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Earliest Evidence of Elephant Butchery at Olduvai Gorge (Tanzania) Reveals the Evolutionary Impact of Early Human Megafaunal Exploitation

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eLife Assessment

In this **valuable** study, the authors present traces of bone modification on ~1.8 million-year-old proboscidean remains from Tanzania, which they infer to be the earliest evidence for stone-tool-assisted megafaunal consumption by hominins. Challenging published claims, the authors argue that persistent megafaunal exploitation roughly coincided with the earliest Achulean tools. Notwithstanding the rich descriptive and spatial data, the behavioral inferences about hominin agency rely on traces (such as bone fracture patterns and spatial overlap) that are not unequivocal; the evidence presented to support the inferences thus remains **incomplete**. Given the implications of the timing and extent of hominin consumption of nutritious and energy-dense food resources, as well as of bone toolmaking, the findings of this study will be of interest to paleoanthropologists and other evolutionary biologists.

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Abstract

The role of megafaunal exploitation in early human evolution remains debated. Occasional use of large carcasses by early hominins has been considered by some as opportunistic, possibly a fallback dietary strategy, and for others a more important survival strategy. At Olduvai Gorge, evidence for megafaunal butchery is scarce in the Oldowan of Bed I, but becomes more frequent and widespread after 1.8 Ma in Bed II, coinciding with the emergence of Acheulean technologies, but not functionally related to the main Acheulean tool types. Here, we present the earliest direct evidence of proboscidean butchery, including a newly documented elephant butchery site (EAK). This shift in behavior is accompanied by larger, more complex occupation sites, signaling a profound ecological and technological transformation. Rather than opportunistic scavenging,

these findings suggest a strategic adaptation to megafaunal resources, with implications for early human subsistence and social organization. The ability to systematically exploit large prey represents a unique evolutionary trajectory, with no direct modern analogue, since modern foragers do so only episodically.

Introduction

Spatially concurrent lithic tools and proboscidean bones have a long history in human evolution. Such concurrency (sometimes in conjunction with other variables) has been frequently interpreted as the result of hominin butchery (Adrien Hannus, 2018 [↗](#); Agam and Barkai, 2018 [↗](#), 2016 [↗](#); Altamura et al., 2020 [↗](#); Barkai, 2019 [↗](#); Ben-Dor and Barkai, 2020 [↗](#); Berthelet and Chavaillon, 2001 [↗](#); Boschian and Saccà, 2015 [↗](#); Chavaillon et al., 1987 [↗](#); Chavaillon and Berthelet, n.d.; Delagnes et al., 2006 [↗](#); Gaudzinski et al., 2005 [↗](#); Gaudzinski-Windheuser et al., 2023a [↗](#), 2023b [↗](#); Gomez et al., 1978 [↗](#); Goren-Inbar et al., 1994 [↗](#); Haynes, 2022 [↗](#); Konidaris et al., 2021 [↗](#); Leakey, 1971 [↗](#); Lemorini et al., 2023 [↗](#); Lev and Barkai, 2016 [↗](#); Mussi and Villa, 2008 [↗](#); Reshef and Barkai, 2015 [↗](#); Rocca et al., 2021 [↗](#); Saccà, 2012 [↗](#); Santucci et al., 2016 [↗](#); Solodenko et al., 2015 [↗](#); Villa et al., 2005 [↗](#); Yravedra et al., 2019 [↗](#), 2010 [↗](#); Rabinovich et al., 2012 [↗](#)). Spatial concurrency is insufficient to establish a causal relationship between tools and megafaunal remains. Given the time-averaged nature of a large part of the Paleolithic record, the deposition of tools and elephants could have occurred sequentially and unrelatedly in several sites; especially taking into account that most of these sites were in paleo-floodplains where elephants and hippos were intensively active and formed natural taphocoenoses. Examples of this abound in the paleobiological record. For example, at BK (upper Bed II, Olduvai Gorge, Tanzania), some *Pelorovis* carcasses were naturally deposited on the same alluvial bar and among the fauna processed by hominins, thereby creating an artificial spatial concurrence between independent depositional events and agencies (Organista et al., 2016 [↗](#)). In the Middle Pleistocene deposits of Torralba and Ambrona (Spain), artifact-littered areas occur in spatial association with naturally-deposited elephant carcasses, only a few of which were also exploited to a limited degree by hominins, as demonstrated by a few proboscidean remains bearing cut marks (Villa, 1990 [↗](#); Villa et al., 2005 [↗](#)). Post-depositional/sedimentation processes also might have artificially created associations of faunal remains and unrelated lithic artifacts (Villa, 1990 [↗](#); Villa et al., 2005 [↗](#)).

Direct taphonomic evidence of hominin exploitation of megafauna (in the form of cutmarked or dynamically-percussed bone; in this study, *megafauna* refers to animals with a body mass exceeding 800 kg) has been so far the main argument to establish a causal link between hominin agency and megafaunal remains (Tappen et al., 2022 [↗](#)). If restricted to the Early Pleistocene, most sites containing partial carcasses of megafauna (e.g., elephant, hippopotamus) either show poor preservation, do not exhibit any of these anthropogenic traces, or these modifications cannot be securely identified (Delagnes et al., 2006 [↗](#); Domínguez-Rodrigo et al., 2007 [↗](#); Haynes, 2022 [↗](#), 1991 [↗](#); Isaac and Isaac, 2023 [↗](#); Leakey, 1971 [↗](#)). In contrast, for the Middle and Upper Pleistocene, there is more abundant evidence of hominin butchery of megafaunal remains, especially of elephants (Gaudzinski-Windheuser et al., 2023a [↗](#), 2023b [↗](#); Haynes, 2022 [↗](#); Yravedra et al., 2010 [↗](#); Rabinovich et al., 2012 [↗](#)); see review of taphonomic evidence in Agam and Barkai, (2018) [↗](#), Haynes (2022) [↗](#) and Konidaris et al. (2021) [↗](#). The question that we address here is if such a behavior has its roots in the early Pleistocene.

Once hominin agency is empirically demonstrated at taphonomically-supported butchery sites, a second inferential step is attributing carcass butchery to hunting or scavenging. Occasionally, the occurrence of embedded flint in proboscidean remains has been taken as direct evidence of predatory behaviors (Agam and Barkai, 2018 [↗](#)). This evidence is marginal and chronologically restricted to the late Upper Pleistocene with composite hafted tools. Recently, a supportive argument used to detect proboscidean hunting lies on the intensity of cut marks on carcasses and mortality profiles dominated by male prime adults (Gaudzinski-Windheuser et al., 2023a [↗](#), 2023b [↗](#)). Prime adult mortality is documented also in other natural palimpsests (Haynes, 1991 [↗](#)), in some cases probably caused by fights leading also to broken tusks (Villa and d'Errico, 2001 [↗](#)).

Ethnoarchaeological observation of modern foragers butchering elephants and hippos shows that they leave very few cut marks after bulk defleshing (Crader, 1983). Modern elephant butchery after culling events (based on a sample of >500 carcasses) also shows that bulk defleshing virtually leaves no traces on bones (Haynes and Krasinski, 2021). Only butchery aiming at the extraction of meat scraps after bulk defleshing imparts most of the cut marks documented experimentally (Haynes and Krasinski, 2021). This casts doubts on whether cutmarking intensity relates to hunting, scavenging or a maximization strategy feasible in all scenarios. To complicate things more, there is a clear mismatch between the butchery intensity documented at several sites and the resulting tool kit associated with it. Some Middle Pleistocene elephant carcasses display abundant cut marks, but there are very few or no stone tools associated with them (Gaudzinski-Windheuser et al., 2023a); whereas at other sites, elephant carcasses exhibit not a single cut mark but they occur with hundreds or thousands of associated tools (Chavaillon et al., 1987; Delagnes et al., 2006; Yravedra et al., 2010) (Table 1). In the latter case, it is probable that in some cases the bulk of tools may have been used to process other non-megafaunal fauna. In the particular case of the Nadunga elephant (Kenya, 1-0.7 Ma), that explanation for the presence of lithics is improbable since the only other mammal carcass remains found are from one bovid and one suid, most likely a background scatter associated with the bird, fish and reptile remains with which they are spatially associated. The question remains as to why such a divergent range of tool sets (both in quantity and typological composition) accompany similar partial megafaunal skeletal remains if they are truly functionally related to them.

To make interpretations even more challenging, many butchery sites exhibit fairly complete and (semi)articulated carcasses with limb bones intact. In some of these instances, elements were dismembered but not demarrowed or degreased (Gaudzinski-Windheuser et al., 2023a). Defleshing or demarrowing/degreasing do not require disarticulating bones, and the energy costs involved in cutting through tendons and ligaments of a proboscidean carcass are better explained as a maximizing strategy aiming at reducing the costs of element transportation (neither defleshing or demarrowing/degreasing requires disarticulation), and/or further exploitation of within-bone fat resources. None of this is clearly documented in those sites. Fat was a crucial resource during human evolution (Ben-Dor and Barkai, 2024; Ben-Dor et al., 2011; Reshef and Barkai, 2015; Solodenko et al., 2015), and the large fat deposits stored in proboscidean carcasses rationally would have been a target of prehistoric butchery, especially in strategies of carcass maximization (as documented in the abundant cut mark record at some megafaunal butchery sites). The question of why our ancestors chose to maximize flesh extraction from proboscideans, and yet frequently abandoned their fat deposits untouched remains unanswered. Modern Bisa people (Zambia) butcher elephants and do not exploit their fat, but they follow a “satisficing” strategy (Haynes and Krasinski, 2021), through bulk defleshing (barely impacting bone surfaces) (Crader, 1983), and not a “maximizing” strategy, as suggested for some highly anthropogenically-impacted archaeological proboscidean sites (Gaudzinski-Windheuser et al., 2023a). It could be argued that the meat of healthy elephants contains already a high amount of fat and that other anatomical areas (like the podal pads) contain extremely nutritious fat, or that the relevance of fat exploitation varies according to latitude and climate, but if the strategy was to maximize food resources, long bone medullary contents should also have been consumed (Ben-Dor et al., 2011; Haynes et al., 2021), as documented in sites like Castel di Guido (Italy), Preresá (Spain) (Boschian and Saccà, 2015; Yravedra et al., 2012), or BK (see below). Megafaunal long bone green breakage (linked to continuous spiral fractures on thick cortical bone accompanied by modification [in some cases, intensive] of cortical and medullary surfaces of breakage planes) is probably a less ambiguous trace of butchery than “cut marks”, since many of the latter could be equifinal and harder to identify in contexts of moderate to poor preservation, especially in contexts of high abrasion and trampling (Haynes et al., 2021, 2020). For example, the purported cut-marked pelvis from Fuentenueva 3 (Yravedra et al. 2024) exhibits intense biostratigraphic -in addition to diagenetic-modifications impacted by abrasive processes, which renders the pristine experimental reference collection inadequate to confidently classify it as human-made. This is further supported by the fact that the experimental trampling collection used depicts trampling marks as extremely shallow and with wide divergent walls. This does not

Table 1. African Early Pleistocene archaeological sites with proboscidean carcasses containing potential evidence of hominin involvement

	Area excavated (m2)	Nº bones	Nº lithics	Megafaunal taxon	Other non megafauna	Age (Ma)	Green breaks	Cut marks
Nyayanga 3 (Kenya)	49	1580* (241 Hippo)	42**	Hippo	Present	3-2.6	Unreported	Ambiguous
Nyayanga 5 (Kenya)	24	196*	14**	Hippo	Present	3-2.6	Unreported	Ambiguous
FLK North 6 (Tanzania)	37	400	123**	Elephant	Present	1.8	Absent	Ambiguous
FLK North Deinotherium site (Tanzania)	-		23	Elephant	Present	1.7	Absent	Absent
Barogali (Djibuti)	37	-	569	Elephant	Absent	1.6-1.3	Unreported	Absent
Nadung'a (Kenya)	53	65	6797	Elephant	Present	1-0.7	Unreported	Absent

- * Numbers in main text and supplementary tables do not coincide.
- **Only artifacts reported as associated to the skeletal remains (total in both excavations is 135)
- ***Excluding purported manuports

include the large diversity of morphologies generated by trampling marks, whose cross-sections frequently are indistinguishable from stone-tool cut marks (Domínguez-Rodrigo et al., 2010b [↗](#)). Given the abrasive sedimentary context, the abundance of abrasion marks on the affected specimens, and the lack of description of microscopic features that could unambiguously be used to identify those traces as human-made, we remain skeptical of their anthropogenic nature.

Ideally, cut marks should complement green breakage patterns to identify butchery episodes, but the virtual lack of cut marks in “satisfying” proboscidean exploitation renders their presence/absence non-indicative of the type of anthropic action. Despite the occurrence of green fractures on naturally-broken bones, such as those trampled by elephants (Haynes et al., 2020 [↗](#)), and those occurring through traumatic fracturing or gnawed by carnivores (Haynes and Hutson, 2020 [↗](#)), these fail to reproduce the elongated, extensive, or helicoidal spiral fractures (uninterrupted by stepped sections), accompanied by the overlapping conchoidal scars (both cortical and medullary), the reflected scarring, the inflection points, or the impact hackled break surfaces and flakes typical of dynamic percussive breakage. Evidence of this type of green breakage had not been documented earlier for the Early Pleistocene proboscidean or hippopotamid carcasses, beyond the documentation of flaked bone with the purpose of elaboration of bone tools (Backwell and d’Errico, 2004 [↗](#); Pante et al., 2020 [↗](#); Sano et al., 2020 [↗](#)). Such type of dynamic breaking, in contrast, has been documented in *Pelorovis* and *Sivatherium* carcasses at the 1.3 Ma site of BK (Olduvai Gorge) (Domínguez-Rodrigo et al., 2014a [↗](#); Labrado, 2017 [↗](#); Organista et al., 2016 [↗](#)).

Regardless of the type of butchery evidence -and with the taphonomic caveat that no unambiguous evidence exists to confirm that megafaunal carcasses were hunted or scavenged other than hominins accessed them in different taphonomically-defined stages (i.e., early or late)- the principal reasons for exploring megafaunal consumption in early human evolution is its origin, its episodic or temporally-patterned occurrence, its impact on hominin adaptation to certain landscapes, and its reflection on hominin group size and site functionality. If hominins actively sought the exploitation of megafauna, especially if targeting early stages of carcass consumption, the recovery of an apparent surplus of resources reflects a substantially different behavior from the small-group/small-site pattern documented at several earlier Oldowan anthropogenic sites (Domínguez-Rodrigo et al., 2019 [↗](#)) -or some modern foragers, like the Hadza, who only exploit megafaunal carcasses very sporadically, mostly upon opportunistic encounters (Marlowe, 2010 [↗](#); O’Connell et al., 1992 [↗](#); Wood, 2010 [↗](#); Wood and Marlowe, 2013 [↗](#)). Determining when the process of becoming megafaunal commensal started has major implications for human evolution, since it has clear implications for our understanding of past social group sizes and social dynamics.

The multiple taphonomic biases intervening in the palimpsestic nature of most of these butchery sites often prevent the detection of the causal traces linking megafaunal carcasses and hominins. Functional links have commonly been assumed through the spatial concurrence of tools and carcass remains; however, this perception may be utterly unjustified as we argued above. Functional association of both archaeological elements can more securely be detected through objective spatial statistical methods. This has been argued to be foundational for heuristic interpretations of proboscidean butchery sites (Giusti, 2021 [↗](#)). Such an approach removes ambiguity and provides a better argument for spatial functional association, as demonstrated at sites like Marathousa 1 (Konidaris et al., 2018 [↗](#)) or TK *Sivatherium* (Panera et al., 2019 [↗](#)). This method will play a major role in the present study.

Here, we present the discovery of a new elephant butchery site (Emiliano Aguirre Korongo, EAK), dated to 1.78 Ma, from the base of Bed II at Olduvai Gorge (Tanzania). It is the oldest unambiguous proboscidean butchery site at Olduvai. In combination with its study, we have carried out extensive survey at a landscape scale on one stratigraphic section of Bed I (Oldowan) and three stratigraphic sections of Bed II: lower Bed II-Lower Augitic Sands (1.8.1.69 Ma), upper middle Bed II (from tuff IIB to IID, 1.5 Ma), and upper Bed II (overlying Tuff IID, 1.3 Ma), which are known to contain Acheulian materials. The goal was to find megafaunal fossils bearing traces of hominin modification across the landscape. Starting at 1.78 Ma, Olduvai Gorge records extensive evidence

of hominin involvement with megafaunal carcasses (Domínguez-Rodrigo et al., 2014b [↗](#), 2009b [↗](#)), namely Proboscidea and Hippopotamidae, followed closely by Giraffidae and big Bovidae. The nature of this interaction is elaborated and analyzed in this paper. We have used a spatial approach, combined with a more general taphonomic analysis, and an analysis of hammerstone-broken bone specimens occurring widespread on the three targeted Bed II stratigraphic intervals. Also provided is a technological study of the lithic artifacts.

Results

The Emiliano Aguirre Korongo (EAK) site

EAK is located in the area of the confluence of the two gorges, next to geo-locality 45a, between the FLK-N and FLK-NN sites (Hay, 1976 [↗](#)) (Fig. 1 [↗](#)). Stratigraphically, the archaeological remains rest on Tuff IF (1.78 M.a), i.e. at the beginning of Bed II (Deino, 2012 [↗](#)). As in the whole area of the gorge, the lowermost Bed II is similar to the uppermost Bed I, which is composed of clays deposited in the margins of the lake. The drying period that characterizes Bed II had not yet taken place during this moment. The sedimentary context of the Olduvai basin in this area is dominated by low energy processes, with predominantly clay deposition, controlled by small seasonal rises and falls in lake level. The lake had a very high pH and high salinity in the central zone (Deocampo et al., 2017 [↗](#)), but this value is lowered at the margins by the arrival of runoff water. EAK is located roughly coinciding with the FLK fault zone (Fig. 1 [↗](#)). The bone and lithic remains lie on a thin layer of clay (<5 cm) on top of tuff IF. They are also covered by the lacustrine clay of the lowermost Bed II. It is therefore the oldest documented archaeological site formed in Bed II in Olduvai.

