Bone tools from beds II–IV, Olduvai Gorge, Tanzania, and implications for the origins and evolution of bone technology

Michael Pante^{a,*}, Ignacio de la Torre^b, Francesco d'Errico^{c,d}, Jackson Njau^{e,f}, Robert Blumenshine^g

^a Department of Anthropology and Geography, Colorado State University, 1787 Campus Delivery, Fort Collins, CO, 80523, USA

^b Instituto de Historia, Spanish National Research Council-CSIC, Albasanz 26-28, 28037, Madrid, Spain

^c UMR 5199 CNRS De la Préhistoire à l'Actuel: Culture, Environnement, et Anthropologie (PACEA), Université de Bordeaux, Allée Geoffroy Saint Hilaire, CS 50023, F - 33615, Pessac CEDEX, Talence, France

^d Centre for Early Sapiens Behaviour, Øysteinsgate 3, Postboks 7805, 5020, University of Bergen, Norway

^e Department of Earth and Atmospheric Sciences, Indiana University, 1001 E Tenth Street, Bloomington, IN, 47405, USA

^f The Stone Age Institute, Bloomington, IN, 47407, USA

^g Palaeontological Scientific Trust and Evolutionary Studies Institute, University of the Witwatersrand, P Bag 3, WITS 2050, South Africa

ARTICLE INFO

Article history:

Received 1 May 2020

Accepted 27 August 2020

Available online xxx

Keywords:

Osseous technology

Earliest barbed point

Homo erectus

Taphonomy

Early Stone Age

ABSTRACT

The advent of bone technology in Africa is often associated with behavioral modernity that began sometime in the Middle Stone Age. Yet, small numbers of bone tools are known from Early Pleistocene sites in East and South Africa, complicating our understanding of the evolutionary significance of osseous technologies. These early bone tools vary geographically, with those in South Africa indicating use in foraging activities such as termite extraction and those in East Africa intentionally shaped in a manner similar to lithic tool manufacture, leading some to infer multiple hominin species were responsible for bone technology in these regions, with *Paranthropus robustus* assumed to be the maker of South African bone tools and *Homo erectus* responsible for those in East Africa. Here, we present on an assemblage of 52 supposed bone tools primarily from beds III and IV, Olduvai Gorge, Tanzania, that was excavated by Mary Leakey in the late 1960s and early 1970s, but was only partially published and was never studied in detail from a taphonomic perspective. The majority of the sites from which the tools were recovered were deposited when only *H. erectus* is known to have existed in the region, potentially allowing a direct link between this fossil hominin and bone technology. Our analysis confirms at least six bone tools in the assemblage, the majority of which are intentionally flaked large mammal bones. However, one of the tools is a preform of the oldest barbed bone point known to exist anywhere in the world and pushes back the initial appearance of this technology by 700 kyr.

© 2020.

1. Introduction

Bone technology has long held significance in assessing the behavioral complexity of human ancestors (Dart, 1957). Dart (1957) proposed that *Australopithecus prometheus* used a bone, tooth, and horn (osteodontokeratic) technology to carry out the predatory behavior he hypothesized for the species. His proposal was in response to the absence of stone technology at the Makapansgat site, but Dart's (1957) osteodontokeratic culture has since been attributed to nonhominin taphonomic processes (Brain, 1981). Yet, the origins and significance of bone technology remains important in understanding the development of human culture. More recently, the advent of formal bone tools—i.e., shaped with techniques specifically conceived for bone material such as scraping, grinding, and grooving (Klein, 1983, 1999; McBrearty and Brooks, 2000)—has become associated with behavioral modernity that began in the Middle Stone Age of Africa and became increasingly sophisticated through the Upper Paleolithic

of Europe (McBrearty and Brooks, 2000; Henshilwood et al., 2001; d'Errico et al., 2012; Bouzouggar et al., 2018). However, evidence indicates that bone technology has much greater antiquity, extending into the Early Pleistocene at sites in South Africa (Brain and Shipman, 1993; Backwell and d'Errico, 2001, 2008; d'Errico et al., 2001; d'Errico and Backwell, 2003, 2009; Stammers et al., 2018) and East Africa (Leakey, 1971; Shipman, 1989; Backwell and d'Errico, 2004). Bone tools from these early sites and others outside of Africa suggest that bone technology in general is not an indicator of modern human behavior (Table 1). Still, bone tools are extremely rare from this time period, complicating our understanding of the evolutionary implications of this technology.

The makers and users of Early Stone Age (ESA) bone tools are currently unknown, with indications that multiple species, including at least *Homo erectus* and *Paranthropus robustus*, may have developed or acquired the technology (Backwell and d'Errico, 2004; Backwell and d'Errico, 2008). Although ESA bone tools have been identified in both East and South Africa, there are clear differences between the bone technology found in these two geographic regions. South African bone tools consist of weathered bone splinters used in

* Corresponding author.

Email address: Michael.Pante@colostate.edu (M. Pante)

Table 1

Prominent Lower and Middle Pleistocene bone tool sites and associated technology.

Site	Geographic location	Age	Associated stone technology	Type of bone technology	Citation
Drimolen	South Africa	2.0–1.5 Ma	Only six artifacts: 3 flakes and 3 cores	14 worn bones due to use in digging activities	Backwell and d'Errico (2008); Stammers et al. (2018)
Olduvai Gorge bed I and II	Tanzania	1.8–1.15 Ma	Oldowan, Developed Oldowan, Acheulean	35 flaked bones and bone anvils mostly from large animals	Backwell and d'Errico (2004)
Swartkrans	South Africa	1.8–1.0 Ma	Acheulean	85 worn bones due to use in digging activities, 6 intentionally shaped horn cores, and 1 shaped ulna	Backwell and d'Errico (2003); d'Errico and Backwell (2003)
Sterkfontein	South Africa	1.4–0.8 Ma	Acheulean	1 worn bone used in digging activities	Kuman and Clarke (2000); d'Errico et al. (2001)
Konso	Ethiopia	1.4 Ma	Acheulean	Bone biface	Sano et al. (2020); Echassoux (2012)
Boxgrove	United Kingdom	MIS13	Acheulean	Retouchers	Roberts and Parfitt (1999)
Gran Dolina	Spain	MIS 9	Acheulean-Mousterian transition	Retoucher and flaked from large bovids	Rosell et al. (2011)
Vertesszöllös	Hungary	MIS 13–9	Acheulean	>100 bone tools, many made from elephant bones	Dobosi (2001)
Revadim	Israel	500–300 ka	Acheulean	2 bone bifaces from elephant bones	Rabinovich et al. (2012)
Schoningen	Germany	478–424 ka	Pre-Mousterian—small flakes mostly scraper and points with no blanks	88 bone tools consisting of mostly retouchers made from the horse limb shaft and rib fragments, innominate used as an anvil in bipolar percussion, metapodial hammers	Van Kolfschoten et al. (2015)
Fontana Ranuccio	Italy	450 ka	Acheulean	2 bone bifaces of elephant bone	Biddittu and Celletti (2001)
Cueva del Angel	Spain	MIS 11–7	Acheulean	4 bone retouchers	Moigne et al. (2016)
Qesem cave	Israel	420–300 ka	Acheulo-Yabrudian Cultural Complex	24 bone retouchers	Blasco et al. (2013); Rosell et al. (2015)
Bilzingsleben	Germany	412–320 ka	Acheulean	Bone bifaces from elephant bones and other bone tools	Mania and Mania (2003); Brühl (2003)
La Polledrara	Italy	340–320 ka	Acheulean	8 bone tools	Anzidei (2001)
Orgnac 3	France	MIS 9–8	Acheulean	4 bone retouchers	Moigne et al. (2016)
Cagny-l'Épinette	France	MIS 9	Acheulean	6 bone retouchers	Moigne et al. (2016)
Castel di Guido	Italy	327–260 ka	Acheulean	270 bone tools made mostly from elephant bones, and some are bifaces.	Radmilli and Boschian (1996)

MIS = Marine Isotope Stage.

unmodified form or occasionally shaped through grinding and implemented in foraging activities such as termite extraction (d'Errico et al., 2001; Backwell and d'Errico, 2008), while those from Olduvai Gorge in Tanzania were intentionally knapped in a manner that mimics lithic manufacture and/or possibly used as anvils/hammers (Shipman, 1989; Leakey and Roe, 1994; Backwell and d'Errico, 2004). These functional and morphological differences between the bone tool assemblages have been hypothesized to be the result of (1) varying subsistence strategies practiced by hominins in the two regions or (2) distinct cultural traditions linked to multiple hominin species (Backwell and d'Errico, 2004). It has been suggested that *P. robustus* was the user of bone tools at the South African sites owing to the species' spatial association with the technology particularly at the Drimolen site, while *H. erectus* has been implicated as the maker of most of bone tools at Olduvai as the knapping strategies applied resemble those used in the Acheulean stone technology that is associated with the species (d'Errico and Backwell, 2003; Backwell and d'Errico, 2004, 2008). Although these interpretations are intriguing, they are tenuous owing to overlap in the temporal and spatial ranges of these species in South Africa, including now the Drimolen site (Herries et al., 2020), and the presence of two additional species (*Paranthropus boisei* and *Homo habilis*) at Olduvai. It is clear that these questions can only be resolved by increasing the sample of tools and sites on which these inferences are based.

