers: layer I ($n=3$), layer II ($n=1$), layer III ($n=6$), and layer IV ($n=21$). Although raw material variability includes phonolite and basalt artifacts, quartzite dominates throughout the sequence (68%), overshadowing the use of volcanic materials. In layers I and II, all retouched flakes are made of quartzite, whereas layers III (83%) and IV (57%) exhibit greater variability.

The standard retouched types characteristic of Acheulean assemblages are well represented at Engaji Nanyori. In layer I, they include a denticulate and two burin-like artifacts, both featuring side-retouch designed to create a prominent tip. Layer II yielded a double-notch artifact on quartzite, shaped through simple retouch on its distal end to form a distinct tip. Layer III comprises five burin-like artifacts and a denticulate. These burins exhibit a relatively standardized configuration, with one side modified through simple or abrupt retouch and a burin-strike removal on the opposite side, producing a dihedral tip (Fig. 5). Additionally, two burins display side-scraper-like simple retouch alongside the burin-strike tip formation. Layer IV yielded a larger sample of these burin-like artifacts ($n=11$), demonstrating a similar degree of standardization (Fig. 6), as well as six denticulates and four scrapers.

Knapping Products

At Engaji Nanyori, the most common knapping products are complete flakes ($n=1149$, 60% of the complete assemblage). Flake fragments ($n=422$) and fragmented flakes ($n=86$) are present throughout the complete sequence although in reduced proportions (Table 1). Technological features of flake fragments were not considered (see Materials and Methods). We have also identified a small amount of shatter material ($n=49$) most likely related to knapping activities but lacking sufficient diagnostic criteria to be ascribed to any technological group. Nevertheless, both flake fragments and shatter material show an identical trend to the rest of knapping products regarding the preference of quartzite material.

Across all layers, complete flakes are technologically similar. They occur predominantly on quartzite, with notably high proportions of this raw material present in layers I (97%), II (99%), III (96%) and IV (86%). Raw material variability contemplates the use of lavas, such as basalts and phonolites, and an instance of sandstone, however it does so in marginal proportions except for layer IV.

Flake dimensions remain remarkably consistent throughout the sequence. In Layer I, flakes (excluding debris, $n=119$) exhibit an average size of [31.2 ± 11.3 mm] in length, [29.9 ± 11.2 mm] in width, and [13.8 ± 6 mm] in thickness. Layer II flakes (excluding debris, $n=36$) display similar metrics, averaging [29.7 ± 9.8 mm] in length, [27.5 ± 10.8 mm] in width, and [13.3 ± 5.7 mm] in thickness. Layer III flakes (excluding debris, $n=19$) align closely with those from Layer I, measuring [32.5 ± 12.7 mm] in length, [32 ± 13.4 mm] in width, and [14.4 ± 6.1 mm] in thickness. Finally, Layer IV flakes (excluding debris, $n=52$) average [28.7 ± 10 mm] in length, [26.6 ± 11.1 mm] in width, and [12.1 ± 4.7 mm] in thickness.

Dorsal surfaces are mainly non-cortical (layers I to IV: 96%, 92%, 91% and 89% respectively) (Supplementary Table 8), and average ~ 2 removals per flake (layers I to IV: 2.2, 2, 2.1 and 2.1 respectively). These removals reflect consistency on their arrangements (Supplementary Table 9), as they primarily reflect unidirectional longitudinal removals in similar quantity across all layers (I to IV: 60%, 62%, 58%, 61% respectively). Centripetal scar arrangements are scarce (layers I to IV: 7%, 8%, 9%, 8% respectively), although this reduction strategy has been furtherly identified through unifacial and bifacial centripetal cores. However, the remaining proportion of flakes with scar arrangements involving mandatory core rotation (removals coming from two or more directions) is well represented and continues to exemplify technological consistency throughout the sequence (layers I to IV: 31%, 32%, 31%, 23% respectively).

