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Older Than the Oldowan? Rethinking the Emergence of Hominin Tool Use

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Intentionally modified stone tools first appear in the hominin archeological record about 2.5 mya. Their appearance has been variously interpreted as marking the onset of tool use by hominins or, less restrictively, the origin of hominin lithic technology.[1,2] Although the 2.5 mya date has persisted for two decades, several related but distinct questions about the origin and evolution of hominin tool use remain to be answered: Did hominins use tools before 2.5 mya? Did hominins use unmodified stones as tools before 2.5 mya? Does the earliest appearance of stone tools in the archeological record represent the earliest use of intentionally modified stones as tools?

Using information from primatology, functional morphology, phylogeny, archeology, and paleoanthropology, we argue that before 2.5 mya hominins may have used tools, including unmodified and possibly modified stone tools (Fig. 1). We consider several scenarios to explain why stone tool manufacture and use might not have left archeological traces prior to 2.5 mya and conclude by suggesting means to test our hypotheses.

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THE EARLIEST KNOWN DIRECT EVIDENCE OF HOMININ TOOL USE

Research on the evolution of tool-based behavior in hominins focuses on modified stone tools and fossilized faunal remains showing wear consistent with tool use. Here, tool use is defined according to Beck[3]: "The external employment of an unattached environmental object to alter . . . another object . . . when the user holds or carries the tool during or just prior to use . . . " (p. 10). "Modified" stone tools are those that have been intentionally modified. "Hominin" refers to members of the human clade or, in other words, components of the lineage that separated from the last common ancestor of *Homo* and *Pan* spp. 8 to 5 mya, and that persist as *Homo sapiens*.[4]

The earliest known tools are modified stone tools belonging to the Oldowan Industry and dating to about 2.5 to 2.0 mya (Table 1). Most Oldowan tools, however, have been recovered from sites dating from 2 to 1.5 mya, and are known primarily from localized occurrences often containing hundreds or even thousands of stone artifacts and associated fossil specimens.[5] Low-density sites with fewer than 100 stone artifacts, referred to as scatters, have also been described.[6] The artifacts range from well-made flakes with clear striking platforms, bulbs of percussion, and dorsal scars indicative of multiple prior flake removals from the core[7] to amorphous lumps and shattered fragments of exotic raw materials.[8]

Hard-hammer percussion, the most frequent technique used to manufacture Oldowan-type tools, apparently involved striking a hand-held hammer stone against a hand-held core.[9] However, it is likely that some Oldowan tools were made by placing a core against a substrate and then striking it with another stone or by striking or throwing a stone against a hard surface.[9] Microwear analyses suggest that some Oldowan tools were used to process large vertebrates by cutting meat from bone or, using percussion techniques, to gain access to bone marrow.[10,11] Other tools may have been used for digging[9] or for cutting wood and siliceous plant tissues.[11,12] Oldowan tools have been described in detail elsewhere.[13,14]

When stone tools are used to process large vertebrates, they often leave distinctive patterns of damage on the fossilized remains.[15,16] Therefore, faunal remains showing modifications inconsistent with natural breakage but consistent with stone tool use provide indirect evidence of stone tool use.[17] Currently, the earliest such evidence also dates to about 2.5 mya.[17]

Bone tools dating to 2 to 1.5 mya have also been found in both East and Southern Africa.[14,18] Although the bones are not extensively modified,

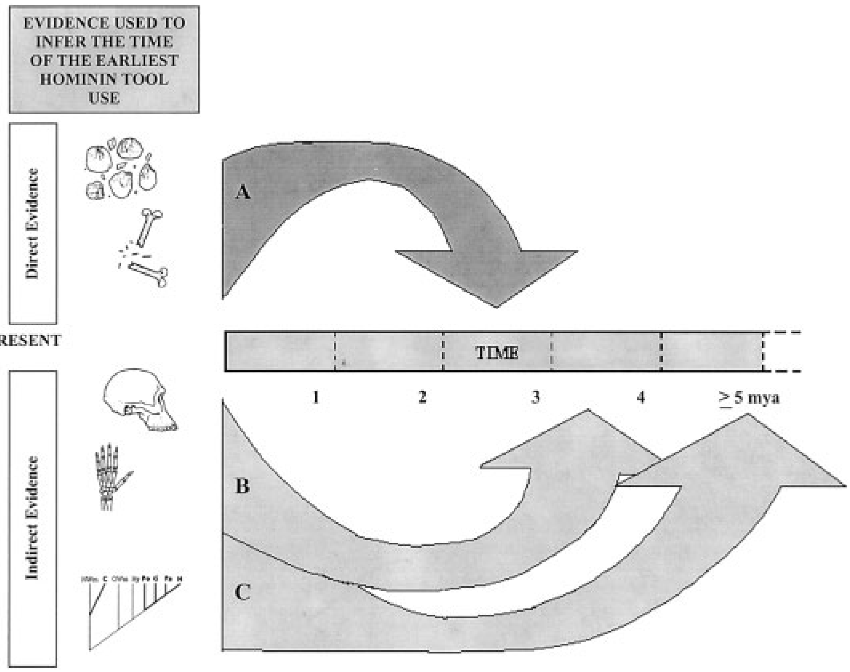

Figure 1. Estimations of the earliest hominin tool use using various lines of evidence. This figure represents the estimated time of the earliest hominin tool use using three different sources of evidence. The Direct Evidence of tool use is represented by accumulated modified stone tools, bone tools, and percussion or cut marks on bones that survive to the present in the fossil or archeological record, the earliest known dating to about 2.5 mya (arrow A). Arrow B represents anatomical traits (such as a relatively large brain and manipulative hands) from the hominin fossil record that are consistent with, correlated with, or necessary for primate tool use, including stone-tool use (modified and unmodified). The earliest known hominins (about 3.2 mya) for which we have appropriate anatomical data have an anatomy consistent with tool use, possibly including modified stone-tool use. Because anatomical evidence necessary for determining relative brain size and hand morphology are currently not available for earlier hominins, this date may change as more information becomes available. Arrow C represents the estimated time of the earliest hominin tool use (comparable to that observed among great apes, including unmodified stone-tool use) derived using phylogenetic inference (see Fig. 2). The related event is the split between the panins and hominins; that is, the origin of the hominin clade at about 8 to 5 mya. Thus, 5 mya is a conservative estimate.