During the recent Holocene, the EAK site was affected by a small landslide which displaced the site 6.25 m vertically and approximately 12 m downslope. Although the stratigraphic sequence remains clearly recognizable, Tuff I-F, which serves as the paleosurface of the site, is fragmented into numerous blocks up to 1 m in diameter (Fig. 2 [↗](#)). The archaeological deposit has moved together with the blocks and their original spatial distribution has been altered by this post-sedimentary deformation.

Olduvai Gorge is located in a sedimentary basin bounded to the south by several volcanoes, and to the north by large outcrops of metamorphic rocks. These two groups are the sources of raw material (basalts and quartzites respectively) during practically the entire Pleistocene at Olduvai. Both, the aforementioned basement rocks and the Plio-Quaternary and Quaternary sedimentary fill are affected by these major east-west faults known as 1st, 2nd, 3rd, 4th, KK, FLK and 5th faults. It should be noted that the FLK fault can only be identified in the landscape through the deformation of the southern escarpment of the gorge, at the beginning of the gully that gives its name to this deposit (EAK). It is a well-known fault because it defines the FLK-5 fault block, described stratigraphically by Hay (1976) [↗](#). Although it is an escarpment degraded by the current geodynamics, it affects the most recent aeolian deposits of Olduvai (Naisiusiu). This geomorphological feature indicates that the FLK fault remained active at least until the Upper Pleistocene to Holocene. The exact direction of the fault is unknown, although the stratigraphy suggests that it must be SW-NE (Fig. 1 [↗](#)), and its vertical drop is several tens of meters. The movement of the fault has probably triggered local earthquakes of varying magnitude. It is well known that earthquakes are one of the main causes of landslides (Keefer, 1984 [↗](#); Ugai et al., 2012 [↗](#); Wasowski et al., 2011 [↗](#)), and in this particular case, they may have triggered several landslides affecting deposits from the base of the present gully -i.e. from the upper part of Bed I to the uppermost Bed (Fig. 2 [↗](#)). The fluvial erosion of the stream at the base of the slopes also destabilized the base of the slopes in this gully, favoring this type of gravitational process. In the case of EAK, this is a very small landslide, although much larger landslides have been recorded in the surrounding area, affecting Bed II units such as the Lower Augitic Sandstone (LAS), which slides over the waxy clay of the lowermost Bed II. Interestingly, there is a similar archaeological site on the Colorado Plateau in northern New Mexico (USA); in this case, a mammoth presenting a similar post-depositional history (Rowe et al., 2022 [↗](#)).

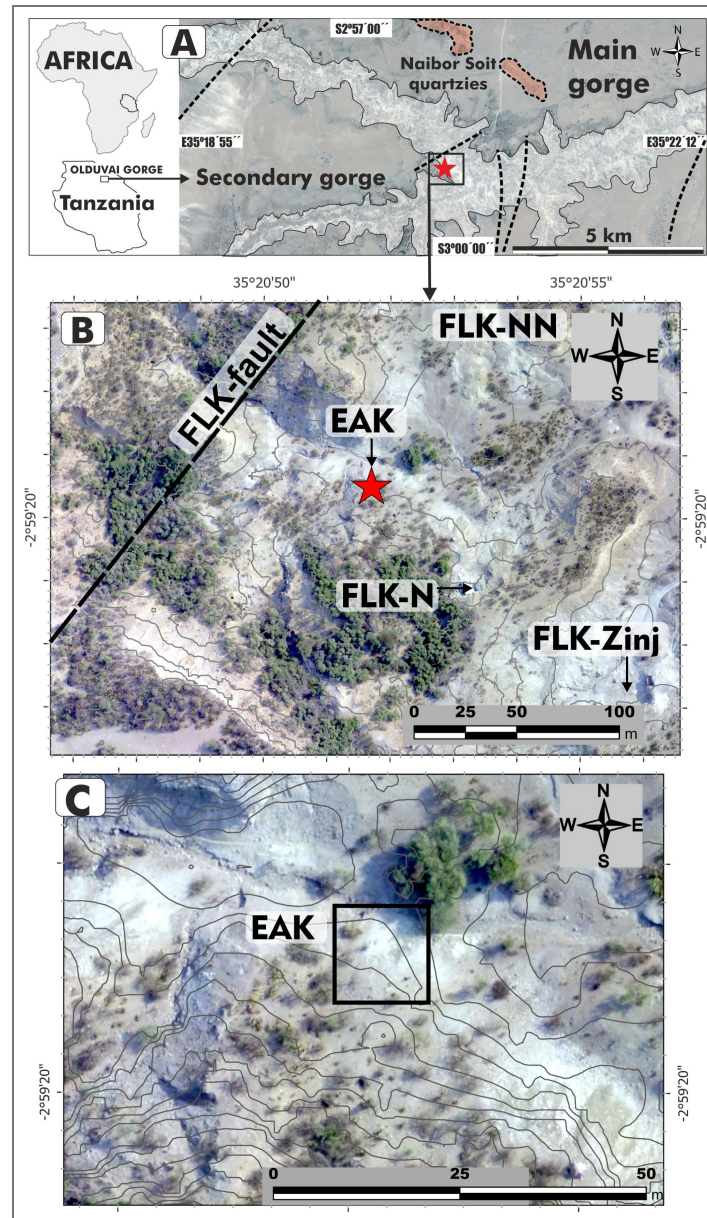


Figure 1. Location of EAK in the junction of the main and secondary branches of Olduvai Gorge, main faults and Naibor Soit quartzites (A), within the area where the Bed I sites cluster at the junction (B), and the specific EAK locus with 1 m contour lines (C).

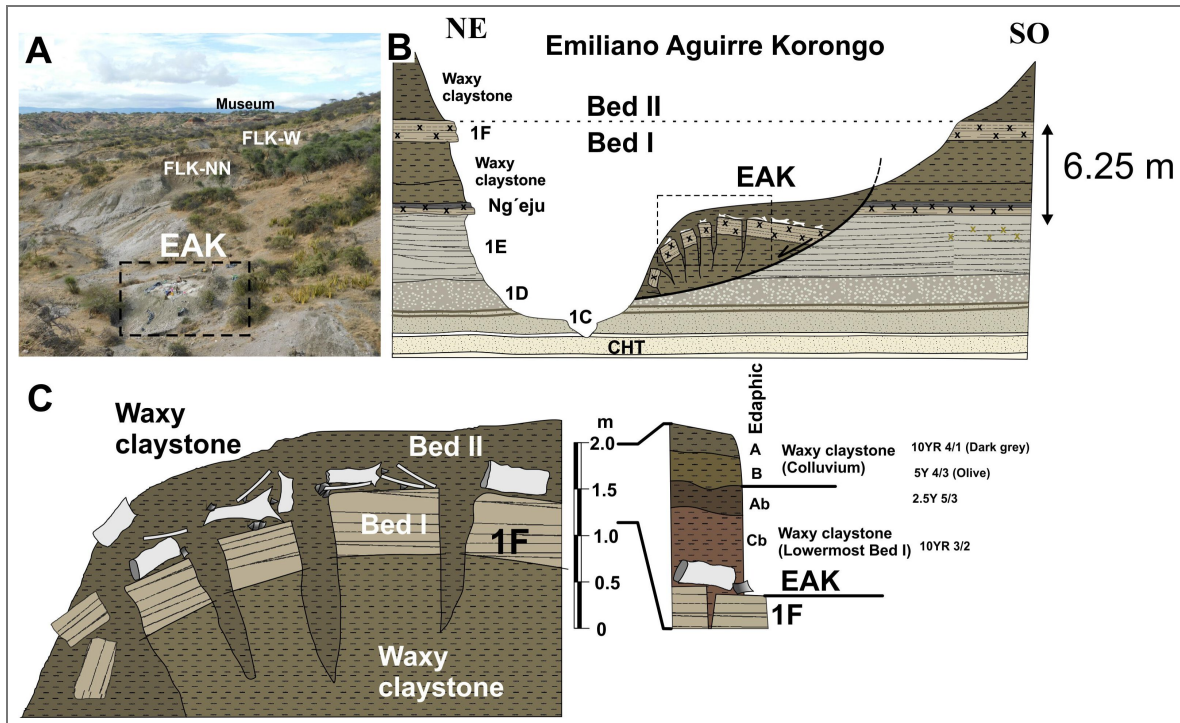


Figure 2.

A, Location of EAK on the south side of the Main Gorge (view to the east). B, Stratigraphic section of the gully (Korongo) showing the correlation between the different marker tuffs of Bed I on either side. The landslide displaced the boundary between Bed I and Bed II, including the following sequence: waxy claystone, tuff 1F, waxy claystone. Vertical displacement is 6.25 m. C, detail of the stratigraphy of the site, showing how the archaeological level rests directly on Tuff 1F and was covered by the clay of the lowermost Bed II. The landslide has created vertical cracks that separate both the Tuff 1F and the archaeological level itself. The archaeological remains have moved along with the tuff blocks. The original clay of the lowermost layer II protected the fossils from erosion after the landslide. An incipient soil formed on this surface and was subsequently buried by colluvium. At present, erosion is acting on the part closest to the stream, affecting some of the fossils.

In June 2022, a partial elephant carcass was found at EAK on a fragmented stratigraphic block situated topographically below FLK North, containing most of the sequence from Tuff ID to the carbonated root clays overlying Tuff IF that constitute the base of Bed II. The carcass must have been eroding over the years, since proboscidean bone fragments and lithics had been found over more than 100 m repeatedly along the seasonally-active stream at the bottom of the gully. In January of the same year, we had not documented anything eroding on the same block, but after the rainy season, several bones emerged, making it obvious that the site contained remains of a proboscidean carcass (Fig. 3 [↗](#)). Excavation started right after the discovery, and uncovered remains from a single *E. recki* juvenile individual. We initially set up a 4×2 m trench, followed by an extension consisting of two additional trenches (Figs. 3 [↗](#)). The northern side presented an erosive front, probably responsible for several of the scattered elephant bones found along the bottom gully. The remaining excavated partial carcass contained the complete pelvis associated with both hindlimbs (Table 2). These included both femora and tibiae, plus one set of tarsal elements (including calcaneus, astragalus) and a fully articulated foot (Figure S1). In addition, several rib fragments belonging to a minimum of 8 ribs, as well as a portion of an ulna were also discovered (Fig. S2). It is interesting to note that no complete vertebrae were discovered (only one fragment was identified), despite the presence of a portion of the axial skeleton. The skull was positioned upside down and the projecting tusks were partially preserved (Fig. 3 [↗](#)). In addition to the elephant carcass, a background scatter of few bones, including a *Parmularius* M², a vertebra, rib, tibia and metatarsal of a small-sized artiodactyl were found.

A total of 80 stone tools, mostly flakes and flake fragments, were spatially distributed in tight connection with 153 bone remains, pertaining to 46 elements of a proboscidean carcass (Fig. 3 [↗](#); Table S1 [↗](#)). Their preservation is exceptional and the edges remain sharp. The close spatial association must be functionally linked. Although the cortical bone in several elements was affected by diagenesis, preventing the preservation of any potential bone surface modifications, the good preservation in the remaining assemblage did not yield any marks created either by hominins or other carnivores. On-going restoration work will provide an accurate estimate of well-preserved and modified fractions of the assemblage. Two elephant bone specimens showed attributes of green breakage, inferred to be of anthropic origin (See Supplementary Information). The tibiae were well preserved, but the epiphyseal portions of the femora were missing, probably removed by carnivores, which would also explain why a large portion of the rib cage and almost all vertebrae are missing. Further support for this likelihood can be found in the deletion of bones from three feet, which are one of the richest sources of fat and affected early in the process of carnivore ravaging (Haynes, 1991 [↗](#), 1988 [↗](#); Haynes and Hutson, 2020 [↗](#)). The absence of the forelimbs could be also explained if carnivores had dragged them away from the core axial area; however, the fact that the carcass was detached from its original depositional locus and gravitationally moved (with its overlying sediment) after faulting might also explain that the missing carcass parts could still be in their original depositional spot. Our testing of the area where the block was supposed to have been originally formed yielded no results, mainly because of the thick overburden of Ndutu sediments in the area. The fact that the carcass was moved while encased in its sedimentary context, along with the close association of stone tools with the elephant bones, is in agreement with the inference that the animal was butchered by hominins. A more objective way to assess this association is through spatial statistical analysis.

The spatial statistical analyses of EAK

The analysis of orientation (azimuth) and slope (plunge) (Fig. S28) has shown that the null hypothesis of spatial isotropy cannot be rejected, whether the entire sample is analysed jointly, or the elephant remains are differentiated from the lithic ones. This result is supported using Rayleigh, Kuiper, and Watson tests, but also by the visualization of the stereograms and rose diagrams, which indeed show the existence of orientations in all directions. Regarding the slope, the stereograms indicate the absence of strong imbrications of remains.

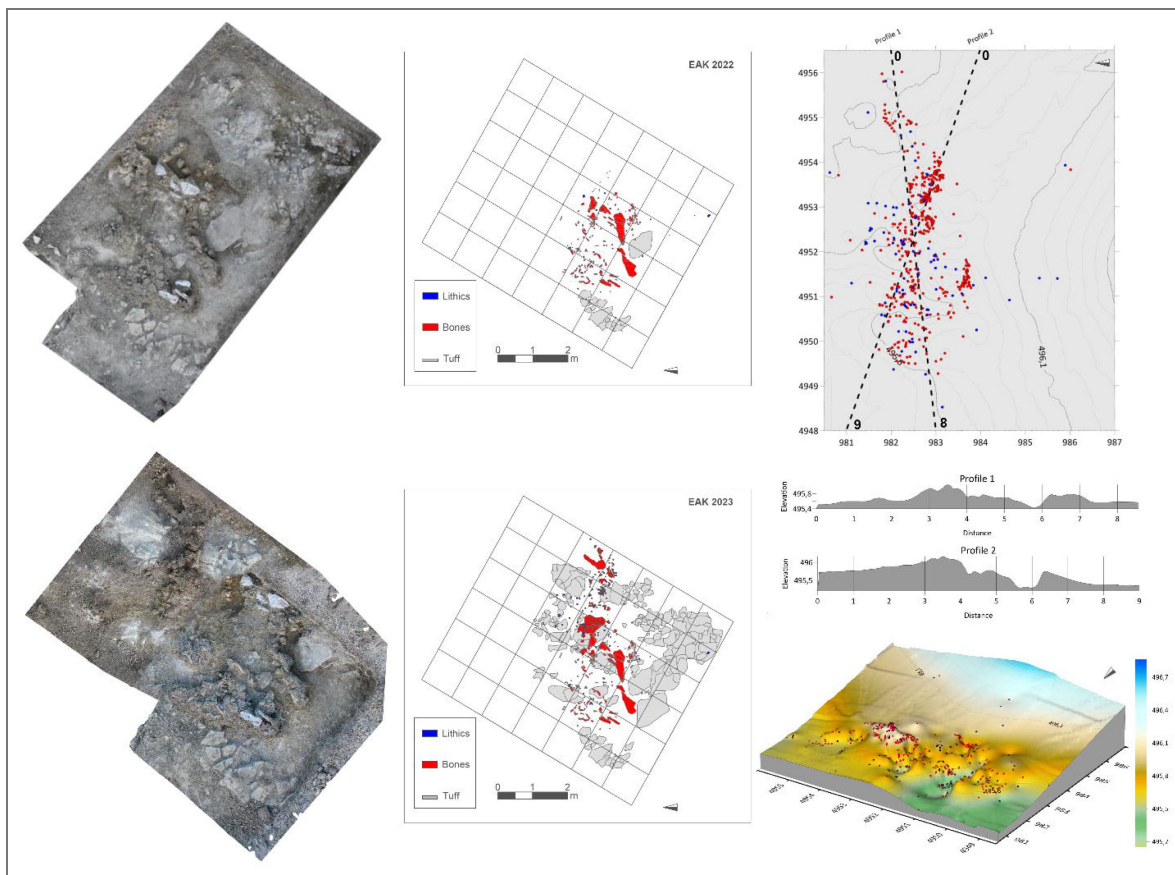


Figure 3. Photogrammetry (left) and planimetry (right) of the EAK site in 2022 and 2023.

The site-wide distribution of materials, lithics (blue) and bones (red), topographic profiles, and the 3D terrain model are shown.

The Spatial Point Pattern (SPP) of the elephant bones has an intensity of 7.74 specimens per square meter. However, this intensity varies significantly across the analyzed surface, with a very high-intensity area in the center of the excavated area and very low intensity surrounding this zone. This pattern is evident both when analyzing the intensity itself and when examining the hot spot maps (Fig. S24 a-c). The use of MAD and DCLF tests has rejected the null hypothesis of spatial randomness with the inhomogeneous K and L functions, as well as with the K_{scaled} and L_{scaled} functions (p-value = 0.025), while it could not be rejected with the F , G , and J functions (p-value = 1). These results align with the use of spatial functions (Fig. S24 d-k), as the F , G , and J functions do not reject the random model, whereas the K , L , K_{scaled} , and L_{scaled} functions reject randomness and suggest a clustered SPP. Additionally, the inhomogeneous K and L functions indicate that this clustering occurs only at short distances and that at distances greater than 1 meter, the SPP follows a regular pattern. The pair correlation function also appears to indicate the presence of a clustered pattern at very short distances. According to the nearest-neighbor cleaning test, most of the faunal assemblage is highly likely to be part of the cluster (Fig. S24 l-n).

