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REVIEW

Paleolithic Technology and Human Evolution

Stanley H. Ambrose

Human biological and cultural evolution are closely linked to technological innovations. Direct evidence for tool manufacture and use is absent before 2.5 million years ago (Ma), so reconstructions of australopithecine technology are based mainly on the behavior and anatomy of chimpanzees. Stone tool technology, robust australopithecines, and the genus *Homo* appeared almost simultaneously 2.5 Ma. Once this adaptive threshold was crossed, technological evolution was accompanied by increased brain size, population size, and geographical range. Aspects of behavior, economy, mental capacities, neurological functions, the origin of grammatical language, and social and symbolic systems have been inferred from the archaeological record of Paleolithic technology.

In the movie *2001: A Space Odyssey* (*1*), a savanna-dwelling ape has a eureka-like flash of inspiration when he realizes the awesome power of the bone tool in his hands. He tosses it skyward, where it morphs into a space station at the dawn of this millennium. What happened between the first tool use by our ape ancestors and the first complex projectile launched into flight with another tool? In this review, conventional wisdom about aspects of Paleolithic technology will be challenged, and new ideas about the coevolution of technology, language, hands, and brains will be proposed.

How did technology influence human evolution? What were the "prime movers" for the origin and development of Paleolithic technologies? Paleoanthropologists once considered making tools to be one of the defining characteristics of the genus *Homo* (*2*). However, the diversity of tool-making and tool-using behaviors among chimpanzees (*Pan troglodytes*) has forced us to completely revise assumptions surrounding the concept of "man the toolmaker," including those about the gender of the first tool users. Chimpanzees have diverse and regionally varied repertoires of tool-using, tool-making, and other "cultural" behaviors (*3–5*). In contrast, *Cebus* monkeys are considered prolific tool users but exhibit no understanding of cause and effect, or of the difference between appropriate and inappropriate tools (*6*).

Chimpanzees make and use several kinds of tools for extractive foraging (*3*), including leaf sponges, termite and ant fishing wands and probes, marrow picks, levers, pestles, stick brushes for honey extraction, leaf

Department of Anthropology, University of Illinois, 109 Davenport Hall, 607 South Mathews Avenue, Urbana, IL 61801, USA. E-mail: ambrose@uiuc.edu

scoops, and hooked sticks to extend their reach. West African chimpanzees use wood and stone hammers and anvils for cracking nuts (*7*). Repeated use produces shallow dimpled and pitted anvils and hammers resembling those made by humans. Sharp-edged stone chips (flakes) are occasionally produced but are not used. Chimpanzee males actively hunt mammals smaller than themselves but rarely use tools during capture and consumption (*8*). Females exhibit greater persistence and skill in several tool-using activities (*7*), which suggests that females may have played a leading role in technological evolution. Tool use among forest-dwelling chimpanzees raises questions about Darwin's (*9*) hypothesis about the role of adaptation to savannas in the origin of technology (*10*).

Assuming that the behaviors of our closest living relatives could also have been performed by our last common ancestor and its descendants, we can infer that the minimum level of technological capacity of hominids between 5 and 2.5 million years ago (Ma) was comparable to that of chimpanzees. Most tools used by chimpanzees are made of organic materials that are rarely preserved in fossil and archaeological sites. Bipedal locomotion in savanna-dwelling hominids was achieved by 4.2 Ma (*11*) but was not accompanied by evidence of tool use (*12*). Broken bones in caves in South Africa, dating from 2.6 to 3.0 Ma, were once considered tools made by *Australopithecus africanus* (*13*) but were probably the product of hyenas and other natural agents (*14*).