macroscopic use-wear patterns and microscopic analyses suggest that the bones were most likely used for digging, cutting, or termite fishing.[18,19] Additionally, some early modified stone tools exhibit wear patterns typical of woodworking, suggesting that wooden tools may also have been part of the early hominin toolkit.[12]

Although it is practical to use early Oldowan tools and fossilized faunal remains having wear consistent with tool use as the earliest indication of hominin tool use we might be better served by turning to more indirect methods. Alternative sources of evidence about the origin of language are routinely explored, for example through information regarding vocal and neural anatomy that is consistent with language,[21] ape-language studies,[22] and archeological and ethnographic studies of symbolic behavior.[23] We suggest that, in much the same way, researchers interested in the evolution of tool use benefit by looking beyond traditional lines of evidence. Potentially important indirect evidence comes from primatology, functional anatomy, and molecular phylogenetics.

DID HOMININS USE TOOLS BEFORE 2.5 MYA?

There is now compelling evidence that the hominins and *Pan* are sister clades[24,25] (but see Satla, Klein, and Takahata,[26] for a more cautious but still supportive interpretation of the data). Because the great apes (especially chimpanzees) and humans use tools, parsimony suggests that the last common ancestor of *Pan* and *Homo* (8 to 5 mya) used tools[27–30] (see Box 1 and Fig. 2).

Because most early hominins are associated with nonarid environments such as riparian forests, densely wooded habitats, and mosaic habitats with some grasslands,[31,32] we assume that such high-energy, difficult-to-access foods such as nuts, social insects, and honey were available. We further assume that raw materials for making tools, among them sticks, grasses, leaves, and appropriate stones, were also available to all early hominins. There is little doubt that hominins, given a body mass comparable to or greater than that of chimpanzees, had the strength to perform a variety of tool-using activities, including the manufacture and use of stone tools. (Capuchins, which, at 2 to 3 kg, are about the size of a house cat, are able to make stone tools). Thus, we assume that the ecological impetus, raw materials, and necessary strength for tool use were available to early hominins from the time of the split between hominins and panins.

TABLE 1. Early Oldowan Tool Sites (Older Than 2 My)

Site or Locality Name	Region, Country	Age	References
Gona	Hadar, Ethiopia	2.6–2.5 My	50
Bouri[a]	Middle Awash, Ethiopia	c. 2.5 My	17
Shungura Formation (Members E and F)	Omo River Valley, Ethiopia	2.4–2.34 My	8
Lokalalei	West Lake Turkana, Kenya	2.34 My	7
Senga 5A[b]	Semliki Valley, Democratic Republic of Congo	c. 2.3 My	105
Kada Hadar Member	Hadar, Ethiopia	c. 2.33 My	36
KS-1 and KS-2	Kanjera South, Kenya	c. 2.2 My	32

[a] Faunal remains with cut marks, but no stone tools, were recovered from this site.
[b] The date and associations for this site are not secure.[13]

Box 1. Nonhuman Primate Tool Use

Tool use has been observed in a wide variety of animal taxa (see Beck[3] for a review), but here we focus on tool use by nonhuman primates here for two specific reasons. First, their close relationship to modern humans makes their tool use particularly relevant to the evolution of tool use by hominins. Second, the type of tool use found among most animals is context-specific and is represented by stereotyped behaviors that show little variation among individuals and populations. "Intelligent" tool use, exhibited by some primates, refers to a more flexible tool-use repertoire[29] and is the type of tool use argued to have important implications for hominin evolution.

Tool manufacture or use by a variety of primates has been reported, but habitual tool use is largely limited to free-ranging and captive *Pongo pygmaeus, Pan troglodytes,* and captive *Pan paniscus, Gorilla gorilla,* and capuchin monkeys (*Cebus* spp.). "Habitual" refers to tool-use events that are repeated by several individuals in a population over time.[67] Chimpanzees (*Pan troglodytes*) in all known populations spontaneously and habitually manufacture and use tools. Some of the most common types of tool use observed in free-ranging chimpanzees are the manufacture and use of probing tools made of sticks, bark, grass, or other vegetation[68] and the manufacture and use of leaf sponges[69] (Fig. 1). (For review, see McGrew[28] and Whiten and co-workers[63]). Several West African chimpanzee populations also use stone and wooden hammers and anvils to access a variety of nuts,[27,69–71] but chimpanzees have never been observed intentionally modifying stone tools in the wild. Recent research has demonstrated that chimpanzee stone-tool use leaves a signal, in the form of stone and plant remains, that is recoverable in the archeological record.[38]

