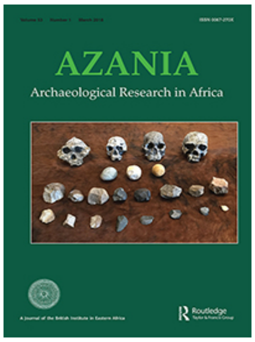

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An overview of the cognitive implications of the Oldowan Industrial Complex

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ABSTRACT

This paper focuses on the empirical evidence for the cognitive abilities of early hominins of the Oldowan Industrial Complex (*c.* ≥2.6 to 1.4 Mya) on the African continent. It profiles various researchers' approaches to and inferences about the cognitive abilities of Oldowan (Mode 1) toolmakers, based on the excavated archaeological evidence, primate models, experimental archaeology and neuroimaging techniques. Although there is a great deal of variation with regard to how to interpret such evidence, a variety of archaeological and palaeoneurological evidence indicates that Oldowan hominins represent a stage of technological and cognitive complexity not seen in modern great apes (chimpanzees, bonobos, gorillas, orangutans), but transitional between a modern ape-like cognition and that of later *Homo* (*erectus*, *heidelbergensis*, *sapiens*). Prevailing evidence and evolutionary models suggest that this new evolutionary stage entailed the growing elaboration of a problem-solving, technological niche that incorporated manufactured tools as a critical component of adaptation, especially to enhance food procurement and processing, as well as enhancements and greater complexity in social behaviours and communication.

RESUMÉ

Cet article examine les données empiriques sur les capacités cognitives des premiers hominins du complexe industriel d'Oldowan (environ ≥2,6 à 1,4 Mya) sur le continent africain. Nous présentons les différentes approches et inférences des chercheurs concernant les capacités cognitives de ceux qui créèrent les outils de l'Oldowan (Mode 1), se basant les données archéologiques, les modèles de primatologie, l'archéologie expérimentale et les techniques de neuro-imagerie. Bien qu'il existe beaucoup de variabilité dans l'interprétation de ces données, un type de données archéologiques et paléonévrologiques indique que les homininés Oldowans représentent un stade de complexité technologique et cognitive que l'on n'observe pas chez les grands singes modernes (chimpanzés, bonobos, gorilles, orangs-outans). Il s'agit plutôt d'un stade transitoire entre la cognition des *Homo* tardifs (*erectus, heidelbergensis, sapiens*) et celle des grands singes actuels. Les données existantes et les modèles évolutionnaires

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suggèrent que cette nouvelle étape évolutive impliqua l'élaboration croissante d'un créneau technologique et de résolution des problèmes. Ce créneau incorpora les outils manufacturés comme un élément essentiel de l'adaptation — en particulier pour améliorer l'acquisition et le traitement des aliments — et un renforcement et un accroissement de la complexité dans les comportements et la communication.

Introduction

The African continent documents the emergence of bipedal hominins, the earliest evidence of stone technology, the origins of the larger-brained genus *Homo*, the earliest Acheulean handaxes and cleavers, early (if not the earliest) evidence of *Homo erectus* and the earliest evidence of anatomically modern humans (Cartmill and Smith 2009). It seems clear that the human lineage evolved from a cognitive state similar to that of modern apes some five million years ago and subsequently went through a series of biological and technological stages leading to the modern human condition.

In this paper we discuss the range of approaches used to investigate Oldowan hominin cognition as this can be gleaned from the African prehistoric record, focusing on the major researchers and their theoretical and methodological approaches. At the outset, we provide a brief summary and update of the Oldowan Industrial Complex, including the location and ages of major sites and contemporary fossil hominins. We then organise our overview of the major approaches used to infer human cognitive evolution into four major sections: a) primate studies; b) the archaeological evidence; c) experimental archaeology; and d) brain imaging studies.

The Oldowan Industrial Complex

The Oldowan Industrial Complex (L. Leakey 1936; M. Leakey 1971, 1975; G. Isaac 1976a) comprises the earliest major group of archaeological sites showing very simple stone technologies, dating back to at least 2.6-2.5 Mya (Semaw *et al.* 1997; Semaw 2006). These technologies tend to be characterised by simple core forms made on cobbles or chunks (choppers, discoids, polyhedrons, heavy-duty scrapers), battered percussors (hammerstones, spheroids, subspheroids) retouched flakes (scrapers, awls), a range of débitage (flakes, broken flakes and fragments) and unmodified stones (manuports) that appear to have been carried to sites (Figure 1). Where preservation is good, faunal remains are often associated as well. Beginning about 1.76 Mya, these Oldowan industries are also contemporary with the rise of handaxe/cleaver/pick industries assigned to the Acheulean Industrial Complex (Lepre *et al.* 2011). Simple Oldowan-like stone technologies continue to be found through time in many parts of the Old World, even into the Holocene in some cases, but the Oldowan *sensu stricto* is usually applied to these simple core/flake industries older than one million years or so.

Mary Leakey (1971, 1975) divided these early sites at the type site of Olduvai Gorge, Tanzania, into the chopper-dominated (and usually lava-dominated) "Oldowan" and, beginning in Bed II, the "Developed Oldowan", which usually takes the form of quartz/quartzite-dominated assemblages with higher proportions of subspheroids/spheroids and retouched flakes and fragments and sometime low frequencies of bifaces (handaxes