When performing different regression models, we found that the linear regression had an AIC of -861.53, the quadratic regression -1990.689, the cubic regression -2076.40, and the 4th-degree polynomial regression -2100.39. However, we used the quadratic regression for the analysis because the cubic and 4th-degree polynomial regressions were found to be unreliable due to issues related to sample size and collinearity. Therefore, we performed modelling using the quadratic regression (Fig. S24 o-r), reinforcing the interpretation of a very high-intensity cluster in the central part of the excavated area. Furthermore, it is proposed that the accumulation should not extend significantly beyond the excavated area. This supports that site erosion may have affected the preserved concentration less than initially suggested.

The analysis of the SPP for lithic remains shows an intensity of 1.67. Although the sample size is much smaller, it exhibits a pattern similar to that of the bone remains. It also presents intensity and hot spot maps (Fig. S25 a-c), with very high intensity in the central area of the spatial window and very low intensity in the surrounding areas. The DCLF and MAD tests yield the same results as those for the elephant remains. However, the functions (Fig. S25 d-k) show some differences. The F , G , J , and pair correlation functions do not reject the null hypothesis, while the K , L , K_{scaled} , and L_{scaled} functions do reject it. In this case, the inhomogeneous functions suggest the presence of a regular pattern, while the scaled functions indicate a clustered pattern. Once again, the nearest-neighbor cleaning test (Fig. S25 l-n) suggests that the lithic remains in the high-intensity area are highly likely to be part of a cluster.

The regression analyses in this case show much higher AIC values compared to the faunal remains. However, as before, the 4th-degree polynomial regression has the lowest AIC (-87.99), followed by the cubic regression (-83.02), the quadratic regression (-71.73), and finally the linear regression (79.5). However, once again, the cubic and 4th-degree polynomial regressions cannot be used due to collinearity and sample size issues, making the quadratic regression the most appropriate choice. Modelling with quadratic regression (Fig. S25 o-r) further reinforces the presence of a large cluster and the possible absence of remains outside the analysed window. Interestingly, the area of maximum intensity does not exactly coincide with that of the elephant remains but is slightly shifted to the left (west) within the spatial window.

The analysis of the SPP with marks (elephant bones vs. lithic tools) shows that, as expected due to the imbalance in sample size, there is always a higher probability of finding elephant remains than lithic remains (Fig. 4 a [↗](#)), with the only exception being at the far left (north) of the spatial window. The analysis of spatial marks reveals a significant segregate correlation between fauna and lithics when using the K_{cross} and L_{cross} functions (Fig. 4 b-c [↗](#)). The pattern is of regular segregation, meaning that although lithics and bones form part of the same cluster, they tend to occupy different positions, with lithics clustered in the periphery, as would correspond to their use and discard upon the processing of the elephant carcass, which occupies the central part of the cluster.

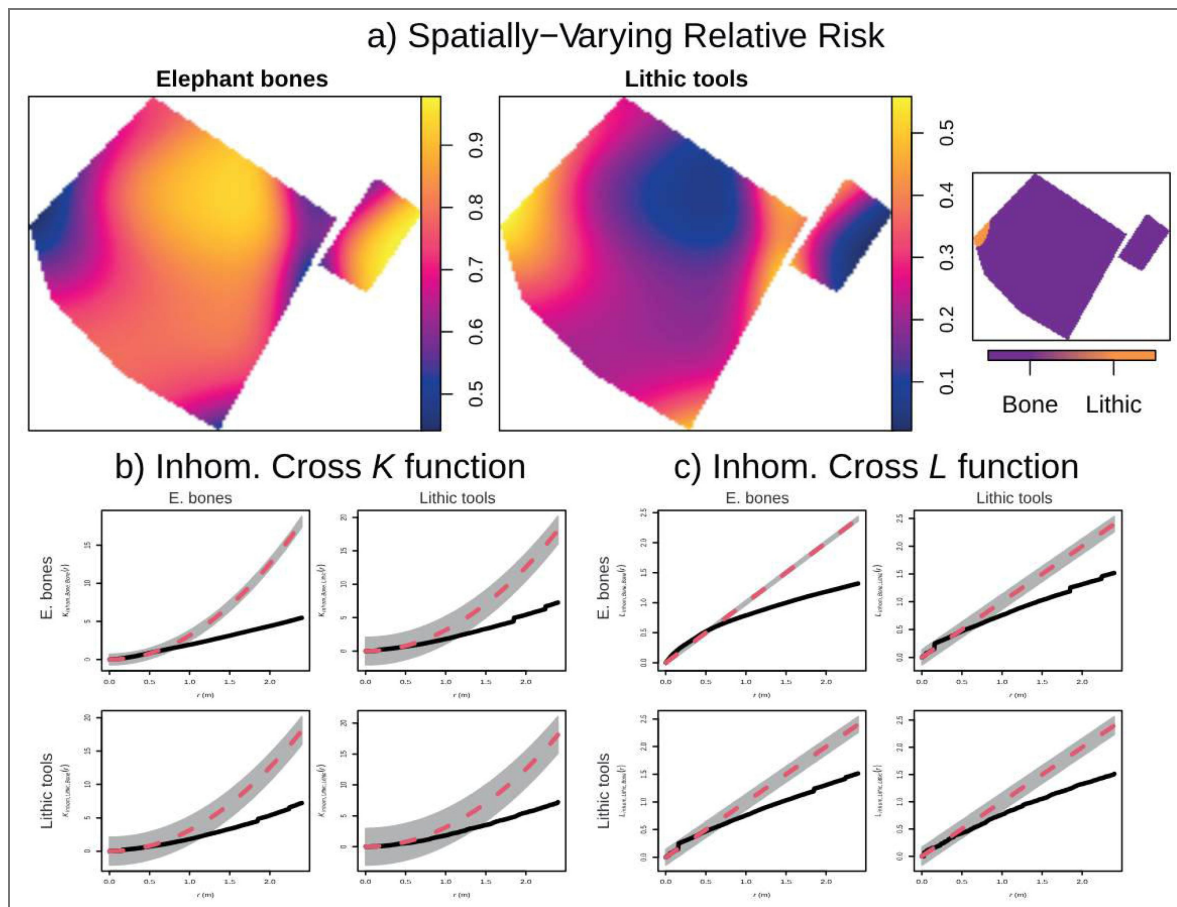


Figure 4. Relative risk (i.e., probability of occurrence) of bones and lithic artifacts at EAK, with second-order functions showing regular correlation between both types of items.

Finally, analyzing the bones as a covariate has further reinforced the presence of high lithic tool intensity in the center of the spatial window and the relation between fauna and lithic artifacts (Fig. 5 [↗](#)). First, modelling intensity based on the covariate and the estimated intensity (ρ) shows that intensity is very high when lithic remains are close to elephant remains, but it drops sharply when moving just 50 cm away. This finding is further supported by the ANOVA test on the model (p -value = $<2.2 \times 10^{-16}$) and the results of the Berman Z_1 (p -value = $<8.456 \times 10^{-16}$) and Z_2 (p -value = $<1.585 \times 10^{-16}$) tests. This also shows that the functional connection between the elephant bones and the tools has been maintained despite the block post-sedimentary movement. This is further supported by the technological analysis (Supplementary Information).

Traces of megafaunal exploitation along the paleolandscape at Olduvai Gorge

Bed I

During our survey of the Bed I targeted strata in 2024, no significant traces of megafaunal green bone breakage were observed, with the exception of one locality (Fig. S3). In previous years, we had observed few megafaunal fossils, mostly restricted to hippopotamus scattered remains. They were not particularly abundant, despite the clearly lacustrine and alluvial depositional settings sampled at the junction.

Bed II

Out of the three targeted units (lower, intermediate and upper), the lower unit yielded the highest concentration of elephant and hippopotamus remains, followed by the upper unit (Figure S3 [↗](#)). The distribution shows a clustered pattern, despite the virtual continuity of most of the sequence in larger areas. The junction area contains the highest density of megafaunal remains for the lower unit. Figure S3 [↗](#) shows the thorough overlap of those elephant and hippopotamus carcasses with areas containing high density of stone artifacts. All the carcasses documented in the lower unit but one (EAK) occur within the Lower Augitic Sands (LAS). This unit contains a landscape-scale concentration of lithic artifacts spreading from HWKE to FLK West (Domínguez-Rodrigo et al., 2023 [↗](#); Uribelarrea et al., 2019 [↗](#), 2017 [↗](#)).

The distribution of carcasses in the intermediate unit is less dense and mostly restricted to a small portion of the junction. This small area also shows concentration of lithic remains, but its extent is still unknown since only two localities have been excavated [one to the west of FLK West (Fujioka et al., 2022 [↗](#)) and BBS] and no much surface material is found that could be securely attributed to this unit in between both sites. BBS (Bob Brain Site) is a recent site discovered in middle Bed II on the same stratigraphic unit as the site named by Fujioka et al. (2022) [↗](#) as FLK West, recently renamed T69 Complex. In the side gorge, SHK represents this unit, with well documented presence of megafauna and cut-marked hippopotamus remains (Diez-Martín et al., 2017 [↗](#); Domínguez-Rodrigo et al., 2014b [↗](#)).

The other large cluster of elephant and hippopotamus carcasses is documented in the upper section of the side gorge (Fig S3). There, most of them concentrate around two sites (BK and SC). These sites are also relevant because they contain other smaller megafauna, such as *Sivatherium* and *Pelorovis* in larger numbers (Domínguez-Rodrigo et al., 2014a [↗](#); Organista et al., 2019 [↗](#), 2017 [↗](#), 2016 [↗](#)). It is at these two sites and the landscape surrounding them that the highest densities of lithic artifacts are also found in the upper section of Bed II (Diez-Martín et al., 2009 [↗](#)).

The clustering of the elephant (and hippopotamus) carcasses in the areas containing the highest densities of landscape surface artifacts is suggestive of a hominin agency in at least part of their consumption and modification. The presence of green broken elephant long bone elements in the area surveyed is only documented within such clusters, both for lower and upper Bed II. This constitutes inverse negative evidence for natural breaks occurring on those carcasses through natural (i.e., non-hominin) pre- and peri-mortem limb breaking (Haynes et al., 2021 [↗](#), 2020 [↗](#); Haynes and Hutson, 2020 [↗](#)). In this latter case, it would be expected for green-broken bones to

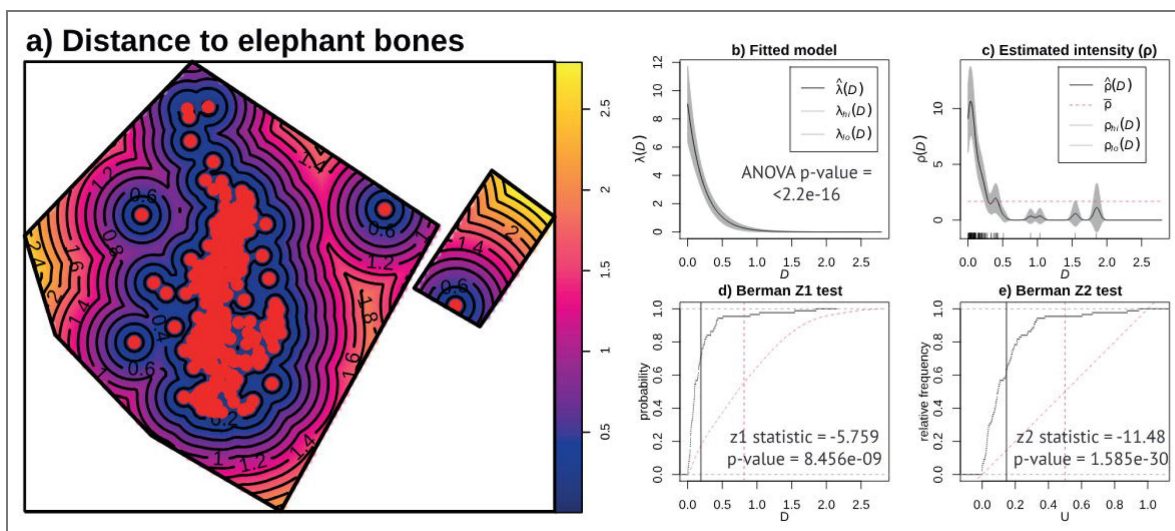


Figure 5. Correlation between lithics and bones at EAK (using the elephant bones as a covariate) with the ρ ('rhat') function and a Z 1 and Z 2 Berman-Lawson-Waller.

show a more random landscape distribution, and occur in similar frequencies in areas with intense hominin landscape use (as documented in high density artifact deposition) and those with marginal or non-hominin intervention (mostly devoid of anthropogenic lithic remains).

This indicates that from lower Bed II (1.78 Ma) onwards, there is ample documented evidence of anthropogenic agency in the modification of proboscidean bones across the Olduvai paleolandscapes. The discovery of EAK constitutes in this respect the oldest evidence thereof at the gorge. The taphonomic evidence of dynamic proboscidean bone breaking across time and space supports, therefore, the inferences made by the spatial statistical analyses of bones and lithics at the site.

Discussion

Evidence shows that the oldest systematic anthropogenic exploitation of proboscidean carcasses is documented (at several paleolandscape scales) in the Late Pleistocene sites of Neumark-Nord (Germany) (Gaudzinski-Windheuser et al., 2023a [↗](#), 2023b [↗](#)). Evidence of at least episodic access to proboscidean remains goes back in time (see review in Agam and Barkai, 2018 [↗](#); Ben-Dor et al., 2011 [↗](#); Haynes, 2022 [↗](#)). Redundant megafaunal exploitation is well documented at some early Pleistocene sites from Olduvai Gorge (Domínguez-Rodrigo et al., 2014a [↗](#), 2014b [↗](#); Organista et al., 2019 [↗](#), 2017 [↗](#), 2016 [↗](#)). At the very same sites, the stone artifactual assemblages, as well as the site dimensions, are substantially larger than those documented in the Bed I Oldowan sites (Diez-Martín et al., 2024 [↗](#), 2017 [↗](#), 2014 [↗](#), 2009 [↗](#)). Whether this reflects larger hominin groups or more prolonged and time-averaged intervention in more productive environments remains to be determined (it will likely vary according to site).

A recent discovery of a couple of hippopotamus partial carcasses at the 3.0-2.6 Ma site of Nyayanga (Kenya), spatially concurrent with stone artifacts, has been argued to be causally linked by the presence of cut marks on some bones (Plummer et al., 2023 [↗](#)). The only evidence published thereof is a series of bone surface modifications on a hippo rib and a tibial crest, which we suggest they might also be the result of byproduct of abiotic abrasive processes; the marks contrast noticeably with the well-defined cut marks found on smaller mammal bones in the same localities (Plummer et al.'s 2023 [↗](#): fig. 3C,D) associated with the hippo remains (Plummer et al., 2023 [↗](#)). The two trenches from which both hippo remains derive are located in the stratigraphic unit NY1, consisting of a channel containing cobble conglomerates and coarse sands in addition to silts. Gravel and coarse sand can generate the same types of marks seen in the figures of the Nyayanga hippo bones (Domínguez-Rodrigo et al., 2009a [↗](#); Manuel Domínguez-Rodrigo et al., 2010b [↗](#)). Hippopotamidae are the most abundant taxa in the Nyayanga excavations, indicating a productive taphocoenotic environment, in which hippopotamus remains co-occur with a large diversity of mammal taxa, most of which could have been naturally deposited and mixed. No green fractures have been reported on the hippopotamus bones as found in some other mammal fauna. Although Nyayanga could potentially be one of the earliest examples of megafaunal butchery, the taphonomic evidence remains ambiguous. Butchery experiments show that complete butchery of animals is reflected in a large percentage of remains bearing traces of butchery marks. In T3, these are documented in <0.9% and in T5 in 1%. This is a magnitude of 10-30 times lower than expected using experimental butchery frameworks (even if using only well-preserved bone specimens) (Domínguez-Rodrigo, 1997 [↗](#); Domínguez-Rodrigo et al., 2014a [↗](#); Pizarro-Monzo et al., 2021 [↗](#)).

The 1.8 Ma *Elephas recki* of FLK North (level 6, Olduvai Bed I) has the potential of being the oldest proboscidean butchery site (Leakey, 1971 [↗](#)). It was argued that cut marks existed on its complete bones (Bunn, 1982 [↗](#); Delagnes et al., 2006 [↗](#)), but a subsequent taphonomic study of those marks suggested that they might have been made by trampling (Domínguez-Rodrigo et al., 2007 [↗](#)). Additionally, it is unclear if the spatial association of stone tools and elephant bones is functional or artificial. Leakey (1971 [↗](#)) did not report on the third dimension of her excavations and this is crucial. In our excavations of FLK N6, we documented that the level was a deposit spanning more than half a meter depth and fossils and stone tools were vertically scattered throughout

(Domínguez-Rodrigo et al., 2010 [a](#)). It would have been essential to document that the FLK N6 tools associated with the elephant were either on the same depositional surface as the elephant bones and/or on the same vertical position.

The ambiguity about the FLK N6 elephant renders EAK the oldest secure proboscidean butchery evidence at Olduvai, and also probably one of the oldest in the early Pleistocene elsewhere in Africa. FLK North *Deinotherium* occupied a position above the EAK stratigraphic level, and evidence of hominin intervention there is missing (Leakey, 1971 [a](#)). A cut-marked bone fragment of a large animal (probably a hippopotamus) was documented at El-Kherba (Algeria) dated to 1.78 Ma (Sahnouni et al., 2013 [a](#)). These findings are suggestive of the beginning of megafaunal exploitation by humans in similar times both in East and North Africa.