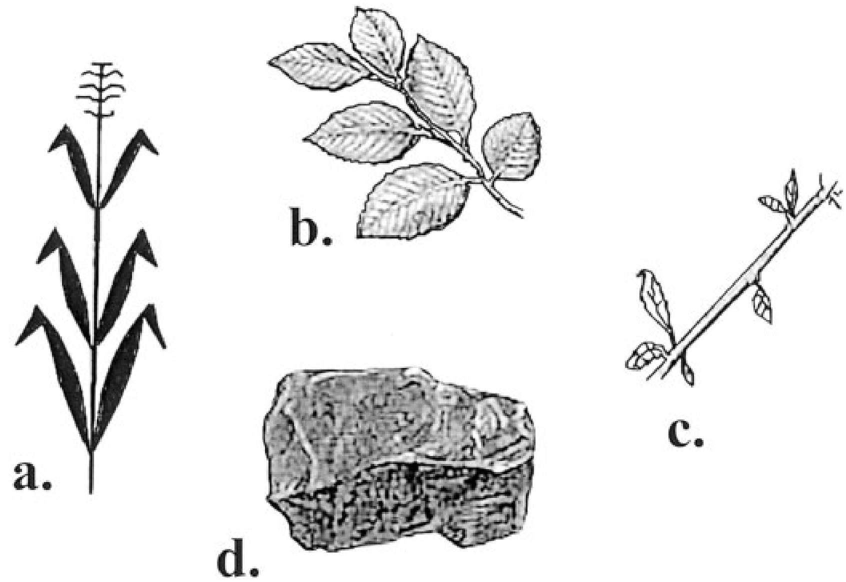

Figure 1. Raw material of tools commonly used by free-ranging chimpanzees. These schematic drawings of materials that chimpanzees commonly use as tools are not to scale and do not necessarily represent the exact species or type actually used: **a.** Grass, used as probing tools, may be intentionally modified before use; **b.** Leaves, when chewed or folded, are used as leaf sponges or "napkins"; **c.** Sticks, used as tools for probing for social insects, honey, and such, may be intentionally modified before use; **d.** Stone, used as hammer or anvil to open hard-shelled nuts, may be unintentionally modified during use.

Some free-ranging orangutan (*Pongo pygmaeus*) populations habitually and spontaneously manufacture and use hammers, probes, and scrapers made of sticks.[72,73] Gorillas (*Gorilla gorilla*) and bonobos (*Pan paniscus*) have yet to be seen habitually manufacturing or using tools in the wild (but see Ingmanson[74]). However, all of the great apes, including orangutans,[75] gorillas,[76] chimpanzees,[77] and bonobos,[78] readily use tools in captivity.

Capuchins (*Cebus* spp.), medium-sized New World monkeys, are the only nonhominoid primates known to use tools habitually. Studies have shown that captive capuchins manufacture and use "ape-equivalent" types of tools.[67,79] Currently, wild capuchins are known to use tools only rarely. The few such observations that have been made include, for example, use of a wooden club by *C. capucinus,*[80,81] wooden probing tools and "leaf-wrapping" by *C. capucinus,*[62,82] hammers and anvils by *C. apella,*[83,84] and leaf containers by *C. albifrons.*[85] As with chimpanzees[28,63] and orangutans,[72,73] complex foraging behaviors, including tool use, are known to vary across capuchin populations.[62]

Several captive primates have been taught to make modified stone tools, among them *Cebus apella,*[86] *Pan paniscus,*[41,87] and *Pongo pygmaeus.*[88] In the *Pan* and *Cebus* studies, although the animals were only shown hard-hammer percussion techniques, the primates not only acquired these techniques, but also developed innovative techniques involving pounding and throwing cores against hard substrates to produce flakes. To date, no stone-tool-making nonhuman primate has attained the skill to produce the acute-edged bifacial and polyhedral cores associated with many Oldowan sites[87] or the multiple sequential flake removals seen even in some of the earliest known Oldowan assemblages.[7]

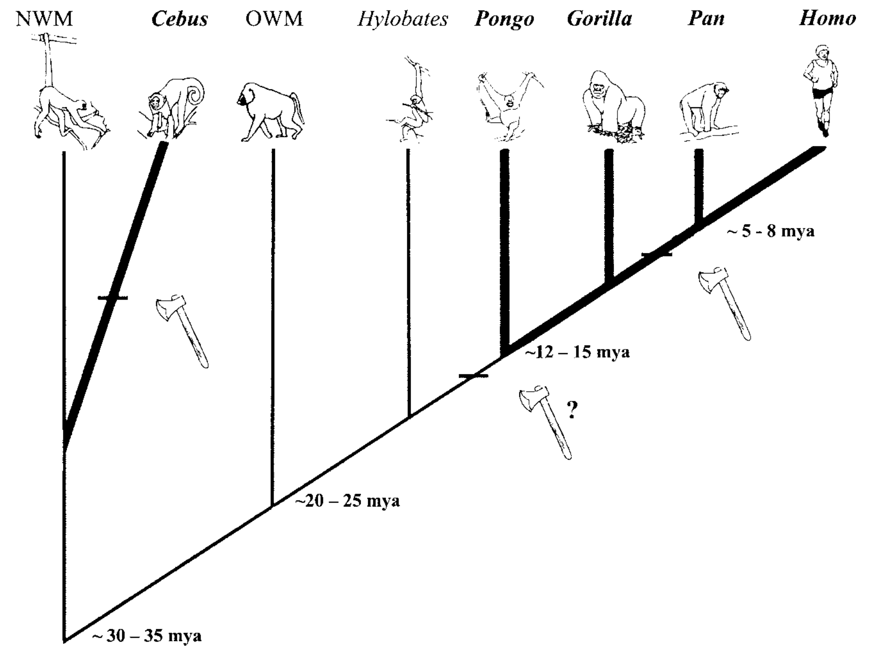

Figure 2. Abbreviated primate phylogeny. Living primate genera that habitually use tools are in bold (see Box 1). NWM = New World monkeys, OWM = Old World monkeys. The axe logos are placed where the principle of parsimony suggests that tool use most likely evolved in primates. The question mark next to the axe logo implies that the data supporting placement of the axe are suggestive but not as compelling as the data supporting placement of the other axe logos.