The earliest direct evidence of hominid technology dates to 2.5 Ma in the Ethiopian Rift Valley (*15*, *16*), comprising sharp-edged slivers and lumps of stone, hammer stones and anvils, and bones with hammer marks and cut marks from butchery and marrow extraction. This simple technology is named the Oldowan Industrial Complex, after the type localities at Olduvai Gorge (*17*). Early hominids possessed an excellent empirical understanding of the mechanical properties of lithic raw materials, fracture mechanics, and geometry. Brittle fine-grained lava, volcanic glass (obsidian), quartzite, limestone, and flint are isotropic (their mineral structure exerts little influence on the orientation of fractures). Striking a hand-held isotropic block or cobble (a core) with a hammerstone initiates a cone-shaped crack at roughly 60° from the axis of force, exemplified by the hole in a plate glass window made by a pellet gun (*18*, *19*). In order to detach thin sharp-edged flakes, the core must be struck obliquely close to the edge of a platform (Fig. 1). Hominids were highly skilled in direct percussion flaking by 2.5 Ma, consistently producing many well-formed flakes from each core with few misdirected blows (*16*, *20*). Where the available raw materials were mainly quartz pebbles smaller than 2.5 cm across, cores were too small for hand-held direct percussion, so they were placed on an anvil and smashed with a hammerstone (bipolar technique) (*21*). Interassemblage variability in the Oldowan thus seems to reflect least-effort strategies for obtaining large sharp-edged flakes from available raw materials, rather than culturally determined stylistic traditions (*22*, *23*). Bone tools were usually flaked like stone or were used without intentional modification (*17*).

Oldowan technology seems simple, reflecting the mental capacities of extant apes (*24*), but it actually reflects manual skills far exceeding those of chimpanzees. For example, Kanzi, a bonobo (pygmy chimpanzee, *Pan paniscus*), was apprenticed for 3 years in stone tool flaking by direct percussion of hand-held cores (*25*, *26*) but was unable to strike forcefully and accurately at the correct angle or position on the platform. His small flakes and battered cores did not resemble Oldowan artifacts.

Kanzi used sharp-edged flakes to cut a rope to open a food reward box. He cut slowly, with little downward pressure, moving his whole arm, mainly from the shoulder, with an immobile wrist. Wild chimpanzees also move their arms mainly from the shoulder and elbow when cracking nuts (*7*). This contrasts dramatically with the human dexterity in precision tool use that is afforded by a mobile wrist. Anatomical limitations on joint motion and power and on precision grips, due to design primarily for quadrupedal and arboreal locomotion (*27–29*), may account for the poor performance of chimpanzees in stone tool-making and use. Long curved fingers and a short thumb hinder opposition of their fingertips in a strong pinch grip. Humans have short straight fingers, a long stout thumb, and fingertips with broad fleshy pads underlain by wide apical tufts of bone, which increase stability when gripping small tools. Chimpanzees have narrow fingertips and lack the forearm muscle for powerful thumb flexion. Palm muscles that strengthen the opposable thumb grip are either absent or relatively weakly developed. *Australopithecus afarensis* (3.8 to 2.9 Ma) had chimpanzee-like narrow fingertips (*27*), but those of *A. africanus* (3.0 to 2.6 Ma) may have been more human-like (*30*). The chimpanzee wrist locks to prevent overextension during knuckle walking, which limits rotation of the wrist (*29*). This may inhibit wrist motions such as those humans use to throw a fastball, flake stone, and manipulate small tools precisely. Additional biomechanical, myographic, anatomical, and neurological (positron emission tomography scan) studies (*27*, *28*, *31*) of the kinematics of chimpanzee and human tool use are needed to evaluate this impression of limited chimpanzee arm and wrist flexibility during tool use.

Meat eating is often considered the prime mover for the adoption of stone tools (*8*, *32*). Cut marks and hammerstone marks on bones of large mammals demonstrate meat and marrow consumption by 2.5 Ma (*15*, *33*, *34*). However, microwear polishes on stone flakes demonstrate their use for cutting and scraping wood and for cutting siliceous plants (reeds, sedges, or grasses) in addition to cutting meat (*35*). Sharp-edged cores also undoubtedly had several potential uses (*23*). Pointed bone fragments from South African cave sites have

Fig. 1. Flaked stone tool production, illustrating right-handed flakes (*32*).

polished tips, possibly from perforating soft materials, and coarser abrasions resembling those resulting from digging in stony soil or termite mounds (*36*, *37*). Oldowan technology was an adaptive threshold (*22*), expanding the abilities of early hominids to modify wood, bone, and other materials and to gain greater access to high-quality food resources, including termite colonies and the meat and marrow of very large thick-skinned mammals. High-quality resources could have fueled the high metabolic energy demands of the large brain of early *Homo* (*38*). Social cooperation, needed to gain access to unpredictable risky resources such as scavenged and hunted animal carcasses in the competitive and unpredictable environments of the African savanna, combined with new tools to exploit the environment, may have been important stimuli to mental development (*39*).