Flakes' platforms were assessed summing complete (including debris) and fragmented flakes (Supplementary Table 10). Cortical, point-shaped and lineal platforms are only in marginal amounts. Single-faceted platforms constitute the largest identified group throughout all layers (I to IV: 97%, 93%, 89% and 89% respectively). Double and multifaceted platforms, which tend to be indicative of core preparation, never compute for more than 6% of the total amount of platform types identified.

Ventral surfaces consistently display diffuse bulbs of percussion (layers I to IV: 98%, 91%, 93%, and 92% respectively), a feature normally associated with the utilization of hard hammerstones and microcrystalline textures such as quartzites.

Manuports and Percussion Materials

Layer I yielded a small sample of percussion materials (Table 1 & Supplementary Table 11) consisting of five basalt hammerstones and two quartzite cobbles exhibiting fractures due to pounding use. In addition, seven *manuports* were recovered, the majority of which (71%) are basalts. Percussion material is present in equal amounts and raw materials in layer II: five complete basalt hammerstones exhibiting similar hand-sized rounded, and two additional hammerstone fragments, also in basalt. In contrast, *manuports* in layer II are in lower frequency and exclusively basalts. In layer III, *manuports* and percussion materials are rare, being present on the lowest frequencies identified at the site. These proportions increase again in layer IV, with one complete basalt hammerstone, three fragmented hammerstones on basalt and quartzite, and four hammerstone fragments on basalt, quartzite and sandstone.

Post-depositional Alterations

The lithics from Engaji Nanyori's layers I, II, and III were all deposited in high-energy sedimentary environments that reworked the artifacts, and thus they are not in primary position. In spite of this, most artifacts exhibit no rounding (layer I: 84% layer II: 92%, layer III: 93%) (Supplementary Table 12). Carbonic concretion, suggestive of surface precipitates and pedogenic processes, are scarce, with high levels of fresh surfaces (layer I: 93% layer II: 92%, layer III: 89%) (Supplementary Table 13). We documented all stages of the operative chain, which suggests limited winnowing. In contrast, layer IV, a low energy environment corresponding to the sinuous pond habitats settled by *Homo erectus*, is in primary position (Mercader et al. 2025). While the proportion of fresh artifacts is comparable to that in high energy layers (93%) (Supplementary Table 12), stone tools in layer IV are the only ones that, when rounded, are so in minimum amounts. Concretion appears in just a few lithics (Supplementary Table 13), and when it is present it affects less than 25% of the stone area. All elements of the operative chain are present. We also recorded one refit: a dorsal-ventral join of two quartzite flakes (Fig. 6).

Discussion

Engaji Nanyori remains the only excavated Acheulean site within Bed III at Oldupai Gorge, providing the only possible glimpse into hominin adaptive strategies during the marked paleoclimatic and environmental shifts from the MPT (Kleindienst 1973; Leakey and Roe 1994; Mercader et al. 2025). Our analysis reveals a consistent technological approach throughout the occupational sequence, suggesting stable tool production methods over time.

Homo erectus primarily exploited adjacent metamorphic outcrops– geochemical characterization points towards Endonyo Osunyai, Naibor Soit and Nasiusiu as main sources (Mercader et al. 2025; Soto et al. 2020a, b). Volcanic rocks, in contrast, were used only sparingly, a pattern already observed in Bed II contexts, where quartzite utilization progressively predominates across all sites in the Gorge (Kyara 1999). This observation is particularly relevant given that the lithological context of Oldupai provides relatively equal access to both metamorphic and volcanic raw materials (Favreau 2024; Hay 1976). Furthermore, the differential selectivity pattern identified at Engaji Nanyori appears to align with broader regional trends, such as those documented at EF-HR, where LCT production is primarily associated with high-quality lavas (McHenry and de la Torre 2018). In this regard, the absence of LCTs at Engaji Nanyori may be a consequence of the overarching preference for quartzite materials. Moreover, the consistent predominance of quartzite across all four layers, coupled with the presence of Oldowan-like exploitation strategies, suggests that local hominins may have been unable to impose controlled reduction sequences on raw materials different than quartzite, as previously suggested for regional Oldowan localities (Cueva-Temprana et al. 2022). At Engaji Nanyori, this would be further reinforced by the use volcanic rocks as percussion material, as these artifacts required no modification through knapping to be effectively utilized.