Data from fossilized cranial remains and endocasts indicate that hominins living before the evolution of *Homo habilis sensu stricto,* perhaps as early as 3.2 mya, had relative brain sizes as large as or larger than those of modern great apes.[33–35] *Australopithecus africanus,* dating to about 2.75 mya, exhibited encephalization greater than that in modern apes (specimens Sts 17 and Sts 5),[34] while *A. afarensis,* dating to about 3.2 mya,[36] had brains comparable in size to those of *Pan* (specimen AL 162-28).[33] The limited information available about brain morphology indicates that the brains of early hominins resembled those of extant hominoids in many ways and had, as well, some similarities to the brains of modern humans.[37] At present, data on brain size and morphology are not available from the hominin fossil record before 3.2 mya. However, the fact that by this time the hominin brain was comparable to that of great apes in discernible morphology and as large in relative size suggests that hominins were sufficiently intelligent to use tools.

The relatively comprehensive sample of early hominin hand bones (from the AL 333 site) attributed to *A. afarensis* date to about 3.2 mya and show morphological features consistent with greater manipulative ability than modern apes have (Box 2). Based on this and the fact that all hominoids have hands capable of fine manipulation, including tool use, it is logical to assume that the earliest hominins also possessed hands capable of tool use.

At this time, the fossil evidence alone does not lead to a definitive conclusion on the absence or presence of tool use among our early ancestors, but it does imply that hominin tool use was possible by at least 3.2 mya. The combination of primatological, phylogenetic, and fossil evidence suggests that hominins living before 2.5 mya almost certainly had the capacity to use tools (Fig. 1).

DID HOMININS USE UNMODIFIED STONES AS TOOLS BEFORE 2.5 MYA?

Chimpanzees in West Africa living under natural conditions habitually use stone tools as hammers and anvils (Box 1). Therefore, because *Pan* and hominins are almost certainly sister clades, it is probable that the common ancestor of chimpanzees and humans used stones as tools, though they may not have intentionally modified them (Fig. 2). Furthermore, given that the use of stone tools as hammers and anvils is within the realm of free-ranging chimpanzees and capuchins, the arguments regarding the morphological requirements necessary for unmodified stone tool use are similar to those in the preceding section. Most notably, by at least 3.2 mya, *A. afarensis* appears to have been capable of manipulative skills that exceeded those of extant apes. In addition, the hominin brain was comparable to that of chimpanzees in morphology and relative size, suggesting that early hominins were sufficiently intelligent to use stones as hammers and anvils.

Unlike tools made of more ephemeral material like sticks and leaves, stone tools are likely to be preserved in the archeological record. The recent excavation of a chimpanzee stone-tool site in West Africa provides one model for how an unintentionally modified stone-tool assemblage might appear in the paleo-archeological record.[38] The chimpanzee assemblage shows some similarities to a few early Oldowan sites, for example in terms of stone piece density. However, the lack of cores and the high proportion of stone shatter smaller than 20 mm in the chimpanzee assemblage suggests that such sites may not be easily recognizable in the archeological record. However, the chimpanzee assemblage does include a few flakes with sharp edges. Because stone hammer use can unintentionally create sharp-edged stones, it is possible that this type of stone-tool use preceded the intentional production of stone flakes. As Sigaut[39] noted, Pitt-Rivers proposed a similar connection 125 years ago. In 1875, Pitt-Rivers, as quoted by Sigaut[39] extrapolated from early reports of chimpanzees using unmodified stone implements to crack nuts to suggest that:

> "In using stones as hammers, they would occasionally split- . . . The creature would be led to perform the motions which had been found effectual in splitting the stone before applying it to

> the purposes for which it was to be used . . . And we may therefore consider it probable that should any evidences of [hu]man[s] be hereafter discovered in [M]iocene beds, they will be associated with . . . large crude flakes" (that is, single-flaked tools) (p. 32–33).

Therefore, Pitt-Rivers argued that long before Oldowan tools were known, early modified stone tools were most likely preceded by stone tools similar to those used by modern chimpanzees. Phylogenetic and available fossil evidence are consistent with this notion.

DOES THE EARLIEST APPEARANCE OF STONE TOOLS IN THE ARCHEOLOGICAL RECORD REPRESENT THE EARLIEST USE OF INTENTIONALLY MODIFIED STONES AS TOOLS?

Much research has been devoted to characterizing morphological traits that are consistent with improved hard-hammer percussion abilities (see Box 2). Hard-hammer percussion is thought to be particularly important for the creation of flake and core tools because it allows for much greater control than do other flaking techniques such as throwing a stone against a hard surface. However, the requisite morphological refinements in the hand would enhance the performance of a variety of manipulative behaviors involving a variety of materials. Therefore, morphological factors that improve the ability to use the hard-hammer percussion technique (for example, those associated with grip capabilities and stress resistance) observed in fossil hominins would be consistent with stone-tool modification and use,[40–42] but might also be related to other manipulative tasks.