Homo habilis is usually considered the first tool maker. Cranial endocasts show that its left hemisphere has an impression of Broca's area (*40*, *41*). Broca's area is involved in oro-facial fine motor control and language and is adjacent to and probably derived from the area for precise hand motor control (*42*). Approximately 90% of humans are right-handed, and hand preference is strongest in skilled tool use with the precision grip (*43*). Individual chimpanzees exhibit long-term consistency of hand preference mainly for complicated tool-using tasks (*44*), but there is no overall preference for right-handedness at the population level (*43*).

Handedness may be reflected in flaked stone tools (*45*). Right-handed individuals tend to rotate the core clockwise when striking a sequence of overlapping flakes (Fig. 1). Cortex (the weathered cobble surface) is preferentially distributed on the right side of the dorsal flake surface in experimental replication of Oldowan tools by right-handed individuals [by a ratio of 56:44, right:left (R:L) cortex] and in Oldowan artifact assemblages (57:43 R:L) (*45*). Direct percussion flaking and precise tool use place different demands on the functions of the left and right hands. The left hand grips the core while the right hand strikes the platform accurately and precisely, with well-controlled force. Humans typically hold a worked object with the left hand while using a tool with the right. Chimpanzees show no clear populational laterality for holding versus manipulating (*43*). Habitual tool-making and tool-using activities involving bimanual coordination of stabilizing objects and precision tool use may have led to lateralization of brain functions and set the stage for the evolution of language.

The hand of *H. habilis* resembles that of modern humans (*46*). Its brain was significantly larger (600 to 800 cm^3) than that of earlier and contemporary australopithecines and extant African apes (450 to 500 cm^3), and its teeth were relatively small for its body size (*12*, *47*), suggesting a relation between tool use, quality of diet, and intelligence. However, several small-brained, large-toothed species of "robust" *Australopithecus* (*A. garhi*, *A. aethiopicus*, *A. boisei*, and *A. robustus*) were also associated with the Oldowan (*15*, *48*), so the identities of the Oldowan toolmakers and the relationship of technology to anatomy remain open questions. Finger and thumb bones from Swartkrans Cave, South Africa, have the anatomy of tool users (*27*). If their attribution to *A.* (*Paranthropus*) *robustus* is correct, there was more than one Oldowan tool-making species. Australopithecines were extinct by 1.0 Ma, but typical Oldowan artifact assemblages were made until at least 0.5 Ma (*49*). *Homo erectus/ergaster*, with a larger brain and smaller teeth, appeared around 1.8 Ma in Africa (*48*), but the Oldowan remained unchanged until 1.5 Ma.

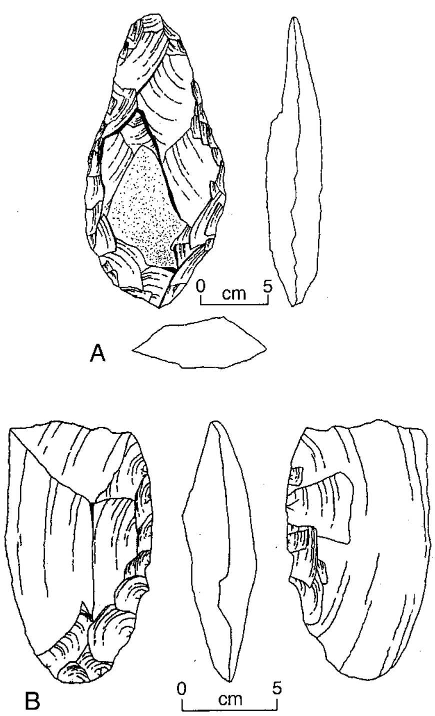

Fig. 2. Acheulean LCTs from Olorgesailie, Kenya. (**A**) Handaxe and (**B**) cleaver (*65*).