Our landscape study of the megafaunal remains at Olduvai show that elephants and hippopotamus overlap on the same clustering areas. In all of them, the geology is indicative of extensive alluvial zones. At the base of Bed II, the gorge junction is characterized by extensive wetlands (Ashley, 2003 [a](#); Ashley et al., 2009 [a](#); Deocampo et al., 2002 [a](#); Hay, 2023; Liutkus and Ashley, 2003 [a](#)). In the overlying LAS, wetlands are crossed by important fluvial systems (Domínguez-Rodrigo et al., 2023 [a](#); Uribelarrea et al., 2017 [a](#)). In the middle and upper Bed II fluvial and wetland systems intertwined as the lake was reduced and moved away from its former shoreline in the Bed I-Bed II transition (Arráiz et al., 2017 [a](#); Garrett, 2017 [a](#); Uribelarrea del Val and Domínguez-Rodrigo, 2017 [a](#)). In all cases, these wet environments must have been preferred places for water-dependent megafauna, like elephants and hippos, and their overlapping ecological niches are reflected in the spatial co-occurrence of their carcasses. Both types of megafauna show traces of hominin use through either cutmarked or percussed bones, green-broken bones or both (Supplementary Information).

Green-broken elephant bones are documented at Olduvai at a landscape scale during the LAS deposition (1.7 Ma) (Diez-Martín et al., 2015 [a](#); Domínguez-Rodrigo et al., 2023 [a](#); Uribelarrea et al., 2017 [a](#)). This record is now added to the newly discovered EAK site, showing tight spatial association (both vertically and horizontally) between bones and stone tools. This trend of spatial association of stone artifacts and proboscidean bones continues through the deposition of Bed II. Although no cut marks have been documented on the proboscidean bones that we identified (part of which had cortical surfaces impacted by biostratinomic and diagenetic modification), the presence of green-broken bones at the sites, the butchery of carcasses as indicated by spatial statistical analyses at sites like EAK and TK (Domínguez-Rodrigo et al., 2014a [a](#); Organista et al., 2016 [a](#); Panera et al., 2019 [a](#)), and the presence of hammerstone-broken bones on the surrounding paleo-landscapes of these and other sites, support the occasional exploitation of megafaunal remains by humans. In most green-broken limb bones, we document the presence of a medullary cavity, despite the continuous presence of trabecular bone tissue on its walls. We do not know if the bone breakage was intended to obtain marrow or to create raw material for making artifacts or tools with functional purposes or both. We have been able to identify only one potential bone tool in our sample (Figures 6 [a](#), S4-S23); the scarcity of bone implements supports the former option. The exploitation of megafauna is not anecdotal, since at sites like BK or TK (upper Bed II), the taphonomic analysis of other megafaunal remains (namely, *Sivatherium* and *Pelorovis*) clearly shows intensive exploitation of complete carcasses in both of these taxa, especially at BK (Domínguez-Rodrigo et al., 2014a [a](#); Organista et al., 2016 [a](#); Panera et al., 2019 [a](#)). The food surplus generated by the exploitation of some of these animals would have been a significant advantage for the survival and adaptation of the hominin groups. These results of widespread conspicuous evidence of hammerstone-breaking behaviors during Bed II partially confirm the recent report on bone artefacts discovered in Bed II by another research team (de la Torre et al., 2025 [a](#)). Excavations at T69 Complex area unearthed a wealth of megafaunal (proboscidean and hippopotamus) remains displaying hammerstone green breakage and hominin modifications. These remains seem to be spatially connected with a highly productive paleolandscape, since at its northern end it connects with BBS, a recently discovered site with

megafaunal (Hippopotamus) remains. Green breakage at BBS also reflects hominin intervention in the palustrine environment congregating so many megafaunal carcasses. This unit would be equivalent to our second unit in Bed II.

We are not confident that the artefacts reported by dela Torre et al. at the T69 Complex are indeed tools. They are similar to the green-broken specimens that we have reported here. They are characterized by repeated number of flake scars along the edges; however, this is not a diagnostic feature, since multiple scars along edges also indirectly result from the repeated battering until the final breakage of the bone during butchery (Haynes et al., 2021 [DOI](#), 2020 [DOI](#); work in progress). In large bovids, it can also be derived from the gnawing of durophagous carnivores (Villa and Bartram, 1996 [DOI](#)) (Fig. S32). Carnivores capable of breaking elephant bones and producing the similar break shapes go back to at least the early Middle Miocene (Fig S33), although no carnivore today can effectively break the dense long bone mid-shafts of adult elephant bones. Another argument used by the authors is that the purported tools are longer and bear more flake scars compared to other faunal fragments (approximate average 13 versus 4). Again, this is documented among durophagous carnivores (Villa and Bartram, 1996 [DOI](#); see examples in the Supplementary Information). A higher scar number in the T69 artifact collection could result from a correlation of different variables (i.e., longer dimension of the compared specimens, or different carcass sizes) and be, therefore, unrelated to anthropic intentionality. A third argument provided is that the items share consistent technological features, such as the production of morphologically similar, elongated, pointed, and notched bone tools, suggesting a patterned behavior. Again, this is equifinal with unintentional breaking of megafaunal remains during butchery (Haynes et al., 2021 [DOI](#), 2020 [DOI](#); Figs.S 6-8-10-11-16-19; experimental work in progress). There are several arguments that could be used to support this alternative:

1. The scars in the T69 artifacts exhibit an asymmetric distribution, characterized by stepped or reflected, incomplete fractures predominantly on the medullary surface, with minimal invasiveness. This contrasts with the expected conchoidal and complete scarring distributed equally across both cortical (i.e., periosteal) and medullary surfaces, as would be anticipated in cases of intentional flaking. Given that bone is more easily flaked than metamorphic rock, and that bifacial knapping of stone typically produces symmetrical, conchoidal scars on both surfaces, this would also be expected in the T69 bone specimens.
2. This bilateral symmetry principle is observed in Middle Pleistocene bone handaxes, where intentional modification is inferred based on the equal treatment of both sides and evidence of artificial shaping (Zutovski and Barkai, 2016 [DOI](#)). It is also documented on the similarly aged 1.4 Ma bone handaxe from Konso (Sano et al., 2020 [DOI](#)), and a purported handaxe from FC (Bed II, Olduvai) (Backwell and d'Errico, 2004 [DOI](#)), but it is absent from the reported items in T69, as well as those of the present study. Why, otherwise, would scars on the medullary surface be mostly limited to the wall of the breakage plane?
3. The repeated presence of incomplete, stepped scars on the medullary surfaces of the artifacts found at T69 aligns more closely with damage resulting from deliberate battering associated with breakage rather than subsequent edge retouching. The latter process would be expected to generate more controlled and complete conchoidal scars indicative of intentional shaping (Backwell and d'Errico, 2004 [DOI](#); Haynes et al., 2021 [DOI](#), 2020 [DOI](#)). This reflected scarring is also documented in Bos/Bison bones broken by hyenas, caused by redundancy in gnawing and the resulting overlapping micro-cracking leading to final collapse (Villa and Bartram, 1996 [DOI](#)) (Fig. S31).
4. Scar frequency is not a taphonomically valid criterion to attribute agency, since elephant bones can be broken in multiple ways, thus impacting experimentally-derived scar patterns. Sequential battering of initial crack lines with handheld hammerstones can generate overlapping notches and scars (work in progress). This is not necessarily reproduced when other experimental studies use alternative methods (such as throwing or bashing against immobile anvils) (Backwell and d'Errico, 2004 [DOI](#); Haynes et al., 2021 [DOI](#)).

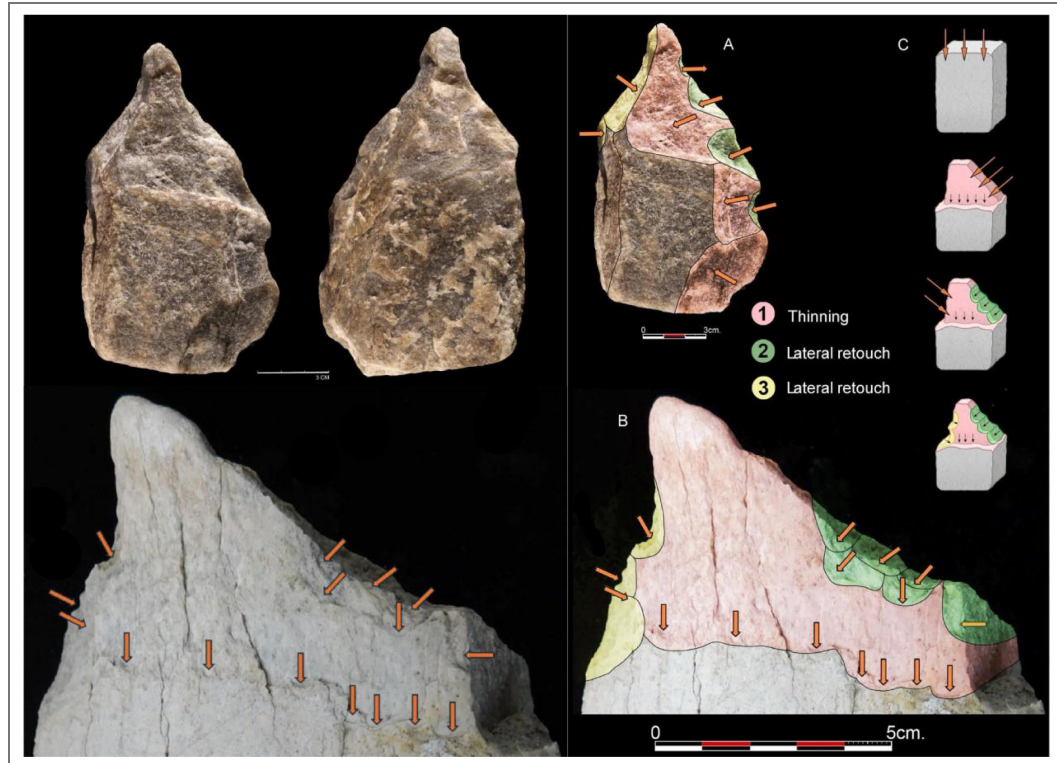


Figure 6.

Left: Intentional shaping of points in a quartzite LCT from FLK West, and on a proboscidean femur shaft. Arrows indicate conchoidal scars probably caused by use (given their location away from the edge) and their reflection and stepped morphology by the pointed area. Notice the polishing at the point, which contrasts with the unpolished state of the remainder of the artifact. More complete cortical and medullary views of this artifact can be seen in [Figures S6-S8](#). Right: Comparison of the configuration strategies identified on the quartz LCT and the LAS proboscidean femur shaft. A. LCT on a quartz slab from FLK West, Level 6; B. The proboscidean femoral shaft from LAS in the vicinity of EAK; C. Diacritical diagram showing point conceptualization sequencing identified in the previous specimens: 1. First thinning work (oblique to the distal end in the quartz LCT and vertical in the bone shaft); 2. Right-sided retouch; 3. Left-sided retouch. Series 2 and 3 determine the final shaping of the distal tip.

5. In several of the artifacts from T69, most of the overlapping scarring occurs in association to notches (and, in some cases, associated percussion marks) derived from dynamic loading. This reinforces that they may have been resulted from repeated battering during bone breaking.
6. The T69 Complex bone artifacts and those reported here are large-sized. If their potential function was for heavy-duty activities, those should have left any visible traces (at the macro and micro-scales) on the scarred edges. These are absent. A faunal assemblage that has good preservation of cut and percussion marks should certainly have good preservation conditions for microwear use and macro-damage scars.
7. If applying the same criteria defining bone tools at T69 Complex to Bos/Bison modified-bones, hyenas would also create similar artifacts (Fig. S32).

A final argument used by the authors to justify the intentional artifactual nature of their bone implements is that the bone tools were found *in situ* within a single stratigraphic horizon securely dated to 1.5 million years ago, indicating systematic production rather than episodic use. This is taphonomically unjustified. In a productive paleosurface where megafauna is abundant and hominin intervention is intense, the presence of this type of highly-scarred green-broken bones can be fairly common, since they result from butchery and carnivore post-depositional ravaging on non-proboscidean megafaunal bones (Domínguez-Rodrigo et al., 2014a [DOI](#), 2014b [DOI](#), 2009b [DOI](#); Villa and Bartram, 1996 [DOI](#)). Here, we have shown that most green-broken elephant bones cluster in three main areas of the Olduvai gorge.

Leakey collected more than a hundred purported bone tools from the same locations of Bed II where we collected our hammerstone-broken bones (Leakey, 1971 [DOI](#)) (Fig S33). All of them derive from Bed II (Backwell and d'Errico, 2004 [DOI](#)). A recent taphonomic review cautiously identified six potential bone tools in that collection (Pante et al., 2020 [DOI](#)). Some of these authors, using the much smaller T69 Complex artifact sample, now argue about systematic bone tool production. Bone artifacts (i.e., hominin-made items) that are used as tools should display evidence thereof through the macroscopic scarring, the polishing of the actively used surface, and the presence of microabrasive modifications on it (Backwell and d'Errico, 2008 [DOI](#), 2001 [DOI](#); d'Errico and Backwell, 2009 [DOI](#); LeMoine, 1994 [DOI](#)). None of that has been documented in the T69 assemblage. We do not deny that the items reported by de la Torre et al. (2025) [DOI](#) have the potential of having been used as tools, but proof is currently missing. The same applies to our reported sample (Fig 6 [DOI](#); S4-S25). Only one artifact shows modifications that are potentially derived from its use as a tool. If confirmed, it is interesting to note the convergence in the point shape targeted in such an implement and those intentionally shaped in the earliest Acheulian implements documented at Olduvai Gorge (Figs 6 [DOI](#), S6-S8). If such a bone implement was a tool, it would be the oldest bone tool documented to date (>1.7 Ma).

Conclusions

Here, we have reported a significant change in hominin foraging behaviors during Bed I and Bed II times, roughly coinciding with the replacement of Oldowan industries by Acheulian tool kits - although during Bed II, both industries co-existed for a substantial amount of time (Domínguez-Rodrigo et al., 2023 [DOI](#); Uribelarrea et al., 2019 [DOI](#), 2017 [DOI](#)). This correlation does not necessarily imply causation, given that most tools documented around some of these butchery sites (e.g. EAK) are typologically Oldowan (mostly flakes and fragments). The traditional Acheulian large cutting tools do not seem to have played any role in megafaunal butchery, since they are most commonly undocumented or under-represented at early butchery sites, and where they are predominant or very common (e.g., TK), they are not functionally associated with faunal exploitation (see the examples of typological changes at TK, when *Elephas* and *Sivatherium* carcasses are exploited) (Panera et al., 2019 [DOI](#)). In contrast, the occurrence of these megafaunal exploitation areas in three Bed II paleolandscape sections containing extremely large sites (e.g., FLK West in the LAS strata; SHK and BK in middle and upper Bed II respectively in the secondary gorge) attests to larger group sizes, which may be in connection with the intensity of exploitation of megafaunal resources. This was argued to be the main trigger in the thorough exploitation of a complete

Sivatherium carcass at BK (Domínguez-Rodrigo et al., 2014a [↗](#)), another one at TK (Panera et al., 2019 [↗](#)), and several *Pelorovis* individuals at BK (Organista et al., 2016 [↗](#)). The documentation of *H. erectus* around this time, with a much bigger anatomy than previous and sympatric hominins, suggests that a meat-based diet was behind these changes (Domínguez-Rodrigo et al., 2021 [↗](#)). Having repeated access to high-yielding megafaunal taxa would have enabled access to a large supply of food for a large group for a substantial amount of time. The same as modern Hadza can fend off predators like lions from large kills, those early hominins might have sustained a similar eco-trophic position, especially given their bigger size. An additional important resource, fat, might have also pushed hominins to target proboscideans, since their long bones contain large amounts of fat, rich in nutritional EPA. This resource is currently under no competition, since modern hyenas cannot break open elephant long bone shafts from adult individuals.

The evidence presented here, together with that documented by de la Torre et al. (2025) [↗](#), represents the most geographically extensive documentation of repeated access to proboscidean and other megafaunal remains at a single fossil locality. The transition from Oldowan sites, where lithic and archaeofaunal assemblages are typically concentrated within 30–40 m² clusters, to Acheulean sites that span hundreds or even over 1000 m² (as in BK), with distinct internal spatial organization and redundancy in space use across multiple archaeological layers spanning meters of stratigraphic sequence (Domínguez-Rodrigo et al., 2014a [↗](#), 2009b [↗](#); Organista et al., 2017 [↗](#)), reflects significant behavioral and technological shifts. This pattern likely signifies critical innovations in human evolution, coinciding with major anatomical and physiological transformations in early hominins (Dembitzer et al., 2022 [↗](#); Domínguez-Rodrigo et al., 2021 [↗](#), 2012 [↗](#)). The causal relationships of these events that appear correlated in the archaeological record remain to be established.

Methods

Excavation of EAK

The systematic excavation of the stratigraphic layers involved a small crew. Materials exceeding 2 cm in size were meticulously plotted using laser theodolites (TOPCON total stations). Each trench was subjected to stereo-photography upon exposure, enabling the creation of photogrammetric 3D reconstructions of the paleosurface and deposited materials prior to recovery. The orientation and inclination of the artifacts were recorded using a compass and an inclinometer, respectively. Sediments removed from the trenches were sieved using 5 mm and 3 mm meshes.

The photogrammetric reconstructions of each trench were subsequently georeferenced and the resulting orthophotos were imported into AutoCAD, facilitating the detailed mapping of archaeological materials. The decision to conduct photogrammetry by individual trenches was made to minimize the exposure time of the excavated materials. Prolonged exposure could accelerate desiccation, potentially causing the most fragile specimens to become brittle and fragmentary. To mitigate this risk, excavation was limited to small, manageable areas, with small trenches proving ideal for efficient excavation due to the limited overburden. Each trench was excavated until the entire archaeological horizon was exposed, followed by comprehensive photogrammetric documentation prior to 3D plotting. Throughout the excavation, professional restoration experts provided necessary treatment for the bones. This was crucial for the recovery and identification of many bone fragments.