1.1. Bone tools from Olduvai Gorge

Bone tools are known from beds I–IV at Olduvai, but only the samples from beds I and II were scrutinized beyond their original description by Leakey (1971, 1994). The confirmed bone tool sample from bed I (~2.04–1.8 Ma; Deino, 2012) and bed II (~1.8–1.2 Ma; McHenry and Stanistreet, 2018) comes from seven sites, six of which are in bed II (Backwell and d'Errico, 2004). Leakey (1971) reported only 125 bone tools among tens of thousands of fossils recovered from her excavations of this time interval. However, this sample was later reduced to 41 specimens by Shipman (1989) based on her reanalysis of the material and comparison with modern control collections produced by both experiments that simulate hominin use of bone as tools and by observation of the signatures left by natural phenomena that could potentially mimic the characteristics of hominin bone tool use (e.g., sedimentary abrasion and bone weathering). A subsequent reanalysis by Backwell and d'Errico (2004), bolstered by larger control collections and improved analytical methods, resulted in a further reduction of the sample to 36 specimens that could be confidentially attributed to hominin bone tool use. We argue here that the number of bone tools should be further reduced to 35 because damage on an elephant patella identified as an anvil by Backwell and d'Errico (2004: Fig. 8) could instead be attributed to since-described feeding marks inflicted by crocodiles (Njau and Blumenschine, 2006, 2012). In sum, the sample of bone tools from Olduvai beds I and II is currently small, and it is challenging to distinguish the taphonomic

signatures of bone tool manufacture from nonhominin taphonomic processes or even other types of hominin damage, such as impact marks from marrow extraction.

Leakey (1994) also reported on 28 modified bones from seven archaeological sites within beds III (~1.15–0.93 Ma) and IV (~0.93–0.8 Ma; Deino et al., in press). Leakey (1994) categorized these bones into five categories: (1) elephant pelves with battered acetabula; (2) pieces of elephant limb bones flaked to pointed extremities; (3) distal parts of large humeri with condyles removed by battering; (4) heads of large femora, broken off at the necks with battering on condylar surfaces; and (5) fragments of large limb bones with one end flaked to a point. However, the majority of these specimens were not shown in photographs in her chapter on the modified bones from beds III and IV in volume 5 of the Olduvai monographs (Leakey, 1994), and none have been further scrutinized to confirm her account of the modifications present.

Here, we report on an assemblage of 52 bones and teeth (Table 2) that Mary Leakey recovered during her excavations at Olduvai in beds II, III, and IV (Leakey, 1994) and subsequently identified as modified on associated collection labels (Supplementary Online Material [SOM] Fig. S1). Some of these specimens ($n = 5$) can be tentatively linked to descriptions provided by Leakey (1994) based on the skeletal part and/or metric measurements, but only one of these is shown in a photograph (specimen 895 from the Peter Davies Korongo [PDK] site). Others may be part of the sample of 28 specimens that she described, but we are unable to link them with the sample studied here owing to a lack of specimen numbers or measurements in the descriptions provided. There are also eleven specimens described in enough detail by Leakey (1994) to conclude they are not part of the 52 specimens described here. These include specimens from the Long Korongo site ($n = 1$), which is not represented in the collection, from skeletal parts not in the collection including all elephant pelves ($n = 2$), most large distal humeri ($n = 3$), all femoral heads ($n = 3$), a plate of a tortoise, and a specimen shown in a photograph from the HEB site that is described as an elephant bone with a pointed end. The whereabouts of these specimens is unknown, whereas the remainder of 52 specimens that were not linked to Leakey's (1994) descriptions were identified as bone tools on associated collection labels in the Olduvai Gorge laboratory in which they were stored. It is possible that Leakey (1994) referred to some of these specimens in her chapter when she noted that there were likely many more fragments of bone that were used and flaked, but only the most obvious were described.

Table 2

The complete assemblage of fossils and teeth in M.D. Leakey's collection of alleged bone tools.

Site	Stratigraphic location	Age (Ma)	Associated stone tool industry	NISP
HWK EE	Bed II	1.7	Oldowan	5
SC	Bed II	1.4–1.2	Developed Oldowan B/Acheulean	6
JK	Bed III	1.15	Acheulean	13
HEB	Bed IV	0.93–0.8	Acheulean	1
HEB West	Bed IV	0.93–0.8	Acheulean	4
PDK	Bed IV	0.93–0.8	Acheulean	2
WK	Bed IV	0.93–0.8	Acheulean	11
WK East A	Bed IV	0.93–0.8	Acheulean	8
WK East C	Bed IV	0.93–0.8	Acheulean	1
WK Hippo Cliff	Bed IV	0.93–0.8	Acheulean	1

NISP = number of individual specimens; WK = Wayland's Korongo; JK = Juma's Korongo; HWK EE = Henrietta Wilfrida Korongo East East; PDK = Peter Davies Korongo.

The assemblage we describe here was rediscovered by one of us (M.P.) among the collections of fossils from beds II–IV that remained on-site at Olduvai Gorge (Pante, 2010). Unlike their earlier excavated counterparts, they were never exported to the National Museums of Kenya in Nairobi for curation. As a result, this material has never received the same attention to which the earlier bone tools were subjected. The assemblage is uniquely positioned to shed light on the maker of bone tools at Olduvai as *H. erectus* is the only known hominin species to exist in the region where the majority of these specimens were deposited. However, confirmation of the bones as tools using standards successfully applied elsewhere (Backwell and d'Errico, 2004) is necessary to assess the significance of the material.

1.2. Background

The outcrops of Olduvai Gorge represent a nearly continuous record of human evolution over the last two million years. A rich sedimentological record with excellent age control is provided by stratigraphic studies (Hay, 1976), radiometry and magnetostratigraphy (Deino, 2012; Deino et al., in press), high-resolution tephrostratigraphy (McHenry et al., 2016; McHenry and Stanistreet, 2018), and sequence-stratigraphic frameworks (Stanistreet, 2012; Stanistreet et al., 2018), while its well-preserved fossils and substantial stone tool assemblages provide a rich record of the behavioral and technological evolution of human ancestors (Leakey, 1971; Leakey and Roe, 1994), particularly with regard to the lower units (i.e., beds I and II).

Much less is known about the stratigraphy and archaeology of the younger beds at Olduvai. Leakey's work in beds III and IV was carried out between 1968 and 1971 and published much later (Leakey and Roe, 1994). Forty-three archaeological sites were excavated from beds III and IV, but only seventeen of these have been reported in detail (Leakey and Roe, 1994). Since Leakey's work, little has been published on the nonhominin material from any sites within beds III and IV (Pante, 2010, 2013; Johnson et al., 2016), and much of the archaeological material, and the fossils in particular, have not been subjected to detailed analyses.

Mary Leakey also excavated two sites (Henrietta Wilfrida Korongo East East [HWK EE] and SC) within bed II while she was conducting excavations in beds III and IV, but she never published detailed descriptions of this work. The artifacts and fossils from HWK EE and the fossils from SC were stored alongside the material from beds III and IV at the Olduvai research station. The good condition and size of the collection from the HWK EE site inspired renewed excavations (de la Torre et al., 2018) at the site with analyses of the new (Arroyo and de la Torre, 2018; Bibi et al., 2018; de la Torre et al., 2018; Pante et al., 2018; Prassack et al., 2018; Proffitt, 2018; Rivals et al., 2018; Uno et al., 2018) and original (Pante and de la Torre, 2018) artifact and fossil assemblages recently published. However, the SC site is yet to receive the same attention, and little is known about the site other than that it produced an ulna of *H. erectus* and it is stratigraphically located above tuff IID, placing it in upper bed II (Hay, 1976; McHenry et al., 2007).

2. Materials and methods

Analyses of the 52 alleged bone tools, which are currently curated in a laboratory in Mary Leakey's camp at Olduvai Gorge, were aimed at testing two hypotheses: (1) hominins modified the bones, if only in the process of consuming carcass parts, and (2) the bones were shaped into tools or used by hominins. We approached these tests in three stages of analysis. Stage 1 primarily took place in 2009 and was a taphonomic analysis by M.P., R.B., and J.N., but was revisited by

M.P. in 2016; stage 2 took place in 2016 and was the analysis by I.d.I.T. of specimens ($n = 9$) that appeared to have been intentionally flaked, providing the perspective of a lithic technology analyst; stage 3 also took place in 2016 and was the analysis of specimens ($n = 2$) that appeared to exhibit possible traces of use or traces of manufacture with techniques specifically conceived for bone material by F.d.