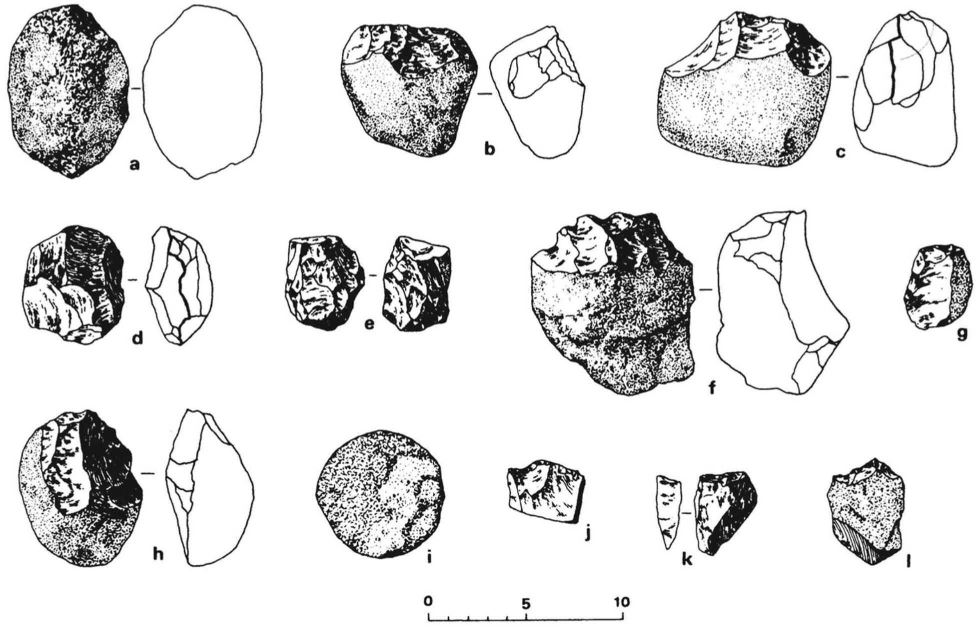

Figure 1. A range of Oldowan artefacts from Olduvai Gorge, using Mary Leakey's (1971) typology: a) battered hammerstone; b) unifacial chopper; c) bifacial chopper; d) discoid; e) polyhedron; f) heavy-duty scraper; g) light-duty retouched scraper; h) "proto-biface"; i) battered spheroid; j) utilised flake; k) burin; l) awl.

or cleavers). Glynn Isaac (1976a) subsumed both the Oldowan and Developed Oldowan into the Oldowan Industrial Complex. Some researchers, such as de la Torre (2005), have argued that "Developed Oldowan" sites contemporaneous with early Acheulean handaxe/cleaver occurrences should be considered to be a facies of the Acheulean.

Other researchers, such as de Lumley *et al.* (2009), have suggested using the term "Pre-Oldowan" or "Archaic Oldowan" for many of the sites that are older than ~1.9 Mya. The stone assemblages from these sites (e.g. Gona, Lokalalei and Fejej) tend to be characterised by simple cores (choppers etc.) that are often preponderantly unifacially flaked, few retouched elements, a lack of spheroids and subspheroids and low transport distances of raw materials.

The Oldowan is by no means a homogeneous entity. Expanding research has shown that sites can show significant differences in assemblage composition and context. Reasons for such variability could include: functional activities; cognitive and biomechanical abilities or constraints; cultural norms; skill levels in a given individual or population; raw material quality, size, shape, proximity and availability; modes of flaking (hard hammer percussion, bipolar technique, anvil technique etc.); stages of reduction represented; discard patterns; proximity to water and other resources; safety from predators; and taphonomic factors such as bone preservation and degree of water disturbance, among others (Toth and Schick 2011).

Claims for early stone technology

During the past decade, two localities have yielded possible evidence of even earlier stone tool manufacture and/or use: Dikika in Ethiopia and Lomekwi 3 in Kenya. These sites are considerably older (by some 800,000 to 700,000 years) than the next oldest Palaeolithic sites at Gona in Ethiopia (Semaw *et al.* 1997, Semaw 2006). If these claims are correct, then it would show that Pliocene hominins were experimenting with stone technology much sooner than has previously been suspected and that they may have no real cultural continuity with later sites. It will be very important to validate/invalidate these claims in the future.

At Dikika, researchers have described surface modification on fossil mammalian bones found on the surface at that locality as cut-mark modification from the use of sharp-edged stone tools, dating to about 3.4 Mya (McPherron *et al.* 2010). As previously noted, if true, this would greatly extend the time range of the archaeological record and of the Palaeolithic, although no stone artefacts were recovered from either the surface or the excavation. However, some researchers have questioned whether these marks on bones were actually hominin-induced, or whether they might have been the product of trampling (Domínguez-Rodrigo 2016) or possibly the product of crocodile predation and consumption (Njau 2012; Pante *et al.* 2016).

Recently, surface and excavated artefacts from the site of Lomekwi 3, West Turkana, northern Kenya, have been reported to date to 3.3 Mya (Harmand *et al.* 2015). Lomekwi 3 is an anomaly both chronologically and technologically (unusually large cores and flakes) and its researchers have proposed a pre-Oldowan "Lomekwian Industry" based on this relatively small sample of artefacts. There has been some question as to whether these artefacts are truly *in situ* in these ancient sediments (Domínguez-Rodrigo 2016; Frank Brown, senior Turkana geologist, pers. comm.) and, although the artefactual nature of this assemblage seems clear, it will be critical to demonstrate that these materials are clearly *in situ* in these 3.3 million-year-old deposits rather than being more recent artefacts redeposited against the older sediments. Even if this site does prove to be *in situ*, it is still debatable, however, whether this technology warrants its own, unique industrial designation or whether it can be subsumed within the Oldowan Industrial Complex.

Major summaries of the Oldowan Industrial Complex that readers may wish to consult include those by G. Isaac (1982, 1984), Harris (1983), Toth (1985a), Toth and Schick (1986, 2005, 2006a, 2006b, 2009b), B. Isaac (1989), Potts (1991), Harris and Capaldo (1993), Schick and Toth (1993, 2009a, 2013), Plummer (2004), Carbonell *et al.* (2008), Braun and Hovers (2008), Klein (2009, Chapter 4), Whiten *et al.* (2009), de la Torre (2011a), Braun (2012), Domínguez-Rodrigo (2012) and Hovers (2012).

Major localities of the Oldowan Industrial Complex and associated hominins

Oldowan sites are found in North, East and South Africa. In North and East Africa, they occur in open-air contexts, usually in lake margin or riverine settings, whereas in South Africa they are found in karstic limestone cave deposits (Table 1 and Figure 2). Note that many of these localities, such as Olduvai Gorge, Tanzania, and East Turkana, Kenya, have numerous sites spanning a considerable amount of time and that some localities, such as Konso Gardula, Ethiopia, and Peninj, Tanzania, are well known for early Acheulean industries, but also have Oldowan-like sites lacking handaxes and cleavers.

Hominins that potentially overlap in time with Oldowan sites are listed in Table 2. Observations regarding the potential association of hominin taxa with archaeological

Table 1. Major Oldowan localities in Africa. Some localities, such as Olduvai Gorge and Koobi Fora, have a large number of sites.