Restoration of the EAK elephant bones

The main interventions were carried out in two locations: in situ, and in the field laboratory at the Emiliano Aguirre Research Station. For the consolidation and extraction of remains at the site, interventions were performed using Paraloid B-72 diluted in acetone at different concentrations, applied exclusively to fossils exhibiting powdering. This methodology strengthened the bones prior to extraction, ensuring better handling and reducing the risk of fractures. The use of Paraloid B-72 is a standard practice in the conservation of osseous remains due to its stability and compatibility with the material, though its limited penetration in some bone types has been

noted (Daura et al., 2017 [↗](#)). During this process, bandaging with sterile gauze impregnated with Paraloid B-72 was selectively applied to necessary areas to further protect fragile sections. Additionally, superficial bandaging was conducted on larger fossils that visibly presented potential fractures and retained their cortical surface, aiming to prevent deterioration during the extraction process.

The greatest challenge was extracting long bones due to their size, weight, and fragility. These bones exhibited a greater presence of cortical surface, although they were not completely preserved, as they were fragmented but still retained significant areas suitable for study. Another significant challenge was the extraction of tusk remains, as the ivory exhibited a high degree of degradation and fragmentation. To recover these, multiple applications of consolidant were performed, allowing certain tusk blocks to be extracted in a controlled manner.

Larger fossils were extracted in block to minimize the risk of structural damage. The extraction process involved:

1. Initial consolidation by applying Paraloid B-72 dropwise to the surface, along with bandaging with sterile gauze in necessary areas to provide additional protection.
2. Surface protection with a sacrificial layer, avoiding direct contact with other reinforcing materials.
3. Creation of a counter-mold using plaster bandages, reinforced with interwoven steel rods to provide rigidity and stability.
4. Insertion of metal spatulas beneath the remains to lift and safely transport them.

In the field laboratory, cleaning of the bone remains was carried out, along with adhesion of fragments and their consolidation when necessary. The primary priority was preparing the remains for study by the rest of the team, opting for a purely conservative intervention, prioritizing detailed cleaning of some fragments for identification. Additionally, reassembly of larger fragments was performed, using Paraloid B-72 diluted in acetone at a higher concentration to ensure effective adhesion. For bone remains, mechanical and chemical cleaning procedures were applied depending on the nature of the adhered deposits.

This restoration procedure enabled the preservation of many bone fragments. Cleaning them properly will require much more time. In their current status, several specimens still have some adhering sedimentary matrix. This has prevented us from thoroughly examining all bone surfaces looking for BSM or conducting comprehensive identification. Some elements and fragments remain unidentified given also the lack of a proper comparative proboscidean collection. Despite this, most of the assemblage has been successfully studied.

Taphonomic analysis of EAK

Skeletal part profiles were determined using the Number of Identifiable Specimens (NISIP) and the Minimum Number of Elements (MNE) (Table S1 [↗](#)). Given that with the exception of a few faunal specimens, the majority of the assemblage belongs to a single elephant individual, we did not use hierarchical units like MNI or MAU. To determine the MNE, ribs have been divided according to Rodríguez-Hidalgo's (2017) system: portion 1 belongs to the epiphysis which includes the head, neck and costal tubercle; portion 2 belongs to the costal angle; portion 3 belongs to the proximal body; portion 4 is composed by the distal body and portion 5 belongs to the sternal zone. The high frequency of fragmentation documented in the EAK's ribs and the lack of landmarks made us determine the rib's MNE through portions 1 and 2, in addition to a side-by-side comparison of rib shaft fragment widths (portions 3 and 4).

In the present study, presence of abrasion and polishing due to water dynamics (i.e., resedimentation, transport, lag) was taken into account. The first issue we analysed regarding the spatial distribution of archaeological remains was the orientation and slope of the items. First, we created stereograms and rose diagrams for the sample of elephant bone remains and lithic artifacts, as well as for both sets combined. These graphs were generated using OpenStereo software. Next, we conducted Rayleigh, Watson, and Kuiper tests to determine whether the isotropy/anisotropy tendency could be rejected (Fisher 1995 [↗](#)).

An evaluation of the cortical surfaces was made, followed by an analysis of bone surface modifications; namely, cut marks, tooth marks, percussion marks and natural marks (i.e., biochemical and abrasion marks). Marks were identified by using hand lenses under strong direct light (60W) following the methodological and mark diagnostic criteria specified in [Blumenschine \(1995\)](#) and [Blumenschine & Selvaggio \(1988\)](#) for tooth and percussion marks, [Dominguez-Rodrigo et al. \(2009a, 2010b\)](#) for cut marks, and [Domínguez-Rodrigo and Barba \(2006\)](#) for biochemical marks. The analysis of bone breakage at EAK is based on the identification of green and dry breakage planes following [Villa and Mahieu's \(1991\)](#) criteria.

Lithic analysis of EAK

A total of 80 lithic specimens have been recovered from EAK. The technological analysis of these materials follows established classification criteria and methodological frameworks ([Diez-Martín et al., 2009](#)), categorizing artifacts into the following groups:

- a. Unmodified Specimens – Naturally occurring cobblestones lacking evidence of anthropogenic modification.
- b. Percussion Tools – Includes hammerstones or cobbles exhibiting diagnostic battering, pitting, and/or impact scars consistent with percussive activities.
- c. Cores – Handheld cores are classified based on key technological attributes: (i) the number of reduction surfaces (unifacial, bifacial, multifacial), (ii) the number of striking platforms (unipolar, bipolar, multipolar), and (iii) the spatial organization of knapping sequences (linear, opposed, orthogonal, centripetal). Bipolar cores are identified based on diagnostic features associated with anvil-supported percussion.
- d. Detached Products – This category encompasses both complete and fragmented flakes, derived from either bipolar or freehand reduction. Technological attributes recorded for detached products include core reduction stage (assessed through the presence and extent of cortical coverage on dorsal surfaces and striking platforms), platform morphology, and dorsal scar patterning.
- e. Knapping By-Products – Includes all non-diagnostic lithic debris resulting from core reduction and flake detachment. This category incorporates non-diagnostic flake fragments with evidence of direct handheld percussion, shatter, blocky/angular undetermined detached fragments, core-like fragments, and debris ≤ 20 mm in size.

The spatial statistical analyses of EAK

The spatial point patterns (SPP) of faunal and lithic remains have been analyzed using the 'spatstat' library ([Baddeley et al., 2015](#)) in R (www.r-project.org). This methodological approach is of great interest for paleontological and archaeological contexts, as it allows for the analysis of aspects such as the degree of randomness of the SPP, potential relationships between different types of materials, or enabling predictions about unexcavated areas. We conducted the analysis in three different ways after selecting the spatial window, i.e. the analysed excavated area (52.56 m²).

First, we analysed the SPPs without marks (i.e., raw SPPs, without considering any specific spatial variable) for the elephant remains and lithic remains independently. In these initial cases, we created intensity maps, hot spot maps, and hot spot maps with a 99% Confidence Interval (C.I.). Next, we applied a chi-squared test with four different grid configurations (5×5, 8×8, 10×10, 12×12) ([Moclán et al., 2023](#)) to determine whether the SPPs are homogeneous or inhomogeneous. These analyses showed that, in all cases, the SPPs can be considered inhomogeneous (p-value <0.05). Therefore, we proceeded to use tests to analyse the type of SPP. We employed the Pair Correlation, *K*, *L*, *F*, *G*, and *J* functions in their inhomogeneous versions, as well as the *Kscaled* and *Lscaled* functions to analyse the typology of the SPPs (i.e., random, cluster, or regular). Both versions of the functions were used because the sample size does not allow us to analyse the type of inhomogeneity through a studentized permutation test. Similarly, we used the DCLF (Diggle-Cressie-Loosmore-Ford) and MAD (Maximum Absolute Deviation) tests with the *K*, *L*, *F*, *G*, *J*, *Kscaled*, and *Lscaled* functions to check the typology of the point patterns (i.e., random vs. non-

random). Finally, we used the ‘nnclean’ function (Baddeley et al., 2015) to detect possible clustering of materials through nearest neighbour clutter removal. Lastly, we performed spatial modelling using linear, quadratic, cubic, and 4th-degree polynomial regressions to delve deeper into the characteristics of the SPPs. The models were evaluated using the Akaike Information Criterion (AIC) index, and subsequently, we compared their validity through ANOVA. Finally, we selected the best-performing model (i.e., the one with the lowest AIC values and that does not show issues of collinearity or suffer from the small sample size) and generated four maps: 1) estimated intensity of the point process based on the fitted model, 2) simulation of a new point pattern using the fitted model with the Metropolis-Hastings algorithm, 3) a difference map subtracting the intensity of the simulated new point pattern from the “real” intensity of the spatial point pattern (Domínguez-Rodrigo et al., 2024), and 4) an extrapolated estimation of potential points within a larger spatial window (308.23 m²) than the original one.

The second analysis consists of examining the degree of statistical correlation between two marks, i.e., spatial variables, in this case, fauna vs. lithic tools. To do this, we first calculated the relative risk to assess the likelihood of each type of material appearing in the analysed window. Then, we applied a chi-square test to verify once again, using the same grid configuration, whether the samples are homogeneous or inhomogeneous. The chi-square test again indicates that the spatial distribution is inhomogeneous. Therefore, we used the K , L , K_{cross} , and L_{cross} inhomogeneous functions to analyse whether there is spatial correlation between the two material types and, if so, what kind it is.

Finally, given the size disparity between the elephant remains and the lithics, we analysed the relationship between both types of materials by considering the location of the elephant remains as a covariate. First, a distance map was generated to the centroids of the bone remains. ANOVA was then conducted to assess the fitted effect of the covariate in the SPPs. This was followed by the application of the ρ function (‘rho-hat’ function) to investigate the influence of the distance to the bones. This test is similar to the previous one but provides a more detailed view of the potential variations in the intensity of remains with respect to distance from the bones. Finally, a Z_1 and Z_2 Berman–Lawson–Waller test was performed.

Megafaunal exploitation along the paleolandscape sequence of Olduvai Gorge

An intensive survey seeking stratigraphically-associated megafaunal bones was carried out in the months of June 2023 and 2024. We targeted the Bed I and Bed II exposures of the main Gorge (From FLK NNN to the KK fault), and the side gorge, from the junction until BK. Linearly, this comprises over 6 km of outcrops. We targeted this area because it contains the highest density of fossils of all the gorge. We focused on proboscidean bones and used hippopotamus bones, some of the most abundant in the megafaunal fossils, as a spatial control. Bones were counted as separate carcasses when enough distance existed in between findings (i.e., localities). Stratigraphic association was carried out by direct observation of the geological context and with the presence of a Quaternary geologist during the whole survey. When fossils found were ambiguously associated with specific strata, these were excluded from the present analysis.

For the sake of analysis, and given that we were not focusing on time-resolution landscapes, we used four time intervals: Bed I, Bed II lower (from Tuff IF to LAS), Bed II intermediate (from Tuff IIB to Tuff IIC, and Bed II upper (from Tuff IID to the interface with Bed III). Only in one case, Bed II lower, were most of the remains circumscribed to a single stratigraphic unit (Lower Augitic Sands [LAS], which mark the beginning of Hay’s middle Bed II). The goals of this survey were: a) collect a spatial sample of proboscidean and megafaunal bones enabling us to understand if carcasses on the Olduvai paleolandscapes were randomly deposited or associated to specific habitats; b) given the water dependence of elephants, we wanted to understand if they showed the same type of ecological association to water-dependent megafauna, like hippopotamus, as their modern counterparts (using taphocoenoses as indicators of past megafaunal biocoenosis); c) approach potential anthropogenic agency in proboscidean exploitation by comparing carcass dispersal and accumulation and productivity of anthropogenic landscapes (i.e., concentrations and

dispersals of lithic artifacts); d) seek anthropogenic traces of proboscidean exploitation in the form of cut and percussion marks and green bone breakage; e) associate this latter point with the hominin use of space, by determining if these taphonomic evidences occurred randomly or clustered and spatially associated with stone tools.

Data availability

It does not apply but data is available upon request

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Additional files

[Supplementary Information](#) 

Additional information

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Peer reviews

Reviewer #1 (Public review):

Domínguez-Rodrigo and colleagues make a largely convincing case for habitual elephant butchery by Early Pleistocene hominins at Olduvai Gorge (Tanzania), ca. 1.8-1.7 million years ago. They present this at a site scale (the EAK locality, which they excavated), as well as across the penecontemporaneous landscape, analyzing a series of findspots that contain stone tools and large-mammal bones. The latter are primarily elephants, but giraffids and bovids were also butchered in a few localities.

The authors claim that this is the earliest well-documented evidence for elephant butchery; doing so requires debunking other purported cases of elephant butchery in the literature, or in one case, reinterpreting elephant bone manipulation as being nutritional (fracturing to obtain marrow) rather than technological (to make bone tools). The authors' critical discussion of these cases may not be consensual, but it surely advances the scientific discourse. The authors conclude by suggesting that an evolutionary threshold was achieved at ca. 1.8 ma, whereby regular elephant consumption rich in fats and perhaps food surplus, more advanced extractive technology (the Acheulian toolkit), and larger human group size had coincided.

The fieldwork and spatial statistics methods are presented in detail and are solid and helpful, especially the excellent description (all too rare in zooarchaeology papers) of bone conservation and preservation procedures. The results are detailed and clearly presented.

The authors achieved their aims, showcasing recurring elephant butchery in 1.8-1.7 million-year-old archaeological contexts. The authors cautiously emphasize the temporal and spatial correlation of 1) elephant butchery, 2) Acheulian toolkits, and 3) larger sites, and discuss how these elements may be causally related.

Overall, this is an interesting manuscript of broad interest that presents original data and interpretations from the Early Pleistocene archaeology of Olduvai Gorge. These observations and the authors' critical review of previously published evidence are an important contribution that will form the basis for building models of Early Pleistocene hominin adaptation.

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Reviewer #2 (Public review):

The manuscript makes a valuable contribution to the Olduvai Gorge record, offering a detailed description of the EAK faunal assemblage. In particular, the paper provides a high-resolution record of a juvenile *Elephas recki* carcass, associated lithic artifacts, and several green-broken bone specimens. These data are inherently valuable and will be of significant interest to researchers studying Early Pleistocene taphonomy. My concerns do not relate to the quality or importance of the data themselves, but rather to the interpretive inferences drawn from these data, particularly regarding the strength of the claim for unambiguous proboscidean butchery.

This review follows the authors' response to an earlier round of reviewer feedback and addresses points raised in that exchange. In their rebuttal, the authors state that some of my initial concerns reflect misunderstandings of their analysis, but after carefully re-reading both the manuscript and their responses, I do not believe this is the case.

In their response, the authors state that they do not treat the EAK evidence as decisive, yet the manuscript repeatedly characterizes the assemblage in very definitive terms. For example, EAK is described as "the oldest unambiguous proboscidean butchery site at Olduvai" and as "the oldest secure proboscidean butchery evidence." These phrases communicate a high level of confidence that does not align with the more qualified position articulated in the rebuttal and extends beyond what the documented evidence securely supports.

I appreciate the authors' clarification regarding the fracture features, and I agree that these are well-established outcomes of dynamic hammerstone percussion. At the same time, several of these traits have been documented in non-anthropogenic contexts, including helicoidal spiral fractures resulting from trampling and carnivore activity (Haynes 1983), adjacent or flake-like scars created by carnivore gnawing (Villa and Bartram 1996), hackled break surfaces produced by heavy passive breakage such as trampling or sediment pressure (Haynes 1983), and impact-related bone flakes observed in carnivore-modified assemblages (Coil et al. 2020). One of the biggest issues is that there is no quantitative data or images of the bone fracture features that the authors refer to as the main diagnostic criteria at EAK. The only figures that show EAK specimens (S21, S22, S23) illustrate general green-bone fracture morphology but none of the specific traits listed in the text. In contrast, clear examples of similar features come from other Olduvai assemblages, which may be misleading to readers if they mistakenly interpret those as images from EAK. The manuscript also states that these traits "co-occur," but it is not defined whether this refers to multiple features on the same fragment or within the broader assemblage. Without images or counts that document these traits on EAK fossils, readers cannot evaluate the strength of the interpretation. Including that information would substantially strengthen the manuscript.

Regarding the statement that "natural elephant long limb breaks have been documented only in pre or peri-mortem stages when an elephant breaks a leg, and only in femora (Haynes et al., 2021)," it is not entirely clear what this example is intended to illustrate in relation to the EAK assemblage. My understanding is that the authors are suggesting that naturally produced green bone fractures in elephants are very limited, perhaps occurring only in pre or peri-mortem broken leg cases, and that fractures on other elements should therefore be attributed to hominin activity. If that is not the intended argument, I would encourage clarifying this point. This appears to conflate pre-mortem injury with the broader issue of equifinality. My original comment was not referring to pre-mortem breaks but to the range of natural (i.e., non-hominin) and post-mortem processes that can generate spiral or green bone fractures similar to those described by the authors.

I fully understand the spatial analyses, and I realize that the association between bones and lithics is statistically significant. My original concern was not about whether the correlation exists, but about how that correlation is interpreted. That point still stands. Statistical co-occurrence cannot distinguish among the multiple depositional and post-depositional processes that can generate similar spatial patterns. However, I agree that the spatial correlation is intriguing, particularly when viewed alongside the possible butchery evidence. The pattern is notable and worthy of publication, even if the behavioral interpretation requires caution.