2.1. Taphonomic analysis

All three authors conducting the taphonomic analysis of the 52 specimens have extensive experience with control collections of bones modified experimentally and by fossil hominins, mammalian carnivores, crocodiles, weathering, fluvial abrasion, and bioerosion that guided our interpretations (Behrensmeyer, 1978; Capaldo and Blumenschine, 1994; Blumenschine et al., 1996, 2007; Njau and Blumenschine, 2006; Pante and Blumenschine, 2010; Gümrukçü and Pante, 2018). All three have also analyzed thousands of fossils from Olduvai Gorge. One of us (M.P.) has conducted detailed taphonomic analyses of several sites represented in the studied collection, including HWK EE, Juma's Korongo (JK), Wayland's Korongo (WK), and HEB, which is ongoing and unpublished (Pante, 2010, 2013; Pante and de la Torre, 2018; Pante et al., 2018; Njau et al., 2020). Our analyses also considered published descriptions of comparative collections of bone tools and previously identified examples from both South Africa and Olduvai Gorge (Backwell and d'Errico, 2001, 2004, 2008; d'Errico et al., 2001; d'Errico and Backwell, 2003, 2009).

Taphonomic analyses were carried out by all three analysts simultaneously, initially independently, but then seeking consensus on the identifications. Each specimen was viewed using a 60-W light source and 10× hand lens following Blumenschine et al. (1996) and inspected for cut marks, percussion marks, carnivoran and crocodile tooth marks, percussion and tooth notches, bone weathering, abrasion (fluvial and other), general breakage patterns (green or dry), and polish. Identifications were discussed and required consensus to be marked in the database. Hypothesis 1 was accepted when bones exhibited modifications consistent with bone breakage for marrow extraction or defleshing including the presence of cut and percussion marks or percussion notches. Assessing hypothesis 2 was more complex as criteria for the identification of shaped and used bones are more ambiguous than the presence of a single modification. At this stage of the analysis, bones were determined to be potential tools if they were modified by hominins, but in a manner inconsistent with the extraction of flesh and marrow from carcasses as observed in comparative collections and in fossil assemblages from Olduvai. These specimens were subjected to additional analysis by I.d.I.T. and F.d. depending on the taphonomic traces (i.e., scraping, flaking, polish) observed. We accept hypothesis 2 when hominin-induced modifications are present but are inconsistent with damage produced through carcass consumption. These include the following: (1) evidence of percussion battering found on bones that do not have a marrow cavity or in areas that are not near a fracture allowing access to the marrow cavity; (2) flake scars that are suggestive of intentional knapping (Backwell and d'Errico, 2004) assessed by the presence of scars that are invasive, bifacial, and/or contiguous and are difficult to explain as resulting from breakage for marrow consumption (i.e., inflicted on already detached splinters); and (3) the presence of localized polish or worked areas inconsistent with natural abrasion. Our initial assessments of flaking and polish were also further evaluated in the manner described in the following section.

2.2. Analysis of flaked specimens

Flake removals were analyzed following conventions in the study of prehistoric knapping, which is mostly based on flaked stones (e.g., Inizan et al., 1999). Description of large cutting tool (LCT) attributes followed recent proposals for the Olduvai assemblages (de la Torre and Mora, 2018b), and core flaking schemes were based on de la Torre (2011) and de la Torre and Mora (2018a).

2.3. Analysis of polished specimens

Specimens with polished and possibly worked areas were examined and photographed at magnifications between 4× and 40× using a motorized Leica Z6 APOA microscope equipped with a DFC420 digital camera and Leica Application Suite (LAS) software, including the multifocus module. With this microscope, digital images are acquired at different heights, and adapted algorithms combine them into a single sharp composite image that significantly extends the depth of field. Interpretation of recorded modifications is based on criteria defined in the literature (Bromage, 1984; Shipman and Rose, 1988; d'Errico, 1993) and on previous analysis of polished areas conducted by Backwell and d'Errico (2004) on Olduvai faunal remains and bone tools.

3. Results

3.1. Assemblage data

Mary Leakey's bone assemblage described here includes a total of 52 specimens from ten archaeological sites distributed through beds II–IV (Table 1). The majority of the specimens (25%) come from the bed III site (JK), with a bed IV site (WK) close behind (21.2%). Forty-five of the specimens are bone fragments, and seven are teeth (Table 2). The assemblage comprised completely mammal bones and teeth (Table 3), with some identifiable as bovids (11.5%), hippopotamids (13.5%), and proboscideans (19.2%), the most common group identified. This is at least in part due to the much larger size of their bones, making even nondescript fragments easy to attribute to the taxonomic group. All but animal size group 1 are represented in the assemblage, which overall has a disproportionate number (52%) of large megafaunal animals (size groups 5 and 6), compared with most faunal assemblages from Olduvai Gorge (Table 2). Limb bones dominate the assemblage (63.5%), followed by teeth (13.5%), and ribs (9.6%; Table 2).

3.2. Taphonomic data

Taphonomic data for the assemblage are summarized in Table 4 and only apply to bones, not teeth. The majority (77.8%) of the assemblage exhibits abrasion/mechanical rounding likely caused by exposure to fluvial action. Some bones (26.7%) exhibit abrasion severe enough to completely obscure bone surface modifications that may have been present before exposure to fluvial action. Subaerial weathering is generally minimal in the assemblage, with 88.9% of bones falling below stage 3, suggesting relatively quick burial. The majority of bones (71.1%) exhibit green bone breakage, suggestive of fracture when bones remained greasy and attractive to consumers.

The bone assemblage exhibits evidence of both hominin and carnivore feeding (Table 4). Of all bones, 13.3% are cut marked (Fig. 1a), whereas 11.1% are percussion marked. However, tooth marks are the most abundant modification in the assemblage at 37.8%. Notches

Table 3

Taxonomic attribution, animal size groups, and skeletal part profiles for complete assemblage in M.D. Leakey's collection of alleged bone tools.

Taxon	NISP
Bovidae	6
Hippopotamidae	7
Mammalia	29
Proboscidean	10
Size group ^a	NISP
2	2
3	10
4	13
5	17
6	10
Skeletal part	NISP
Astragalus	1
Cranium	1
Femur	5
Horn core	1
Humerus	8
Indeterminate	1
Innominate	1
Limb bone	12
Metatarsal	2
Radius	5
Radius/ulna	1
Rib	5
Scapula	2
Teeth	7

NISP = number of individual specimens.

^a Size groups based on Bunn and Kroll (1986): size 1 = <50 lb (23 kg); size 2 = 50–250 lb (23–114 kg); size 3 = 250–750 lb (114–341 kg); size 4 = 750–2000 lb (341–907 kg); size 5 = 2000–6000 lb (907–2722 kg); size 6 = >6000 lb (>2722 kg).

Table 4

Taphonomy for the collection of fossils only in M.D. Leakey's collection of alleged bone tools.

Abrasion	NISP
Major	12
Minor	23
None	10
Weathering ^a	NISP
Stage 0	5
Stage 1	20
Stage 2	15
Stage 3	4
Stage 4	1
Stage 5	0
Stage 6	0
General breakage	NISP
Dry	12
Green	32
Unbroken	1
Cut marks	NISP
Absent	39
Present	6
Tooth marks	NISP
Absent	28
Present	17
Percussion marks	NISP
Absent	40
Present	5
Notches	NISP
Absent	36
Tooth	3
Percussion	7

NISP = number of individual specimens.

^a Weathering stages based on Behrensmeier (1978).

exhibit the reverse pattern, with a greater number of percussion notches (15.5%) than tooth notches (6.7%) in the assemblage. The poor condition of bone surfaces likely reduced the overall percentage of modifications in the assemblage.

3.3. Tools or other?

The majority of specimens in the collection could not be attributed to hominin bone tool manufacture or use because they do not demonstrate evidence for intentional shaping and lack localized polish consistent with use (Backwell and d'Errico, 2004, Table 5). However, six specimens (11.5%) of the collection are identified as bone tools by this study, whereas an additional 15.4% of the collection shows evidence of hominin modification resulting from defleshing and demarrowing of carcasses, but not intentional manufacture. Carnivores/crocodiles are responsible for modifications recorded on 26.9% of the assemblage, whereas 50% of the collection does not bear traces attributable to a specific taphonomic agent. Notably, all tooth fragments only show natural modifications produced during the lifetimes of the animals during feeding, digging, or through use in intraspecific competition (Fig. 1b). One of these teeth (HEB West 112) was described by Leakey (1994: 314) as “chipped and battered,” but we interpret this as natural damage.

3.4. The confirmed bone tool assemblage

The confirmed bone tool assemblage comes from six of the ten sites that comprise the entire collection (Table 6). All three beds (II–IV) are represented, with the oldest tool coming from the ~1.7 Ma HWK EE site in bed II. All but a single bone tool (WK East A 494) are made from the bones of large animals in size group 5 or 6. Of the bone tools, 71.4% are made from limb bones and 42.9% are made from proboscidean bones. In the following section, we describe and show photographs of each tool to justify our interpretations.

HWK EE 386A

The oldest of the bone tools, HWK EE 386A, is a large ungulate distal humerus that is well preserved and unabraded (Fig. 2a). It exhibits carnivore tooth furrows on the distal epiphysis, but has also been knapped. With at least two scars on the medullar side and three scars on the cortical surface, flaking follows a bifacial simple partial scheme (i.e., de la Torre and Mora, 2018a) in a fashion that resembles knapping of a chopping tool (sensu Leakey, 1971). The flaking also closely follows the knapping schemes typical of the HWK EE stone assemblage (Pante and de la Torre, 2018; de la Torre and Mora, 2018a). Although the pointed end could be suggestive of the specimen being used as a tool, no damage was observed macroscopically.