Locality	Country	Age (Mya)	References
Gona	Ethiopia	2.6-2.5 2.2-2.1	Roche and Tiercelin 1980; Harris 1983; Semaw *et al.* 1997, 2003; Semaw 2000, 2006; Stout *et al.* 2005, 2010; Toth *et al.* 2006
Hadar	Ethiopia	2.3	Kimbel *et al.* 1996; Hovers *et al.* 2002; Hovers 2003, 2009
Konso Gardula	Ethiopia	1.7	Suwa *et al.* 1997; Beyene *et al.* 2015
Melka Kunture	Ethiopia	1.7	Chevaillon *et al.* 1979 ; Morgan *et al.* 2012; Galloti and Mussi 2015
Gadeb	Ethiopia		Clark 1987; de la Torre 2011b
Fejej	Ethiopia	1.96	Asfaw *et al.* 1991; de Lumley and Beyene 2004
Omo Valley	Ethiopia	2.4-2.3	Chevaillon 1970; Chevaillon and Chevaillon 1976; Merrick 1976; Howell *et al.* 1987; de la Torre 2004
Koobi Fora (East Turkana)	Kenya	1.9-1.3	G. Isaac 1997
Lomekwi 3 (West Turkana)	Kenya	3.3	Lewis and Harmand 2016
Lokalalei (West Turkana)	Kenya	2.34	Kibunjia *et al.* 1992; Roche and Kibunjia 1994; Roche *et al.* 1999; Brown and Gathago 2002; Delagnes and Roche 2005
Chesowanja	Kenya	1.42	Harris and Gowlett 1980; Gowlett *et al.* 1981
Kanjera	Kenya	2.2	Ditchfield *et al.* 1999; Plummer *et al.* 1999; Braun *et al.* 2009
Olduvai Gorge	Tanzania	2.0-1.35	M. Leakey 1971, 1975; Peters and Blumenschine 1995, 1996; Blumenschine and Peters 1998; de la Torre and Mora 2005; Domínguez-Rodrigo *et al.* 2007; Blumenschine *et al.* 2012
Peninj	Tanzania	1.6-1.4	Domínguez-Rodrigo *et al.* 2002, 2009; de la Torre *et al.* 2003
Nyabusosi	Uganda	1.5	Texier 1993, 1995
Sterkfontein	South Africa	~2.0-1.4	Kuman 1994, 2005; Field 1999; Pickering *et al.* 2000
Swartkrans	South Africa	~1.8-1.0	Brain 1981; Clark 1991; Field 1999; Kuman 2005
Kromdraai	South Africa	~2.0-1.0	Kuman *et al.* 1997; Field 1999; Kuman 2005
Ain Hanech El-Kherba	Algeria	1.8	Sahnouni *et al.* 1996, 1997, 2002; Sahnouni and de Heinzelin 1998; Sahnouni 2005, 2006; Sahnouni and van der Made 2009
Ain Boucherit	Algeria	2.2	Sahnouni and van der Made 2009

localities are noted below. Holloway *et al.* (2004) and Cartmill and Smith (2009) provide more details regarding these taxa.

If the early date (3.3 Mya) holds for Lomekwi 3, Kenya, then the hominin taxa broadly contemporaneous with this assemblage in East Africa would include:

- *Australopithecus afarensis* (cranial capacity range 380-430 cm^3) ~3.9 to 2.9 Mya;
- *Kenyanthropus platyops* (cranial capacity of 450 cm^3, but based on a single cranial specimen) ~3.5 to 3.2 Mya.

The cranial capacity of these taxa is within the range of that seen in modern chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).

The earliest Gona sites, between 2.6 and 2.5 Mya, are contemporaneous in East Africa with:

- *Austalopithecus garhi* (cranial capacity of 450 cm^3, but based on a single cranial specimen);

Figure 2. Distribution of the major Oldowan localities in Africa: 1 Ain Boucherit, Ain Hanech and El-Kherba, Algeria; 2 Gona and Hadar, Ethiopia; 3 Melka Kunturé, Ethiopia; 4 Gadeb, Ethiopia; 5 Omo, Ethiopia; 6 Fejej, Ethiopia; 7 East Turkana (Koobi Fora), Kenya; 8 West Turkana, Kenya; 9 Nyabusosi, Uganda; 10 Chesowanja, Kenya; 11 Kanjera, Kenya; 12 Peninj, Tanzania; 13 Olduvai Gorge, Tanzania; 14 Sterkfontein, Swartkrans and Kromdraai, South Africa.

- *Paranthropus aethiopicus* (cranial capacity of 410 cm^3, likewise based on a single cranial specimen);
- *Homo sp.* — a mandible from Ledi-Geraru, Ethiopia, dated to 2.8 Mya and assigned to early *Homo* (Villmoare *et al.* 2015), plus a maxilla from Hadar, also in Ethiopia (Kimbel *et al.* 1997), dated to 2.33 Mya, would indicate the presence of some form of early *Homo* in this region during this time period, although its cranial capacity is unknown.

The cranial capacities of *A. garhi* and *P. aethiopicus* are, once again, within the range seen in chimpanzees and bonobos.

Table 2. Hominin taxa that could have potentially produced Oldowan artefactual assemblages. Taxa with an asterisk are known to be associated with Oldowan tools in nearby contemporaneous sediments or at actual Oldowan sites. Oldowan tools are associated with *Homo* sp. at Hadar at 2.3 Ma. If the early date of the Lomekwi 3 artefacts holds at 3.3 Ma, then *Australopithecus afarensis* and *Kenyanthropus platyops* would have been the contemporary hominins in that region of East Africa. By ~1.2 Ma, the genus *Paranthropus* appears to have gone extinct, leaving *Homo erectus* as the surviving hominin taxon. There is no *a priori* reason why *Paranthropus* could not have produced Oldowan tools; however, its massive posterior dentition and smaller cranical capacity relative to *Homo* makes it more likely that the genus *Homo* was the major tool-making lineage.