Acheulean Industrial Complex

Large cutting tools (LCTs), typically about 10 to 17 cm long (Fig. 2), were added to the Oldowan toolkit around 1.5 Ma, marking the advent of the Acheulean Industrial Complex. The Acheulean was manufactured by *H. erectus* and its larger-brained descendant *H. heidelbergensis*, and dates between 1.5 and 0.3 Ma (*50*, *51*). With a few exceptions in China and Korea, Acheulean-like industries do not occur east or north of the "Movius Line" (*52*, *53*), which arcs from the India-Bangladesh border to northern England. The dispersal of *H. erectus* to east Asia 1.6 to 1.8 Ma (that is, before the invention of the Acheulean) may explain the absence of the Acheulean east of the Movius line (*53*–*55*) but does not explain its absence in northern Europe after 0.5 Ma. Early dispersal to Asia may not have been facilitated by Acheulean lithic technology or control of fire.

Large flakes, slabs, and cobbles were shaped into LCTs by bidirectional or unidirectional invasive trimming of lateral edges. Handaxes (Fig. 2A) typically have a tear-drop-shaped plan form and a lenticular cross section. Cleavers (Fig. 2B) have a sharp, thin, usually unmodified edge transverse to the long axis (the cleaver bit). Picks and knives have convergent tips, like handaxes. Picks have a thick cross section at the midline, and knives have one thick lateral margin. Microwear studies show that LCTs may have been multipurpose tools (*56*). Experiments show that they are excellent for heavy-duty butchery, woodworking, and other tasks (*35*, *57*). Acheulean LCTs were probably hand-held. Their use as projectiles (*58*) cannot be discounted but cannot be confirmed. Although the descriptive names imply different functions for handaxes, cleavers, knives, and picks, this notion remains unproved. If the most important functional attribute of LCTs was a long straight cutting edge rather than a finished form, then all LCT classes may have had equivalent functions.

Unlike simple Oldowan stone tools, whose shapes are largely controlled by the primary form, size, and mechanical properties of raw materials (*22*), LCTs are assumed to reflect arbitrary preconceived designs imposed on a diverse range of primary forms. Bilateral symmetry and the high degree of standardization of handaxe shape over a wide range of sizes imply a well-defined concept of shape and proportion, reflecting higher conceptual and cognitive abilities than in the Oldowan (*24*, *59*). Subclasses of handaxes and cleavers are defined mainly by plan form (*60*). However, the meaning of variation in the frequencies of classes and subclasses and in the modal sizes and shapes of LCTs between sites is unclear. The shapes of LCTs are usually assumed to conform to the mental template of the cultural group. If so, LCT style can be used to identify regional cultural traditions (*61*). This assumption is challenged by stochastic variation in the modal sizes and shapes of LCT assemblages at Olduvai Gorge (*62*) and other site complexes (*63*–*65*). Evaluation of the existence of style with Isaac's (*22*) five-step "method of residuals" (MR), which systematically examines noncultural influences on form first and cultural ones last, suggests that mechanical properties (*57*, *65*); the abundance, size, and shape of available raw materials; the primary form of the blank (flake, cobble, or slab) (*65*); and the amount of resharpening done (*65*, *66*) account for most interassemblage differences in form modalities. Finished artifact forms may thus be the unintended byproduct of several nonstylistic factors rather than intended target types. For example, flaking a thick cobble of tough raw material will usually produce a pick-like form. Trimming the lateral margins of a large flat flake may initially produce a cleaver, but after several bouts of resharpening, the margins converge to a point, and the cleaver becomes a handaxe. The MR (*22*) and reduction/resharpening intensity approaches to explaining morphological and typological diversity (*67*) are useful for all Paleolithic industries. They raise provocative questions about the existence of style in the Acheulean and about functional differences between the four LCT classes. The cultural and cognitive capacities of Acheulean hominids may have been substantially overestimated.

Burned bones from Swartkrans Cave in South Africa suggest that hominids systematically used fire beginning 1.0 to 1.5 Ma (*68*). Fire would have substantially improved the nutritional qualities of plant and animal foods, among other adaptive advantages (*69*, *70*). Nonlithic Acheulean technology is poorly documented. Bone tools were still shaped mainly by direct percussion. The poor preservation of plant materials effectively hides an important dimension of Paleolithic technology. The oldest wood tools are well-made javelin-like spears dated ~0.4 Ma, from Schöningen, Germany (*71*).