JK 3109

The only bone tool from bed III is a proboscidean astragalus that shows pitting typical of stone anvils (Fig. 2b; SOM Video S1). The distal surface of the astragalus shows no human-inflicted marks and is flat, which suggests it was used as the resting side. The convex proximal face of the astragalus (i.e., the articulation with the tibia) contains at least three clusters of impacts. These battered areas are heart shaped, with deep impacts that have dented and rectilinear walls; these features are consistent with those produced on stone anvils through bipolar percussion (Arroyo and de la Torre, 2018). The bone also exhibits tooth marks on the articular surface, with the tibia that were likely inflicted before their use as an anvil. Leakey (1994) also observed depressions on the convex surface of the specimen and noted their similarity to pits on stone anvils and hammerstones.

Figure 1. Pseudo and potential bone tools. (a) Size 2 bovid radius from JK (163) that has been cut marked. Mary Leakey may have identified this as a tool owing to the cortical flake that was removed from the end of the specimen. We interpret this as resulting from marrow extraction with a hammerstone-on-anvil technique. (b) Hippopotamid canine from HEB West (1518) interpreted by Leakey as a tool, but as natural modified here. (c) Proboscidean incisor fragment from JK (276) that exhibits polish and a point-like shape (scale = 1 cm). (d) Superior view of the proximal portion of the JK 276 fragment (scale = 1 mm). (e) Superior view of the proximal portion of the JK 276 fragment (scale = 1 mm). (f) Close-up of polish on JK 276 fragment (scale = 1 mm). (g) Size 4 limb bone fragment from WK East A (2749). One end has flake scars that suggest the possibility of intentional shaping. (h) Proboscidean limb bone shaft fragment from WK (526) that exhibits multiple flake scars indicative of marrow extraction using a hammerstone-on-anvil technique (arrows indicate the direction of impact). Black and white scales = 2 cm. JK = Juma's Korongo; WK = Wayland's Korongo.

Table 5
Interpretation of taphonomic processes leading to the signatures on the fossils and teeth in the assemblage in M.D. Leakey's collection of alleged bone tools.

Interpretation	NISP
Bone tool	7
Butchery	5
Carnivore	10
Carnivore/butchery	3
Carnivore/crocodile	1
Natural	26
Total	52

NISP = number of individual specimens.

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jhevol.2020.102885>.

HEB 326

HEB 326 is a fragment of proboscidean limb bone of nearly 20 cm in length (Table 6) that has a shape suggestive of a LCT (Fig. 2c; SOM Video S2). The bone exhibits abrasion/mechanical rounding, and thus, use-wear cannot be observed on the bone. Nonetheless, the specimen shows clear contiguous removals/flake scars produced

by a hammer. The medullary surface shows one scar, which is flat and noninvasive. This surface was used as a striking platform for flake removals of the cortical surface, which form an acute angle and penetrate deeply into the edge of the shaft. Overall, this tool shows the typical features of early LCTs made on stone at Olduvai (de la Torre and Mora, 2018b), with unifacial shaping of one edge of the blank aided by occasional flaking of the ventral side on the distal end.

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jhevol.2020.102885>.

PDK 895

PDK 895 is a distal hippopotamid humerus that has a large battered area (Fig. 2d). This is the only bone in the collection that was shown in photographs in Leakey (1994). She interpreted the damage to the distal epiphysis as the result of battering. We interpret the distal epiphysis damage as carnivore gnawing, but note that the shaft has many impact marks concentrated on a flat area. These are unlikely to be impacts resulting from attempts to extract marrow from the bone, as they are not near any fractured edge. The marks suggest the bone was either used as an anvil or as a soft hammer to manufacture stone tools.

Table 6

Data for confirmed bone tool and potential bone tool assemblage.

Site	Specimen number	Stratigraphic location	Taxonomic ID	Size group ^a	Skeletal part	Abrasion	Length (mm)	Width (mm)	Thickness (mm)	Weathering stage	Breakage	Cut marks	Tooth marks	Percussion marks	Notch	Determination
HWK EE	386A	Bed II	Ungulata	5	Humerus	None	168	74	72	2	Green	Yes	Yes	No	Tooth	Bone tool
JK	3109	Bed III	Proboscidea	6	Astragalus	Minor	210	170	115	0	Unbroken	No	Yes	Yes	None	Bone tool
HEB	326	Bed IV	Proboscidea	6	Limb bone	Major	186	65	47	1	Green	No	No	No	None	Bone tool
PDK	895	Bed IV	Hippopotamidae	5	Humerus	Minor	216	129	91	2	Green	No	Yes	Yes	None	Bone tool
WK	4601	Bed IV	Proboscidea	6	Limb bone	Minor	206	131	50	2	Green	No	No	No	Percussion	Bone tool
WK East A	494	Bed IV	Mammalia	3	Rib	Major	88	21	13	1	Green	No	No	No	None	Bone tool
JK	276	Bed III	Mammalia	6	Incisor tooth	Minor	64	22	8	NA	NA	NA	NA	NA	NA	Natural
WK	526	Bed IV	Proboscidea	6	Limb bone	Major	325	113	73	4	Green	No	No	No	Percussion	Butchery
WK East A	2749	Bed IV	Mammalia	4	Limb bone	Minor	105	41	20	1	Green	No	No	No	None	Butchery/natural

NA = not applicable; WK = Wayland's Korongo; JK = Juma's Korongo; HWK EE = Henrietta Wilfrida Korongo East East; PDK = Peter Davies Korongo.

^a Size groups based on Bunn and Kroll (1986): size 1 = <50 lb (23 kg); size 2 = 50–250 lb (23–114 kg); size 3 = 250–750 lb (114–341 kg); size 4 = 750–2000 lb (341–907 kg); size 5 = 2000–6000 lb (907–2722 kg); size 6 = >6000 lb (>2722 kg).

Figure 2. Confirmed bone tools. (a) Size 5 mammal humerus from HWK EE (386a) that has been tooth marked by carnivores and intentionally shaped proximally. Arrows indicate the direction of impact, whereas circles identify scars on the opposing surface. (b) Proboscidean astragalus from JK (3109) that has been used as an anvil likely for bipolar percussion. (c) Proboscidean limb bone from HEB (326) that exhibits evidence of intentional shaping. Arrows indicate the direction of impact, whereas circles identify scars on the opposing surface. (d) Hippopotamid humerus from PDK (895) that has been battered through use as an anvil or through use as a soft hammer implement. Distal epiphysis has been gnawed by carnivores. (e) Proboscidean limb bone shaft fragment from WK (4601) that has been intentionally shaped through knapping. Arrows indicate the direction of flaking, whereas circles identify scars on the opposing surface. Black and white scales = 2 cm. JK = Juma's Korongo; WK = Wayland's Korongo; PDK = Peter Davies Korongo.

WK 4601

WK 4601 is a proboscidean limb bone shaft fragment that has been knapped (Fig. 2e; SOM Video S3). The bone exhibits minor abrasion/mechanical rounding, which prohibits identification of microwear damage to the flaked area. No carnivore damage is observed on the specimen. Flaking is concentrated on a straight edge, opposite a V-shaped green fracture that splits the proboscidean limb with extreme dynamic loading, of which no carnivore was capable, and thus, we attribute to human percussive action. This bezel-like edge, transverse to the long axis of the limb, contains at least three removals that could be caused by use-wear, rather than by shaping. One flake removal bearing a percussion point penetrates deeply into the medullary surface adjacent to the bezel-like edge. Opposite this edge and on the cortical surface, there are two more flake removals with percussion points that also penetrate deeply into the edge adjacent to

the straight end of the blank. Overall, the shape of this tool is reminiscent of Acheulean cleavers on stone, wherein a transverse edge is left unshaped, but often presents chipping, and wherein flaking is focused on shaping the lateral sides parallel to the long axis of the blank.

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jhevol.2020.102885>.

WK East A 494

The most intriguing specimen in the collection is WK East A 494, a rib fragment from a size 3 mammal that measures 88 mm in length and has been shaped through either flaking/scraping or a combination of both (Fig. 3; SOM Video S4). The specimen preserves three barbs that are each approximately 1 cm in length, with the first having been damaged postdepositionally. The outer profiles of the barbs are curved, and under high magnification, there appears to be eroded

Figure 3. Evidence of anthropogenic modification on a preform of a barbed point from WK East A (494). Specimen is a size 3 mammal rib: (a and b) close-up of region 1 in complete view; (c–e) close-up of region 2 in complete view; (g–i) close-up of region 3 in complete view. All demonstrate localized polish (scales = 1 mm). Arrows in d highlight evidence of scraping striations. (f) Evidence of scraping highlighted by arrows (scale = 1 cm). (j) Close-up of region 4 in complete view showing potential chatter marks along the edge of the piece that leads to the barbs (scale = 1 mm). WK = Wayland's Korongo.

scraping marks directed toward the barb tip and polish covering the barb surface, particularly at the tip. There are also three invasive and thin flake scars at the origin of the first barb. These features suggest an anthropogenic origin as they contrast with the remainder of the object's surface, which is rough. Subparallel striations close to a barb, highlighted with white arrows in Figure 3f, also point toward anthropogenic modification possibly produced by scraping the bone surface. Distal from the barbs are small discontinuities on the object edge that could be chatter marks produced by vigorously scraping the edge of the specimen, but subsequent erosion has reduced our confidence in attributing these traces to an anthropogenic origin (Fig. 3j). Together, the traces on the piece indicate it is a preform of a functional object, such as a barbed point.

