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The First Million Years of Technology: The Lomekwian and the Early Oldowan

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Abstract

During the course of human evolution, lithic technology became a critical element of hominin foraging ecology and a contributor to feedback loops selecting for increasingly sophisticated tool use, cognition, and language. Here we review the first million years of technology, from 3.3 million years ago (Ma) to 2.3 Ma. This time interval includes the two oldest archaeological industries (the Lomekwian and the early Oldowan) known exclusively from Africa, which collectively overlap with four genera of hominins (human relatives and ancestors). These Early Stone Age (ESA) industries focused on the production and use of sharp edges for cutting, as well as the use of larger, sometimes unworked stones for pounding. We review our current understanding of these technologies, where they were found, how they were made, what they were used for, and the hominins that could have produced them, and consider them in the context of nonhuman primate archaeology.

INTRODUCTION

We consider tools to be objects that can modify other materials, organisms, or the user of the tool and can help insulate organisms from environmental stresses (Beck 1980, McGrew 1992, Shea 2017). Humans are a technologically dependent species, and our lives are guided and facilitated by the types of tools we use. Nonhuman primate tool users frequently make tools from nonlithic materials, and it is highly likely that hominin tool users made tools from perishable materials as well. However, because of preservation biases, the record of the oldest industries is based exclusively on stone tools, the origins, uses, and adaptive significance of which are poorly understood.

The oldest stone tool industry, termed the Lomekwian, comes from the site of Lomekwi 3 (LOM3) in West Turkana, Kenya, dated to 3.3 million years ago (Ma) (Harmand et al. 2015, Lewis & Harmand 2016) (**Figure 1**). The controversy over the in situ context of the lithic assemblage after its initial publication (Domínguez-Rodrigo & Alcalá 2016, 2019) has been addressed (Harmand et al. 2019), and excavations between 2014 and 2024 extended the excavation footprint, increasing the composition of the Lomekwian industry by more than 250 artifacts (S. Harmand, X. Boës, N. Taylor, V. Arrighi, S. Prat, et al., manuscript in preparation).

The Oldowan industry first appears in eastern Africa 2.9–2.6 Ma (Plummer et al. 2023) and by 2.4 Ma is found as far north as modern-day Algeria. Both industries created effective stone tools to process a variety of materials but are clearly distinguished from each other by artifact size and methods of flake production.

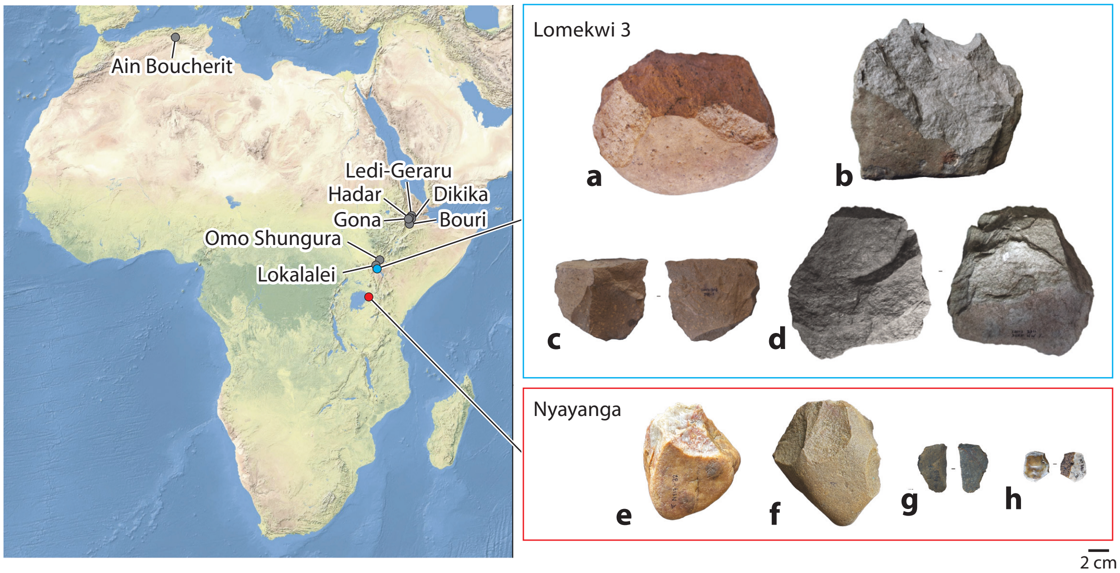

Figure 1

A map showing the potential archaeological localities that date between 3.3 Ma and 2.3 Ma (*left*) and photographs of selected cores and flakes from Lomekwi 3 and Nyayanga, Kenya (*right*). (*a*) Lomekwian core LOM3-2012-H18-1, (*b*) Lomekwian core LOM3-2011-I16-3, (*c*) Lomekwian flake LOM3-2012-J17-3, (*d*) Lomekwian flake LOM3-2011 surf NW7, (*e*) Oldowan core NY17-32, (*f*) Oldowan core NY15-134, (*g*) Oldowan flake Exc3-1413, (*h*) Oldowan flake Exc3-281. Basemap of Africa image is the intellectual property of Esri and is used herein under license (**https://services.arcgisonline.com/arcgis/rest/services/USA_Topo_Maps/MapServer/0**). Copyright © 2013 National Geographic Society, i-cubed. All rights reserved. Artifact figures provided by (*a–d*) Sonia Harmand, (*e,f*) James S. Oliver, and (*g,h*) Emma Finestone.

CONTEXT AND CHARACTERISTICS OF THE LOMEKWIAN INDUSTRY

The Lomekwian core-and-flake technology exhibits the earliest evidence of intentional hard-hammer percussion, where one stone was struck against another to fracture pieces off of it. These detached pieces include sharp-edged flakes and angular fragments, while the stone that was flaked is called a flaked piece or core. The stones used to percuss other stones to initiate fracture are called hammerstones, while large stationary blocks of stone used as flat bases for tool manufacture or food processing are called anvils.

The focus of Lomekwian technological practices was the production of sharp-edged tools (Harmand et al. 2015). Flakes and other products of hard-hammer percussion could be used for cutting, like a knife today, whereas cores or unmodified stones such as hammerstones and anvils could be used for pounding. The lithic assemblage includes large and heavy cores (average of 3.1 kg, maximum dimension >25 cm), flakes and flake fragments, and hammerstones and large anvils (up to 15 kg) from locally selected lava rocks. Flakes were produced using two relatively simple percussive techniques: the passive hammer technique, in which the core is held in both hands and struck downward onto a stationary block on the ground to fracture off flakes, with both arms performing the same motion; and the bipolar technique, in which one hand stabilizes the core on an anvil and the other hand strikes the hammer down vertically onto the core. Most cores were flaked in one direction from one striking platform onto one single surface (**Figure 1**). Flaking often resulted in several superimposed and contiguous unidirectional removals along a longer part of the perimeter of the core. A few specimens show flaking of a single face from multiple directions (multidirectional removals), whereas others show flaking along an axis from two opposing sides (bifacial flaking) (Harmand et al. 2015).

Conglomerates with a wide range of cobble and block sizes were found within a few hundred meters of LOM3. Hominins consistently selected the larger clasts of higher-quality stone (mainly basalt, phonolite, and trachy-phonolite) for artifact manufacture (Harmand et al. 2015). Specific rock shapes were chosen for different modes of flake production. The blocks selected for bipolar reduction have naturally acute angles and are thicker and more quadrangular in shape than are the cores selected for passive hammering (Harmand et al. 2015). Unifacial passive hammer cores tend to be exploited on flatter blocks with naturally obtuse angles. Although numerous hinge and step fracture terminations on cores document significant knapping accidents during flaking, more invasive and feather-terminating flakes were also often successfully removed.