Early hominins predating the stone-tool record have some of the human-like adaptations for manual dexterity that characterize the earliest known stone tool-makers, *Homo habilis s. s.* and *Paranthropus robustus*. Hand fossils attributed to *A. africanus* boast a broad apical tuft, apical spines, a marked insertion site for flexor pollicis longus on the pollical distal phalanx,[43] a third metacarpal designed for stability,[43,44] and a flat distal radius.[4,45] These human-like characteristics suggest that the hand of *A. africanus* dating to 2.4 to 3 mya was adapted for manipulation to a degree not evident in earlier hominins (Box 2). Furthermore, faunal remains with stone tool cut marks have been found coeval with another australopithecine, the recently discovered taxon *Australopithecus garhi*, which dates to about 2.5 mya.[17]

The hand of *A. afarensis* is more primitive than those of the later hominins,[46] but it is still derived relative to that of apes in features that are important for manipulation.[47] Most importantly, the ratio of the thumb length to finger length resembles that of the modern human hand more closely than it does the hands of extant nonhuman hominoids.[48] The hand of *A. afarensis* also features a second metacarpal with the distinctly human ability to rotate for grasping and cupping the hand.[48] It has been argued that the second metacarpal of *A. afarensis* has characteristics that would facilitate the firm pad-to-side pinch and three-jaw chuck grips that modern humans often use when replicating and using Oldowan tools.[47] These features were present by about 3.2 mya. Thus, adaptations for manual dexterity appear well before the earliest known evidence of modified stone tools. These adaptations suggest that early hominins used or made tools, possibly including modified stone tools, or engaged in other manipulative tasks, such as food preparation, that are more complex than those practiced by extant great apes before the earliest-known stone tool record. It remains to be seen whether or not these features appear in hominins earlier than *A. afarensis*.

The recent excavation of a chimpanzee stone-tool site in West Africa provides one model for how an unintentionally modified stone-tool assemblage might appear in the paleo-archeological record.

The proposal that hominins manufactured and used modified stone tools before 2.5 mya is indirectly supported by some of the earliest-known Oldowan tools. A subset of early Oldowan tools, although crude compared to later tool industries, includes well-made flakes with clear striking platforms, bulbs of percussion, and dorsal scars indicative of multiple prior flake removals from the core, implying that their makers understood the fracture mechanics of stone.[7,36,49,50] At some of the earliest known Oldowan sites such as Gona[50] and Lokalalei,[7] the stone assemblages show relatively elaborate debitage schemes in which various raw materials were gathered from stream beds, transported throughout the landscape, and reduced as part of a complete stone-reduction sequence in which as many as thirty flakes were removed from a single core. In addition, a few of the flakes were retouched. Therefore, it is unlikely that these tools represent the first attempts at stone knapping, the earliest lithic technology, or the first hominin tools.

FUTURE DIRECTIONS

If hominins used tools, possibly including modified stone tools, before 2.5 mya, why is there no evidence of that tool use? Tools made of ephemeral material such as wood and grass are unlikely to have been preserved. Furthermore, unmodified stone tool use, if similar to the chimpanzee case, may be difficult to recognize in the archeological record. But why has no direct evidence of modified stone-tool use before 2.5 mya been found? At many of the sites that contain the earliest Oldowan assemblages, earlier deposits are devoid of flaked stone. For example, in places like Hadar, in East Africa, abundant fossil hominin remains have been found in deposits dated between 3.4 and 2.8 mya, but stone artifacts do not appear until 2.3 mya.[13] Tools dating to about 2.5 mya have been found at nearby Gona[50] and

Box 2. Morphology Associated With Primate Tool Use

The behavioral convergence between the great apes and capuchins (see Box 1) helps identify the minimum morphological requirements for primate tool use. The great apes have relatively opposable thumbs and thus are able to make pad-to-pad contact between the index finger and thumb, although not as completely as humans can. They are also capable of a wide range of manipulative behaviors.[40,87] Capuchins have a pseudo-opposable thumb[89] and are capable of both power and precision grips.[90] In addition, the great apes and capuchins have large brains relative to body size when compared with other nonhuman primates.[91]

A bonobo, an orangutan, and several capuchin monkeys have made and used modified stone tools in captivity. Thus, these species possess the minimum morphological requirements for stone-tool use and manufacture. However, these and other primates with comparable hand morphology do not habitually make stone tools. Thus, the fact that all hominins known to date have these "minimum" requirements shows that they have the ability to modify stone but does not provide evidence of such behavior. Hard-hammer percussion, which provides greater control than do cruder flaking techniques such as throwing a stone against a hard surface, almost certainly has different morphological requirements than the stone modification by nonhuman primates seen to date.

Some of the oldest known fossil hand bones, those of *A. afarensis* and *A. africanus,* exhibit derived features that are related to enhanced manipulative function as compared to that of apes. The hand of *A. afarensis* (for example, those from the AL 333 site) has a second metacarpal with an asymmetric head and volar-proximal projection of the joint surface, features that are thought to allow slight pronation of the proximal phalanx to accommodate object shape during grasp; relatively transverse orientations of the second metacarpal joints with the capitate and trapezium, which are thought to allow more flexion and pronation of the metacarpal; and, most importantly, a high thumb-to-finger-length ratio. Hand fossils belonging to *A. africanus* have skeletal features such as broad distal phalangeal tuberosities and ungual spines, which are associated with broad, fleshy fingertips that improve object handling. They also show an insertion area on the pollical distal phalanx, which is evidence of the presence of a flexor pollicis longus muscle; that muscle, which is rare in great apes but present in humans, is important for strength in thumb flexion. Also, the styloid process of the third metacarpal in *A. africanus* might have helped to stabilize its articulation with the carpal bones and transfer stresses associated with tool-related activities. The flat distal radius of *A. africanus* probably increased the range of wrist extension, which is important for hand and finger movements. Thus, before the oldest current evidence of stone tools, fossil hominin hands had derived features related to enhanced manipulative skills.