In addition, reduction systems across the four archaeological layers remained notably uniform, with high frequencies of unifacial unipolar, bifacial orthogonal, and bifacial centripetal core strategies to produce flakes, which dominate each layer, with retouched flakes remaining minimal, except for layer IV. In general, the standardized characteristics of flakes and consistency in dorsal surfaces and platform attributes express a preference for a flake-based approach over complex tool shaping. The overall integrity of the assemblage is highest in layer IV, while it is also considerable in the rest of the layers, where post-depositional alterations are scarce despite their reworked nature.

Acheulean sites across Africa often exhibit two technological pathways: one oriented towards flake production and the other one towards LCTs (de la Torre and Mora 2018b; Santonja et al. 2014; Stout 2011; Texier 2018). At Engaji Nanyori, *Homo erectus* relied on flake knapping strategies comparable to preceding Oldowan technologies, a choice also identified in other local Acheulean sites, such as EF-HR (de la Torre and Mora 2018b). As previously mentioned, LCT production is infrequent, and when it appears it generates tools with limited configuration beyond cursory reduction of the original blank shape. It seems improbable that this scarcity in LCT products come from sampling bias, as similar observations were made by Kleindienst and Leakey in their own collection of 21,368 artifacts, of which only 51 were LCTs—a mere 0.2% of the assemblage. We cannot assess the possibility that LCT manufacture occurred off site. However, the available evidence suggests that *Homo erectus* may have prioritized flake-based toolkits, potentially because these better suited their functional requirements compared to LCTs.

While LCTs are often considered the defining feature of Acheulean industries (Leakey 1971; de la Torre and Mora 2014; Gowlett 1986), the coexistence of LCT-bearing and LCT-absent assemblages has been documented throughout the Acheulean (Beyene et al. 2013; Goren-Inbar & Sharon 2006; Lepre et al. 2011; Sánchez-Yustos et al. 2018; Uribelarrea et al. 2017). At Oldupai Gorge, both types of assemblages co-occur from middle Bed II onwards (Leakey 1971). This interstratification was traditionally interpreted as evidence for the coexistence of two cultural traditions– the Developed Oldowan A & B (DOA & DOB)– preceding the Acheulean and representing different phases of cultural development (de la Torre and Mora 2014). However, recent research has questioned this view (de la Torre and Mora 2014; Proffitt 2018; Semaw et al. 2009), and the appearance of LCTs in Acheulean assemblages is currently understood to represent variable techno-economic expressions within the same tradition (Sánchez-Yustos et al. 2018).

Furthermore, the sustained use of Oldowan-like knapping strategies during the initial MPT challenges the notion of a sharp boundary between Oldowan and Acheulean technocomplexes (Mussi et al. 2023), suggesting that Acheulean industries in certain contexts incorporated, rather than replaced, pre-existing technological behaviors (Clark 1969; Cueva-Temprana et al. 2019; Stout 2011; Stout et al. 2015). Therefore, the stone tool assemblage of Engaji Nanyori invites a reassessment of the continuity of Lower Pleistocene technological traditions and the variability within the Acheulean itself (Gallotti and Mussi 2017) and how it might reflect regional differences, ecological adaptions, functionality or technological evolution throughout time.