During the later Acheulean, LCTs became more refined in shape, in part reflecting flaking with soft hammers of hardwood or bone, which make straighter edges and more regular plan forms (*51*). However, refinement does not always correlate with age, because poor raw materials produce unrefined artifacts (*57*, *65*). New strategies of tool manufacture and regionally distinct industries appeared at the end of the Acheulean, around 0.3 to 0.5 Ma (*72*). Cores were carefully shaped by variants of the Levallois prepared core technique (named after a suburb of Paris) to produce very large flakes that were close to the finished form, and blades were struck from prismatic cores (*72*–*74*). Large, thick-core axes, picks, and lances in the Sangoan industry suggest a new emphasis on heavy-duty woodworking in tropical Africa (*75*).

Middle Paleolithic Technologies

Technological and cultural evolution accelerated ~300,000 years ago (300 ka), during the Middle Paleolithic (MP) and its sub-Saharan African correlate, the Middle Stone Age (MSA). These advances were made by Neanderthals, late archaic humans, and anatomically modern humans (*72*, *76*). Regional stylistic and technological variants are clearly identifiable, suggesting the emergence of true cultural traditions and culture areas (*77*). LCTs were supplanted by smaller tools from Levallois and radial cores (Fig. 3). Levallois core technology is a sophisticated strategy for efficiently producing relatively standardized artifacts, and may reflect more complex cognitive abilities (*78*). Stemmed (tanged) points and other tools (*77*), microwear traces from mounts (*79*), and organic residues of mastic (*80*) indicate hafted composite tools, probably as early as the Acheulean to the MP/MSA transition. Stone-tipped spears, knives, and scrapers mounted in shafts and handles represent an order-of-magnitude increase in technological complexity that may be analogous to the difference between primate vocalizations and human speech.

Hand-held Oldowan and Acheulean tools are single techno-units made by reduction (percussion flaking of stone and scraping and whittling of wood), but composite tools are conjunctions of at least three techno-units, involving the assembly of a handle or shaft, a stone insert, and binding materials (*81*). Reductive technologies are linear sequences of behaviors (*24*) that involve predominantly repetitive coarse motor control (percussion flaking). Primate vocalizations are also repetitive sequences of coarse motor actions. Conjunctive technologies are hierarchical and involve nonrepetitive fine hand motor control to fit components to each other. Assembling techno-units in different configurations produces functionally different tools. This is formally analogous to grammatical language, because hierarchical assemblies of sounds produce meaningful phrases and sentences, and changing word order changes meaning. Speech and composite tool manufacture involve sequences of nonrepetitive fine motor control and both are controlled by adjacent areas of the inferior left frontal lobe (*42*, *82*). A composite tool may be analogous to a sentence, but explaining how to make one is the equivalent of a recipe or short story. If composite tool manufacture and grammatical language coevolved ~300 ka, then Neanderthals and modern humans could speak. This is consistent with reconstructions of fossil hominid vocal tracts that suggest that their last common ances-