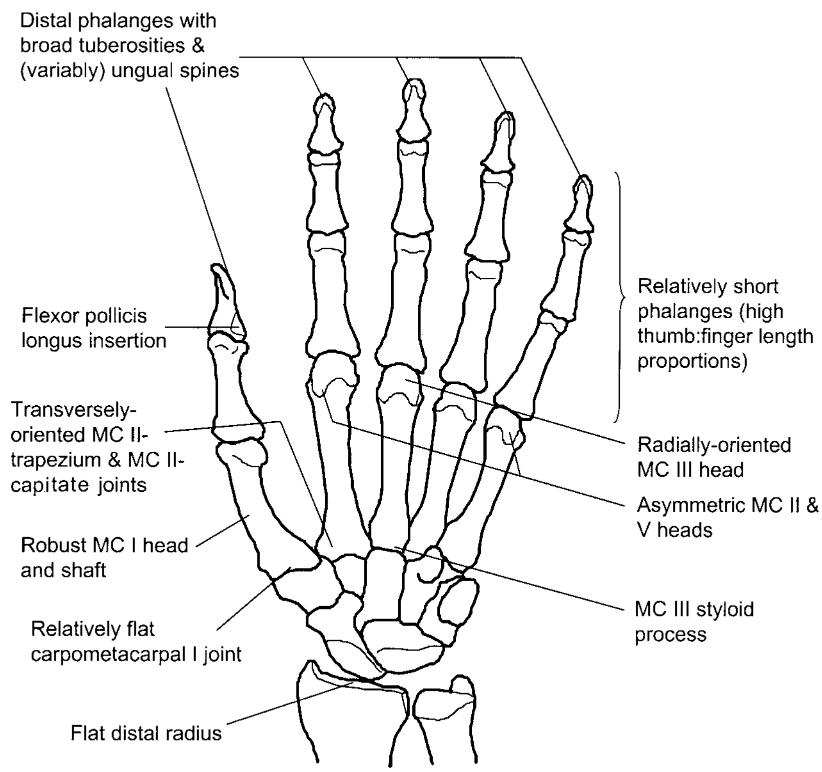

Figure 1. Hand anatomy related to manipulative skills and stress resistance. Many of these features have been related to tool use and manufacture, but might also be related to other uses of the hand (for example, manipulation involved in food processing). See text and Box 2 for the likely functional significance of these features and their presence in some early hominin taxa. MC = metacarpal.

Hand bones attributed to *Homo habilis s.s.* (for example, OH 7), which are coeval with Oldowan tools,[92,93] also have broad distal phalangeal tuberosities[94] and show evidence of a flexor pollicis longus tendon[92] (but see Susman and Creel[94]). The hand of *H. habilis s.s.* also resembles that of humans in having a broader, less contoured pollical carpo-metacarpal joint than does the ape hand.[94,95] This feature is thought to improve stress dissipation across the joint. Evidence tentatively suggests that the hand of *H. habilis s.s.* had relatively human-like thumb-to-finger proportions.[96] These features suggest that *H. habilis s.s.* had grasping abilities consistent with complex manipulation including stone-tool manufacture using hard-hammer percussion.

Box 2. Morphology Associated With Primate Tool Use (continued)

Although the connection is not universally accepted (see Trinkaus and Long[97]) the robust australopith *Paranthropus* (or *Australopithecus*) *robustus* has been linked with the Oldowan tools at Swartkrans.[98,99] The Swartkrans fossils exhibit broad distal phalangeal tuberosities, a site for insertion of the flexor pollicis longus,[98] a broad pollical metacarpal head and shaft with a human-like base,[99] and a relatively mobile, human-like wrist joint.[45,100] All of these features are consistent with adaptations for manual dexterity and power that would be useful for the manufacture and use of stone tools. If the Swartkrans hand bones are attributable to *P. robustus,* then its hand was as well, if not better, adapted for manipulation than was that of *H. habilis s.s.*[98] However, the morphological factors that facilitate hard-hammer percussion techniques might also facilitate other manipulative tasks.[40,41]

faunal remains with tool-cut marks dating to approximately 2.5 mya have been found at Bouri, in the Middle Awash, coeval with *Australopithecus garhi.*[17] Similarly, in Southern Africa, sites such as Sterkfontein and Makapansgat have yielded hominin fossils dated to between 3 and 2.5 mya,[51,52] but flaked stone tools do not appear in these areas until about 2 mya.[53]

Direct evidence older than 2.5 mya may be absent because hominins were not using any tools, or at least modified stone tools, before 2.5 mya. For example, the earliest known appearance of modified stone tools could have coincided with a dietary shift, such as a new reliance on large vertebrates. The processing of large vertebrates is a behavior not seen in any living nonhuman primate, although a variety of nonhuman primates do eat vertebrate prey smaller than 10 kg. Therefore, it is possible that modified stone-tool use was first developed to aid in the processing of large prey, although microwear analyses indicate that early Oldowan tools were also used in a variety of ways not directly related to the processing of vertebrates.

It is also possible, however, that around 2.5 mya changes occurred that caused behaviors that previously had been archeologically "invisible" to become archeologically "visible" (see Box 3). The chance of finding a lone artifact in situ, especially one with only one or two flakes struck, is like finding the proverbial needle in a haystack. Moreover, a single-surface stone artifact is difficult to date and could easily be dismissed due to the possibility of contamination from later sites (for example, see Howell, Haesaerts, and de Heinzelin[54]). In other words, hominins could have been manufacturing and using modified stone tools long before the earliest currently known Oldowan tools. However, if these tools were not concentrated in time and space (especially if they involved lone artifacts with minimal flaking episodes), they would essentially be archeologically "invisible" (see also Klein[13]).

Several lines of potential evidence may, in the future, help to test the hypothesis that hominins used tools, including stone tools, before 2.5 mya. Obviously, the discovery of modified and unmodified stone and nonlithic tools dating to before 2.5 mya in the fossil record would support the hypothesis. However, there are two minimum requirements for finding such tools: they have to exist, and they must be recognizable as artifacts.