Taxon	Region	Age (Mya)	Cranial capacity (cm^3)	Key sites
Australopithecus afarensis	East Africa	3.9-2.9	380-430	Hadar, Ethiopia; Laetoli, Tanzania
Kenyanthropus platyops	East Africa	3.5-3.2	450	Lomekwi, West Turkana, Kenya
Australopithecus africanus	South Africa	3.3-2.1	400-500	Taung, Sterkfontein, Makapansgat and Gladysvale (South Africa)
Homo sp.*	East Africa	2.8-2.3	(Only jaws and teeth)	Hadar and Ledi-Geraru, Ethiopia
Paranthropus aethiopicus	East Africa	2.7-2.5	410	West Turkana, Kenya
Australopithecus garhi	East Africa	2.5	450	Bouri and Middle Awash, Ethiopia
*Paranthropus boisei**	East Africa	2.4-1.4	500-550	Olduvai Gorge, Tanzania; East Turkana, Kenya; Konso Gardula, Ethiopia
*Homo habilis**	East and South Africa	2.1-1.5	510-690	Olduvai Gorge, Tanzania; East Turkana, Kenya
Australopithecus sediba	South Africa	2.0	420-450	Malapa, South Africa
*Paranthropus robustus**	South Africa	2.0-1.2	410-530	Swartkrans, Kromdraai and Drimolen, South Africa
*Homo rudolfensis**	East Africa	1.9	750	East Turkana, Kenya
Early *Homo erectus/ ergaster**	East and South Africa	1.9-1.0	800-1070	Olduvai Gorge, Tanzania; Koobi Fora, Kenya; Daka, Ethiopia; Buia, Eritrea; Swartkrans, South Africa

In South Africa the Gona sites are contemporaneous with:

- *Australopithecus africanus* (cranial capacities ranging from 400 to 500 cm^3) ~3.3 to 2.1 Mya, but so far no definitive stone artefacts have been found associated with this species.

Other Oldowan sites (spanning 2.3-1.4 Mya) are contemporaneous in East Africa with:

- *Paranthropus boisei* (cranial capacity range 500-550 cm^3) ~ 2.4-1.4 Mya;
- *Homo rudolfensis* (cranial capacity of ~750 cm^3, but based on a single cranial specimen) ~2.4-1.9 Ma;
- *Homo habilis* (cranial capacity range 510-690 cm^3) ~2.1 to 1.5 Ma;
- *Homo ergaster/erectus* (cranial capacity range 800-1070 cm^3) ~1.9 to <1.0 Ma.

In South Africa Oldowan sites would be contemporary with:

- *Australopithecus africanus* (later forms, 2.3 to 2.1 Mya), but without any known association with stone tools;

- *Australopithecus sediba* (cranial capacity 420-450 cm^3) ~1.98 Mya, but without any known association with stone tools;
- *Paranthropus robustus* (cranial capacities ranging from 410 to 530 cm^3) ~2.0 to 1.2 Mya;
- *Homo habilis* (see above);
- *Homo erectus* (see above).

Assuming that they do indeed all derive from one taxon, the remarkable range of variation seen in the penecontemporaneous early *Homo* fossil skulls from Dmanisi, Georgia, dating to 1.8 Mya suggests to some that our division of early *Homo* skulls from Africa into the taxa *H. rudolfensis*, *H. habilis* and *H. ergaster/erectus* may be an instance of "over-splitting" (Lordkipanidze *et al.* 2013). Taking a contrary position, some researchers would, for example, lump *H. rudolfensis* and *H. habilis* into one taxon (e.g. Miller 1991, 2000; Tobias 1991; Wolpoff 1999).

By 1.2 Mya, it appears that the genus *Paranthropus* (the "robust australopithecines") had become extinct, leaving the only known surviving hominin taxon, the larger-brained *Homo erectus*, to continue on the evolutionary path that eventually led to modern humans. During the duration of the Oldowan (from at least 2.6 Mya to 1.4 Mya), it appears that brain size had effectively doubled by the time of *Homo erectus* (Figures 3 and 4).

Approaches to human cognitive evolution

This article primarily focuses on *cognitive archaeology* or, as it is sometimes called "the archaeology of mind", which is an approach that attempts to assess the level of intelligence, problem solving abilities and symbolic behaviour of past hominins by examining the patterns that can be gleaned from the archaeological record through evolutionary time. We give examples of the various approaches adopted by those researchers who have made attempts to assess levels of cognitive complexity. Overviews and examples of cognitive archaeological studies include those by G. Isaac (1976b, 1986), Wynn (1989, 1991, 2002), Boëda *et al.* (1990), Gibson and Ingold (1993), Mellars and Gibson (1996), Mithen (1996, 2006), Noble and Davidson (1996), McBrearty and Brooks (2000), Ambrose (2001), Stout (2002), d'Errico (2003), Coolidge and Wynn (2009), de Beaune *et al.* (2009), Renfrew *et al.* (2009), Davidson (2010, in press), Toth and Schick (2010), Wynn and Coolidge (2010), Stout *et al.* (2011), Gowlett *et al.* (2012), Mahaney (2015) and Overmann and Coolidge (in press).

Primate considerations

McGrew (1992, 2004) has documented in detail chimpanzee tool manufacture and use, as well as a range of other cultural patterns (e.g. hand-clasping). Wynn and McGrew (1989) have argued that the range of behaviours that can be inferred from the Oldowan are cognitively and behaviourally comparable to those of modern apes in terms of range of tool types, their roles in subsistence behaviour and patterns of manufacture, with two notable exceptions: a) Oldowan hominins appear to have carried stone for several kilometres from its geological sources; and b) Oldowan hominins were moving into an adaptive niche