To situate Engaji Nanyori within both Acheulean and late Oldowan technological frameworks and examine patterns of technological continuity and assemblage variation, we compared key attributes across 40 sites in Tanzania, Kenya, Ethiopia, South Africa, Algeria, and Morocco (Table 2, Supplementary Table 14). The temporal scope of this analysis spans 1.75 to 1 million years, enabling an investigation of diachronic shifts within Acheulean assemblages across diverse environmental settings. To assess whether technotypological attributes exhibit consistency within the Acheulean record or reflect localized phenomena, we selected ten categories, as detailed under **Materials and Methods**. Additionally, we considered the environmental context of occupation to determine whether assemblages display ecological imprints. Principal Component Analysis (PCA) was employed to identify clustering patterns indicative of chronological, geographical, and/or paleoenvironmental structuring.

Two initial PCAs (Fig. 7A and B) examined differences based on the proportions of selected artifact types, including percussion material, complete and fragmented flakes,

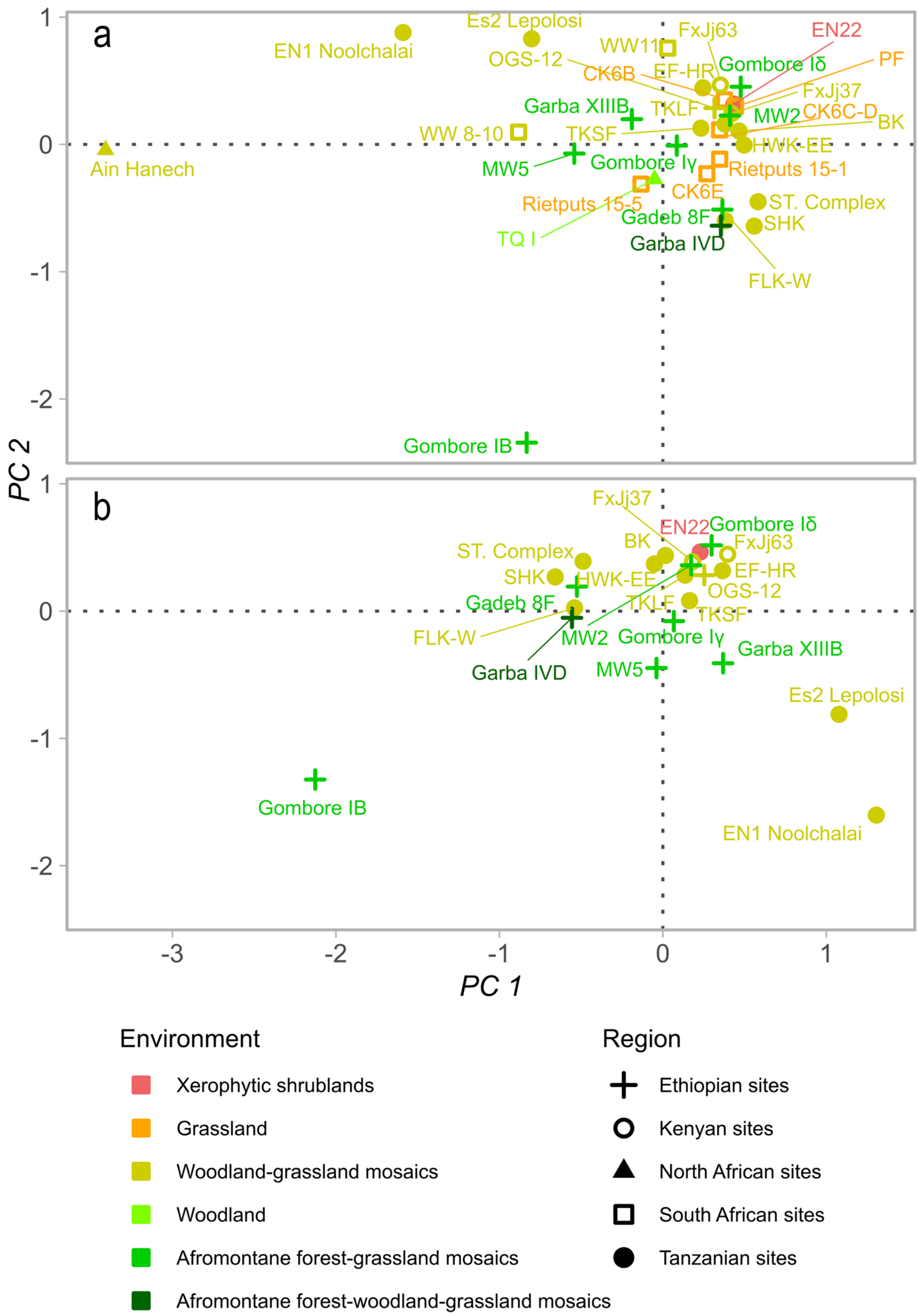

Fig. 7 **A**: PCA and Loadings for Late Oldowan/Acheulean sites older than 1 Ma by frequency of percussion material, complete and fragmented flakes, retouched flakes, complete and fragmented LCTs and total of cores, as seen in Table 2. **B**: PCA and Loadings for East African Late Oldowan/Acheulean sites older than 1 Ma by frequency of percussion material, complete and fragmented flakes, retouched flakes, complete and fragmented LCTs and total of cores, as seen in Table 2. In all PCAs, no sites of Table 2 with N/A values were included. Site abbreviations in plot: **CK6B** = Canteen Kopje Pit 6B; **CK6C-D** = Canteen Kopje Pit 6 C-D; **CK6E** = Canteen Kopje Pit 6E; **EN22** = Engaji Nanyori 2022; **MW2** = Melka Wakena 2; **MW5** = Melka Wakena 5; **PF** = Penhill Farm; **TQI** = Thomas Quarry I; **WW 8–10** = Wonderwerk Strata 8–10; **WW11** = Wonderwerk Stratum 11