Specific use-wear patterns on stones not associated with deliberate flaking would provide evidence of hominin tool use before 2.5 mya.[9] For example, the repeated use of stone hammers and anvils to open hard nuts produces distinctive use-wear patterns on both the hammers and anvils that can be recognized in the archeological record.[27,55,56] In addition, the stone assemblage recently excavated at a chimpanzee nut-cracking site in West Africa demonstrates that low-density, unintentionally modified stone tool assemblages are recoverable through excavation.[38] It also provides one model for what a pre-Oldowan stone tool technology might look like in the archeological record.

Faunal remains exhibiting cut or percussion marks due to modified stone-tool use dating to before 2.5 mya would also provide support for the hypothesis that modified stone tools were being used before 2.5 mya.[16,17] Current collection strategies for pre-2.5 mya sites emphasize identifiable faunal remains, but a shift toward recovery of samples of unidentifiable long bone fragments would increase chances of finding cut marks or percussion before 2.5 mya. These types of data, unless directly associated with primate remains, would not indicate which species made and used the tools, but they would support the hypothesis that stone tool use existed before 2.5 mya.

Methods for obtaining data on tool use independent of the recovery of modified tools and bones processed by tools would also be helpful. One promising avenue of research involves examining aspects of hand skeletal morphology that are sensitive to biomechanical stresses.[57] Some aspects of bone, such as cortical robusticity,[58] trabecular architecture,[59] and shaft curvature[60] model and remodel in response to biomechanical loads and are thus sensitive to daily use. Ways in which the biomechanics of tool-making and tool use are distinct from other uses of the hand[42,61] suggest that significant tool-related activities may leave stress signatures in the hand skeleton. Therefore, important areas of future research include improving our understanding of how tool-related activities are biomechanically distinct from other (for example, locomotor) hand uses and investigating what osteological evidence might provide a durable record of an individual's biomechanical history.

An important point that researchers interested in hominin tool use should keep in mind is that because tool use varies intraspecifically among primate populations,[62,63] uniform tool use across hominin populations should not be expected. Therefore, absence of evidence of a specific type of tool use

Box 3. Site Formation Models to Explain the "Sudden" Appearance of Modified Stone Tools 2.5 Mya

Oldowan tools have almost always been found in large concentrations, leading several researchers to suggest that early lithic sites represent areas where stone tools were concentrated by early hominins in both space and time (for example, home bases, butchering sites, and "workshops" for making tools).[13,101,102] In most of these cases, the hypothesis is that when hominins began to make modified stone tools they accumulated the tools in the same geographic area over a relatively short period (see Fig. 1, A → C), resulting in the conclusion that the early "accumulated" sites represent the origin of modified stone tool use. But this interpretation is only one of several possible explanations of the evidence (Fig. 1).

For example, Potts[102] suggested that hominins may have manufactured and used stone tools before 2.5 mya, but that the tools do not show up in the fossil record because they were not cached before 2.5 mya (see Fig. 1, B → C). Another scenario for the appearance of stone tools in the archeological record at 2.5 mya has been proposed by Brooks and Laden,[103] who attribute it to climate change that led to an alteration in habitat and available foods that changed the way hominins used the landscape (Fig. 1, D).

Brooks and Laden[103] argue that the differences in the stability of certain landscape features can make the difference between artifact-producing behaviors being "visible" and "invisible" in the archeological record. For example, trees have a much shorter life span than do geologic formations like rock outcrops. Let us assume that two populations engage in a shade-dependent, artifact-producing behavior at similar frequencies. One population lives in an environment with a limited number of shade trees and no other options for shade (for example, a savanna), while the other population lives in an area with no trees but a similar number of areas where shade is provided by rock outcrops (for example, a desert). Thus, shade trees and rocky outcrops represent the focal points for the artifact-producing behavior. Because rock outcrops have a much longer potential life span than trees do, behaviors would be concentrated around the rock outcrops over a much longer period than they would be around the trees. Therefore, landscape use around the rocks would be much more stable over a geologic time scale, and would produce sites with higher artifact density than would the