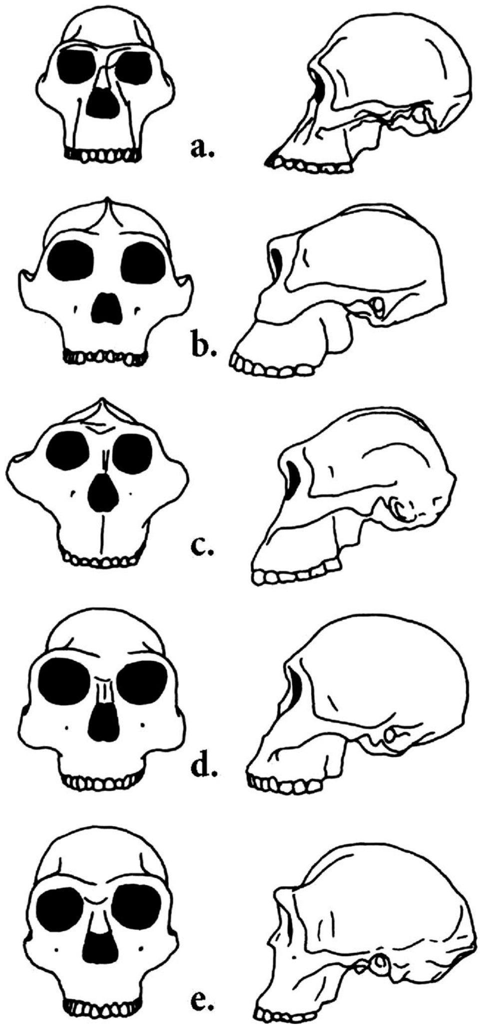

Figure 3. Schematic crania of some of the hominin fossil forms contemporaneous with the Oldowan: a) *Australopithecus africanus*; b) *Paranthropus robustus*; c) *Paranthropus boisei*; d) early *Homo* (*Homo rudolfensis*); e) *Homo ergaster/erectus* (from Toth and Schick 1986: 4).

where they began to compete with large carnivores for access to animal carcasses. This subject was subsequently revisited (Wynn *et al.* 2011) with similar conclusions and citing even more types of ape tool behaviour that had been documented over the intervening period.

In a study of the spatial patterning of chimpanzee nesting and feeding debris in Congo-Kinshasa, Sept (1992) argued that the pattern produced (i.e. one made from organic materials that would have little or no visibility in the prehistoric record) was in many ways analogous with the spatial patterning at Oldowan localities. She questioned whether interpretations of Oldowan "home bases" might, in fact, have been the product of hominins with behavioural capabilities similar to those of chimpanzees.

Whiten *et al.* (1999) undertook a major synthesis of the distribution of chimpanzee cultural traits in East and West Africa. They then used their database to examine the number

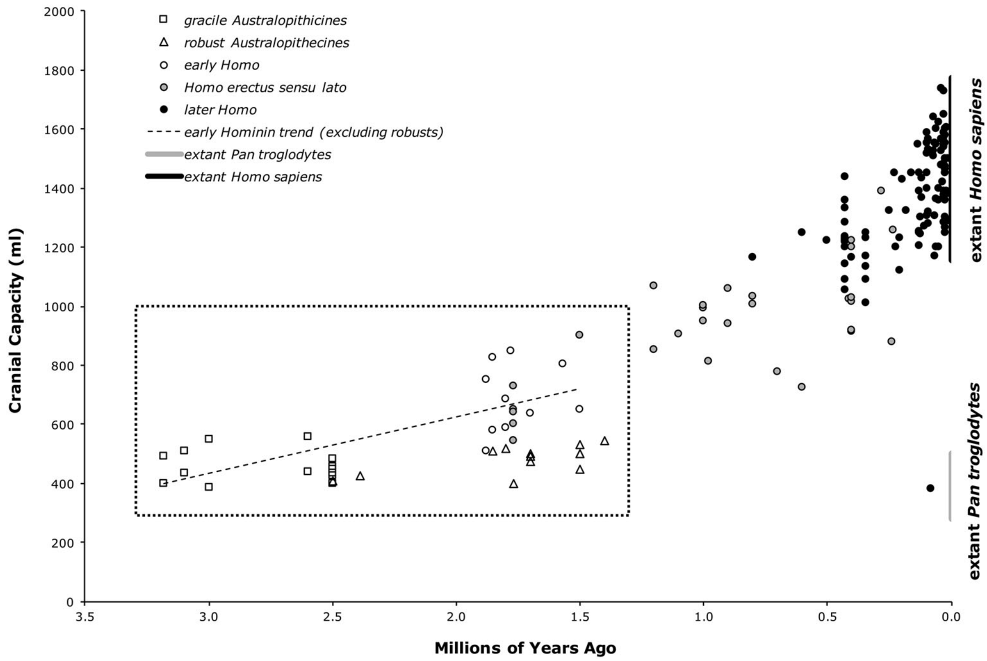

Figure 4. Hominin cranial capacities through time by taxa. The Oldowan time period considered here is outlined in the rectangle. The range of extant *Homo sapiens* and chimpanzees is at far right. Note that between 2.0 and 1.5 Ma there is a notable increase in cranial capacity of some of these hominin forms and that between 2.4 and 2.0 Ma there is a major gap in the fossil record of relatively complete hominin crania. Graph courtesy of Tom Schoenemann with data from Holloway *et al.* (2004), Schoenemann (2013), Arsuaga *et al.* (2014) and Sutikna *et al.* (2016).

of shared chimpanzee cultural traits relative to geographical proximity (see also Toth and Schick 2009b). At the subspecies level (western chimpanzees (*Pan troglodytes verus*); western chimpanzees (*P. t. schweinfurthii*)), there was a very strong correlation between the number of shared traits and the proximity of chimpanzee populations, suggesting strong regional spheres of shared culture, with half the shared traits dropping off between groups at distances of about 700 km. A similar pattern at the subspecies level was discerned by Lycett *et al.* (2007) based on a cladistic analysis of cultural traits.

In a long-term study of the toolmaking capabilities of bonobos using a combination of primatology and experimental archaeology (Toth *et al.* 1993, 2006; Schick *et al.* 1999; Savage-Rumbaugh and Fields 2006) two individuals (a male, Kanzi, and a female, Panbanisha) learned to flake lava, quartzite and flint and to use the flakes that they produced for cutting activities in order to access food rewards. It is clear that these African apes have the basic capabilities to flake stone through hard-hammer percussion and other techniques (such as throwing and the bipolar technique). In a comparative study of skill levels, the bonobos were given lava cobbles from the 2.6 million-year-old conglomerates at Gona (the same raw material that early hominins used), while representatives of modern humans also flaked these cobbles (Toth *et al.* 2006). Although the bonobos could flake the cobbles and produce usable flakes, they were clearly the out-group of the three samples: their cores were less heavily reduced, produced smaller flakes on average with steeper angles between the striking platform and the dorsal surface and showed heavy battering on edges from failed attempts to remove flakes with a hammerstone. The Gona cores and flakes were intermediate in skill levels between those of bonobos and modern humans, but much closer to the human sample. Interestingly, it appeared that the early stages of flaking were not represented at the Gona sites, indicating transport of partially flaked cores and percussors to these sites from some other locality for further reduction.