Flake production in the Lomekwian may have been part of a dietary adaptation to a broad C3 (e.g., bush, shrub, trees) to C4 (e.g., grasses using C4 photosynthetic pathway) feeding niche (Quinn et al. 2021). Fossil specimens, including identifiable fragments of large mammal bones and teeth, were collected in situ at LOM3 and on the surface around the site. While stone tool–modified bones have yet to be found associated with Lomekwian artifacts, linear marks on roughly coeval (3.39 Ma) surface fossils from Dikika, Ethiopia, may have been produced by hominins cutting meat off of bones using stone tools (McPherron et al. 2010, 2011; though see Domínguez-Rodrigo et al. 2010, 2012; Pante 2019; and Sahle et al. 2017 for nonbutchery interpretations of mark formation). The taxonomic composition of the fauna from LOM3 suggests that there were tree-rich habitats nearby, probably riverine forest with wooded savanna (Harmand et al. 2015). Stable carbon isotopic analysis of soil carbonates suggests that Lomekwian knappers were active in a woodland/bushland/thicket/shrubland environment (Quinn et al. 2021). The isotope results are comparable to those from other East African hominin sites between 3.4 Ma and 3.2 Ma but woodier than the early Oldowan sites at Gona, Ethiopia, at 2.6 Ma and Nyayanga at ca. 2.9 Ma (Harmand et al. 2015, Plummer et al. 2023). Furthermore, recent paleoecological reconstructions show that significant freshwater resources existed for LOM3 hominins, altering current hypotheses on the role played by aridity and environmental stress in the development of early technology and the emergence of our genus (Boës et al. 2024). The Lomekwian thus represents a technological system where large blocks from local conglomerates were transported a short distance to be used in pounding and cutting activities in a well-shaded area in proximity to fresh water. Faunal remains found in spatial association with artifacts may have been transported there for processing, although this conclusion awaits detailed taphonomic analysis. The size and weight of many of the tools limited their transportability, though hominins could have carried flakes off-site for use. At this point, LOM3 is the only excavated Lomekwian site, but surface finds of Lomekwian tools from erosional surfaces indicate that additional sites with in situ artifacts exist in the vicinity.

CONTEXT AND CHARACTERISTICS OF THE EARLY OLDOWAN INDUSTRY (Ca. 2.9–2.3 MA)

The Oldowan industry appears possibly as early as 2.9 Ma (Plummer et al. 2023) but definitely by 2.6 Ma (Braun et al. 2019, Semaw 2000) in eastern Africa. Oldowan artifact production was usually carried out with smaller stones than those used during the Lomekwian (**Figure 1**), using a method termed handheld percussion. One stone, often a rounded hammerstone, was held in the dominant hand and used to hit another stone held in a fixed position in the opposite hand in order to flake it. Bipolar percussion using a hammer and anvil was also important at some sites. Here we focus on the earliest Oldowan sites (2.9–2.3 Ma) for our comparison with the Lomekwian. Early Oldowan sites are known over a far larger geographic area than are Lomekwian sites, but that greater range reflects discoveries published in just the last 10 years, showing that sampling error has a major impact on our understanding of the timing and geographic distribution of ESA sites. In eastern Africa, localities include Nyayanga (3.032–2.581 Ma; favored age of ca. 2.9 Ma) and Lokalalei (2.34 Ma) in Kenya, and Ledi-Geraru (2.61–2.58 Ma), Gona (2.58–2.3 Ma), Hadar (2.36 Ma), and the Omo Shungura Formation (2.34–2.3 Ma) in Ethiopia; and in North Africa, they include Ain Boucherit (2.4 Ma) in Algeria (Plummer & Finestone 2018, Sahnouni et al. 2018). Possible Oldowan artifacts from the Zarqa Valley, Jordan (Parenti et al. 2024), may fall within this time interval but need further documentation.

Oldowan assemblages can vary in core form and the frequency of different artifact types defined by Leakey (1971) (e.g., the iconic chopper is a cobble flaked unifacially or bifacially along a single axis). However, artifact form is strongly influenced by the size, shape, and flaking characteristics of the clasts of available raw material and the duration of flaking (Potts 1991, Toth 1985). For example, the small quartz pebbles flaked using handheld and bipolar percussion at the ca. 2.3 Ma Shungura Formation Member F sites in Ethiopia produced assemblages dominated by angular fragments, whole flakes, and flake fragments (de la Torre 2004), whereas at the coeval locality of Lokalalei 2C in West Turkana, Kenya, blocks and cobbles of volcanic rocks (mainly basalt and phonolite) were reduced exclusively through handheld percussion, producing an assemblage of generally larger-sized artifacts, including whole and broken cores, flakes, and hammerstones. The assemblages look very different, but much of the distinction between them is explained by the characteristics of the raw material being reduced and how flaking was carried out. Many researchers propose that there was uniform knapping competency through the roughly one-million-year time span (ca. 2.6 Ma–1.7 Ma) of the Oldowan (Finestone et al. 2024; Hovers 2009; Ludwig & Harris 1998; Semaw 2000; Semaw et al. 1997, 2003). The primary exception to this view is Lokalalei 1, which has a small lithic assemblage with a high frequency of step fractures, small flakes, and impact damage on cores from repeated percussion that failed to remove flakes (Delagnes & Roche 2005, Harmand 2009, Kibunjia 1994).

Early Oldowan sites exhibit variable degrees of raw material selectivity, from relatively low to more complex (Goldman-Neuman & Hovers 2012, Harmand 2009, Stout et al. 2005). What this selectivity variability, ranging from simply choosing cobbles with relatively homogeneous groundmass (e.g., A.L. 894 at Hadar, Ethiopia) to choosing specific raw materials and specific cobble shapes (e.g., Lokalalei 2C), represents is unclear. Some suggest that it reflects differing levels of cognitive sophistication or technical skills between different groups (or species) of hominins (e.g., Delagnes & Roche 2005, Harmand 2009), as it is likely that more than one hominin utilized Oldowan tools (see below). Going back to the Lokalalei 1 example, the high frequency of flaking mistakes may reflect the selection of rounded cobbles without the natural angles used elsewhere as platforms to initiate fracture (Harmand 2009). This lack of foresight restricted the reduction strategies that the hominins could deploy. Comparison of the Lokalalei 1 reduction strategies with the "organized" (sensu Delagnes & Roche 2005) reduction of the Lokalalei 2C cores, which were selected for their natural angles and sequentially flaked, provides one of the strongest contrasts in reduction strategies around 2.3 Ma.

Analysis of artifact raw material composition coupled with the degree of core reduction and the relative frequency of flakes struck from cores at different reduction stages indicates that there was a dynamic flow of lithic material both into and out of Oldowan archaeological sites (Isaac 1984, Potts 1988, Semaw 2006, Toth 1987). Moreover, sites with particularly dense accumulations of artifacts were likely located in resource-rich places through which hominins recurrently foraged, leading to an accretion of archaeological materials over time (Plummer 2004, Shick 1987). These assemblages in turn could be used as secondary raw material sources (Potts 1984), enhancing hominin access to resources requiring tool use (Reeves et al. 2021, 2023).