Finally, in considering the authors' response on the Nyayanga material, I still find the basis for their dismissal of that evidence difficult to follow and the contrasting treatment of the Nyayanga and EAK evidence raises concerns about interpretive consistency. Plummer et al. (2023) specify that bone surface modifications were examined using low-power magnification (10×-40×) and strong light sources to identify modifications and that they attributed agency (e.g., hominin, carnivore) to modifications only after excluding possible alternatives. The rebuttal does not engage with the procedures reported. The existence of newer analytical techniques does not diminish the validity of long-standing methods that have been applied across many studies. It is also unclear why abrasion is presented as a more

likely explanation than stone tool cutmarks. The authors dismiss the Nyayanga images as "blurry," but this is irrelevant to the interpretation, since the analysis was based on the fossils, not the photographs. The Nyayanga dataset is dismissed without a thorough engagement, while the EAK material, despite similar uncertainties and potential for alternative explanations, is treated as definitive.

These concerns do not diminish the significance of the EAK assemblage, and addressing them would allow the interpretations to more fully reflect the scope of the available data.

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Author response:

The following is the authors' response to the original reviews

Public Reviews:

Reviewer #1 (Public review):

Domínguez-Rodrigo and colleagues make a moderately convincing case for habitual elephant butchery by Early Pleistocene hominins at Olduvai Gorge (Tanzania), ca. 1.8-1.7 million years ago. They present this at the site scale (the EAK locality, which they excavated), as well as across the penecontemporaneous landscape, analyzing a series of findspots that contain stone tools and large-mammal bones. The latter are primarily elephants, but giraffids and bovids were also butchered in a few localities. The authors claim that this is the earliest well-documented evidence for elephant butchery; doing so requires debunking other purported cases of elephant butchery in the literature, or in one case, reinterpreting elephant bone manipulation as being nutritional (fracturing to obtain marrow) rather than technological (to make bone tools). The authors' critical discussion of these cases may not be consensual, but it surely advances the scientific discourse. The authors conclude by suggesting that an evolutionary threshold was achieved at ca. 1.8 ma, whereby regular elephant consumption rich in fats and perhaps food surplus, more advanced extractive technology (the Acheulian toolkit), and larger human group size had coincided.

The fieldwork and spatial statistics methods are presented in detail and are solid and helpful, especially the excellent description (all too rare in zooarchaeology papers) of bone conservation and preservation procedures. However, the methods of the zooarchaeological and taphonomic analysis - the core of the study - are peculiarly missing. Some of these are explained along the manuscript, but not in a standard Methods paragraph with suitable references and an explicit account of how the authors

recorded bone-surface modifications and the mode of bone fragmentation. This seems more of a technical omission that can be easily fixed than a true shortcoming of the study. The results are detailed and clearly presented.

By and large, the authors achieved their aims, showcasing recurring elephant butchery in 1.8-1.7 million-year-old archaeological contexts. Nevertheless, some ambiguity surrounds the evolutionary significance part. The authors emphasize the temporal and spatial correlation of (1) elephant butchery, (2) Acheulian toolkits, and (3) larger sites, but do not actually discuss how these elements may be causally related. Is it not possible that larger group size or the adoption of Acheulian technology have nothing to do with megafaunal exploitation? Alternative hypotheses exist, and at least, the authors should try to defend the causation, not just put forward the correlation. The only exception is briefly mentioning food surplus as a "significant advantage", but how exactly, in the absence of food-preservation technologies? Moreover, in a landscape full of aggressive scavengers, such excess carcass parts may become a death trap for hominins, not an advantage. I do think that demonstrating habitual butchery bears very significant implications for human evolution, but more effort should be invested in explaining how this might have worked.

Overall, this is an interesting manuscript of broad interest that presents original data and interpretations from the Early Pleistocene archaeology of Olduvai Gorge. These observations and the authors' critical review of previously published evidence are an important contribution that will form the basis for building models of Early Pleistocene hominin adaptation.

This is a good example of the advantages of the eLife reviewing process. It has become much too common, among traditional peer-reviewing journals, to reject articles when there is no coincident agreement in the reviews, regardless of the heuristics (i.e., empirically-supported weight) of the arguments on both reviewers. Reviewers 1 and 2 provide contrasting evaluations, and the eLife dialogue between authors and reviewers enable us to address their comments differentially. Reviewer 1 (R1), whose evaluation is overall positive, remarks that the methods of the zooarchaeological and taphonomic analysis are missing. We have added them now in the revised version of our manuscript. R1 also remarks that our work highlights correlation of events, but not necessarily causation. We did not establish causation because such interpretations bear a considerable amount of speculation (and they might have fostered further criticism by R2); however, in the revised version, we expanded our discussion of these issues substantially. Establishing causation among the events described is impossible, but we certainly provide arguments to link them.

Reviewer #2 (Public review):

The authors argue that the Emiliano Aguirre Korongo (EAK) assemblage from the base of Bed II at Olduvai Gorge shows systematic exploitation of elephants by hominins about 1.78 million years ago. They describe it as the earliest clear case of proboscidean butchery at Olduvai and link it to a larger behavioral shift from the Oldowan to the Acheulean.

The paper includes detailed faunal and spatial data. The excavation and mapping methods appear to be careful, and the figures and tables effectively document the assemblage. The data presentation is strong, but the behavioral interpretation is not supported by the evidence.

The claim for butchery is based mainly on the presence of green-bone fractures and the proximity of bones and stone artifacts. These observations do not prove human activity. Fractures of this kind can form naturally when bones break while still fresh, and spatial overlap can result from post-depositional processes. The studies cited to support these

points, including work by Haynes and colleagues, explain that such traces alone are not diagnostic of butchery, but this paper presents them as if they were.

The spatial analyses are technically correct, but their interpretation extends beyond what they can demonstrate. Clustering indicates proximity, not behavior. The claim that statistical results demonstrate a functional link between bones and artifacts is not justified. Other studies that use these methods combine them with direct modification evidence, which is lacking in this case.

The discussion treats different bodies of evidence unevenly. Well-documented cut-marked specimens from Nyayanga and other sites are described as uncertain, while less direct evidence at EAK is treated as decisive. This selective approach weakens the argument and creates inconsistency in how evidence is judged.

The broader evolutionary conclusions are not supported by the data. The paper presents EAK as marking the start of systematic megafaunal exploitation, but the evidence does not show this. The assemblage is described well, but the behavioral and evolutionary interpretations extend far beyond what can be demonstrated.

We disagree with the arguments provided by Reviewer 2 (R2). The arguments are based on two issues: bone breakage and spatial association. We will treat both separately here.

Bone breakage

R2 argues that:

“The claim for butchery is based mainly on the presence of green-bone fractures and the proximity of bones and stone artifacts. These observations do not prove human activity. Fractures of this kind can form naturally when bones break while still fresh, and spatial overlap can result from post-depositional processes. The studies cited to support these points, including work by Haynes and colleagues, explain that such traces alone are not diagnostic of butchery, but this paper presents them as if they were.”

In our manuscript, we argued that green-breakage provides an equally good (or even better) taphonomic evidence of butchery if documented following clear taphonomic indicators. Not all green breaks are equal and not all “cut marks” are unambiguously identifiable as such. First, “natural” elephant long limb breaks have been documented only in pre/peri-mortem stages when an elephant breaks a leg. As a matter of fact, they have only been reported in publication on femora, the thinnest long bone (Haynes et al., 2021). Unfortunately, they have been studied many months after the death of the individuals, and the published diagnosis is made under the assumption that no other process intervened in the modification of those bones during this vast time span. Most of the breaks resulting from pre-mortem fractures produce long smooth, oblique/helical outlines. Occasionally, some flake scarring may occur on the cortical surface. This has been documented as uneven, small-sized, spaced, and we are not sure if it resulted from rubbing of broken fragments while the animal was alive and attempting to walk or some may have resulted from dessication of the bone after one year. When looking at them in detail, such breaks contain sometimes step-microfractures and angular (butterfly-like) outlines. Sometimes, they may be accompanied by pseudo-notches, which are distinct and not comparable to the deep notches that hammerstone breaking generates on the same types of bones. Commonly, the edges of the breaks show some polishing, probably from separate break planes rubbing against each other. It should be emphasized that the experimental work on hammerstone breaking documented by Haynes et al. (2021) is based on bone fracture properties of bones that are no longer completely green. The cracking documented in their hammerstone experimentation, with very irregular outlines differs from the cracking that we are documented in butchery of recently dead elephants.

All this contrasts with the overlapping notches and flake scars (mostly occurring on the medullary side of the bone), both of them bigger in size, with clear smooth, spiral and longitudinal trajectories, with a more intensive modification on the medullary surface, and with sharp break edges resulting from hammerstone breaking of the green bone. No “natural” break has been documented replicating the same morphologies displayed in the Supplementary File to our paper. We display specimens with inflection points, hackle marks on the breaks, overlapping scarring on the medullary surface, with several specimens displaying percussion marks and pitting (also most likely percussion marks). Most importantly, we document this patterned modification on elements other than femora, for which no example has been documented of purported morphological equifinality caused by pre-mortem “natural” breaking. In contrast, such morphologies are documented in hammerstone-broken completely green bones (work in progress). We cited the works of Haynes to support this, because they do not show otherwise. As a matter of fact, Haynes himself had the courtesy of making a thorough reading of our manuscript and did not encounter any contradiction with his work.

Spatial association

R2 argues in this regard:

“The spatial analyses are technically correct, but their interpretation extends beyond what they can demonstrate. Clustering indicates proximity, not behavior. The claim that statistical results demonstrate a functional link between bones and artifacts is not justified. Other studies that use these methods combine them with direct modification evidence, which is lacking in this case.”

We should emphasize that there is some confusion in the use and interpretation of clustering by R2 when applied to EAK. R2 appears to interpret clustering as the typical naked-eye perception of the spatial association of different items. In contrast, we rely on the statistical concept of clustering, more specifically on spatial interdependence or covariance, which is different. Items may appear visually clustered but still be statistically independent. This could, for example, result from two independent depositional episodes that happen to overlap spatially. In such cases, the item-to-item relationship does not necessarily show any spatial interdependence between classes other than simple clustering (i.e., spatial coincidence in intensity).

Spatial statistical interdependence, on the other hand, reflects a spatial relationship or co-dependence between different items. This goes beyond the mere fact that classes appear clustered: items between classes may show specific spatial relationships — they may avoid each other or occupy distinct positions in space (regular co-dependence), or they may interact within the same spatial area (clustering co-dependence). Our tests indicate the latter for EAK.

Such patterns are difficult to explain when depositional events are unrelated, since the probability that two independent events would generate identical spatial patterns in the same loci is very low. They are also difficult to reconcile when post-depositional processes intervene and resediment part of the assemblage (Domínguez-Rodrigo et al. 2018).

Finally, R2 concludes:

“The discussion treats different bodies of evidence unevenly. Well-documented cut-marked specimens from Nyayanga and other sites are described as uncertain, while less direct evidence at EAK is treated as decisive. This selective approach weakens the argument and creates inconsistency in how evidence is judged.”

The Nyayanga hippo remains bearing modifications have not been well-documented cut marks. Neither R2 nor we can differentiate those marks from those inflicted by natural

abrasive processes in coarse-grained sedimentary contexts, where the carcasses are found. The fact that the observable microscopic features (through low-quality photographs as appear in the original publication) differ between the cut marks documented on smaller animals and those inferred for the hippo remains makes them even more ambiguous. Nowhere in our manuscript do we treat the EAK evidence (or any other evidence) as decisive, but as the most likely given the methods used and the results reported.

References

Haynes G, Krasinski K, Wojtal P. 2021. A Study of Fractured Proboscidean Bones in Recent and Fossil Assemblages. *Journal of Archaeological Method and Theory* 28:956–1025.

Domínguez-Rodrigo, M., Cobo-Sánchez, L., yruveda, J., Uribealarea, D., Arriaza, C., Organista, E., Baquedano, E. 2018. Fluvial spatial taphonomy: a new method for the study of post-depositional processes. *Archaeological and Anthropological Sciences* 10: 1769-1789.

Recommendations for authors:

Reviewer #1 (Recommendations for the authors):

I have several recommendations that, in my opinion, could enhance the communication of this study to the readers. The first point is the only crucial one.

(1) A detailed zooarchaeological methods section must be added, with explanations (or references to them) of precisely how the authors defined and recorded bone-surface modifications and mode of bone fragmentation.

This appears in the revised version of the manuscript in the form of a new sub-section within the Methods section.

(2) The title could be improved to better represent the contents of the paper. It contains two parts: the earliest evidence for elephant butchery (that's ok), and revealing the evolutionary impact of megafaunal exploitation. The latter point is not actually revealed in the manuscript, just alluded to here and there (see also below).

We have elaborated on this in the revised version, linking megafaunal exploitation and anatomical changes (which appear discussed in much more detail in the references indicated).

(3) The abstract does not make it clear whether the authors think that the megafaunal adaptation strongly correlates with the Acheulian technocomplex. It seems that they do, so please make this point apparent in the abstract.

From a functional point of view, we document the correlation, but do not believe in the causation, since most butchering tools around these megafaunal carcasses are typologically non Acheulian. We have indicated so in the abstract.

(4) Please define what you mean by "megafauna". How large should an animal be to be considered as megafauna in this particular context?

We have added this definition: we identify as “megafauna” those animals heavier than 800 kg.

*(5) In the literature survey, consider also this Middle Pleistocene case-study of elephant butchery, including a probable bone tool: Rabinovich, R., Ackermann, O., Aladjem, E., Barkai, R., Biton, R., Milevski, I., Solodenko, N., and Marder, O., 2012. Elephants at the middle Pleistocene Acheulian open-air site of Revadim Quarry, Israel. *Quaternary International*, 276, pp.183-197.*

Added to the revised version

(6) The paragraph in lines 123-160 is unclear. Do the authors argue that the lack of evidence for processing elephant carcasses for marrow and grease is universal? They bring forth a single example of a much later (MIS 5) site in Germany. Then, the authors state the huge importance of fats for foragers (when? Where? Surely not in all latitudes and ecosystems). This left me confused - what exactly are you trying to claim here?

We have explained this a little more in the revised text. What we pointed out was that most prehistoric (and modern) elephant butchery sites leave grease-containing long bones intact. Evidence of anthropogenic breakage of these elements is rather limited. The most probably reason is the overabundance of meat and fat from the rest of the carcass and the time-consuming effort needed to access the medullary cavity of elephant long bones.

(7) The paragraph in lines 174-187 disrupts the flow of the text, contains previously mentioned information, ends with an unclear sentence, and could be cut.

(8) Results: please provide the MNI for the EAK site (presumably 1, but this is never mentioned).

Done in the revised version.

(9) Lines 292 - 295: The authors found no traces of carnivorous activity (carnivorous remains, coprolites, or gnawing marks on the elephant bones), yet they attribute the absence of some non-dense skeletal elements to carnivore ravaging. I cannot understand this rationale, given that other density-mediated processes could have deleted the missing bones and epiphysis.

This interpretation stems from our observations of several elephant carcasses in the Okavango delta in Botswana. Those that were monitored showed deletion of remains (i.e., disappearance of certain bones, like feet) without necessarily imprinting damage on the rest of the carcass. Carnivore intervention in an elephant death site can result in deletion of a few remains without much damage (if any), or if hyena clans access the carcass, much more conspicuous damage can be documented. There is a whole range of carnivore signatures in between. We are currently working on our study of several elephant carcasses subjected to these highly variable degrees of carnivore impact.

(10) Lines 412 - 422: "The clustering of the elephant (and hippopotamus) carcasses in the areas containing the highest densities of landscape surface artifacts is suggestive of a hominin agency in at least part of their consumption and modification." - how so? It could equally suggest that both hominins and elephants were drawn to the same lush environments.

We agree. Both hominins and megafauna must have been drawn to the same ecological loci for interaction to emerge. However, the fact that the highest density clusters of artifacts coincide with the highest density of carcasses "showing evidence of having been broken", is suggestive of hominin use and consumption.

(11) Discussion: I suggest starting the Discussion with a concise appraisal of the lines of evidence detailed in the Results and their interpretation, and only then, the critical reassessment of other studies. Similarly, a new topic starts in line 508, but without any subheading or an introductory sentence that could assist the readers.

We added the introductory lines of the former Conclusion section to the revised Discussion section, as suggested by R1.

(12) Line 607: Neumark-Nord are Late Pleistocene sites (MIS 5), not Middle Pleistocene.

Corrected.

(13) Regarding the ambiguity in how megafaunal exploitation may be causally related to the other features of the early Acheulian, the authors can develop the discussion. Alternatively, they should explicitly state that correlation is not causation, and that the present study adds the megafaunal exploitation element to be considered in future discussion of the shifts in lifestyles 1.8 million years ago.

We have done so.

Reviewer #2 (Recommendations for the authors):

The following detailed comments are provided to help clarify arguments, ensure accurate representation of cited literature, and strengthen the logical and methodological framing of the paper. Line numbers refer to the version provided for review.

(1) Line 55: Such concurrency (sometimes in conjunction with other variables)

The term "other variables" is very vague. I would suggest expanding on this or taking it out altogether.

(2) Line 146: Megafaunal long bone green breakage (linked to continuous spiral fractures on thick cortical bone) is probably a less ambiguous trace of butchery than "cut marks", since many of the latter could be equifinal and harder to identify, especially in contexts of high abrasion and trampling (Haynes et al., 2021, 2020).

This reasoning is not supported by the evidence or the cited sources. Green-bone spiral fractures only show that a bone broke while it was fresh and do not reveal who or what caused it. Carnivore feeding, trampling, and natural sediment pressure can all create the same patterns, so these fractures are not clearer evidence of butchery than cut marks. Cut marks, when they are preserved and morphologically clear, remain the most reliable indicator of human activity. The Haynes papers actually show the opposite of what is claimed here. They warn that spiral fractures and surface marks can form naturally and that fracture patterns alone cannot be used to infer butchery. This section should be revised to reflect what those studies actually demonstrate.