Mercader *et al.* (2002, 2007) have examined modern and excavated (*c.* 4300-year-old) chimpanzee nut-cracking activity areas in Ivory Coast, arguing for a "Chimpanzee Stone Age" that included nut-cracking hammers and anvils, as well as the (accidental) fractured debris resulting from these activities. They go on to argue that these materials are reminiscent (technologically and possibly also cognitively) of prehistoric Oldowan assemblages. It should be kept in mind, however, that Oldowan assemblages are, in contrast, clearly the result of the intentional controlled fracture of stone by Oldowan hominins. Carvalho *et al.* (2008) employed a *chaîne opératoire* approach to analyse chimpanzee nut-cracking activities and also suggested that they could identify organisational patterns (assemblage diversity, spatial patterning, tool transport) with affinities with the Oldowan. More recently, a special issue of the *Philosophical Transactions of the Royal Society B* (de la Torre and Hirata 2015) has highlighted a range of percussive technologies documented across a number of primate species and stressed a need to better understand the cognitive, anatomical and ecological constraints of such percussive behaviours, not only in stone tool-making but also in various food-processing activities.

Hunt (2006) has pointed out that in modern chimpanzee studies in the wild females use tools for processing foods more than males (e.g. nut-cracking, termite-fishing). He suggests that a similar pattern may have been the case with Oldowan hominins, with female hominins likely using tools in a wider variety of circumstances and extracting a greater percentage of their caloric intake with the use of tools than did males (although males may have been more involved in tool-related processing of animal carcasses). He further suggests that early stone toolmaking hominins were likely still partly arboreal in their food-gathering activities and for sleeping at night and avoiding predators.

Humans are unique in the animal world in having a very strong asymmetry in preferential handedness, with approximately 90% of the modern human population being right-handed for most tasks. It has been suggested (e.g. Holloway *et al.* 2004) that preferential right-handedness may be a product of the reorganisation of the hominin brain, with left-hemispherical laterality increasingly specialised for many language tasks, as well as for controlling the right hand. Asymmetries in hominin endocasts include the appearance of a "Broca's cap" in the left hemisphere. Examining chimpanzee tool use and hand preference/laterality, Marchant and colleagues (Marchant *et al.* 2005, 2010; Marchant 2015) found that there was no preferential handedness in chimpanzee populations, although individual chimpanzees often manifested left- or right-handedness. Marchant suggests that increased reliance on technology and emphasis on skill in human evolution favoured this bias toward right-handedness over time.

Analysis of patterns at Oldowan sites (primarily non-experimental)

Many of our insights into African Oldowan cognitive abilities come from the analysis of stone artefact assemblages and their context (for a succinct history of these approaches, see de la Torre 2011a). Experimental archaeology and other actualistic studies allow the researcher to see the possible relationships between *processes* and *products*, whereas in the prehistoric record we only see the products and have to deduce the processes.

Patterns in stone artefact assemblages at the early (2.6-2.5 Mya) sites at Gona, Ethiopia, have been interpreted as exhibiting a high level of knapping skills, although technological variation among three penecontemporary sites indicates variability in raw material selection and reduction strategies. Using similar knapping techniques, the strategies pursued show variability, particularly an emphasis on unifacial flaking at two of the sites compared to one on bifacial flaking at the third (Stout *et al.* 2010). This differentiation among flaking strategies was inferred to represent the influence of cultural transmission on these archaeological patterns.

Gona also provides evidence that Oldowan hominins preferentially selected higher-quality materials from rock sources. Stout *et al.* (2005) compared the range and frequency of raw materials represented at six Gona sites relative to their geological abundance in the nearby contemporaneous river gravels. They concluded that these early toolmakers were able to identify and preferentially select higher quality materials (finer-grained volcanic materials with fewer phenocrysts that could produce hard, sharp edges when flaked). They also highlighted the high quality of the trachyte raw material selected as a prominent rock type in the Gona artefact assemblages. In experiments with novice stone knappers, this trachyte was relatively easy to flake and beginning stone toolmakers readily produced flakes very similar to those in the Gona assemblages.

Hovers (2009) examined flaking "accidents" (e.g. stepped and hinged flakes seen on cores and the dorsal surfaces of flakes) at the site of A.L. 894, Hadar, Ethiopia, dating to ~2.36 Mya. She argues that such accidents are not necessarily a good proxy for knapping skill levels, as different stages of cobble reduction can produce markedly different frequencies of these incomplete flakes. On the other hand, there was evidence at this site that hominins could recover from such accidents and continue to remove potentially usable flakes from cores.

In a study of refitted stone artefacts at the 2.34 million-year-old site of Lokalalei 2C using a *chaîne opératoire* approach, Delagnes and Roche (2005) identified how the toolmakers had a well-developed mastery of knapping skills and techniques and, moreover, argued that the overall lithic assemblage shows 'planning and foresight in raw material procurement and management' (Delagnes and Roche 2005: 435). Approximately 40% of the cores at the site had refitting pieces, sometimes involving up to 39 refits per core, plus, in many instances, missing pieces in the core reduction, indicating possible transport away from the immediate site area. In addition, there is a pattern here of prior flake removals before many of the cores were brought into the site area, indicating probably "testing" of raw material and planned transport of raw materials over the landscape. Harmand (2009) also pointed out that different Lokalalei sites display different patterns of selectivity for raw materials, with Lokakalei 2C showing more selection for higher-quality volcanic rocks and clast morphologies amenable to efficiently reduce cores for flake reduction than Lokalalei 1.

In a reassessment of the lithic industries from Member F (~2.33 Mya) from the Omo Valley, Ethiopia, de la Torre (2004) pointed out that the raw materials available to toolmaking hominins here were primarily low-quality, smallish pebbles of quartz. Although the resultant cores and flakes may superficially appear to exhibit a low level technological skill, once the nature of the raw materials available is factored in they actually show advanced cognitive and manipulative skills beyond what chimpanzees could be expected to produce.