retouched flakes, complete and fragmented LCTs, and total core count. The first PCA (Fig. 7A) presents a continental comparison of all sites listed in Table 2, explaining 76.7% of the variance through the first two principal components (Supplementary Fig. 1). The distribution does not exhibit clear clustering by geography, paleoenvironment, or chronology, suggesting that the selected variables do not singularly define assemblage composition.

The second PCA (Fig. 7B), based on the same variables but restricted to East African sites, similarly reveals no discernible pattern. This analysis accounts for 75.9% of the variance through the first two components (Supplementary Fig. 1). Here, site distribution predominantly reflects variation in the total number of complete and fragmented flakes and cores, reinforcing the notion that artifact proportions rather than chronology, geographic location, or environmental factors drive assemblage differences.

Two additional PCAs (Fig. 8A and B) focused on technological variation, using core types as proxies for reduction strategies. These analyses explain over 70% of the variance (**Supplementary Fig. 2**) and similarly exhibit no clear clustering by region, period, or environment. Instead, site distribution appears to be primarily influenced by the frequencies of bifacial knapping strategies and the application of the bipolar-on-anvil technique.

Engaji Nanyori compares to other local sites (HWK-EE, EF-HR, and TK-LF, Oldupai Gorge), Koobi Fora in Kenya (Jjx37, Jjx63), several localities in the Ethiopian Highlands (Melka Wakena 2, Gombore Iδ), and South African siters (Canteen Kopje, Wonderwerk Cave, Rietputs-15). These places share similar proportions of bifacial centripetal and bifacial orthogonal core strategies, the use of bipolar-on-anvil, and low frequencies of LCTs. Notably, HWK-EE– a Late Oldowan assemblage lacking LCTs– shows some of the most important technological similarities with Engaji Nanyori. These findings highlight the need to define the Acheulean technocomplex beyond the presence or absence of LCTs. Our comparison suggests that assemblage compositions exhibit limited technological variation beyond the LCT component, warranting deeper investigation.