All early Oldowan sites were formed near a stream or river, where overbank deposits sealed the archaeological levels, within or in proximity to riparian woodlands or riparian woodland/grassland ecotones (Plummer & Finestone 2018, Quade et al. 2004, Rogers & Semaw 2009). These occurred in the broader eastern African context of heterogeneous woodlands/bushlands and wooded grassland mosaics with seasonal rainfall that existed during most of the last 7 Ma (Negash et al. 2024), though the vegetation mosaics that most Oldowan sites were situated in likely had a higher proportion of C4 vegetation than did LOM3 (Harmand et al. 2015, Plummer et al. 2023, Quade et al. 2004). The large mammal communities in eastern Africa, of which the hominins forming the Lomekwian and the early Oldowan were a part, were almost certainly structured differently than modern African mammalian communities, due largely to a greater richness of nonruminants and megaherbivore (>1,000 kg) species (Faith et al. 2019). Given the disproportionate ecological impacts of large-bodied herbivores on factors such as vegetation structure, hydrology, and fire regimes, it follows that the Lomekwian and early Oldowan activities may have been carried out within ecosystems that were not that different from each other but were functionally different from modern ones. The well-watered habitat mosaics in which these early archaeological sites were found would have provided hominins with a variety of foraging opportunities (Su 2024).

Oldowan tools were used to cut, scrape, and pound materials, as evidenced by the abundance of sharp-edged flakes, angular fragments, and pounding tools discarded at archaeological sites (Plummer & Finestone 2018, Rogers & Semaw 2009). Cut marks and percussion damage on associated fauna provide direct documentation of butchery activities at three localities (Nyayanga, Gona, and Ain Boucherit), and artifact use-wear traces at Nyayanga indicate animal processing as well as the processing of underground storage organs (USOs) and other plants (Cáceres et al. 2017, 2023; Plummer et al. 2023).

At Nyayanga, hominins butchered two megafaunal (hippopotamid) carcasses excavated in association with artifacts at the ca. 2.9 Ma excavations 3 and 5, as well as individual small and medium bovid bones recovered both in situ and from the surface (Plummer et al. 2023). Similarly, the ca.

2.6 Ma sites at Gona, Ethiopia, have yielded a small sample of surface bovid and equid bones with cut mark locations suggesting skinning and defleshing, as well as bone breakage for marrow acquisition (Cáceres et al. 2017, Domínguez-Rodrigo et al. 2005). DAN2, the Gona Oldowan site with the best-preserved fauna, is somewhere between 2.4 and 2.0 million years old. Eighteen surface-collected small- and medium-sized antelope fossils have cut mark locations suggesting skinning, defleshing, and evisceration of fleshy carcasses. Four bones with percussion marks indicate that marrow was being consumed as well. The 2.4 Ma Ain Boucherit bone assemblage in Algeria provides an in situ sample of small- and medium-sized bovid fossils associated with artifacts. Skeletal part representation and butchery damage suggest that hominins had early access to relatively complete carcasses, and skinned, eviscerated, defleshed, and demarrowed them, and it is likely that these carcasses were transported at least short distances to the site locale (Cáceres et al. 2023). Carnivore damage frequencies are low in all these assemblages. Together, these findings hint that early toolmakers did have access to flesh and marrow from carcasses ranging from small antelopes to megafauna and that competition with carnivores was not necessarily intense or at least not always intense. However, the overall frequency of meat eating (here, referring to all soft tissue within the body, e.g., muscle, viscera, brains, and marrow) and relative importance of large mammal flesh in the diet of hominins making Oldowan tools remain unclear. What seems certain is that animal tissue made a more substantial contribution to their diet than the ~5% annual caloric intake that animal tissue contributes in some chimpanzee populations (Stanford 1996).

THE LOMEKWIAN AND OLDOWAN WITHIN THE CONTEXT OF NONHUMAN PRIMATE ARCHAEOLOGY

Over the past 50 years, primatologists have been documenting the use of technology by nonhuman primates at the same time that archaeologists have been studying ESA sites. Cross-pollination between these research streams is becoming increasingly common, allowing researchers to assess similarities and define unique attributes in the primate and hominin archaeological records (see review in Harmand & Arroyo 2023). The study of nonhuman primate technological usage provides a phylogenetically broader window for thinking about ESA hominin behavior and can help generate scenarios for the origin(s) of hominin lithic technology.

The most common use of stone by nonhuman primates is for pounding, the action of striking one object against another to modify or fragment it (Harmand & Arroyo 2023). Primate taxa that use stone to pound open encased foods include West African chimpanzees (*Pan troglodytes verus*; e.g., Boesch & Boesch-Achermann 2000), capuchin monkeys (*Sapajus libidinosus*, *Cebus capucinus*; e.g., Visalberghi et al. 2009), and long-tailed macaques (*Macaca fascicularis*; e.g., Proffitt et al. 2023).

Capuchin monkeys use stone tools (including hammers and anvils) to process foods (e.g., nuts, seeds, fruit), to dig holes, and to pound other stones to produce dust that they consume (Falótico et al. 2017, Falótico & Ottoni 2016). This latter behavior can unintentionally generate stone flakes resembling flakes produced in ESA industries (Proffitt et al. 2016). Long-tailed macaques in Thailand use stones to access gastropod flesh and to crack nuts (Proffitt et al. 2023). Their nut-cracking can also unintentionally produce flakes morphologically similar to those produced in the Oldowan, but in both this and the capuchin cases these flakes are not utilized for any tasks.

Chimpanzees have a rich repertoire of pounding behaviors that can be classified predominantly as hammer and anvil and passive hammer (Harmand & Arroyo 2023). Hammer-and-anvil percussion is used by some (mostly western African) chimpanzee communities living in forested areas to process nuts. It is a bimanual activity, as one hand is used to place the nut on an anvil and the other hand holds the hammerstone that strikes the nut, and then the first hand is used to retrieve the nut meat to eat it. This process can also unintentionally fracture stone, though generally the flakes produced are not similar to the conchoidally fractured stones of Lomekwian and Oldowan flaking (Harmand & Arroyo 2023). Passive hammer percussion is used by chimpanzee communities over the entire geographic range of the species, in habitats ranging from forest to wooded savanna. The processed food (usually fruits but occasionally animals such as snails or tortoises) is held in one hand and struck against a passive hammer (a fixed root, branch, or stone) to fracture or crush it. Primate studies demonstrate that pounding behaviors are important for processing a variety of foods but particularly fruit and nuts and that they are widespread in *P. troglodytes*, one of our closest living relatives. This finding may suggest that hammer-and-anvil and passive hammer processing of food was a shared trait derived from the last common ancestor between humans and chimpanzees (Panger et al. 2002). Even if that were not the case, the parallel development of stone-assisted food processing in multiple nonhuman primate lineages indicates that it is a recurrent evolutionary strategy to access encased food (Harmand & Arroyo 2023).

How nonhuman primates use stone tools and how their material culture was distributed across the landscape provide important reference points for considering reconstructions of stone age lifeways (Haslam et al. 2009, Reeves et al. 2023). Some western African chimpanzee populations form sites by moving hammers and/or anvils underneath trees that produce nuts ready to be processed and consumed. Artifacts, artifact fragments, and discarded nut shells accumulate there and can ultimately form archaeological accumulations (e.g., Mercader et al. 2002, 2007), though useful stone tools such as hammerstones may be transported to the next spot they are needed for processing activities. It is this cumulative short-distance movement of hammerstones from one nut-processing spot to another that can distribute chimpanzee pounding tools up to 2 km away from their source (Luncz et al. 2016). Some short-distance transport of hominin artifacts likely occurred this way as well (Reeves et al. 2024). However, the shorter use-life of cores compared with primate percussive tools, as well as differences in the environmental context of ESA sites compared with chimpanzee habitats, limits the explanatory power of a chimpanzee transport analogy for the Oldowan (Reeves et al. 2021, 2023). Nonetheless, ESA hominin foraging across landscapes would have been similarly influenced by the locations of predictable food sources (such as seasonally fruiting trees or patches of USOs), raw materials for tools, sleeping sites, potable water, and ephemeral resources such as animal carcasses (Almeida-Warren et al. 2022).