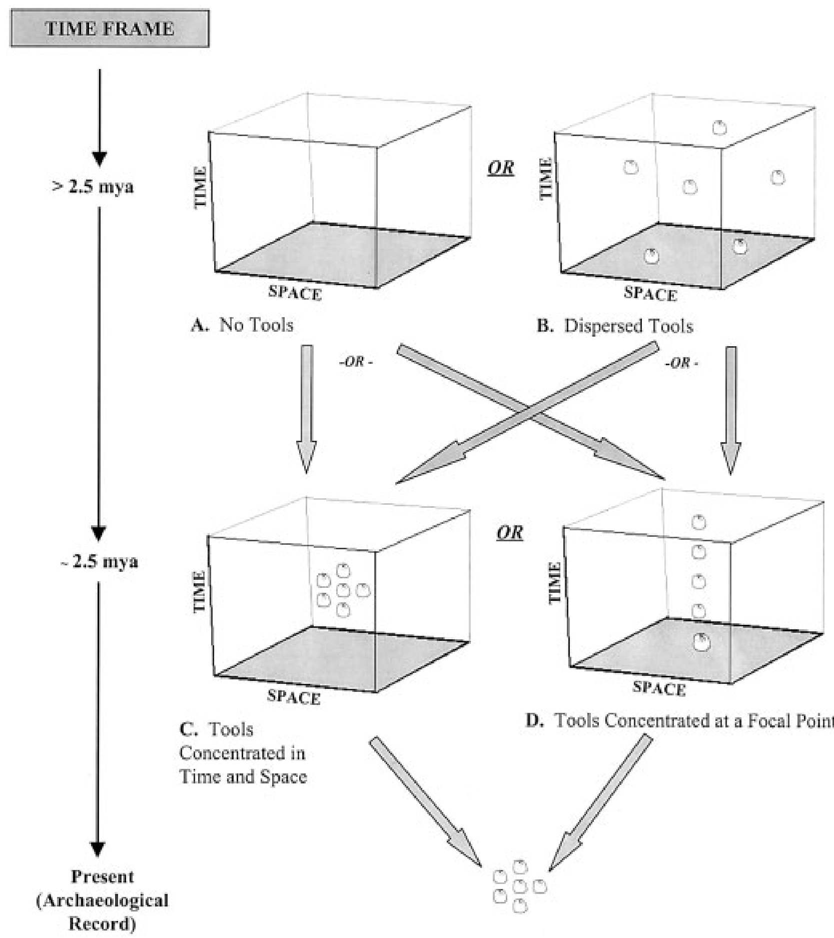

Figure 1. Site formation models that could explain the "sudden" appearance of modified stone tools at 2.5 mya. This figure represents a range of site-formation scenarios consistent with accumulated stone-tool sites in the archeological record dating to 2.5 mya. The figure is separated into three main time frames: before 2.5 mya (an unspecified period between 5 and 2.5 mya), about 2.5 mya, and the present. Time is represented vertically in the entire figure, and space is represented three-dimensionally in the subfigures A–D. The rounded objects represent modified stone tools. The tools to the right of the Present time frame represent an Oldowan tool "site." A: Modified stone tools were not made or used by hominins at the specified time frame; B: Modified stone tools were distributed at low density in both time and space; C: Modified stone tools were concentrated in both time and space; D: Modified stone tools were deposited at low density per use event, but at the same location over a long period of time. These are schematic figures demonstrating general distribution patterns; the represented tools are not necessarily to scale in time or space. Before 2.5 mya, A and B are possible, and either situation could lead to C or D at about 2.5 mya. Any one of the four scenarios (A to C, A to D, B to C, or B to D) could produce the accumulation of modified stone tools represented by Oldowan sites in the contemporary archeological record.

Box 3. Site Formation Models to Explain the "Sudden" Appearance of Modified Stone Tools 2.5 Mya (continued)

more dispersed sites associated with trees. Thus, the sites around the outcrops would be more "visible" in the archeological record, and would mimic cached sites. This pattern is supported by ethnoarcheological data from two regions in Africa, the Kalahari Desert in Western Botswana and the Ituri Forest in the Democratic Republic of Congo.

These site-formation scenarios do not exhaust the possible scenarios for concentrations of stone tools in the early archeological record. They do show, however, that 2.5 mya may not mark the emergence of modified stone tool use, but instead may be the first time that the behavior became archeologically visible.

at one hominin site does not necessarily imply that other populations within the same species did not use that specific tool type. In addition, as recent research has demonstrated, crucial information about human origins may come from outside East and Southern Africa, such as the Sahel and rainforests of Central and West Africa.[64,65] An archeological record dominated by evidence from East and Southern Africa may not fully reflect the technological chronology of hominin populations elsewhere on that continent.

CONCLUSIONS

Regarding the questions posed in this paper:

1. Did hominins use tools before 2.5 mya? Because panins and hominins are sister clades, parsimony suggests the last common ancestor of *Pan* and *Homo* (8 to 5 mya) used tools. Furthermore, the earliest available data on hominin brain size and morphology and hand morphology imply that hominin tool use was possible by at least 3.2 mya. The combination of primatological, phylogenetic, and fossil evidence suggests that hominins living as early as 8 to 5 mya, and almost certainly by 3.2 mya, had the capacity to use tools.

2. Did hominins use unmodified stones as tools before 2.5 mya? Because the use of unintentionally modified stone tools is within the realm of free-ranging chimpanzees and capuchins, the evidence of the possible use of unmodified stone tools by early hominins is similar to that for question 1. Therefore, the combination of primatological, phylogenetic, and fossil evidence suggests that hominins living as early as 8 to 5 mya, and almost certainly by 3.2 mya, had the capacity to use unmodified stones as tools.

3. Does the earliest appearance of stone tools in the archeological record represent the earliest use of intentionally modified stones as tools? The relative complexity of a subset of early Oldowan tools implies that hominins most likely had experience modifying stone tools before 2.6 mya. Morphological evidence older than 2.6 mya does not preclude stone tool manufacture.

Therefore, the available direct evidence of tool use in the archeological record potentially underestimates the origin of hominin tool use by millions of years (Fig. 1). What we may be detecting at 2.5 mya is an intensification or spatial reorganization of previous tool-related behaviors resulting from ecological exigency, related or unrelated to new dietary opportunities such as a drier climate or the consumption of large mammals by hominins.

Early modified stone tools provide insights into the behavior and ecology of early hominin taxa. However, placing all our emphasis on the stone tools and the products of tool use that have been recovered from the fossil or archeological record to the exclusion of alternative sources of evidence may strongly skew reconstructions of early hominin life ways. Moreover, by focusing on lithic evidence we inevitably constrain investigations of the origin and evolution of tool use by hominins. Our questions are restricted to the evolution of the earliest known, accumulated modified stone tools. This omits important aspects of the evolution of tool use and the emergence of modified stone tool use.

This review has re-evaluated the way we study the origin and evolution of hominin tool use. It also encourages integrative studies of early hominin life ways, and has drawn attention to nontraditional lines of research that may help refute or support the hypothesis that hominins used tools, possibly including modified stone tools, before 2.5 mya. Evidence from a range of disciplines will provide a more comprehensive understanding of the evolution of tool use by hominins than will an approach that is limited to lithic evidence and the products of stone tool use. With characteristic prescience several decades ago, Isaac[66] implied that researchers need to look beyond the conventional archeological record for evidence about the evolution of human behavior. He stated, in regard to stone tools, that "we need to assess the limits to the amount of blood that can realistically be squeezed from these stones" (p. 5).

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