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jhevol.2020.102885>.

3.5. Possible bone tools

There are three additional specimens (JK 276, WK 526, WK East A 2749) that may be bone tools, but we conservatively attribute them

to natural processes and butchery (Table 5). Still, we have chosen to describe them in further detail as others may develop their own viewpoints based on the images and descriptions provided. There is also one additional specimen (Johnson et al., 2016) described by Leakey (1994), but not considered a possible tool here. She described a large hippopotamus radius, with a broken and flaked shaft, noting that the flake scars do not follow any pattern and likely resulted from use. We attribute the piece to hammerstone breakage for marrow removal.

JK 276

JK 276 is a flake of what appears to be the tip of a proboscidean incisor (Fig. 1c–f). The impact or striking platform of the specimen corresponds to a portion of the animal's tusk that is susceptible to both mechanical damage and flaking. A small flake removal, which occurred before the detachment of the piece itself, is visible on the left side of Figure 1d, e. Part of the tip is highly polished (visible in Fig. 1e, f) and bears parallel deep striations with randomly oriented thinner striations that are almost certainly the result of the animals' use of the tooth before the fracture that detached the flake. Had these thinner striations resulted from postdepositional processes, there

would be similar abrasion on the remainder of the specimen's surface, but this is not the case. The shape is suggestive of a blade. We conclude that the evidence is most consistent with natural damage observed on elephant incisors (Villa and d'Errico, 2001).

WK 526

WK 526 is a massive limb bone fragment of a proboscidean (Fig. 1h). It exhibits at least one percussion notch and has potentially been shaped at the tip, but we cannot rule out percussion damage resulting from marrow extraction as the cause of the shape of the bone. The surface exhibits pitting that may indicate the use of the bone as an anvil, but again, percussion resulting from marrow extraction cannot be ruled out, especially given the tremendous force required to dynamically fracture a proboscidean limb bone. The medial part of the left edge on the cortical surface bears two scars, one of which preserves a percussion point that is potentially indicative of shaping. Leakey (1994: 314) described this specimen as an elephant bone with a pointed tip that was "formed by detaching a single flake from either side" and argued the point had been "chipped and blunted by use," the latter of which we did not observe.

WK East A 2749

WK East A 2749 is a size 4 mammal limb bone fragment that shows evidence of flake removal at one end (Fig. 1g). The bone appears shaped into a point with three individual flake removals. It exhibits minor rounding and no other modifications to the surface. The limited number of flake scars prevents confident attribution to intentional shaping, and similarly shaped bones are known to result from the process of marrow removal (Backwell and d'Errico, 2004).

4. Discussion

Our analysis of Mary Leakey's largely unpublished bone tool collection from beds II–IV has confirmed at least six bone tools dating to the ESA, adding to the very small sample of known bone tools from this time period. It is not surprising that the majority of specimens in the collection were ruled out as bone tools, as the same was true for earlier analyses of specimens that Mary Leakey identified as bone tools from beds I and II of Olduvai (Shipman, 1989; Backwell and d'Errico, 2004). The protocols and general taphonomic knowledge that allow a more confident identification of bone tools were unavailable to Leakey during her original analysis in the early 1970s. Yet, she successfully discovered and recognized multiple bone tools during her excavations, and many of the bones that are unlikely to be tools still show evidence of hominin butchery.

The general assemblage characteristics for the complete collection of 52 specimens show a dominance of large animals, especially proboscideans. Bones of large size 5 and 6 animals are relatively uncommon in faunal assemblages from Olduvai Gorge compared with their smaller and much more abundant size 1–3 counterparts, such as gazelle, impala, and wildebeest. For example, only 2.4% of bones in Leakey's collection from HWK EE are from size 5 and 6 animals, and only two specimens are attributed to proboscideans, both of them teeth (Pante and de la Torre, 2018). It is possible Leakey may have suspected some large bones in the collections were used as tools based on their size alone. This assumption is not unreasonable, given that 83.3% of the bones confirmed to be tools are from large animals. It is interesting that hominins may have been preferentially and likely opportunistically selecting these large bones for knapping, as the rarity of large bones in fossil assemblages from Olduvai may in part explain the scarcity of bone tools. The use of these large bones as a raw material source may have been further limited by the difficulty of

knapping fresh bones of this size. In elephant bone breakage and knapping experiments, Backwell and d'Errico (2004) noted that fresh elephant bones were very difficult to knap, but were shapeable after a period of drying.

We cannot conclusively attribute any of the teeth in the assemblage to hominin modification. Proboscidean incisors and the canines and incisors of hippopotamids have a tool-like appearance even when unmodified. They are prone to polish at their tips and are typically striated owing to abrasion that occurs during an animal's lifetime (Haynes, 1993; Villa and d'Errico, 2001). They are also prone to fracture at their tips, which can mimic the appearance of intentional knapping. The single tooth in the collection that Leakey described in her monograph was a chipped and battered hippopotamus canine, and she may have attributed similar damage on other teeth to anthropogenic modification. Nearly all of the teeth in this collection bear randomly oriented striations and do not exhibit subparallel striations or polish inconsistent with natural modification. The exception is the JK 276 specimen, which is attributed to natural fracture and polishing, but also cannot be completely ruled out as a bone tool given its blade-like shape, impact marks, and highly localized polish.

The complete collection is generally poorly preserved owing to the fluvial contexts in which the bones were buried (Pante, 2010). Although bone weathering is in general minimal, the majority of bones are abraded, and this has prohibited identification of use-wear that may have been present on the edges of bones. As a result, it is possible that other specimens in the assemblage were used as tools. Abrasion of the bone surfaces is not surprising, given the high-energy depositional environments of many of the bed III and IV assemblages (Hay, 1976; Leakey and Roe, 1994). Abrasion is also likely to have obscured surface modifications in the assemblage that are evidence of hominin and carnivore feeding preventing half of the bone tool collection from being attributed to any specific taphonomic agent. Still, when visible, carnivore tooth marks and hominin butchery marks provide strong evidence that many of the bones in the collection have been processed for food even if they were not used as tools. Carnivore damage and percussion battering to the bones of large mammals are known to resemble the signatures of intentional shaping, and it is only the consistent presence of contiguous and/or invasive flake scars that implicates the latter, as these signatures are not observed in experimental breakage of large size 6 mammal bones (Backwell and d'Errico, 2004).

The collection of six confirmed bone tools is generally morphologically similar to those previously identified from bed II (Backwell and d'Errico, 2004). The confirmed bone tools from beds III and IV indicate that most bone tools at Olduvai were made by *H. erectus*. While the lone specimen from the ~1.7 Ma HWK EE site in bed II was flaked as many other Oldowan cores in the same assemblage and predates the known first appearance of *H. erectus* at Olduvai (de la Torre and Mora, 2018a). The bones have either been used as anvils or have been shaped through flaking in a manner that is consistent with the manufacture of stone tools, a pattern that Leakey (1994) also observed. The exception is the WK East A 494 preform, the significance of which is discussed in the following section. The flaked bone tools are consistently produced from the limb bones of large mammals, which are relatively rare in fossil assemblages from Olduvai and may be why flaked bone tools are also scarce. Together, the evidence suggests that bone tool manufacturing was episodic and may have only occurred when suitable lithic raw materials were not immediately available. This is in contrast to the South African bone tool assemblages, wherein implements made of bone appear to have been used for specific foraging activities (Backwell and d'Errico, 2001; d'Errico et al., 2001).

The preform that resembles an unfinished barbed point from WK East A is unique among all bone tools from the ESA. Barbed points were previously unknown from the ESA and are considered a signal of behavioral modernity that blurs the distinction between the MSA and LSA in Africa (Yellen et al., 1995; Yellen, 1998; McBrearty and Brooks, 2000). The earliest known barbed bone points date to ~90 ka and come from Katanda (Yellen et al., 1995) in the Democratic Republic of Congo (formerly known as Zaire). The seven barbed points from that site are part of a larger assemblage of 10 worked bones and are inferred to have been produced through a combination of grinding and scraping techniques (Yellen et al., 1995). Although the preform from WK East A is not as sophisticated as the Katanda points and does not preserve evidence of hafting, it does bear a superficial similarity to the Kt9:7 barbed point (Yellen et al., 1995). The localized polish and linear indentations on the WK East specimen are consistent with scraping rather than with grinding, but nonetheless are solid evidence for anthropogenic shaping of the bone. Outside of Africa, barbed points are known from China as early as 23 ka from the sites Ma'anshan and Xigashan (Huang et al., 1986; Zhang et al., 2010, 2016) and from Europe at sites in France that date to around 16 ka including Fontales (Tisnerat-Laborde et al., 1997), Espalungue (Pétillon et al., 2015), and Isturitz (Szmidi et al., 2009). The WK East specimen pushes back the origin of barbed bone points by at least 700 kyr and implicates *H. erectus* as the inventor of this technology. The sudden appearance in the archaeological record of what seems to be a relatively well-made preform of a barbed point is suggestive that the species may have produced similar objects from perishable materials such as wood, but this speculation may never be supported by direct evidence. Regardless, it is clear the use of bone technology and its refinement into point-like forms is not exclusive to modern humans and likely developed along a continuum beginning after the appearance of the genus *Homo*.