At Kanjera South, Kenya (Braun *et al.* 2008, 2009; Plummer and Bishop 2016), toolmaking hominins were highly selective regarding raw material procurement, bringing in stone from distant conglomerate sources often in much greater proportion that their presence in those conglomerates, while conversely often avoiding and largely leaving some rock types that were quite abundant in those distant sources. Moreover, they transported some of these rocks (~30% of the stone artefact assemblage) up to 10-13 km from sources to the excavated sites between 1.95 and 2.3 Mya. This is well outside the range of carrying stone seen in modern apes, which is usually much less than one kilometre. Overall, hominins seem to have transported and utilised more local stone sources at levels considerably lower than their immediate availability. For both the more distant and the more local conglomerate sources, some rock types were incorporated into the site assemblages in proportions either considerably greater or lesser than their proportions in those conglomerates.

Braun and Harris (2003) compared and contrasted the flakes produced by the earlier hominins at sites in the KBS Member at Koobi Fora (1.89-1.65 Mya) with the flakes produced at sites in the later Okote Member (1.65-1.39 Mya) in the same locality. Using digital image analysis, they were able to demonstrate that the Okote Member assemblages had cores that were much more heavily flaked with a greater amount of cutting edge versus mass, suggesting that their makers had a much more efficient way of producing usable flakes and reducing cores, something that would have given them an adaptive advantage relative to earlier hominins. In a separate study, Braun and Harris (2009) also examined assemblages from the KBS Member at Koobi Fora. Earlier KBS sites, in a deltaic swamp setting, exhibit lower densities of stone artefacts and less extensively flaked cores, which might indicate that the hominins responsible for them were less reliant on stone tools to access resources in these settings (perhaps focusing more on fruit trees). Later KBS sites, in drier grassland environments, show higher site densities and more heavily flaked cores that could indicate a more intensive use of stone tools, perhaps with increased reliance on animal carcasses that required processing with stone tools.

Olduvai Gorge has long provided a case study in raw material selection and transport by early hominins (e.g. M. Leakey 1971; Hay 1976; Kyara 1999; Blumenschine *et al.* 2009). Quartzite sources include the outcrops at Naibor Soit and Naisiusiu, basalt from lava flows in the sedimentary basin and cobbles in streams flowing out of the Ngorongoro volcanic highlands to the south, fine-grained phonolite from Engelosin to the north, chert from the exposed lake sediments during regressions and gneiss from the outcrops at Kelogi to the west. Again, there is good evidence of tool-using hominins transporting rock several kilometres from their primary (outcrop) or secondary (conglomerate) sources to excavated sites, sometime in appreciable quantities (Potts 1988).

An early study of refitting at the 1.5 million-year-old site of FxJj 50 at Koobi Fora, East Turkana, Kenya (Bunn *et al.* 1980; Toth 1985a; Schick 1987; Isaac and Isaac 1997), indicated that there had been transport of stone raw materials to the site area, often with flaking of the stone at another location prior to this and also sometimes subsequent transport of flaked stone away from the site area. Stages of flaking were assigned to an "early stage" (first flake removed from cobble refitting one or more flakes), a "middle stage" (refits not including first flake or resultant core) and a "late stage" (one or more flakes refitting onto core).

In Oldowan assemblages at Peninj, Tanzania (de la Torre *et al.* 2003), and at some sites in Bed II of Olduvai Gorge (de la Torre and Mora 2005), researchers have noted the emergence of heavily flaked, bifacial, radially flaked discoidal cores. Such cores, made on cobbles or thick flakes, allow the knapper to maintain the acute core edges essential for efficient flake removal as the core is reduced. The increased number of such bifacial discoids in later Oldowan sites is likely a technological precursor for the large bifacial forms (handaxes, cleavers, picks) in the early Acheulean, an idea first advanced by Gowlett (1984, 1986, 1996).

Texier (1993, 1995) examined the technological patterns at the Oldowan site of Nyabusosi 18, Uganda, which dates to *c.* 1.5 Mya. The cores here also exhibit a radially flaked pattern with carefully prepared striking platforms for the efficient removal of flakes. Texier suggests that the technology at Nyabusosi shows a good level of flaking skill. Summing up, he notes that 'this is a minimal definition of the concept of predetermination' (Texier 1995: 652) and shows that these toolmakers show a higher level of skill than that seen in earlier Oldowan assemblages. This is perhaps no surprise, as the site is contemporaneous with early Acheulean sites in Africa and may well be the product of *Homo erectus*.

Based upon his observations of the material culture and behavioural patterns of Australian Aboriginal foragers, Hayden (2008) argued that Oldowan hominins probably had a rich non-lithic technology, including throwing sticks, digging sticks and spears, and that in addition to usable flakes many of the Oldowan "core tools" (choppers, heavy-duty scrapers etc.), as well as light-duty retouched flakes, were probably important implements used to work wood. He also argued that we may be underestimating the behavioural and cultural abilities of these early toolmakers and that home bases would have been an expected feature of Oldowan adaptation based on the spatial arrays of materials at Oldowan sites.

Although many of the assessments of early hominin cognition focus on stone artefacts and their prehistoric context, the detailed analysis of fossil animal bones from archaeological sites shows great potential for the future. Pante (2013) examined the patterns of bone modification at the Olduvai Gorge Bed III site of JK2 dating to between 1.15 and 0.8 Mya. Although both human-induced and carnivore-induced modification can be seen on animal bone surfaces and broken bones, the pattern suggested that hominins (*Homo erectus*), as well as carnivores, had early access to carcasses (early access to flesh and marrow) and significantly better access than earlier hominins (represented by *Homo habilis* and *Paranthropus boisei*) at the famous FLK Zinj site in Bed I (*c.* 1.84 Mya).

Experimental archaeological studies

Experiments in making and using stone tools date back to the nineteenth century (Coles 1979). Casual experimentation in producing Oldowan artefact forms was conducted by prehistorians such as Louis Leakey and Desmond Clark, but beginning in the 1970s more systematic experimental research began to be conducted in East Africa, notably in Tanzania and Kenya.

Some of the first experimental research focusing on the Oldowan includes studies was carried out by Jones (1980, 1981, 1994) at Olduvai Gorge, Tanzania. He emphasised the profound effect that different raw materials (quartz/quartzite, lava, chert etc.) had on stone artefact manufacture (Oldowan and Acheulean) and use (animal butchery, scraping wood or hide etc.), with the characteristic size, shape and flaking qualities of different stone sources influencing the eventual morphology and typology of the flaking products.