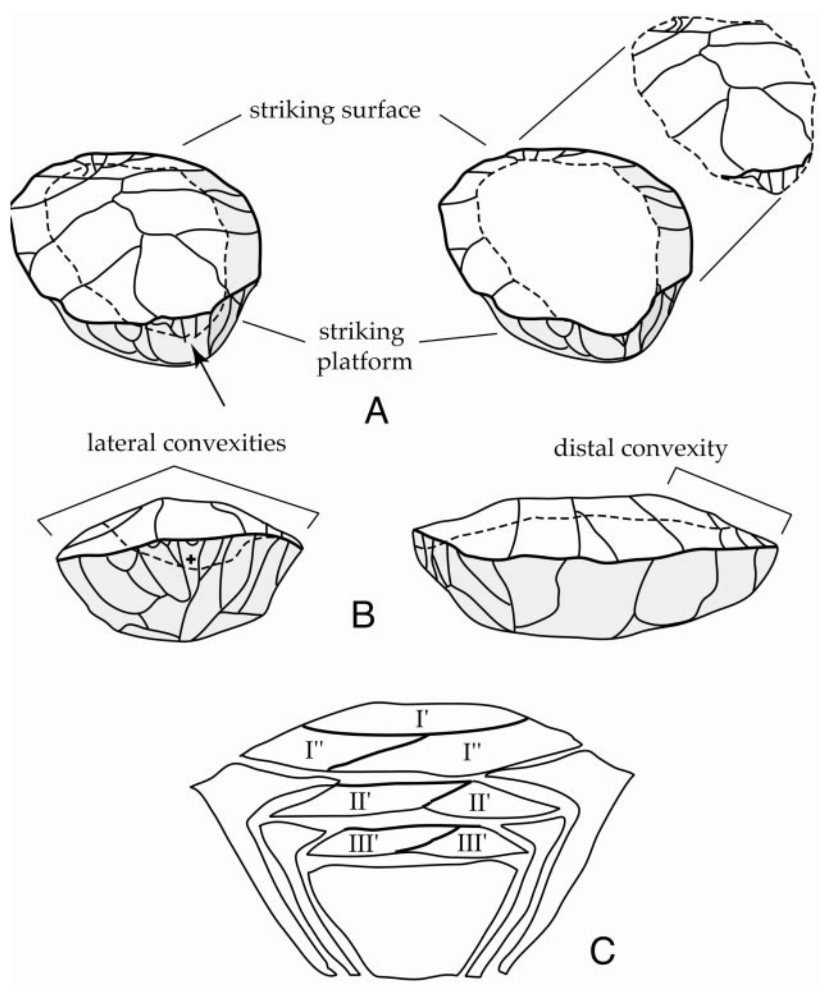

Fig. 3. Levallois core technology. A tortoise core, illustrating (**A**) the main Levallois flake, (**B**) the geometry of the upper and lower faces, and (**C**) the stages of reduction to produce additional Levallois flakes (*101*).

tor, *H. heidelbergensis*, could also speak (*83*).

The acquisition and modification of each component of a composite tool involve planned sequences of actions that can be performed at different times and places, such as flaking a stone point, cutting and shaping a wooden shaft, and collecting and processing binding materials. The complex problem solving and planning demanded by composite tool manufacture may have influenced the evolution of the frontal lobe. Functional magnetic resonance imaging demonstrates that the frontopolar prefrontal cortex selectively activates only when imagining a main objective while performing related secondary tasks (*84*). Switching between unrelated tasks has no effect. Composite tool manufacture demands the planning and coordination of different kinds of subsidiary tasks and may have coevolved with this frontal lobe parallel processing module.

Upper Paleolithic Technologies

Although blade-based lithic technologies occurred throughout the MSA/MP (*72–74*, *85*), more sophisticated ones appeared around 50 ka in East Africa and the Levant (*85*, *86*). Blade production substantially increases the number of usable sharp edges that can be obtained from a core. Standardized blade blanks were shaped into a diverse array of functionally and stylistically distinct tool types (Fig. 4), often as components of tools of greater complexity (*81*). Of greater significance are ground, polished, drilled, and perforated bone, ivory, antler, shell, and stone, shaped into projectiles, harpoons, buttons, awls, needles, and ornaments. Such artifacts are extraordinarily rare in MP/MSA sites but are a consistent feature of Upper Paleolithic (UP) and Later Stone Age (LSA) sites after 40 ka (*72*, *76*). Bone, antler, and ivory are far less brittle than stone and make very reliable, durable armatures for projectile weapons (*87*). The spear thrower dramatically extended the power and velocity of a projectile, transforming a short-range attack weapon into a deadly missile. Traces of more perishable materials, including string and woven fibers that may have been made into nets, ropes, bags, and clothing are also well documented (*88*). These innovations are among many that signify modern human behavior, including art, ornamentation, symbolism, ritual burial, sophisticated architecture, land use planning, resource exploitation, and strategic social alliances, and may have originated in Africa during the late MSA/MP (*72*, *86*). Among the important consequences of this diverse new technological repertoire were increases in population density, reflected indirectly by the genetic structure of living human populations (*89*) and by intensified exploitation of small prey (*90*, *91*); expansion to higher, colder latitudes and altitudes (*76*); the dispersal of modern humans from Africa to Eurasia and Australia (by watercraft) 50 to 70 ka (*92*); and the accelerated extinction of Late Pleistocene megafauna (*93*) and archaic humans (*86*).