The provenance of the preform is of great importance, given the implications for its discovery. Notes detailing the specific location of the preform within the WKE A assemblage have yet to be discovered, but it is extremely unlikely that the preform comes from sediments younger than upper bed IV. Leakey and Roe (1994: Fig. 5.1) showed the WKE A assemblage having accumulated primarily at the base of an aggrading channel that completely incised tuff IVB, which marks the beginning of upper bed IV. The incision surface is shown roughly 2 m below the beginning of the younger Masek beds, which have recently been demonstrated to preserve the Bruhnes-Matuyama reversal (781 ka), based on paleomagnetic analysis of sediment cores recovered by the Olduvai Gorge coring project (Stanistreet et al., 2020; Deino et al., in press). The preform is also similarly preserved to the fauna from WKE A and nearby bed IV sites PDK and WK (M.P., pers. obs.). The abrasion of the surface is consistent with deposition in a fluvial setting, and the mottled red/brown coloring taken from the color of iron-rich surrounding sediments is common only for fossils recovered from beds III and IV at Olduvai (Pante, 2010). Therefore, it is unlikely that the preform was reworked from sediments younger than bed IV, and we are confident in its designated provenance.

The identification of bone tools is not always straightforward, especially when bone surfaces are in less than pristine condition. For example, pseudo bone tools are known to be produced by carnivores, and we acknowledge that three of six bone tools also preserve evidence of carnivore modification (Villa and Bartram, 1996). However, we remain confident that the multifaceted approach used by this study, involving experts in vertebrate fossil taphonomy, bone modification, and lithic and bone tool manufacture, has allowed accurate identification of at least six bone tools in the collection. Our approach was conservative, and new analyses could reveal additional bone tool

specimens in the collection. Flakes that would have been produced through the shaping of bone are superficially indistinguishable from flakes produced through marrow extraction. Use-wear studies of these flakes may prove important in understanding ESA bone technology. Regardless, the six bone tools here, along with the previously confirmed 35 specimens (Backwell and d'Errico, 2004), make up an extremely small proportion of the fossils from Olduvai Gorge and demonstrate the rarity of these artifacts in the ESA worldwide, suggesting their manufacture was certainly episodic and probably opportunistic.

5. Conclusions

Mary Leakey's collection of 52 bones that she identified as tools from Olduvai Gorge has long waited to be rediscovered. Although only a small portion of the assemblage can be confirmed as bone tools, the addition of at least six specimens to the 35 known from Olduvai is invaluable in improving our understanding of bone tool culture in the ESA and sheds light on the behaviors of the hominin species that wielded them. Our results confirm that *H. erectus* produced bone tools through knapping methods that resemble those applied in lithic tool manufacture. We suggest that the rarity of bone tools in the record could be the result of a lack of suitable specimens from large mammals for knapping, the greater suitability of readily available stone, and/or the fundamentally opportunistic nature of ESA bone tool manufacture and use that may rely on the availability of large mammal bones that are suitable for producing tools. Furthermore, the similarity between the later examples of bone technology presented here and earlier examples from Olduvai, an observation also made by Leakey (1994), implicates *H. erectus* as the principal maker of bone tools at Olduvai.

The preform resembling a barbed bone point from WK East A has implications for the emergence of modern human behavior. Previously only known from sites dating to the MSA and later, barbed points have become an important indicator of behavioral modernity. The discovery of the preform from WK East A pushes back the initial appearance of this technology considerably and implicates *H. erectus* as the inventor, while also indicating that the ability to conceive of and produce barbed bone points is not an indicator of behavioral modernity, but rather part of the behavioral and cognitive repertoire of hominins that preceded *Homo sapiens*.

Together, our results suggest that cultural innovations attributed to the MSA may have emerged long before in Africa and were not necessarily transmitted. Conducting new excavations and revisiting museum collections will undoubtedly help contextualize the behavioral complexity implicated by the use and manufacture of bone technology, likely blurring the lines between species as the gaps in the time represented by our data decrease. The use of bone as a raw material is likely to have been more prevalent than is currently understood owing to the greater effect of taphonomic processes on bone than on stone and the extensive effort required to distinguish the signatures of bone tool use and manufacture from other taphonomic processes, including hominin and carnivore carcass consumption (Shipman, 1989). This is particularly true for high-energy fluvial deposits like those found in beds III and IV (Hay, 1976) where bone surfaces are often heavily abraded and poorly preserved (Pante, 2010), which respectively can mimic or obscure the characteristics of bone tool use and manufacture (Shipman, 1989).

The use of bone as a raw material would have provided *H. erectus* a substantial advantage when lithic materials were unavailable. Bones from large mammals are a resource that would have been both less reliably located than outcrops of lithic raw materials, but also more

widely dispersed across the landscape, including in areas where lithic sources were absent. The ability of *H. erectus* to exploit this resource suggests the species was both adaptable and opportunistic, taking advantage of many resources offered by its environment. This characteristic is likely in part responsible for the species' success in Africa and in new environments into which it dispersed and demonstrates that human adaptability has great antiquity within our lineage.

Acknowledgments

We would like to thank the Tanzanian Antiquities Department, Commission for Science and Technology, and Ngorongoro Conservation Area Authority for supporting this research. This research was funded by Wenner-Gren Foundation for Anthropological Research (grant numbers 7640 and 9245); the European Research Council (European Union's Seventh Framework Programme [FP7/2007e2013]/ERC grant agreement n° 283366 [ORACEAF]), and the Rutgers University Center for Human Evolutionary Studies. I.d.I.T. is currently funded by a European Research Council-Advanced Grant (BICAE-HFID; grant agreement no. 832980). F.d.'s work was partially founded by the Research Council of Norway through its Centre of Excellence funding scheme (SFF Centre for Early Sapiens Behaviour – SapienCE – project number 262618), and the Talents program of the University of Bordeaux 'Initiative d'Excellence.' We also respectfully acknowledge the years of work by Mary Leakey and her research team that recovered, curated, and initially identified the archaeological collection reported here along with the curatorial work of the late Jesuit Temba for initiating conservation efforts to salvage the material at the Olduvai Gorge research station. Finally, we would like to acknowledge the efforts of three anonymous reviewers, an associate editor, and David Alba for their comments, which served to greatly improve this manuscript.

Appendix A. Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2020.102885>.

Uncited references

Pé tillon, 2009, Tourloukis et al., 2018, Zutovski and Barkai, 2016.