The analysis presented here suggests that the Acheulean represented a stable technological tradition throughout the Early Pleistocene (Gallotti and Mussi 2017). Variability in assemblage composition– reflected in differing artifact proportions across sites– appears to be primarily driven by functional factors. This interpretation, however, is reached by exclusion, as chronological, geographical, and paleoenvironmental variables do not appear to exert a significant influence. Given the limited number of functional studies conducted in Oldupai Gorge (Bello-Alonso et al. 2019), future comparative research between assemblages is warranted to further investigate these issues. Nevertheless, Engaji Nanyori demonstrates repeated occupation of arid shrublands, contrasting with Acheulean sites older than 1 Ma, which are typically linked to *Acacia-Commiphora* woodlands and grassland mosaics of the Somalia-Masai ecoregion or forest-grassland mosaics found at mid-elevation zones (2000–2200 m a.s.l.), such as Melka Kunture, Melka Wakena, and Gombore. Altogether, this is evidence that Acheulean toolkits support highly complex human ecology profiles across diverse, unstable, and sometimes extreme biomes and speak to the generalist ecological versatility of *Homo erectus*.

Conclusions

Engaji Nanyori's lithic assemblage stands as the sole artifact collection directly associated with *Homo erectus* fossils within a hyper-arid environmental context during the early Middle Pleistocene Transition. The assemblage reveals a stable technological system centered on the exploitation of locally available quartzites and reduction strategies geared toward flake production. The limited presence of LCTs and associated products, consistent with earlier findings, suggests a technological paradigm in which the hallmark features of the Acheulean were secondary to a more streamlined toolkit. This toolkit, while less complex, likely catered more effectively to the ecological demands faced by these hominins. The reduction strategies employed—unifacial unipolar longitudinal, bifacial orthogonal, multifacial multipolar, and bipolar-on-anvil techniques—reflect technological continuity with earlier Oldowan traditions. A multivariate analysis of key technological markers from a broad sample of African Acheulean sites highlights variability primarily driven by differences in artifact proportions, rather than manufacturing processes. However, no clear association was detected between specific technological behaviors and geographic, chronological, or paleoenvironmental factors. These findings emphasize the generalist nature of the Acheulean technocomplex, which demonstrates remarkable adaptability, remaining functionally consistent across diverse ecological contexts and temporal frameworks without substantial technological innovation.