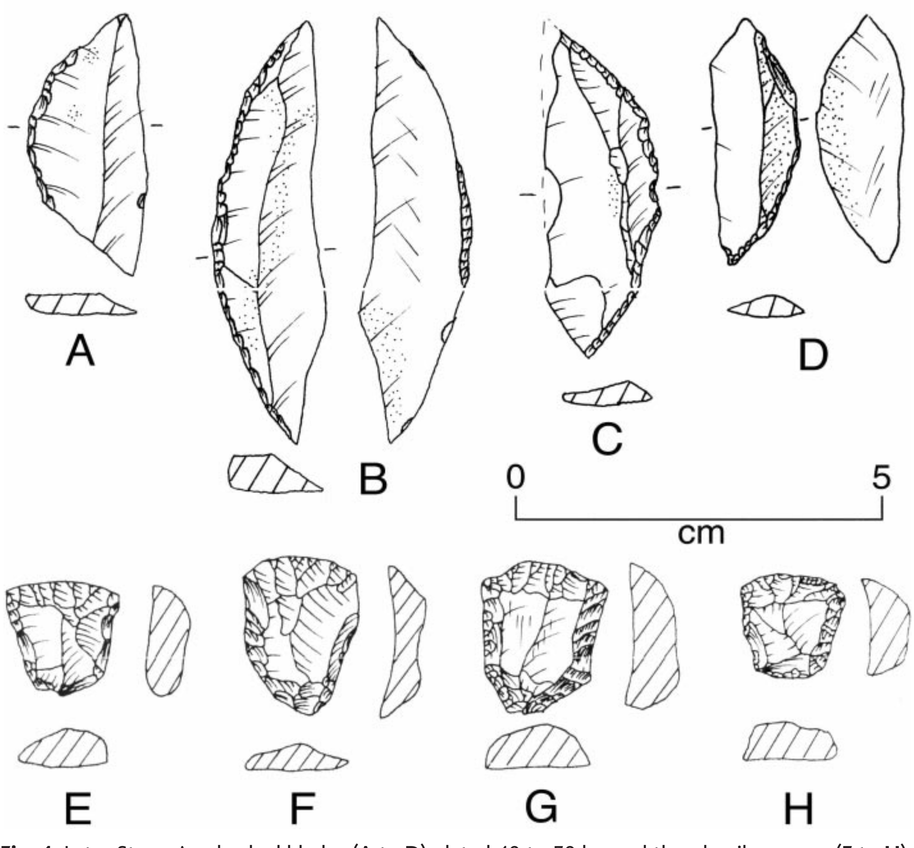

Fig. 4. Later Stone Age backed blades (**A** to **D**), dated 40 to 50 ka, and thumbnail scrapers (**E** to **H**), dated 35 to 40 ka, from Enkapune Ya Muto rockshelter, Kenya (*86*). The stippling on (A) to (D) indicates red ochre residues, probably from mastic. (D) was hafted parallel to the long axis with the sharp edge exposed.

Conclusion

The Oldowan and Acheulean industrial complexes are remarkable for their slow pace of progress between 2.5 and 0.3 Ma and for limited mobility and regional interaction. Distances of stone tool raw materials from their geological sources are rarely more than 10 km in the Oldowan and 20 km in the Acheulean (*94*), indicating very small home ranges. The proportions of materials originating from 40 to >300 km away increase during the late MP/MSA and early UP/LSA (*95*, *96*), suggesting larger home ranges and regional interaction and exchange networks that could have facilitated long-distance population movements. Did the challenges posed by the increasingly variable, severe, and risky environments of glacial/interglacial cycles over the past 800,000 years (*97–99*), as well as more dramatic short-term climatic events (*100*), influence behavioral and biological evolution? Or were changes increasingly autocatalytic, driven by language and by cultural systems of knowledge and understanding of nature and society? With the appearance of near-modern brain size, anatomy, and perhaps of grammatical language ~0.3 Ma, the pace quickens exponentially, suggesting the latter. *Ex terra ad astra*: A mere 12,000 years separate the first bow and arrow (*87*) from the International Space Station.

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