Experiments with nut-cracking chimpanzees in Bossou, Guinea, indicate that chimpanzee raw material preferences can be as refined as those exhibited by Oldowan hominins, with selectivity focused on finding hammers and anvils of the right size and hardness (harder stone for hammers, softer stone for anvils) for the pounding tasks being carried out (Braun et al. 2025). While the transport dynamics of Oldowan sites 2 Ma and younger are likely more sophisticated than those of chimpanzees (Reeves et al. 2024, Toth & Schick 2009), more work needs to be done to document the movement of stone into and out of the oldest Oldowan assemblages.

The focus on flake (cutting edge) production for use in processing tasks is a fundamental distinction between nonhuman primate technologies and ESA technological systems. Lithic selectivity in both the Lomekwian and the Oldowan reflects this concern with a frequent focus on raw materials that were hard, flaked well, and had clast shapes facilitating flake initiation (Harmand et al. 2015, Plummer & Finestone 2018). The flaking strategy at LOM3 required the careful selection of blocks, a mental representation of the objective (sharp flakes), and an appropriate grip and movement for the specific raw materials being utilized (Lewis & Harmand 2016). The passive hammer and especially the bipolar approaches to Lomekwian flake production are likely cognitively more sophisticated than the mental processes in chimpanzee nut-cracking today (Harmand & Arroyo 2023, Lombard et al. 2019). Oldowan handheld stone knapping was even more sophisticated, requiring improved bimanual dexterity, perception, and learning abilities relative to nut-cracking by nonhuman primates (Bril et al. 2015).

Artifact usage at LOM3 is still under investigation, so the range of processing tasks carried out there is unclear. Even at the oldest Oldowan sites, pounding and cutting tools were used to process animal carcasses and plant foods and to work wood (Cáceres et al. 2017, 2023; Plummer et al. 2023). At many occurrences, one can infer that at least some materials were transported to the site locale for processing, highlighting an important distinction between nonhuman primate and Oldowan site formation. Nonhuman primate accumulations form where stone tools are transported to an area with resources to be processed. Oldowan site formation included the transport of both stone tools and food to particular points on the landscape. This dual transport strategy is one of the hallmarks of Oldowan landscape usage (Potts 1991).

POTENTIAL MANUFACTURERS OF STONE TOOLS 3.3–2.3 Ma

The Oldowan tools first discovered in Bed I at Olduvai Gorge, Tanzania, were initially credited to the robust OH 5 cranium found nearby, at the time known as "Zinjanthropus" (now *Paranthropus boisei*; L.S.B. Leakey 1959). However, just a year later, the discovery of another hominin at Olduvai Gorge—one with smaller teeth, a slightly larger brain, and hand morphology suggesting manual dexterity—challenged the idea that OH 5 was the toolmaker (L.S.B. Leakey 1960, L.S.B. Leakey et al. 1964, M.D. Leakey 1966, Napier 1962). This new fossil, OH 7, became the type specimen for *Homo habilis*, named "handy man" for its presumed toolmaking capabilities (L.S.B. Leakey et al. 1964, Tobias 1965). Although hominins belonging to the genus *Homo* were certainly skilled stone toolmakers, whether they were the earliest or sole manufacturers of lithic technology remains uncertain. Recent findings suggest that other hominins also engaged with stone tools, particularly at the earliest archaeological sites.

The artifacts from Lomekwi 3 in Kenya predate the appearance of the genus *Homo* in the fossil record by nearly 500,000 years (Harmand et al. 2015, Villmoare et al. 2015) and by almost 1 Ma in West Turkana (Prat 2023, Prat et al. 2005). In addition, Oldowan tools were found alongside fossilized molars of *Paranthropus* sp. at Nyayanga, Kenya (Plummer et al. 2023), making *Paranthropus* the first hominin genus found in direct association with stone tools. The complexity of the hominin fossil record, coupled with the long duration of the Oldowan, suggests that tool behaviors were not restricted to a single genus. Instead, multiple taxa likely contributed to the development and use of stone tools over time (Finestone 2025, Hammond & Mongle 2023, Panger et al. 2002, Plummer 2004, Prat 2023, Susman 1991, Wood 1997).

The earliest species within the genus *Australopithecus*, *Australopithecus anamensis* (M.G. Leakey et al. 1995) and *Australopithecus bahrelghazali* (Brunet et al. 1996), predate the appearance of stone tools in the archaeological record. However, *Australopithecus afarensis* (Johanson et al. 1978), *Australopithecus deyiremeda* (Haile-Selassie et al. 2015), and *Kenyanthropus platyops* (M.G. Leakey et al. 2001) overlap temporally with the Lomekwian industry. *Au. deyiremeda* is found only in the Afar region in Ethiopia, more than 1,000 km away from the Lomekwian tools. *Au. afarensis* is distributed widely through eastern Africa, including in the Turkana Basin. *K. platyops* (M.G. Leakey et al. 2001) is known exclusively from the West Turkana study area, making it perhaps the most plausible candidate for Lomekwian toolmaker. The LOM3 finds occur in the same geographic and chronological range as the paratype of *K. platyops* (KNM-WT 38350) (M.G. Leakey et al. 2001), other hominin fossils generally referred to as *K. platyops* (Wood & Leakey 2011), and one unpublished hominin tooth (KNM-WT 64060) found by the West Turkana Archaeological Project in 2012.

Fossils attributed to *Australopithecus garhi* (Asfaw et al. 1999) have been found near fauna from the 2.5 Ma Bouri Formation, Ethiopia, with putative stone tool damage (de Heinzelin et al. 1999). However, these marks have been reassessed as crocodile tooth marks (Pante 2019, Sahle et al.

2017), casting doubt on *Au. garhi*'s status as a stone tool user. In eastern Africa, the *Paranthropus* genus is represented by *Paranthropus aethiopicus* (∼2.7–2.3 Ma) and *P. boisei* (∼2.3–1.3 Ma). *Paranthropus* spp. are characterized by robust jaws and chewing muscles and the largest postcanine teeth of any primate. It is often assumed that their powerful masticatory apparatus signified an emphasis on within-mouth food processing rather than extraoral preparation of food with stone tools (e.g., Plummer 2004). However, the tooth morphology of *P. boisei* appears unsuited for processing many food items (e.g., tropical grasses and sedges; see Sponheimer et al. 2023) thought likely to have been important to their diet (Cerling et al. 2011, 2013; Sponheimer et al. 2013; Ungar et al. 2008; Van der Merwe et al. 2008). Opportunistic stone tool–assisted foraging may have allowed some members of *Paranthropus* to access food resources that they were otherwise anatomically ill-equipped to process (Finestone 2025).