References

- Anzidei, A.P., 2001. Tools from elephant bones at la Polledrara di Cecanibbio and Rebbia-Casal de'Pazzi. In: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M.R. (Eds.), *The World of Elephants. Proceedings of the First International Congress. Consiglio Nazionale Delle Ricerche, Rome*, pp. 415–418.
- Arroyo, A., de la Torre, I., 2018. Pounding tools in HWK EE and EF-HR (Olduvai Gorge, Tanzania): Percussive activities in the Oldowan-Acheulean transition. *J. Hum. Evol.* 120, 402–421.
- Backwell, L., d'Errico, F., 2008. Early hominid bone tools from Drimolen, South Africa. *J. Archaeol. Sci.* 35, 2880–2894.
- Backwell, L.R., d'Errico, F., 2001. Evidence of termite foraging by Swartkrans early hominids. *Proc. Natl. Acad. Sci. USA* 98, 1358–1363.
- Backwell, L., d'Errico, F., 2003. Additional evidence on the early hominid bone tools from Swartkrans with reference to spatial distribution of lithic and organic artefacts. *South Afr. J. Sci.* 99, 259–267.
- Backwell, L.R., d'Errico, F., 2004. The first use of bone tools: a reappraisal of the evidence from Olduvai Gorge. *Palaeontol. Afr.* 40, 95–158.
- Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Bibi, F., Pante, M., Souron, A., Stewart, K., Varela, S., Werdelin, L., Boisserie, J.-R., Fortelius, M., Hlusko, L., Njau, J., 2018. Paleoecology of the Serengeti during the Oldowan-Acheulean transition at Olduvai Gorge, Tanzania: The mammal and fish evidence. *J. Hum. Evol.* 120, 48–75.
- Biddittu, I., Celletti, P., 2001. Plio-Pleistocene Proboscidea and Lower Palaeolithic bone industry of Southern Latium (Italy). In: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M.R. (Eds.), *The World of Elephants. Proceedings of the First International Congress. Consiglio Nazionale Delle Ricerche, Rome*, pp. 91–96.
- Blasco, R., Rosell, J., Cuartero, F., Peris, J.F., Gopher, A., Barkai, R., 2013. Using bones to shape stones: MIS 9 bone retouchers at both edges of the Mediterranean Sea. *PLoS One* 8, e76780.
- Blumenschine, R.J., Marean, C., Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *J. Archaeol. Sci.* 23, 493–507.
- Blumenschine, R.J., Prassack, K.A., Kreger, C.D., Pante, M.C., 2007. Carnivore tooth-marks, microbial bioerosion, and the invalidation of test of Oldowan hominin scavenging behavior. *J. Hum. Evol.* 53, 420–426.
- Bouzouggar, A., Humphrey, L.T., Barton, N., Parfitt, S.A., Balzan, L.C., Schwenninger, J.-L., Hajraoui, M.A.E., Nespolet, R., Bello, S.M., 2018. 90,000 year-old specialised bone technology in the Aterian Middle Stone Age of North Africa. *PLoS One* 13, e0202021.
- Brain, C.K., 1981. *The Hunters or the Hunted?: An Introduction to African Cave Taphonomy*. University of Chicago Press, Chicago.
- Brain, C.K., Shipman, P., 1993. The Swartkrans bone tools. *A Cave's Chronicle of Early Man. Transvaal Museum, Pretoria*, 195–215.
- Bromage, T.G., 1984. Interpretation of scanning electron microscopic images of abraded forming bone surfaces. *Am. J. Phys. Anthropol.* 64, 161–178.
- Brühl, E., 2003. The small flint tool industry from Bilzingsleben-Steinrinne. In: Burdukiewicz, J., Ronen, A. (Eds.), *Lower Palaeolithic Small Tools in Europe and the Levant. British Archaeological Reports, Oxford*, pp. 49–64.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthropol.* 27, 431–452.
- Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *Am. Antiq.* 59, 724–748.
- d'Errico, F., 1993. La vie sociale de l'art mobilier paléolithique. Manipulation, transport, suspension des objets on os, bois de Cervidés, ivoire. *Oxf. J. Archaeol.* 12, 145–174.
- d'Errico, F., Backwell, L., 2009. Assessing the function of early hominid bone tools. *J. Archaeol. Sci.* 36, 1764–1773.
- d'Errico, F., Backwell, L.R., 2003. Possible evidence of bone tool shaping by Swartkrans early hominids. *J. Archaeol. Sci.* 30, 1559–1576.
- d'Errico, F., Backwell, L.R., Berger, L.R., 2001. Bone tool use in termite foraging by early hominids and its impact on our understanding of early hominid behaviour. *South Afr. J. Sci.* 97, 71–75.
- d'Errico, F., Backwell, L.R., Wadley, L., 2012. Identifying regional variability in Middle Stone Age bone technology: The case of Sibudu Cave. *J. Archaeol. Sci.* 39, 2479–2495.
- Dart, R., 1957. The Osteodontokeratic culture of Australopithecus prometheus: Discussion. *Transvaal Mus. Mem.* 10, 87–101.
- de la Torre, I., 2011. The Early Stone Age lithic assemblages of Gadeb (Ethiopia) and the Developed Oldowan/early Acheulean in East Africa. *J. Hum. Evol.* 60, 768–812.
- de la Torre, I., Albert, R.M., Arroyo, A., Macphail, R., McHenry, L.J., Mora, R., Njau, J.K., Pante, M.C., Rivera-Rondón, C.A., Rodríguez-Cintas, J., 2018. New excavations at the HWK EE site: Archaeology, paleoenvironment and site formation processes during late Oldowan times at Olduvai Gorge, Tanzania. *J. Hum. Evol.* 120, 140–202.
- de la Torre, I., Mora, R., 2018b. Technological behaviour in the early Acheulean of EF-HR (Olduvai Gorge, Tanzania). *J. Hum. Evol.* 120, 329–377.
- de la Torre, I., Mora, R., 2018a. Oldowan technological behaviour at HWK EE (Olduvai Gorge, Tanzania). *J. Hum. Evol.* 120, 236–273.
- Deino, A.L., 2012. ⁴⁰Ar/³⁹Ar dating of Bed I, Olduvai Gorge, Tanzania, and the chronology of early Pleistocene climate change. *J. Hum. Evol.* 63, 251–273.
- Deino, A.L., King, J., McHenry, L.J., Stanistreet, I.G., Stollhofen, H., Toth, N., Schick, K., Njau, J.K., in press. Chronostratigraphy and age modeling of Quaternary drill cores from the Olduvai Basin, Tanzania (Olduvai Gorge Coring Project). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*
- Dobosi, V., 2001. Ex proboscideis-proboscidean remains as raw material at four Palaeolithic sites, Hungary. In: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M.R. (Eds.), *The world of Elephants. Proceedings of the First International Congress. Consiglio Nazionale Delle Ricerche, Rome*, pp. 429–431.
- Echassoux, A., 2012. Comportements de subsistance et modifications osseuses à l'aube de l'Acheuléen à Konso, Éthiopie. *L'Anthropologie* 116, 291–320.
- Gümürkçü, M., Pante, M.C., 2018. Assessing the effects of fluvial abrasion on bone surface modifications using high-resolution 3-D scanning. *J. Archaeol. Sci.: Rep.* 21, 208–221.
- Hay, R.L., 1976. *Geology of the Olduvai Gorge: A Study of Sedimentation in a Semi-arid Basin*. University of California Press, Berkeley and Los Angeles.
- Haynes, G., 1993. *Mammoths, Mastodonts, and Elephants: Biology, Behavior and the Fossil Record*. Cambridge University Press, Cambridge.