The reasoning referred to in line 146 is further explained below in the original text as follows:

“Despite the occurrence of green fractures on naturally-broken bones, such as those trampled by elephants (Haynes et al., 2020), those occurring through traumatic fracturing or gnawed by carnivores (Haynes and Hutson, 2020), these fail to reproduce the elongated, extensive, or helicoidal spiral fractures (uninterrupted by stepped sections), accompanied by the overlapping conchoidal scars (both cortical and medullary), the reflected scarring, the inflection points, or the impact hackled break surfaces and flakes typical of dynamic percussive breakage. Evidence of this type of green breakage had not been documented earlier for the Early Pleistocene proboscidean or hippopotamid carcasses, beyond the documentation of flaked bone with the purpose of elaboration of bone tools (Backwell and d’Errico, 2004; Pante et al., 2020; Sano et al., 2020).”

The problem in the way that R2 uses Haynes et al.’s works is that R2 uses features separately. Natural breaks occurring while the bone is green can generate spiral smooth breaks, for example, but it is not the presence of a single feature that invalidates the diagnosis of agency or that is taphonomically relevant, but the concurrence of several of them. The best example of a naturally (pre-mortem) broken bone was published by Haynes et al.

The natural break shows helical fractures, subjugated to linear (angular) fracture outlines. Notice how the crack displays a zig-zag. The break is smooth but most damage occurs on the cortical surface, with flaking adjacent to the break and step micro-fracturing on the edges. The cortical scarring is discontinuous (almost marginal) and very small, almost limited to the very edge of the break. No modification occurs on the medullary surface. No extensive conchoidal fractures are documented, and certainly none inside the medullary surface of the break.

Compare with Figure S8, S10, S17 and S34 (all specimens are shown in their medullary surface):

In these examples, we see clearly modified medullary surfaces with multiple green breaks and large-sized step fractures, accompanied in some examples by hackle marks. Some show large overlapping scars (of substantially bigger size than those documented in the natural break image). Not a single example of naturally-broken bones has been documented displaying these morphologies simultaneously. It is the comprehensive analysis of the co-occurrence of these features and not their marginal and isolated occurrence in naturally-broken bones that make a difference in the attribution of agency. Likewise, no example of naturally-broken bone has been published that could mimic any of the two green-broken bones documented at EAK. In contrast, we do have bones from our on-going experimentation with green elephant carcasses that jointly reproduce these features. See also Figure 6 of the article to find another example without any modern referent in the naturally-broken bones documented.

We should emphasize that R2 is inaccurately portraying what Haynes et al.'s results really document. Contrary to R2's assertion, trampling does not reproduce any of the examples shown above. Neither do carnivores. It should be stressed that Haynes & Harrod only document similar overlapping scarring on the medullary surface of bones, when using much smaller animals. In all the carnivore damage repertoire that they document for elephants, durophagous spotted hyenas can only inflict furrowing on the ends of the biggest long bones, especially if they are adults. Long bone midshafts remain inaccessible to them. The mid-shaft portions of bones that we document in our Supplementary File and at EAK cannot be the result of hyena (or carnivore damage) for this reason, and also because their intense gnawing on elephant bones leaves tooth marking on most of the elements that they modify, being absent in our sample.

(3) Line 176: *other than hominins accessed them in different taphonomically-defined stages- stages - the "Stages" is repeated twice*

Defined in the revised version

(4) Line 174: *Regardless of the type of butchery evidence - and with the taphonomic caveat that no unambiguous evidence exists to confirm that megafaunal carcasses were hunted or scavenged other than hominins accessed them in different taphonomically-defined stages- stages - the principal reasons for exploring megafaunal consumption in early human evolution is its origin, its episodic or temporally-patterned occurrence, its impact on hominin adaptation to certain landscapes, and its reflection on hominin group size and site functionality.*

This sentence is confusing and needs to be rewritten for clarity. It tries to combine too many ideas at once, and the phrasing makes it hard to tell what the main point is. The taphonomic caveat in the middle interrupts the sentence and obscures the argument. It should be broken into separate, clearer statements that distinguish what evidence exists, what remains uncertain, and what the broader goals of the discussion are.

We believe the ideas are displayed clearly

(5) Line 179: landscapes, and its reflection on hominin group size and site functionality. If hominins actively sought the exploitation of megafauna, especially if targeting early stages of carcass consumption, the recovery of an apparent surplus of resources reflects a substantially different behavior from the small-group/small-site pattern documented at several earlier Oldowan anthropogenic sites (Domínguez-Rodrigo et al., 2019) -or some modern foragers, like the Hadza, who only exploit megafaunal carcasses very sporadically, mostly upon opportunistic encounters (Marlowe, 2010; O'Connell et al., 1992; Wood, 2010; Wood and Marlowe, 2013).

This sentence makes a reasonable point, but is written in a confusing way. The idea that early, deliberate access to megafauna would represent a different behavioral pattern from smaller Oldowan or modern foraging contexts is valid, but the sentence is awkward and hard to follow. It should be rephrased to make the logic clearer and more direct.

We believe the ideas are displayed clearly

(6) Line 186: When the process started of becoming megafaunal commensal started has major implications for human evolution.

This sentence is awkward and needs to be rewritten for clarity. The phrasing "when the process started of becoming megafaunal commensal started" is confusing and grammatically incorrect. It could be revised to something like "Determining when hominins first began to interact regularly with megafauna has major implications for human evolution," or another version that clearly identifies the process being discussed.

Modified in the revised version

(7) Line 189: The multiple taphonomic biases intervening in the palimpsestic nature of most of these butchery sites often prevent the detection of the causal traces linking megafaunal carcasses and hominins. Functional links have commonly been assumed through the spatial concurrence of tools and carcass remains; however, this perception may be utterly unjustified as we argued above. Functional association of both archaeological elements can more securely be detected through objective spatial statistical methods. This has been argued to be foundational for heuristic interpretations of proboscidean butchery sites (Giusti, 2021). Such an approach removes ambiguity and solidifies spatial functional association, as demonstrated at sites like Marathousa 1 (Konidaris et al., 2018) or TK Sivatherium (Panera et al., 2019). This method will play a major role in the present study.

This section overstates what spatial analysis can demonstrate and misrepresents the cited studies. The works by Giusti (2021), Konidaris et al. (2018), and Panera et al. (2019) do use spatial statistics to examine relationships between artifacts and faunal remains, but they explicitly caution that spatial overlap alone does not prove functional or behavioral association. These studies argue that clustering can support such interpretations only when combined with detailed taphonomic and stratigraphic evidence. None of them claims that spatial analysis "removes ambiguity" or "solidifies" functional links. The text should be revised to reflect the more qualified conclusions of those papers and to avoid implying that spatial statistics can establish behavioral causation on their own.

We disagree. Both works (Giusti and Panera) use spatial statistical tools to create an inferential basis reinforcing a functional association of lithics and bones. In both cases, the anthropogenic agency inferred is based on that. We should stress that this only provides a basis for argumentation, not a definitive causation. Again, those analyses show much more than just apparent visual clustering.

(8) Line 200: *Here, we present the discovery of a new elephant butchery site (Emiliano Aguirre Korongo, EAK), dated to 1.78 Ma, from the base of Bed II at Olduvai Gorge. It is the oldest unambiguous proboscidean butchery site at Olduvai.*

It is fine to state the main finding in the introduction, but the phrasing here is too strong. Calling EAK "the oldest unambiguous proboscidean butchery site" asserts certainty before the evidence is presented. The claim should be stated more cautiously, for example, "a new site that provides early evidence for proboscidean butchery," so that the language reflects the strength of the data rather than pre-judging it.

We understand the caution by R2, but in this case, EAK is the oldest taphonomically-supported evidence of elephant butchery at Olduvai (see discussion about FLK North in the text). Whether this is declared at the beginning or the end of the text is irrelevant.

(9) Line 224: *The drying that characterizes Bed II had not yet taken place during this moment.*

This sentence reads like a literal translation. It should be rewritten for clarity.

Modified in the revised version

(10) Line 233: *During the recent Holocene, the EAK site was affected by a small landslide which displaced the...*

This section contains far more geological detail than is needed for the argument. The reader only needs to know that the site block was displaced by a small Holocene landslide but retains its stratigraphic integrity. The extended discussion of regional faults, seismicity, and slope processes goes well beyond what is necessary for context and distracts from the main focus of the paper.

We disagree. The geological information is what is most commonly missing from most archaeological reports. Here, it is relevant because of the atypical process and because it has been documented only twice with elephant butchery sites. Explaining the dynamic geological process that shaped the site helps to understand its spatial properties.

(11) Line 264: *In June 2022, a partial elephant carcass was found at EAK on a fragmented stratigraphic block...*

This section reads like field notes rather than a formal site description. Most of the details about the discovery sequence, trench setup, and excavation process are unnecessary for the main text. Only the basic contextual information about the find location, stratigraphic position, and anatomical composition is needed. The rest could be condensed or moved to the methods or supplementary material.

We disagree. See reply above.

(12) Line 291: *hominins or other carnivores. Ongoing restoration work will provide an accurate estimate of well-preserved and modified fractions of the assemblage.*

This sentence is unclear and needs to specify what kind of restoration work is being done and what is meant by well-preserved and modified fractions. It is not clear whether modified refers to surface marks, diagenetic alteration, or something else. If the bones are still being cleaned or prepared, the analysis is incomplete, and the counts cannot be considered final. If restoration only means conservation or stabilization, that should be stated clearly so the reader understands that it does not affect the results. As written, it is not clear whether the data presented here are preliminary or complete.

We added: For this reason, until restoration is concluded, we cannot produce any assertion about the presence or absence of bone surface modifications.

(13) Line 294: The tibiae were well preserved, but the epiphyseal portions of the femora were missing, probably removed by carnivores, which would also explain why a large portion of the rib cage and almost all vertebrae are missing.

This explanation is not well supported. The missing elements could be the result of other forms of density-mediated destruction, such as sediment compaction or post-depositional fragmentation, especially since no tooth marks were found. Given the low density of ribs, vertebrae, and femoral epiphyses, these processes are more likely explanations than carnivore removal. The text should acknowledge these alternatives rather than attributing the pattern to carnivore activity without direct evidence.

Sediment compaction and post-depositional can break bones but cannot make them disappear. Our excavation process was careful enough to detect bone if present. Their absence indicates two possibilities: erosion through the years at the front of the excavation or carnivore intervention. Carnivores can take elephant bones without impacting the remaining assemblage (see our reply above to a similar comment).

(14) Line 304: The fact that the carcass was moved while encased in its sedimentary context, along with the close association of stone tools with the elephant bones, is in agreement with the inference that the animal was butchered by hominins. A more objective way to assess this association is through spatial statistical analysis.

The authors state that "the carcass was moved while encased in its sedimentary context, along with the close association of stone tools with the elephant bones, is in agreement with the inference that the animal was butchered by hominins." This does not logically follow. Movement of the block explains why the bones and tools remain together, not how that association was created. The preserved association alone does not demonstrate butchery, especially in the absence of cut marks or other direct evidence of hominin activity.

Again, we are sorry that R2 is completely overlooking the strong signal detected by the spatial statistical analysis. The way that the block moved, it preserved the original association of bones and tools. This statement is meant to clarify that despite the allochthonous nature of the block, the original autochthonous depositional process of both types of archaeological materials has been preserved. The spatial association, as statistically demonstrated, indicates that the functional link is more likely than any other alternative process. The additional fact that nowhere else in that portion of the outcrop do we identify scatters of tools (all appear clustered at a landscape scale with the elephant) adds more support to this interpretation. This would have been further supported by the presence of cut marks, no doubt, but their absence does not indicate lack of functional association, since as Haynes' works have clearly shown, most bulk defleshing of modern elephant leaves no traces on most bones.

(15) Line 370: This also shows that the functional connection between the elephant bones and the tools has been maintained despite the block post-sedimentary movement.

The spatial analyses appear to have been carried out appropriately, and the interpretations of clustering and segregation are consistent with the reported results. However, the conclusion that the "functional connection" between bones and tools has been maintained goes beyond what spatial correlation alone can demonstrate. These analyses show spatial proximity and scale-dependent clustering but cannot, by themselves, confirm a behavioral or functional link.

R2 is making this comment repeatedly and we have addressed it more than once above. We disagree and we refer to our replies above to sustain it.

(16) Line 412: The clustering of the elephant (and hippopotamus) carcasses in the areas containing the highest densities of landscape surface artifacts is suggestive of a hominin agency in at least part of their consumption and modification. The presence of green broken elephant long bone elements in the area surveyed is only documented within such clusters, both for lower and upper Bed II. This constitutes inverse negative evidence for natural breaks occurring on those carcasses through natural (i.e., non-hominin) pre- and peri-mortem limb breaking (Haynes et al., 2021, 2020; Haynes and Hutson, 2020). In this latter case, it would be expected for green-broken bones to show a more random landscape distribution, and occur in similar frequencies in areas with intense hominin landscape use (as documented in high density artifact deposition) and those with marginal or non-hominin intervention (mostly devoid of anthropogenic lithic remains).

The clustering of green-bone fractures with stone tools is intriguing but should be interpreted cautiously. The Haynes references are misrepresented here. Those studies address both cut marks and green-bone (spiral) fractures, emphasizing that each can arise through non-hominin processes such as trampling, carcass collapse, and sediment loading. They do not treat green fractures as clearer evidence of butchery; in fact, they caution that such breakage patterns can occur naturally and even form clustered distributions in areas of repeated animal activity. The claim that these studies support spiral fractures as unambiguous indicators of hominin activity, or that natural breaks would be randomly distributed, is not accurate.

We would like to emphasize again that the Haynes references are not misrepresented here. See our extensive reply above. If R2 can provide evidence of natural breakage patterns resulting from pre-mortem limb breaking or post-mortem trampling resulting in all limb bones being affected by these processes and resulting in smooth spiral breaks, accompanied with extensive and overlapping scarring on the medullary surface, in conjunction with the other features described in our replies above, then we would be willing to reconsider. With the evidence reported until now, that does not occur simultaneously on specimens resulting from studies on modern elephant bones.

R2 seems to contradict him(her)self here by saying that Haynes studies show that cut marks are not reliable because they can also be reproduced via trampling. Until this point, R2 had been saying that only cut marks could demonstrate a functional link and support butchery. Haynes' studies do not deal experimentally with sediment loading.

(17) Line 424: This indicates that from lower Bed II (1.78 Ma) onwards, there is ample documented evidence of anthropogenic agency in the modification of proboscidean bones across the Olduvai paleolandscapes. The discovery of EAK constitutes, in this respect, the oldest evidence thereof at the gorge. The taphonomic evidence of dynamic proboscidean bone breaking across time and space supports, therefore, the inferences made by the spatial statistical analyses of bones and lithics at the site.

This conclusion is overstated. The claim of "ample documented evidence of anthropogenic agency" is too strong, given that the main support comes from indirect indicators like green-bone fractures and spatial clustering rather than clear butchery marks. It would be more accurate to say that the evidence suggests or is consistent with possible hominin involvement. The final sentence also conflates association with causation; spatial and taphonomic data can indicate a relationship, but do not confirm that the carcasses were butchered by hominins.

The evidence is based on spatially clustering (at a landscape scale) of tools and elephant (and other megafaunal taxa) bones, in conjunction with a large amount of green-broken elements.

This interpretation, if we compare it against modern referents is supported even stronger. In the past few years, we have been conducting work on modern naturally dead elephant carcasses in Botswana and Zambia, and of the several carcasses that we have seen, we have not identified a single case of long bone shaft breaks like those described by Haynes as natural or like those we describe here as anthropogenic. This probably means that they are highly unlikely or marginal occurrences at a landscape scale. This seems to be supported by Haynes' work too. Out of the hundreds of elephant carcasses that he has monitored and studied over the years for different works, we have managed to identify only two instances where he described natural pre-mortem breaks. This certainly qualifies as extremely marginal.

Most of the Results section is clearly descriptive, but beginning with "The clustering of the elephant (and hippopotamus) carcasses..." the text shifts from reporting observations to drawing behavioral conclusions. From this point on, it interprets the data as evidence of hominin activity rather than simply describing the patterns. This part would be more appropriate for the Discussion, or should be rewritten in a neutral, descriptive way if it is meant to stay in the Results.

This appears extensively discussed in the Discussion section, but the data presented in the results is also interpreted in that section, following a clear argumental chain.

(18) Line 433: A recent discovery of a couple of hippopotamus partial carcasses at the 3.0-2.6 Ma site of Nyayanga (Kenya), spatially concurrent with stone artifacts, has been argued to be causally linked by the presence of cut marks on some bones (Plummer et al., 2023). The only evidence published thereof is a series of bone surface modifications on a hippo rib and a tibial crest, which we suggest may be the result of byproduct of abiotic abrasive processes; the marks contrast noticeably with the well-defined cut marks found on smaller mammal bones (Plummer et al.'s 2023: Figure 3C, D) associated with the hippo remains (Plummer et al., 2023).

The authors suggest that the Nyayanga marks could result from abiotic abrasion, but this claim does not engage with the detailed evidence presented by Plummer et al. (2023). Plummer and colleagues documented well-defined, morphologically consistent cut marks and considered the sedimentary context in their interpretation. Raising abrasion as a general possibility without addressing that analysis gives the impression of selective skepticism rather than an evaluation grounded in the published data.

We disagree again on this matter. R2 does not clarify what he/she means by well-defined or morphologically consistent. We provide an alternative interpretation of those marks that fit their morphology and features and that Plummer et al did not successfully exclude. We also emphasize that the interpretation of the Nyayanga marks was made descriptively, without any analytical approach and with a high degree of subjectivity by the researcher. All of this disqualifies the approach as well defined and keeps casting an old look at modern taphonomy. Descriptive taphonomy is a thing of the 1980s. Today there are a plethora of analytical methods, from multivariate statistics, to geometric morphometrics to AI computer vision (so far the most reliable) which represent how taphonomy (and more specifically, analysis of bone surface modifications) should be conducted in the XXI century. This approaches would reinforce interpretations as preliminarily published by Plummer et al, provided they reject alternative explanations like those that we have provided.