Members of the genus *Paranthropus* are frequently found at Oldowan sites (Finestone 2025, Prat 2023). At Nyayanga, a *Paranthropus* sp. molar was found in situ with 42 Oldowan tools and a butchered hippopotamid carcass (Plummer et al. 2023). The same geological bed has yielded another *Paranthropus* sp. molar as well as hundreds of stone tools. Notably, remains of early *Homo* have not been found on the Homa Peninsula, and the nearest fossil attributed to *Homo* of comparable age to the Nyayanga tools (2.6 Ma and older) is located ∼1,300 km away in Ethiopia's Afar Triangle (Villmoare et al. 2015). Elsewhere in eastern Africa, both *Homo* and *Paranthropus* were regionally present in areas yielding significant Oldowan tool assemblages, including West Turkana, Kenya (Prat et al. 2003, 2005; Roche et al. 2003; Walker & Leakey 1988; Wood & Constantino 2007), Koobi Fora, Kenya (M.G. Leakey et al. 2012, Wood 1991, Wood & Leakey 2011), and the Lower Omo Valley of Ethiopia (Alemseged 2003, Alemseged et al. 2002, Howell et al. 1987, Suwa et al. 1996). It is also notable for this discussion that at sites closer to 2 Ma in eastern and southern Africa, including Olduvai Gorge, Tanzania, Koobi Fora, Kenya, and in the Cradle of Humankind in South Africa, there are frequent associations between *Paranthropus* and Oldowan tools (Finestone 2025; Susman 1988, 1991, 1998).

Hominins belonging to the genus *Homo* are widely recognized as definitive tool users and remain the only hominins with a geographic distribution extensive enough to encompass the entire range of the Oldowan. While other genera may have manufactured stone tools, *Homo* clearly relied on and refined lithic technology on an unparalleled scale, demonstrating sustained and habitual tool use over time and across diverse environments. Given their higher degree of encephalization relative to *Australopithecus* and *Paranthropus*, it is possible that all species within the genus *Homo* used stone tools. Between 2.8 and 1.7 Ma, several species of *Homo* are documented in the fossil record. The earliest fossils attributed to *Homo* have not been assigned to a specific species (Villmoare et al. 2015; see Schwartz & Tattersall 2015 for challenges in defining the genus *Homo*). After 2 Ma, there is evidence for several distinct species: *H. habilis* (L.S.B. Leakey et al. 1964), *Homo rudolfensis* (M.G. Leakey et al. 2012), and the larger-bodied *Homo erectus* (Mayr 1950; or *Homo ergaster* to some; Antón 2003, Rose 1984, Wood 1992).

The emergence of the genus *Homo* in the fossil record corresponds temporally and geographically with regional appearances of Oldowan tools. Some of the earliest known Oldowan tools come from the Ledi-Geraru research area in Ethiopia, where the oldest fossil assigned to the genus *Homo* (LD 350-1) was also found (Braun et al. 2019, Villmoare et al. 2015). The first artifacts in West Turkana, Kenya, and Hadar, Ethiopia, roughly coincide with the regional appearances of early *Homo* (Kimbel et al. 1996, Prat et al. 2005). There are no hominin fossils in North Africa as old as Ain Boucherit in Algeria; however, at 2.4 Ma, the most likely toolmaker was *Homo*, given that lithic assemblages north of the Omo-Turkana Basin are exclusively linked to the genus *Homo* (Gabunia et al. 2001; Kimbel et al. 1996, 1997; Mussi et al. 2023; Semaw et al. 2020; Zanolli et al. 2017).

DISCUSSION

Humans are obligatory tool users; our survival is dependent on tool use. Obligatory tool use is uniquely human among primates (Shea 2017). More often, tool use in animals is occasional, where the fitness benefit accrued using tools is not substantial, or habitual, where tool use is carried out in stereotypical ways at variable times with varying fitness consequences. Nonhuman primate stone tool use is occasional, as not all populations in a stone tool–using species actually use stone tools, and some individuals use them infrequently or not at all (Harmand & Arroyo 2023).

That pounding using hammers and anvils or through indirect percussion evolved independently in multiple nonhuman primate lineages has led some to posit that hominin use of stone tools emerged from a background of food processing using percussive behaviors (e.g., Carvalho et al. 2008, 2013; Panger et al. 2002). If this were the case, early industries using cutting and pounding tools such as the Lomekwian and the Oldowan may have been preceded by, and developed from, lithic traditions that focused on pounding using hammers and anvils (Harmand et al. 2015). These pre-Lomekwian traditions might become apparent with focused research in the late Miocene and early to middle Pliocene.

At 3.3 Ma, the Lomekwian is the first tangible evidence of hominin food processing using both cutting and pounding tools, reflecting a broadening of extractive foraging behaviors beyond plant foods (e.g., nuts, fruits) and/or animal products (e.g., marrow from long bones, brains from crania; Thompson et al. 2019) that required percussion to access. Differences in artifact size and mode of flaking clearly distinguish the Lomekwian from the Oldowan. The focus on flake production is often taken to reflect hominin butchery of carcasses (e.g., Rogers & Semaw 2009), but cutting tools are also useful for plant processing tasks (e.g., USO processing, working wood to make simple spears or digging sticks) (Lemorini et al. 2014, Plummer et al. 2023). The cutting component of the technology likely reflects dietary expansion by Lomekwian tool users incorporating foods that are not typically consumed by nonhuman primates today. What these foods were is unclear, but further study of artifact damage, use-wear, and associated fossils may point to the processing of both fauna and plant foods.

The evolutionary significance of the Lomekwian can be addressed only with additional research in Pliocene deposits. Expanding the range of the Lomekwian geographically and temporally would establish it as more than a localized phenomenon, and if Lomekwian and Oldowan sites ultimately approximate each other in time, it might be possible to assess whether they represent independent cultural traditions or have an evolutionary relationship. Lomekwian stone tool production may have happened predominantly at sites such as LOM3 where large blocks to be used as anvils and cores were transported, much like chimpanzees transport hammerstones to activity areas for nut-cracking today. Unlike chimpanzees, there was likely more resource flow into Lomekwian sites, including both lithic materials and possibly plant and animal foods. Flakes were the most portable component of the Lomekwian tool kit. They are at a deficit at LOM3 relative to their cores, suggesting that hominins carried flakes with them when they left the site, presumably for processing tasks elsewhere (S. Harmand, X. Boës, N. Taylor, V. Arrighi, S. Prat, et al., manuscript in preparation).

One of the hallmarks of the Oldowan technology is its portability, which, at little energetic cost, allowed hominins to both produce tools and process foods as they ranged and reduce larger packets of food (e.g., carcasses) into segments that could be transported and eaten elsewhere. An evolutionary scenario where the fitness benefits of habitual lithic technology led to the evolution of a handheld tool kit (the Oldowan) from a technological system that was more static (the Lomekwian) is therefore conceivable.

The oldest Oldowan localities have a geographic distribution that has expanded greatly over the last ten years, starting from the Afar Triangle in Ethiopia, where 2.6 Ma Oldowan sites have been known for decades (Semaw et al. 2003), to as far north as Algeria (Sahnouni et al. 2018) and as far west as Lake Victoria (Plummer et al. 2023). This geographic expansion, covering thousands of kilometers, reflects the persistent problem sampling error poses to the investigation of hominin biological and cultural evolution. The expanded geography very early in the known time span of the Oldowan may be a hint that populations of hominins were adopting this technology more rapidly and widely than hitherto realized. The breadth of materials being processed at Nyayanga (plant foods, wood, animals as large as hippos), as well as evidence for hominin access to fleshy carcasses at Gona and Ain Boucherit, suggests that this broad geographic distribution reflects the fitness benefit of lithic technology. However, there was not an increase in hominin body size until ∼2 Ma, roughly coinciding with the appearance of *H. erectus* (Pontzer 2012), possibly reflecting an intensification of stone tool use and a significant increase in dietary quality with the emergence of this taxon.