- Henshilwood, C.S., D'errico, F., Marean, C.W., Milo, R.G., Yates, R., 2001. An early bone tool industry from the Middle Stone Age at Blombos Cave, South Africa: implications for the origins of modern human behaviour, symbolism and language. *J. Hum. Evol.* 41, 631–678.
- Herries, A.I.R., Martin, J.M., Leece, A.B., Adams, J.W., Boschian, G., Joannes-Boyau, R., Edwards, T.R., Mallett, T., Massey, J., Murszewski, A., Neubauer, S., Pickering, R., Strait, D.S., Armstrong, B.J., Baker, S., Caruana, M.V., Denham, T., Hellstrom, J., Moggi-Cecchi, J., Mokobane, S., Penzo-Kajewski, P., Rovinsky, D.S., Schwartz, G.T., Stammers, R.C., Wilson, C., Woodhead, J., Menter, C., 2020. Contemporaneity of Australopithecus, Paranthropus, and early Homo erectus in South Africa. *Science* 368, eaaw7293.
- Huang, W., Zhang, Z., Fu, R., Chen, B., Liu, J., Zhu, M., Wu, H., 1986. Bone artifacts and ornaments from Xiaogushan site of Haicheng, Liaoning Province. *Acta Anthropol. Sin.* 5, 259–266.
- Inizan, M.-L., Reduron-Ballinger, M., Roche, H., 1999. Technology and Terminology of Knapped Stone. CREP, Nanterre.
- Johnson, C.C., Njau, J.K., Damme, D.V., Schick, K., Toth, N., 2016. Paleoecologic significance of malacofauna, Olduvai Gorge, Tanzania. *Palaio* 31, 319–326.
- Klein, R.G., 1983. Anthropology: What do we know about neanderthals and Cro-Magnon man? *Am. Scholar* 52, 386–392.
- Klein, R.G., 1999. *The Human Career: Human Biological and Cultural Origins*. University of Chicago Press, Chicago.
- Kuman, K., Clarke, R.J., 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *J. Hum. Evol.* 38, 827–847.
- Leakey, M., Roe, D.A., 1994. Olduvai Gorge: Volume 5, Excavations in Beds III, IV and the Masek Beds. Cambridge University Press, Cambridge.
- Leakey, M.D., 1971. Olduvai Gorge: Volume 3, Excavations in Beds I and II, 1960–1963. Cambridge University Press, Cambridge.
- Leakey, M., 1994. Modified bones from Beds III and IV. In: Leakey, M., Roe, D. (Eds.), Olduvai Gorge: Volume 5, Excavations in Beds III, IV and the Masek Beds. Cambridge University Press, Cambridge, pp. 311–314.
- Mania, D., Mania, U., 2003. Bilzingsleben Homo erectus, his culture and his environment. The most important results of research. In: Burdukiewicz, J., Ronen, A. (Eds.), Lower Palaeolithic Small Tools in Europe and the Levant. British Archaeological Reports, Oxford, pp. 29–48.
- McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39, 453–563.
- McHenry, H.M., Brown, C.C., McHenry, L.J., 2007. Fossil hominin ulnae and the forelimb of Paranthropus. *Am. J. Phys. Anthropol.* 134, 209–218.
- McHenry, L.J., Stanistreet, I.G., 2018. Tephrochronology of Bed II, Olduvai Gorge, Tanzania, and placement of the Oldowan–Acheulean transition. *J. Hum. Evol.* 120, 7–18.
- Moigne, A.-M., Valensi, P., Auguste, P., Garcia-Solano, J., Tuffreau, A., Lamotte, A., Barroso, C., Moncel, M.-H., 2016. Bone retouchers from Lower Palaeolithic sites: Terra Amata, Orgnac 3, Cagny-l'Épinette and Cueva del Angel. *Quat. Int.* 409, 195–212.
- Njau, J.K., Blumenschine, R.J., 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. *J. Hum. Evol.* 50, 142–162.
- Njau, J.K., Blumenschine, R.J., 2012. Crocodylian and mammalian carnivore feeding traces on hominid fossils from FLK 22 and FLK NN 3, Plio-Pleistocene, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 63, 408–417.
- Njau, J.K., Herrmann, E.W., Ruck, L., Pante, M., Farrugia, P., Toth, N., Schick, K., Stollhofen, H., Stanistreet, I.G., 2020. Core stratigraphy constrains Bed IV archaeological record at HEB site, Olduvai Gorge, Tanzania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 552, 109773.
- Pante, M.C., 2010. The larger mammal fossil assemblages from Beds III and IV, Olduvai Gorge, Tanzania: Implications for the feeding behavior of Homo erectus. Ph.D. Dissertation Rutgers The State University of New Jersey-New Brunswick.
- Pante, M.C., 2013. The larger mammal fossil assemblage from JK2, Bed III, Olduvai Gorge, Tanzania: implications for the feeding behavior of Homo erectus. *J. Hum. Evol.* 64, 68–82.
- Pante, M.C., Blumenschine, R.J., 2010. Fluvial transport of bovid long bones fragmented by the feeding activities of hominins and carnivores. *J. Archaeol. Sci.* 37, 846–854.
- Pante, M.C., de la Torre, I., 2018. A hidden treasure of the Lower Pleistocene at Olduvai Gorge, Tanzania: the Leakey HWK EE assemblage. *J. Hum. Evol.* 120, 114–139.
- Pante, M.C., Njau, J.K., Hensley-Marschand, B., Keevil, T.L., Martín-Ramos, C., Peters, R.F., de la Torre, I., 2018. The carnivorous feeding behavior of early Homo at HWK EE, Bed II, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 120, 215–235.
- Prassack, K.A., Pante, M.C., Njau, J.K., de la Torre, I., 2018. The paleoecology of Pleistocene birds from Middle Bed II, at Olduvai Gorge, Tanzania, and the environmental context of the Oldowan–Acheulean transition. *J. Hum. Evol.* 120, 32–47.
- Pétillon, J.-M., 2009. What are these barbs for? Preliminary study on the function of the Upper Magdalenian barbed weapon tips. *P@lethnology* 1, 66–97.
- Proffitt, T., 2018. Is there a Developed Oldowan A at Olduvai Gorge? A diachronic analysis of the Oldowan in Bed I and Lower-Middle Bed II at Olduvai Gorge, Tanzania. *J. Hum. Evol.* 120, 92–113.
- Radmilli, A.M., Boschian, G., 1996. Gli Scavi a Castel di Guido: Il Più Antico Glacimento di Cacciatori del Paleolitico Inferiore nell'Agro Romano. Istituto Italiano di Preistoria e Protostoria, Firenze.
- Rivals, F., Uno, K.T., Bibi, F., Pante, M.C., Njau, J., de la Torre, I., 2018. Dietary traits of the ungulates from the HWK EE site at Olduvai Gorge (Tanzania): Diachronic changes and seasonality. *J. Hum. Evol.* 120, 203–214.
- Rabinovich, R., Ackermann, O., Aladjem, E., Barkai, R., Biton, R., Milevski, I., Solodenko, N., Marder, O., 2012. Elephants at the Middle Pleistocene Acheulean open-air site of Revadim Quarry, Israel. *Quat. Int.* 276–277, 183–197.
- Roberts, M.B., Parfitt, S.A., 1999. Boxgrove: A Middle Pleistocene Hominid Site at Eartham Quarry, Boxgrove, West Sussex. English Heritage, London.
- Rosell, J., Blasco, R., Campeny, G., Díez, J.C., Alcalde, R.A., Menéndez, L., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2011. Bone as a technological raw material at the Gran Dolina site (Sierra de Atapuerca, Burgos, Spain). *J. Hum. Evol.* 61, 125–131.
- Rosell, J., Blasco, R., Fernández Peris, J., Carbonell, E., Barkai, R., Gopher, A., 2015. Recycling bones in the Middle Pleistocene: Some reflections from Gran Dolina TD10-1 (Spain), Bolomor Cave (Spain) and Qesem Cave (Israel). *Quat. Int.* 361, 297–312.
- Sano, K., Beyene, Y., Katoh, S., Koyabu, D., Endo, H., Sasaki, T., Asfaw, B., Suwa, G., 2020. A 1.4-million-year-old bone handaxe from Konso, Ethiopia, shows advanced tool technology in the early Acheulean. *Proc. Natl. Acad. Sci. USA* <https://doi.org/10.1073/pnas.2006370117>.
- Shipman, P., 1989. Altered bones from Olduvai Gorge, Tanzania: Techniques, problems, and implications of their recognition. In: Bonnicksen, R., Sorg, M. (Eds.), Bone Modification. Center for the Study of the First Americans, Orono, pp. 247–258.
- Shipman, P., Rose, J.J., 1988. Bone tools: an experimental approach. In: Oslen, S. (Ed.), Scanning Electron Microscopy in Archaeology. British Archaeological Reports, Oxford, pp. 303–335.
- Stammers, R.C., Caruana, M.V., Herries, A.I.R., 2018. The first bone tools from Kromdraai and stone tools from Drimolen, and the place of bone tools in the South African Earlier Stone Age. *Quat. Int.* 495, 87–101.
- Stanistreet, I.G., 2012. Fine resolution of early hominin time, Beds I and II, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 63, 300–308.
- Stanistreet, I.G., McHenry, L.J., Stollhofen, H., de la Torre, I., 2018. Bed II Sequence Stratigraphic context of EF-HR and HWK EE archaeological sites, and the Oldowan/Acheulean succession at Olduvai Gorge, Tanzania. *J. Hum. Evol.* 120, 19–31.
- Stanistreet, I.G., Stollhofen, H., Deino, A.L., McHenry, L.J., Toth, N.P., Schick, K.A., Njau, J.K., 2020. New Olduvai Basin stratigraphy and stratigraphic concepts revealed by OGCP cores into the Palaeolake Olduvai depocentre, Tanzania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 554, 109751.
- Szmidt, C., Pétillon, J.-M., Cattelain, P., Normand, C., Schwab, C., 2009. Premières dates radiocarbones pour le Magdalénien d'Isturitz (Pyrénées Atlantiques). *Bull. la Société Préhistorique Française* 106, 588–592.
- Tisnerat-Laborde, N., Valladas, H., Ladier, E., 1997. Nouvelles datations carbone 14 en SMA pour le Magdalénien supérieur de la vallée de l'Aveyron. *Préhist. Ariégeoise* 52, 129–136.
- Tourloukis, V., Thompson, N., Panagopoulou, E., Giusti, D., Konidaris, G.E., Karkanas, P., Harvati, K., 2018. Lithic artifacts and bone tools from the Lower Palaeolithic site Marathousa 1, Megalopolis, Greece: Preliminary results. *Quat. Int.* 497, 47–64.
- Uno, K.T., Rivals, F., Bibi, F., Pante, M., Njau, J., de la Torre, I., 2018. Large mammal diets and paleoecology across the Oldowan–Acheulean transition at Olduvai Gorge, Tanzania from stable isotope and tooth wear analyses. *J. Hum. Evol.* 120, 76–91.
- Van Kolfschoten, T., Parfitt, S.A., Serangeli, J., Bello, S.M., 2015. Lower Paleolithic bone tools from the 'Spear Horizon' at Schöningen (Germany). *J. Hum. Evol.* 89, 226–263.
- Villa, P., Bartram, L., 1996. Flaked bone from a hyena den. *Paléo* 8, 143–159.
- Villa, P., d'Errico, F., 2001. Bone and ivory points in the Lower and Middle Paleolithic of Europe. *J. Hum. Evol.* 41, 69–112.
- Yellen, J.E., 1998. Barbed bone points: tradition and continuity in Saharan and Sub-Saharan Africa. *Afr. Archaeol. Rev.* 15, 173–198.
- Yellen, J.E., Brooks, A.S., Cornelissen, E., Mehlman, M.J., Stewart, K., 1995. A Middle Stone Age worked bone industry from Katanda, Upper Semliki Valley, Zaire. *Science* 268, 553–556.
- Zhang, S., d'Errico, F., Backwell, L.R., Zhang, Y., Chen, F., Gao, X., 2016. Ma'anshan cave and the origin of bone tool technology in China. *J. Archaeol. Sci.* 65, 57–69.
- Zhang, Y., Stiner, M.C., Dennell, R., Wang, C., Zhang, S., Gao, X., 2010. Zooarchaeological perspectives on the Chinese Early and Late Paleolithic from the Ma'anshan site (Guizhou, South China). *J. Archaeol. Sci.* 37, 2066–2077.

Zutovski, K., Barkai, R., 2016. The use of elephant bones for making Acheulian handaxes: A fresh look at old bones. *Quat. Int.* 406, 227–238.

UNCORRECTED PROOF