(19) Line 459: It would have been essential to document that the FLK N6 tools associated with the elephant were either on the same depositional surface as the elephant bones and/or on the same vertical position. The ambiguity about the FLK N6 elephant renders EAK the oldest secure proboscidean butchery evidence at Olduvai, and also probably one of the oldest in the early Pleistocene elsewhere in Africa.

The concern about vertical mixing is fair, but the tone makes it sound like the association is definitely not real. It would be more accurate to say that the evidence is ambiguous, not that it should be dismissed altogether.

We have precisely done so. We do not dismiss it, but we cannot take it for anything solid since we excavated the site and show how easily one could make functional associations if forgetting about the third dimension. It is not a secure butchery site. This is what we said and we stick to this statement.

(20) Line 479: In all cases, these wet environments must have been preferred places for water-dependent megafauna, like elephants and hippos, and their overlapping ecological niches are reflected in the spatial co-occurrence of their carcasses. Both types of megafauna show traces of hominin use through either cutmarked or percussed bones, green-broken bones, or both (Supplementary Information).

The environmental part is good, but the behavioral interpretation is too strong. Saying elephants and hippos "must have been" drawn to these areas is too certain, and claiming that both "show traces of hominin use" makes it sound like every carcass was modified. It should be clearer that only some have possible evidence of this.

The sentence only refers to both types of fauna taxonomically. No inference can be drawn therefor that all carcasses are modified.

(21) Line 496: In most green-broken limb bones, we document the presence of a medullary cavity, despite the continuous presence of trabecular bone tissue on its walls.

This sentence is confusing and doesn't seem to add anything meaningful. All limb bones naturally have a medullary cavity lined with trabecular bone, so it's unclear why this is noted as significant. The authors should clarify what they mean here or remove it if it's simply describing normal bone structure.

No. Modern elephant long bones do not have a hollow medullary cavity. All the medullary volume is composed of trabecular tissue. Some elephants in the past had hollow medullary cavities, which probably contained larger amounts of marrow and fat.

(22) Line 518: We are not confident that the artefacts reported by de la Torre et al are indeed tools.

While I generally agree with this statement, the paragraph reads as defensive rather than comparative. It would help if they briefly summarized what de la Torre et al. actually argued before explaining why they disagree.

We devote two full pages of the Discussion section to do so precisely.

(23) Lines 518-574: They are similar to the green-broken specimens that we have reported here...

This part is very detailed but inconsistent. They argue that the T69 marks could come from natural processes, but they use similar evidence (green fractures, overlapping scars) to argue for human activity at EAK. If equifinality applies to one, it applies to both.

We are confused by this misinterpretation. Features like green fractures and overlapping scars (among others) can be used to detect anthropogenic agency in elephant bone breaking; that is, any given specimen can be determined to have been an "artifact" (in the sense of human-created item), but going from there to interpreting an artifact as a tool, there is a large distance. Whereas an artifact (something made by a human) can be created indirectly through several processes (for example, demarrowing a bone resulting in long bone

fragments), a tool suggest either intentional manufacture and use or both. That is the difference between de la Torre et al.'s interpretation and ours. We believe that they are showing anthropogenically-made items, but they have provided no proof that they were tools.

(24) Line 576: A final argument used by the authors to justify the intentional artifactual nature of their bone implements is that the bone tools were found in situ within a single stratigraphic horizon securely dated to 1.5 million years ago, indicating systematic production rather than episodic use. This is taphonomically unjustified.

The reasoning here feels uneven in how clustering evidence is used. At EAK, clustering of bones and artifacts is taken as meaningful evidence of hominin activity, but here the same pattern at T69 is treated as a natural by-product of butchery or carnivore activity. If clustering alone cannot distinguish between intentional and incidental association, the authors should clarify why it is interpreted as diagnostic in one case but not in the other.

Again, we are confused by this misinterpretation. It applies to two different scenarios/questions:

a) is there a functional link between tools and bones at EAK and T69? We have statistically demonstrated that at EAK and we think de la Torre et al. is trying to do the same for T69, although using a different method.

b) Are the purported tools at T69 tools? Are those that we report here tools? In this regard there is no evidence for either case and given that several bones from T69 come from animals smaller than elephants, we do not discard that carnivores might have been responsible for those, whereas hominin butchery might have been responsible for the intense long limb breaking at that site. It remains to be seen how many (if any) of those specimens were tools.

(25) Line 600: If such a bone implement was a tool, it would be the oldest bone tool documented to date (>1.7 Ma).

The comparison to prior studies is useful, and the point about missing use-wear traces is well taken. However, the last lines feel speculative. If no clear use evidence has been found, it's premature to suggest that one specimen "would be the oldest bone tool." That claim should be either removed or clearly stated as hypothetical.

It clearly reads as hypothetical.

(26) Line 606: Evidence documents that the oldest systematic anthropogenic exploitation of proboscidean carcasses are documented (at several paleolandscape scales) in the Middle Pleistocene sites of Neumark-Nord (Germany)(Gaudzinski-Windheuser et al., 2023a, 2023b).

This is the first and only mention of Neumark-Nord in the paper, and it appears without any prior discussion or connection to the rest of the study. If this site is being used for comparison or as part of a broader temporal framework, it needs to be introduced and contextualized earlier. As written, it feels out of place and disconnected from the rest of the argument.

This is a Late Pleistocene site and we do not see the need to present it earlier, given that the scope of this work is Early Pleistocene.

(27) Line 608: Evidence of at least episodic access to proboscidean remains goes back in time (see review in Agam and Barkai, 2018; Ben-Dor et al., 2011; Haynes, 2022).

The distinction between "systematic" and "episodic" exploitation is useful, but the authors should clarify what criteria define each. The phrase "episodic access...goes back in time"

is vague and could be replaced with a clearer statement summarizing the nature of the earlier evidence.

It is self-explanatory

(28) Line 610: Redundant megafaunal exploitation is well documented at some early Pleistocene sites from Olduvai Gorge (Domínguez-Rodrigo et al., 2014a, 2014b; Organista et al., 2019, 2017, 2016).

The phrase "redundant megafaunal exploitation" needs clarification. "Redundant" is not standard terminology in this context. Does this mean repeated, consistent, or overlapping behaviors? Also, while these same Olduvai sites are mentioned earlier, this phrasing also introduces new interpretive language not used before and implies a broader behavioral generalization than what the data actually show.

Webster: Redundant means repetitive, occurring multiple times.

(29) Line 612: At the very same sites, the stone artifactual assemblages, as well as the site dimensions, are substantially larger than those documented in the Bed I Oldowan sites (Diez-Martín et al., 2024, 2017, 2014, 2009).

The placement and logic of this comparison are unclear. The discussion moves from Middle Pleistocene Neumark-Nord to early Pleistocene Olduvai sites, then to Bed I Oldowan contexts without clearly signaling the temporal or geographic transitions. If the intent is to contrast Acheulean vs. Oldowan site scale or organization, that connection needs to be made explicit. As written, it reads as a disjointed shift rather than a continuation of the argument.

We disagree. Here, we finalize by bringing in some more recent assemblages where hominin agency is not in question.

(30) Line 616: Here, we have reported a significant change in hominin foraging behaviors during Bed I and Bed II times, roughly coinciding with the replacement of Oldowan industries by Acheulian tool kits -although during Bed II, both industries co-existed for a substantial amount of time (Domínguez-Rodrigo et al., 2023; Uribelarra et al., 2019, 2017).

This section should be restructured for flow. The reference to behavioral change during Bed I-II and the overlap of Oldowan and Acheulean industries is important, but feels buried after a long detour. Consider moving this earlier or rephrasing so the main conclusion (behavioral change across Beds I-II) is clearly stated first, followed by supporting examples.

It is not within the scope of this work and is properly described in the references mentioned.

(31) Line 620: The evidence presented here, together with that documented by de la Torre et al. (2025), represents the most geographically extensive documentation of repeated access to proboscidean and other megafaunal remains at a single fossil locality.

The phrase "most geographically extensive documentation of repeated access" overstates what has been demonstrated. The evidence presented is site-specific and does not justify such a broad superlative. This should be toned down or supported with comparative quantitative data.

We disagree. There is no other example where such an abundant record of green-broken elements from megafauna is documented. Neumark-Nord is more similar because it shows extensive evidence of butchery, but not so much about degreasing.

(32) Line 623: *The transition from Oldowan sites, where lithic and archaeofaunal assemblages are typically concentrated within 30-40 m² clusters, to Acheulean sites that span hundreds or even over 1000 m² (as in BK), with distinct internal spatial organization and redundancy in space use across multiple archaeological layers spanning meters of stratigraphic sequence (Domínguez-Rodrigo et al., 2014a, 2009b; Organista et al., 2017), reflects significant behavioral and technological shifts.*

This sentence about site size and spatial organization repeats earlier claims without adding new insight. If it's meant as a synthesis, it should explicitly say how the spatial expansion relates to changes in behavior or mobility, not just describe the difference.

In the Conclusion section these correlations have been explained in more detail to add some causation.

(33) Line 628: *This pattern likely signifies critical innovations in human evolution, coinciding with major anatomical and physiological transformations in early hominins (Dembitzer et al., 2022; Domínguez-Rodrigo et al., 2021, 2012).*

The conclusion that this "signifies critical innovations in human evolution" is too sweeping, given the data presented. It introduces physiological and anatomical transformation without connecting it to any evidence in this paper. Either cite the relevant findings or limit the claim to behavioral implications.

The references cited elaboration in extension this. The revised version of the Conclusion section also elaborates on this.

Overall, the conclusions section reads as a loosely connected set of assertions rather than a focused synthesis. It introduces new interpretations and terminology not supported or developed earlier in the paper, and the argument jumps across temporal and geographic scales without clear transitions. The discussion should be restructured to summarize key results, clarify the scope of interpretation, and avoid speculative or overstated claims about evolutionary significance.

We have done so, supported by the references used in addition to extending some of the arguments

(34) Line 639: *The systematic excavation of the stratigraphic layers involved a small crew.*

This sentence is not necessary.

No comment

(35) Line 643: *The orientation and inclination of the artifacts were recorded using a compass and an inclinometer, respectively.*

What were these measurements used for (e.g., post-depositional movement analysis, spatial patterning)? A short note on the purpose would make this more meaningful.

Fabric analysis has been added to the revised version.

(36) Line 659: *Restoration of the EAK elephant bones*

This section could be streamlined and clarified. It includes procedural detail that doesn't contribute to scientific replicability (e.g., the texture of gauze, number of consolidant applications), while omitting some key information (such as how restoration may have affected analytical results). It also contains interpretive comments ("most of the assemblage has been successfully studied") that don't belong in Methods.

No comment

(37) Line 689: In the field laboratory, cleaning of the bone remains was carried out, along with adhesion of fragments and their consolidation when necessary.

Clarify whether cleaning or adhesion treatments might obscure or alter bone surface modifications, as this has analytical implications.

These protocols do not impact bone like that anymore.

(38) Line 711: (b) Percussion Tools - Includes hammerstones or cobbles exhibiting diagnostic battering, pitting, and/or impact scars consistent with percussive activities.

Define how diagnostic features (battering, pitting) were identified - visual inspection, magnification, or quantitative criteria?

Both macro and microscopically

(39) Line 734: We conducted the analysis in three different ways after selecting the spatial window, i.e., the analysed excavated area (52.56 m²).

Clarify why the 52.56 m² spatial window was chosen. Was this the total excavated area or a selected portion?

It was what was left of the elephant accumulation after erosion.

(40) Line 728: The spatial statistical analyses of EAK.

Adding one or two sentences at the start explaining the analytical objective, such as testing spatial association between faunal and lithic materials, would help readers understand how each analysis relates to the broader research questions.

This is well explained in the main text

(41) Line 782: An intensive survey seeking stratigraphically-associated megafaunal bones was carried out in the months of June 2023 and 2024.

It would help to specify whether the same areas were resurveyed in both field seasons or if different zones were covered each year. This information is important for understanding sampling consistency and potential spatial bias.

Both areas were surveyed in both field seasons. We were very consistent.

(42) Line 787: We focused on proboscidean bones and used hippopotamus bones, some of the most abundant in the megafaunal fossils, as a spatial control.

Clarify how the hippopotamus remains functional as a "spatial control." Are they used as a proxy for water-associated taxa to test habitat patterning, or as a baseline for comparing carcass distribution? The meaning of "control" in this context is ambiguous.

As a proxy for megafaunal distribution given their greater abundance over any other megafaunal taxa.

(43) Line 789: Stratigraphic association was carried out by direct observation of the geological context and with the presence of a Quaternary geologist during the whole survey.

This is good methodological practice, but it would be helpful to describe how stratigraphic boundaries were identified in the field (for example, by reference to tuffs or

marker beds). That information would make the geological framework more replicable.

This is basic geological work. Of course, both tuffs and marker beds were followed.

(44) Line 791: When fossils found were ambiguously associated with specific strata, these were excluded from the present analysis.

You might specify what proportion of the total finds were excluded due to uncertain stratigraphic association. Reporting this would indicate the strength of the stratigraphic control.

This was not quantified but it was a very small amount compared to those whose stratigraphic provenience was certain.

(45) Line 799: The goals of this survey were: a) collect a spatial sample of proboscidean and megafaunal bones enabling us to understand if carcasses on the Olduvai paleolandscapes were randomly deposited or associated to specific habitats.

You might clarify how randomness or habitat association was tested.

Randomness was tested spatially and comparing density according to ecotone. Same for habitat association.

(46) The Methods section provides detailed information about excavation, restoration, and spatial analyses but omits critical details about the zooarchaeological and taphonomic procedures. There is no explanation of how faunal remains were analyzed once recovered, including how cut marks, percussion marks, or green bone fractures were identified or what magnification or diagnostic criteria were used. The authors also do not specify the analytical unit used for faunal quantification (e.g., NISP, MNI, MNE, or other), making it unclear how specimen counts were generated for spatial or taphonomic analyses. Even if these details are provided in the Supplementary Information, the main text should include at least a concise summary describing the analytical framework, the criteria for identifying surface modifications and fracture morphology, and the quantification system employed. This information is essential for transparency, replicability, and proper evaluation of the behavioral interpretations.

See reply above. There is a new subsection on taphonomic methods now.

Supplementary information:

(47) The Supplementary Information includes a large number of green-broken proboscidean specimens from other Olduvai localities (BK, LAS, SC, FLK West), but it is never explained why these are shown or how they relate to the EAK study. The main analysis focuses entirely on the EAK elephant, including so much unrelated material without any stated purpose, which makes the supplement confusing. If these examples are meant only to illustrate the appearance of green fractures, that should be stated. Otherwise, the extensive inclusion of non-EAK material gives the impression that they were part of the analyzed assemblage when they were not.

This is stated in the opening paragraph to the section.

(48) Line 96: A small collection of green-broken elephant bones was retrieved from the lower and upper Bed II units.

It would help to clarify whether these specimens are part of the EAK assemblage or derive from other Bed II localities. As written, it is not clear whether this description refers to material analyzed in the main text or to comparative examples shown only in the Supplementary Information.

No, EAK only occupies the lower Bed II section. They belong in the Bed II paleolandscape units.

(49) Line 97: One of them, a proximal femoral shaft found within the LAS unit, has all the traces of having been used as a tool (Figure 6).

This says the bone tool in Figure 6 is from LAS, but the main text caption identifies it as from EAK. If I am not mistaken, EAK is a site at the base of Bed II, and LAS is a separate stratigraphic unit higher in the sequence, so the authors should clarify which is correct.

Our mistake. It provenience is from LAS in the vicinity of EAK.

(50) Line 186: Figure S20. Example of other megafaunal long bone shafts showing green breaks.

Not cited in text or SI narrative. No indication where these bones come from or why they are relevant.

It appears justified in the revised version.

(51) Line 474: Figure S28-S30. Hyena-ravaged giraffe bones from Chobe (Botswana).

These figures are not discussed in the text or SI, and their relevance to the study is unclear. The authors should explain why these modern comparative examples were included and how they inform interpretations of the Olduvai assemblages.

It appears justified in the revised version.

(52) Line 498: Figure S31. Bos/Bison bone from Bois Roche (France).

This figure is not mentioned in the text or Supplementary Information. The authors should specify why this specimen is shown and how it contributes to the study's taphonomic or behavioral comparisons.

It appears justified in the revised version.

(53) Line 504: Figure S32. Miocene Gomphotherium femur from Spain.

This figure is never referenced in the paper. The authors should clarify the purpose of including a Miocene specimen from outside Africa and explain what it adds to the interpretation of Bed II material.

It appears justified in the revised version.

(54) Line 508: Figure S33. Elephant femoral shaft from BK (Olduvai).

This figure appears to show comparative material but is not cited or discussed in the text. The authors should explain why the BK material is presented here and how it relates to EAK or the broader analysis.

There are two figures labeled S33.

It appears justified in the revised version.

(55) Line 515: Figure S33. Tibia fragment from a large medium-sized bovid displaying multiple overlapping scars on both breakage planes inflicted by carnivore damage.

Because this figure repeats the S33 label and is not cited or explained in the text, it is unclear why this specimen is included or how it contributes to the study. The authors should correct the duplicate numbering and clarify the purpose of this figure.

It appears justified in the revised version.

(56) Line 522: Same specimen as shown in Figure S30, viewed on its medial side.

This is not the same bone as S30. This figure is not discussed in the text or Supplementary Information. The authors should clarify why it is included and how it relates to the rest of the analysis.

It appears justified in the revised version.

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