Stone tool technology appears to have been used in multiple hominin lineages over time, rather than emerging as an isolated, species-specific adaptive breakthrough. The possibility of more than one hominin toolmaker may explain some of the variation seen in technological skill and raw material selection observed in contemporaneous assemblages (e.g., Lokalalei 1 and 2C). For example, it is possible that members of both the genus *Paranthropus* and the genus *Homo* utilized Oldowan tools, potentially inheriting this behavior from a shared, stone tool–using ancestor belonging to the genus *Australopithecus* or *Kenyanthropus*. At sites where *Homo* and *Paranthropus* coexisted, tools may have been used occasionally by both genera. In cases where one group produced and left behind tools at resource-rich locations, these artifacts could have been opportunistically reused by other hominins frequenting the same sites.

Our understanding of the earliest stone technologies has increased substantially over the last 10 years with the discovery of the Lomekwian and the geographic and temporal range expansion of the Oldowan. While the processes by which tools were produced have been documented, our understanding of the adaptive significance of the Lomekwian and Oldowan is at a nascent stage. We hope that further paleoanthropological research will flesh out the identity, ecology, and behaviors of these ancient toolmakers and situate them within their broader ecosystems.

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LITERATURE CITED

Alemseged Z. 2003. An integrated approach to taphonomy and faunal change in the Shungura formation (Ethiopia) and its implication for hominid evolution. *J. Hum. Evol.* 44(4):451–78

Alemseged Z, Coppens Y, Geraads D. 2002. Hominid cranium from Omo: description and taxonomy of Omo-323-1976-896. *Am. J. Phys. Anthropol.* 117(2):103–12

Almeida-Warren K, Camara HD, Matsuzawa T, Carvalho S. 2022. Landscaping the behavioural ecology of primate stone tool use. *Int. J. Primatol.* 43(5):885–912

Antón SC. 2003. Natural history of *Homo erectus*. *Am. J. Phys. Anthropol.* 122(S37):126–70

Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999. *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Science* 284(5414):629–35

Beck BB. 1980. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. Garland

Boës X, Van Bocxlaer B, Prat S, Feibel C, Lewis J, Arrighi V, et al. 2024. Aridity, availability of drinking water and freshwater foods, and hominin and archeological sites during the Late Pliocene-Early Pleistocene in the western region of the Turkana Basin (Kenya): a review. *J. Hum. Evol.* 186:103466

Boesch C, Boesch-Achermann H. 2000. *The Chimpanzees of the Taï Forest: Behavioral Ecology and Evolution*. Oxford University Press

Braun DR, Aldeias V, Archer W, Ramon Arrowsmith J, Baraki N, Campisano C, et al. 2019. Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *PNAS* 116:11712–17

Braun DR, Carvalho S, Kaplan RS, Beardmore-Herd M, Plummer T, Biro D, et al. 2025. Stone selection by wild chimpanzees shares patterns with Oldowan hominins. *J. Hum. Evol.* 199:103625

Bril B, Parry R, Dietrich G. 2015. How similar are nutcracking and stone-flaking? A functional approach to percussive technology. *Phil. Trans. R. Soc. B.* 370:20140355

Brunet M, Beauvilain A, Coppens Y, Heintz É, Moutaye AHE, Pilbeam D. 1996. *Australopithecus bahrelghazali*, une nouvelle espèce d'Hominidé ancien de la région de Koro Toro (Tchad). *C. R. Séances Acad. Sci. Paris* 322:907–13

Cáceres I, Chelli Cheheb R, van der Made J, Harichane Z, Boulaghraief K, Sahnouni M. 2023. Assessing the subsistence strategies of the earliest North African inhabitants: evidence from the Early Pleistocene site of Ain Boucherit (Algeria). *Archaeol. Anthropol. Sci.* 15(6):87

Cáceres I, Rogers MJ, Semaw S, Leiss AC. 2017. Crocodiles in the diet of the first Oldowan toolmakers: evidence from ogs-6 at Gona (Afar, Ethiopia). *III Jorn. Prehist. Afr*. p. 20

Carvalho S, Cunha E, Sousa C, Matsuzawa T. 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *J. Hum. Evol.* 55:148–63

Carvalho S, Matsuzawa T, McGrew WC. 2013. From pounding to knapping: how chimpanzees can help us to model hominin lithics. In *Tool Use in Animals: Cognition and Ecology*, ed. CM Sanz, J Call, C Boesch. Cambridge University Press

Cerling TE, Manthi FK, Mbua EN, Leakey LN, Leakey MG, Leakey RE, et al. 2013. Stable isotope-based diet reconstructions of Turkana Basin hominins. *PNAS* 110(26):10501–6

Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, et al. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *PNAS* 108(23):9337–41

de Heinzelin J, Clark JD, White T, Hart W, Renne P, WoldeGabriel G, et al. 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284(5414):625–29

de la Torre I. 2004. Omo revisited: evaluating the technological skills of Pliocene hominids. *Curr. Anthropol.* 45(4):439–65

Delagnes A, Roche H. 2005. Late Pliocene hominid knapping skills: the case of Lokalalei 2C, West Turkana, Kenya. *J. Hum. Evol.* 48:435–72

Domínguez-Rodrigo M, Alcalá L. 2016. 3.3-million-year-old stone tools and butchery traces? More evidence needed. *PaleoAnthropology* 2016:46–53

Domínguez-Rodrigo M, Alcalá L. 2019. Pliocene archaeology at Lomekwi 3? New evidence fuels more skepticism. *J. Afr. Archaeol.* 17(2):173–76

Domínguez-Rodrigo M, Pickering TR, Bunn HT. 2010. Configurational approach to identifying the earliest hominin butchers. *PNAS* 107:20929–34

Domínguez-Rodrigo M, Pickering TR, Bunn HT. 2012. Experimental study of cut marks made with rocks unmodified by human flaking and its bearing on claims of ∼3.4-million-year-old butchery evidence from Dikika, Ethiopia. *J. Archaeol. Sci.* 39(2):205–14

Domínguez-Rodrigo M, Pickering TR, Semaw S, Rogers MJ. 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *J. Hum. Evol.* 48(2):109–21

Faith JT, Rowan J, Du A. 2019. Early hominins evolved within non-analog ecosystems. *PNAS* 116(43):21478–83

Falótico T, Ottoni EB. 2016. The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. *Behaviour* 153(4):421–42

Falótico T, Siqueira JO, Ottoni EB. 2017. Digging up food: excavation stone tool use by wild capuchin monkeys. *Sci. Rep.* 7(1):6278

Finestone EM. 2025. Early stone tool technology in hominin evolution. *Oxford Encyclopedia of Anthropology*. **https://doi.org/10.1093/acrefore/9780190854584.013.637**

Finestone EM, Plummer TW, Vincent TH, Blumenthal SA, Ditchfield PW, et al. 2024. New Oldowan locality Sare-Abururu (ca. 1.7 Ma) provides evidence of diverse hominin behaviors on the Homa Peninsula, Kenya. *J. Hum. Evol.* 190:103498

Gabunia L, Antón SC, Lordkipanidze D, Vekua A, Justus A, Swisher CC III. 2001. Dmanisi and dispersal. *Evol. Anthropol.* 10(5):158–70

Goldman-Neuman T, Hovers E. 2012. Raw material selectivity in late Pliocene Oldowan sites in the Makaamitalu Basin, Hadar, Ethiopia. *J. Hum. Evol.* 62(3):353–66

Haile-Selassie Y, Gibert L, Melillo SM, Ryan TM, Alene M, Deino A, et al. 2015. New species from Ethiopia further expands middle Pliocene hominin diversity. *Nature* 521:483–88

Hammond AS, Mongle C. 2023. Pleistocene hominin fossil record of Africa. In *Handbook of Pleistocene Archaeology of Africa: Hominin Behavior, Geography, and Chronology*, ed. A Beyin, DK Wright, J Wilkins, DI Olszewski. Springer