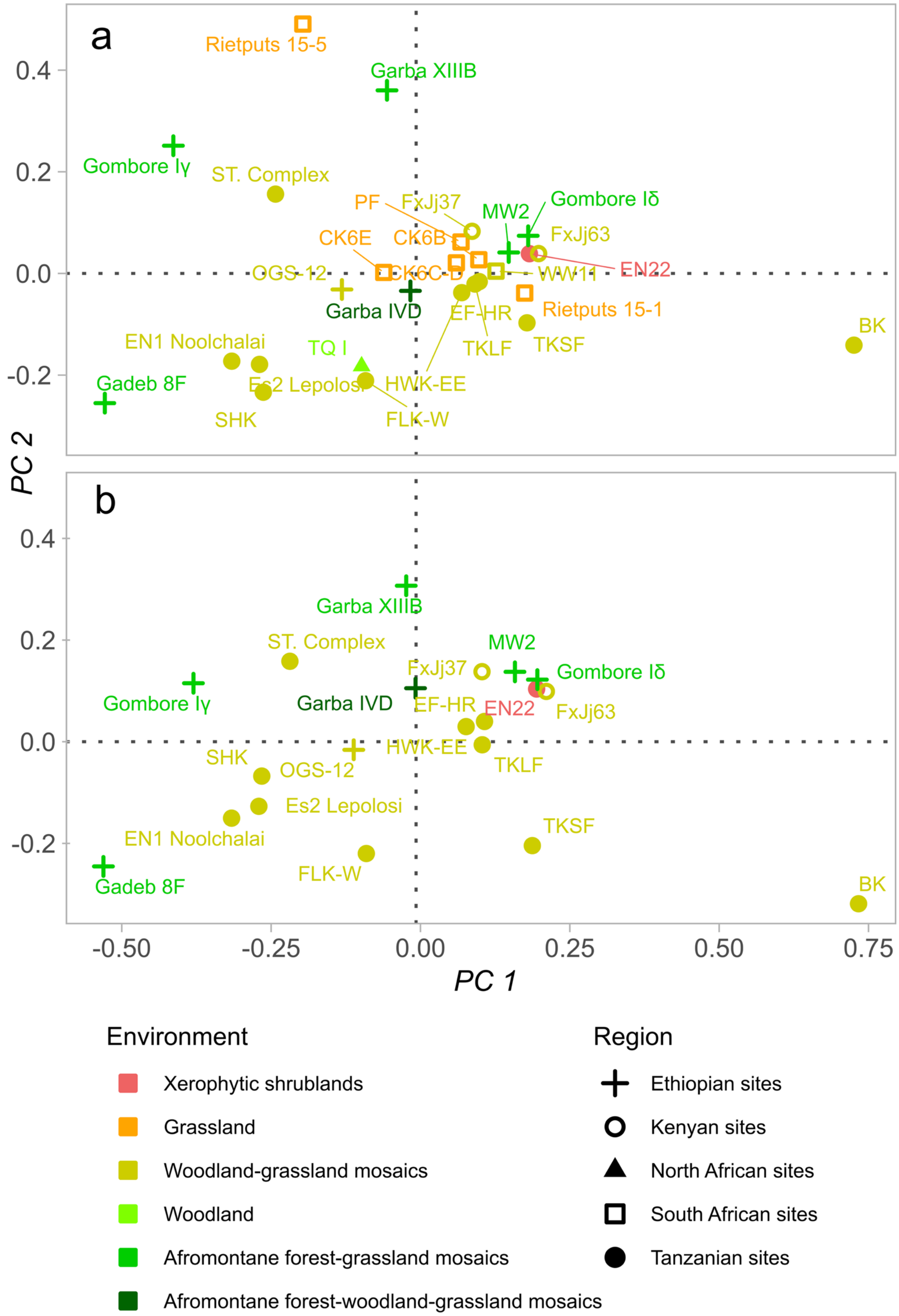

Fig. 8 **A**: PCA for Late Oldowan/Acheulean sites older than 1 Ma by frequency of unifacial/chopper cores, bifacial centripetal cores, bifacial orthogonal cores, multifacial cores/polyhedrons and bipolar-on-anvil cores, as seen in Table 2. **B**: PCA for East African Late Oldowan/Acheulean sites older than 1 Ma by frequency of unifacial/chopper cores, bifacial centripetal cores, bifacial orthogonal cores, multifacial cores/polyhedrons and bipolar-on-anvil cores, as seen in Table 2. In all PCAs, no sites of Table 2 with N/A values were included. Site abbreviations in plot: **CK6B** = Canteen Kopje Pit 6B; **CK6C-D** = Canteen Kopje Pit 6 C-D; **CK6E** = Canteen Kopje Pit 6E; **EN22** = Engaji Nanyori 2022; **MW2** = Melka Wakena 2; **MW5** = Melka Wakena 5; **PF** = Penhill Farm; **TQI** = Thomas Quarry I; **WW 8–10** = Wonderwerk Strata 8–10; **WW11** = Wonderwerk Stratum 11

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Author contributions Corresponding author ACT provided formal analysis, investigation, methodology, visualization, writing original draft, review, and editing. MS provided conceptualization, investigation, methodology, visualization, review and editing. PA, RH, SC, JF, SM, AM and AMw provided investigation, review, and editing. NB provided review and editing. MP provided supervision, review, and editing. Corresponding author JM provided conceptualization, funding, acquisition, investigation, methodology, project administration, resources, supervision, writing, review, and editing.

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Declarations

Competing interests The authors declare no competing interests.

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