Harmand S. 2009. Variability in raw material selectivity at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In *Interdisciplinary Approaches to the Oldowan*, ed. E Hovers, DR Braun. Springer

Harmand S, Arroyo A. 2023. Linking primatology and archaeology: the transversality of stone percussive behaviors. *J. Hum. Evol.* 181:103398

Harmand S, Lewis JE, Feibel CS, Lepre CJ, Prat S, Lenoble A, et al. 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521:310–15

Harmand S, Lewis JE, Taylor N, Feibel CS, Boës X, et al. 2019. Reply to Domínguez-Rodrigo and Alcalá: interpretation without accurate evidence is fantasy. *J. Afr. Archaeol.* 17(2):177–81

Haslam M, Hernandez-Aguilar A, Ling V, Carvalho S, de la Torre I, DeStefano A, et al. 2009. Primate archaeology. *Nature* 460:339–44

Hovers E. 2009. Learning from mistakes: flaking accidents and knapping skills in the assemblage of A.L. 894 (Hadar, Ethiopia). In *The Cutting Edge: New Approaches to the Archaeology of Human Origins*, ed. KD Schick, NP Toth. Stone Age Institute Press

Howell FC, Haesaerts P, de Heinzelin J. 1987. Depositional environments, archaeological occurrences and hominids from Members E and F of the Shungura Formation (Omo basin, Ethiopia). *J. Hum. Evol.* 16:665–700

Isaac G. 1984. The archaeology of human origins: studies of the Lower Pleistocene in East Africa. In *Advances in World Archaeology*, ed. F Wendorf, A Close. Academic Press

Johanson DC, White TD, Coppens Y. 1978. A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia* 28:1–14

Kibunjia M. 1994. Pliocene archaeological occurrences in the Lake Turkana basin. *J. Hum. Evol.* 27:159–71

Kimbel WH, Johanson DC, Rak Y. 1997. Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* 103(2):235–62

Kimbel WH, Walter RC, Johanson DC, Reed KE, Aronson JL, et al. 1996. Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *J. Hum. Evol.* 31:549–61

Leakey LSB. 1959. A new fossil skull from Olduvai. *Nature* 184(4685):491–93

Leakey LSB. 1960. Recent discoveries at Olduvai Gorge. *Nature* 188(4755):1050–52

Leakey LSB, Tobias PV, Napier JR. 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202(4927):7–9

Leakey MD. 1966. A review of the Oldowan culture from Olduvai Gorge, Tanzania. *Nature* 210(5035):462–66

Leakey MD. 1971. *Olduvai Gorge*, Vol. 3: *Excavations in Beds I and II, 1960–1963*. Cambridge University Press

Leakey MG, Feibel CS, McDougall I, Walker A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376(6541):565–71

Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, et al. 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410(6827):433–40

Leakey MG, Spoor F, Dean MC, Feibel CS, Antón SC, et al. 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. *Nature* 488(7410):201–4

Lemorini C, Plummer TW, Braun DR, Crittenden AN, Ditchfield PW, et al. 2014. Old stones' song: use-wear experiments and analysis of the Oldowan quartz and quartzite assemblage from Kanjera South (Kenya). *J. Hum. Evol.* 72:10–25

Lewis JE, Harmand S. 2016. An earlier origin for stone tool making: implications for cognitive evolution and the transition to *Homo*. *Phil. Trans. R. Soc. B* 371:20150233

Lombard M, Högberg A, Haidle MN. 2019. Cognition: from capuchin rock pounding to Lomekwian flake production. *Camb. Archaeol. J.* 29(2):201–31

Ludwig BV, Harris JWK. 1998. Towards a technological reassessment of East African Plio-Pleistocene lithic assemblages. In *Early Human Behaviour in Global Context: The Rise and Diversity of the Lower Palaeolithic Record*, ed. MD Petraglia, R Korisettar. Routledge

Luncz LV, Proffitt T, Kulik L, Haslam M, Wittig RM. 2016. Distance-decay effect in stone tool transport by wild chimpanzees. *Proc. Biol. Sci.* 283(1845):20161607

Mayr E. 1950. Taxonomic categories in fossil hominids. *Cold Spring Harbor Symp. Q. Biol*. 15:109–18

McGrew WC. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press

McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, et al. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466(7308):857–60

McPherron SP, Alemseged Z, Marean C, Wynn JG, Reed D, et al. 2011. Tool-marked bones from before the Oldowan change the paradigm. *PNAS* 108(21):E116

Mercader J, Barton H, Gillespie J, Harris J, Kuhn S, et al. 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *PNAS* 104:3043–48

Mercader J, Panger M, Boesch C. 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296(5572):1452–55

Mussi M, Skinner MM, Melis RT, Panera J, Rubio-Jara S, et al. 2023. Early *Homo erectus* lived at high altitudes and produced both Oldowan and Acheulean tools. *Science* 382(6671):713–18

Napier J. 1962. Fossil hand bones from Olduvai Gorge. *Nature* 196(4853):409–11

Negash EW, Alemseged Z, Barr WA, Behrensmeyer AK, Blumenthal SA, et al. 2024. Modern African ecosystems as landscape-scale analogues for reconstructing woody cover and early hominin environments. *J. Hum. Evol.* 197:103604

Panger MA, Brooks AS, Richmond BG, Wood B. 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol. Anthropol.* 11:235–45

Pante MC. 2019. Comment on Thompson et al. "Origins of the Human Predatory Pattern." *Curr. Anthropol.* 60:12–13

Parenti F, Varejão FG, Scardia G, Okumura M, Araujo A, et al. 2024. The Oldowan of Zarqa Valley, Northern Jordan. *J. Paleolithic Archaeol.* 7(1):3

Plummer TW. 2004. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. *Am. J. Phys. Anthropol.* 125(S39):118–64

Plummer TW, Finestone EM. 2018. Archeological sites from 2.6–2.0 Ma: toward a deeper understanding of the Early Oldowan. In *Rethinking Human Evolution*, ed. JH Schwartz. MIT Press

Plummer TW, Oliver JS, Finestone EM, Ditchfield PW, Bishop LC, et al. 2023. Expanded geographic distribution and dietary strategies of the earliest Oldowan hominins and *Paranthropus*. *Science* 379:561–66

Pontzer H. 2012. Ecological energetics in early *Homo*. *Curr. Anthropol.* 53(S6):S346–58

Potts R. 1984. Home bases and early hominids: reevaluation of the fossil record at Olduvai Gorge suggests that the concentrations of bones and stone tools do not represent fully formed campsites but an antecedent to them. *Am. Sci.* 72(4):338–47

Potts R, ed. 1988. *Early Hominid Activities at Olduvai: Foundations of Human Behaviour*. Routledge

Potts R. 1991. Why the Oldowan? Plio-Pleistocene toolmaking and the transport of resources. *J. Anthropol. Res.* 47(2):153–76

Prat S. 2023. Beyond the genus stereotype. Who were the first tool-markers in Africa? Crossed views between archaeology and anatomy. *Anthropologie* 127(4):103187

Prat S, Brugal J-P, Roche H, Texier PJ. 2003. Nouvelles découvertes de dents d'hominidés dans le membre Kaitio de la formation de Nachukui (1,65–1,9 Ma), ouest du lac Turkana (Kenya). *C. R. Palevol* 2(8):685–93

Prat S, Brugal J-P, Tiercelin J-J, Barrat J-A, Bohn M, et al. 2005. First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3–2.4 Myr. *J. Hum. Evol.* 49:230–40

Proffitt T, Luncz LV, Falótico T, Ottoni EB, de la Torre I, Haslam M. 2016. Wild monkeys flake stone tools. *Nature* 539(7627):85–88

Proffitt T, Reeves JS, Braun DR, Malaivijitnond S, Luncz LV. 2023. Wild macaques challenge the origin of intentional tool production. *Sci. Adv.* 9(10):eade8159

Quade J, Levin N, Semaw S, Stout D, Renne P, Rogers M, et al. 2004. Paleoenvironments of the earliest stone toolmakers, Gona, Ethiopia. *Geol. Soc. Am. Bull.* 116(11–12):1529–44

Quinn RL, Lewis J, Brugal J-P, Lepre C, Trifonov A, Harmand S. 2021. Influences of dietary niche expansion and Pliocene environmental change on the origins of stone tool making. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 562:110074

Reeves JS, Proffitt T, Almeida-Warren K, Luncz LV. 2023. Modeling Oldowan tool transport from a primate perspective. *J. Hum. Evol.* 181:103399

Reeves JS, Proffitt T, Luncz LV. 2021. Modeling a primate technological niche. *Sci. Rep.* 11(1):23139

Reeves JS, Proffitt T, Pacome SS, Luncz LV. 2024. Searching for the earliest archaeological record: insights from chimpanzee material landscapes. *J. R. Soc. Interface* 21(217):20240101

Roche H, Brugal J-P, Delagnes A, Feibel C, Harmand S, Kibunjia M, et al. 2003. Les sites archéologiques Plio-Pléistocènes de la formation de Nachukui, Ouest-Turkana, Kenya: Bilan synthétique 1997–2001. *C. R. Palevol* 2(8):663–73

Rogers MJ, Semaw S. 2009. From nothing to something: the appearance and context of the earliest archaeological record. In *Sourcebook of Paleolithic Transitions: Methods, Theories, and Interpretations*, ed. M Camps, P Chauhan. Springer

Rose MD. 1984. A hominine hip bone, KNM-ER 3228, from East Lake Turkana, Kenya. *Am. J. Phys. Anthropol.* 63(4):371–78

Sahle Y, El Zaatari S, White TD. 2017. Hominid butchers and biting crocodiles in the African Plio-Pleistocene. *PNAS* 114(50):13164–69

Sahnouni M, Parés JM, Duval M, Cáceres I, Harichane Z, et al. 2018. 1.9-million- and 2.4-million-year-old artifacts and stone tool-cutmarked bones from Ain Boucherit, Algeria. *Science* 362(6420):1297–301

Schwartz JH, Tattersall I. 2015. Defining the genus *Homo*. *Science* 349(6251):931–32

Semaw S. 2000. The world's oldest stone artefacts from Gona, Ethiopia: their implications for understanding stone technology and patterns of human evolution between 2.6–1.5 million years ago. *J. Archaeol. Sci.* 27(12):1197–214

Semaw S. 2006. The oldest stone artifacts from Gona (2.6–2.5 Ma), Afar, Ethiopia: implications for understanding the earliest stages of stone knapping. In *The Oldowan: Case Studies into the Earliest Stone Age*, ed. NP Toth, K Schick. Stone Age Institute Press

Semaw S, Renne P, Harris JWK, Feibel CS, Bernor RL, et al. 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385:333–36

Semaw S, Rogers MJ, Quade J, Renne PR, Butler RF, et al. 2003. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Ethiopia. *J. Hum. Evol.* 45:169–77

Semaw S, Rogers MJ, Simpson SW, Levin NE, Quade J, Dunbar N, et al. 2020. Co-occurrence of Acheulian and Oldowan artifacts with *Homo erectus* cranial fossils from Gona, Afar, Ethiopia. *Sci. Adv.* 6(10):eaaw4694

Shea JJ. 2017. Occasional, obligatory, and habitual stone tool use in hominin evolution. *Evol. Anthropol.* 26:200–17

Shick KD. 1987. Modeling the formation of Early Stone Age artifact concentrations. *J. Hum. Evol.* 16(7–8):789–807

Sponheimer M, Alemseged Z, Cerling T, Grine F, Kimbel W, et al. 2013. Isotopic evidence of early hominin diets. *PNAS* 110(26):10513–18

Sponheimer M, Daegling DJ, Ungar PS, Bobe R, Paine OC 2023. Problems with *Paranthropus*. *Quat. Int.* 650:40–51

Stanford CB. 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. *Am. Anthropol.* 98:96–113

Stout D, Quade J, Semaw S, Rogers MJ, Levin NE. 2005. Raw material selectivity of the earliest stone toolmakers at Gona, Afar, Ethiopia. *J. Hum. Evol.* 48:365–80

Su DF. 2024. Early hominin paleoenvironments and habitat heterogeneity. *Annu. Rev. Anthropol.* 53:21–35

Susman RL. 1988. Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil evidence for tool behavior. *Science* 240(4853):781–84

Susman RL. 1991. Who made the Oldowan tools? Fossil evidence for tool behavior in Plio-Pleistocene hominids. *J. Anthropol. Res.* 47(2):129–51

Susman RL 1998. Hand function and tool behavior in early hominids. *J. Hum. Evol.* 35(1):23–46

Suwa G, White TD, Howell FC. 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. *Am. J. Phys. Anthropol.* 101(2):247–82

Thompson JC, Carvalho S, Marean CW, Alemseged Z. 2019. Origins of the human predatory pattern: the transition to large-animal exploitation by early hominins. *Curr. Anthropol.* 60:1–23

Tobias PV. 1965. *Australopithecus*, *Homo habilis*, tool-using and tool-making. *S. Afr. Archaeol. Bull.* 20(80):167–92

Toth N. 1985. The Oldowan reassessed: a close look at early stone artifacts. *J. Archaeol. Sci.* 12(2):101–20

Toth N. 1987. Behavioral inferences from early stone artifact assemblages: an experimental model. *J. Hum. Evol.* 16(7–8):763–87

Toth N, Schick K. 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. *Annu. Rev. Anthropol.* 38:289–305

Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLOS ONE* 3(4):e2044

Van der Merwe NJ, Masao FT, Bamford MK. 2008. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *S. Afr. J. Sci.* 104(3):153–55

Villmoare B, Kimbel WH, Seyoum C, Campisano CJ, DiMaggio E, Rowan J, et al. 2015. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* 347:1352–55

Visalberghi E, Addessi E, Truppa V, Spagnoletti N, Ottoni E, et al. 2009. Selection of effective stone tools by wild bearded capuchin monkeys. *Curr. Biol.* 19(3):213–17

Walker AC, Leakey RE. 1988. The evolution of *Australopithecus boisei*. In *Evolutionary History of the "Robust" Australopithecines*, ed FE Grine. Aldine de Gruyter

Wood B. 1991. *Koobi Fora Research Project*, Volume 4: *Hominid Cranial Remains*. Clarendon Press

Wood B. 1992. Origin and evolution of the genus *Homo*. *Nature* 355(6363):783–90

Wood B. 1997. The oldest whodunnit in the world. *Nature* 385(6614):292–93

Wood B, Constantino P. 2007. *Paranthropus boisei*: fifty years of evidence and analysis. *Am. J. Phys. Anthropol.* 134(S45):106–32

Wood B, Leakey MG. 2011. The Omo-Turkana Basin fossil hominins and their contribution to our understanding of human evolution in Africa. *Evol. Anthropol.* 20:264–92

Zanolli C, Dean MC, Assefa Y, Bayle P, Braga J, et al. 2017. Structural organization and tooth development in a *Homo* aff. erectus juvenile mandible from the Early Pleistocene site of Garba IV at Melka Kunture, Ethiopian Highlands. *Am. J. Phys. Anthropol.* 162(3):533–49