Toth (1982, 1985b, 1987, 1997) focused on the experimental replication of the stone artefacts from the KBS and Okote Member archaeological sites at Koobi Fora (~1.9-1.4 Mya) and argued that many of the Oldowan so-called "core tool" forms may have simply served as cores for the production of sharp flakes and that their morphology could often represent "least effort" core reduction and not necessarily the mental templates of Oldowan toolmakers; size, shape and raw material type could all have a major effect on the type of core produced and the resulting flakes and fragments. At most sites, partial and usually later stages of flaking appeared to be preferentially represented, suggesting significant transport of partially flaked lithic material to and from sites. Cortical flakes also showed an asymmetry of preferentially "right oriented" flakes, suggesting that Oldowan toolmakers were preferentially right-handed, with the right hand holding the percussor and preferential rotation of the left hand (that holding the core) in a clockwise direction as flakes were sequentially removed (Toth 1985b).

Experiments in the production of battered subspheroids and spheroids in quartz (Schick and Toth 1994) and in lava (Toth and Schick 2009a) suggested that these forms were probably well-curated percussors that had been used for a considerable amount of time, implying either caching at a locality to be returned to at a later date or long-term transport of them in anticipation of future use. Experiments in the production of limestone "facetted spheroids" at Ain Hanech, Algeria, suggested that these forms could simply be heavily reduced globular cores (Sahnouni *et al.* 1997).

Experiments with expert, intermediate and novice stone knappers by Nonaka *et al.* (2010) showed that only expert stone toolmakers could accurately predict the shape of the flake to be detached and tended to remove longer flakes with optimal percussion forces than was seen in intermediate and novice groups. They suggest that the organised flaking seen at the 2.3 million-year-old site of Lokalalei 2C, Kenya (Roche *et al.* 1999), shows the ability to control the products of flaking to some extent.

Focusing on quartzite and lava flake production at the site of DK in Bed I of Olduvai Gorge, Reti (2016) has argued that, based on experiments using the null hypothesis of least-effort reduction of these raw materials, toolmaking hominins showed more efficiency than expected in flaking higher-cost quartzite from the Nabor Soit outcrop, which was transported from several kilometres away, and that some of the flakes were produced off-site and transported to DK; hominins also showed less efficiency when flaking the lower-cost local basalt, which outcrops in the vicinity of the site.

In a study of teaching novices to produce Oldowan-like artefacts, Morgan *et al.* (2015) examined the premise that, in view of its probable social transmission, stone toolmaking spurred the evolution of teaching and language in our lineage. Using experiments in teaching novices to make stone tools, they explored five different avenues of learning the task: reverse engineering (from observation of the final artefact product); imitation/emulation (simple observation of the knapping operation); basic teaching (soliciting attention from trainee during the knapping); gestural teaching (emphasising aspects of the task with gestures); and verbal teaching (accompanying the knapping procedure with verbal instructions). They found that teaching with language was far superior to either imitation or emulation in transferring toolmaking skills among individuals.

They concluded, however, that Oldowan toolmaking may have depended on imitation and emulation (observational learning) for transmission among groups and across generations, which they refer to as "low-fidelity social transmission" and suggest this as a reason for the relatively low rate of change in the Oldowan over many hundreds of thousands of years, while contending that Acheulean technology may have required teaching or "proto-language."

Mahaney (2014, 2015) studied skilled modern flint knappers producing Early Stone Age artefact forms. He developed a protocol for documenting and analysing each sequential action of these toolmakers and concluded that both Oldowan and Acheulean flaking required working memory, but that Oldowan flaking was much more rudimentary. Acheulean handaxe manufacture required much more inhibition (not removing flakes in some places and selectively removing them in other places). He thus proposed that later Acheulean technology had a generative action planning that was analogous to language (syntax), a "language-like phrase-structure" (Mahaney 2015: 280) functionally lateralised in the brains of these toolmakers.

Putt (2015) examined novice stone-knappers and how effective different techniques were in flaking stone. Four conditions (techniques) were studied: 1) novice freehand knapping (hard hammer percussion); 2) bipolar flaking (hand-held hammerstone, core on anvil); 3) indirect projectile percussion (bipolar flaking with a core set on an anvil with a thrown percussor); 4) direct projectile percussion (dropping or throwing one rock on a core). Putt found that direct projectile percussion was the best way for novices to exploit a core, that bipolar flaking was the most expedient approach and that freehand knapping produced the most usable flakes (large, with sharp cutting edges). She suggests that projectile throwing or pounding techniques could have been a precursor to the Oldowan (Putt 2015). Interestingly, the bonobo Kanzi became more adept at hand-held, hard-hammer percussion after learning to throw a core against a hard floor or another stone (Schick *et al.* 1999; Savage-Rumbaugh and Fields 2006).

Brain imaging studies

In 1989, at a Wenner-Gren Foundation conference on "Tools, Language, and Intelligence: Evolutionary Implications" in Cascais, Portugal, we proposed the employment of relatively new brain imaging techniques such as PET (positron emission tomography) to address questions pertaining to human evolution, including the manufacture of stone tools (Toth and Schick 1993). After consulting with brain imaging authorities such as Marcus Raichle (Washington University), we designed pilot projects employing PET with Dietrich Stout, using modern toolmaking subjects (including ourselves flaking Oldowan cobble cores and manufacturing late Acheulean handaxes from large flake blanks).

These pilot studies into PET brain imaging during stone artefact manufacture include those of Stout (2006) and Stout *et al.* (2000, 2006, 2008). The initial, pioneering study used PET to elucidate areas of relatively intense brain activation during the making of Oldowan tools and indicated that activated brain areas were located in the superior parietal lobe and involved with complex spatial cognition. These areas of high activation were seen to be 'requiring integration of diverse sensory inputs (e.g. vision, touch, and proprioception, or sense of body position and motion') (Stout *et al.* 2000: 1215).

Stout and his colleagues have subsequently gone on to develop much more detailed brain imaging studies, setting theoretical and methodological standards that other researchers have followed. Further application of PET imaging to toolmaking indicated that activation areas had some overlap with language circuits, suggesting that toolmaking and language 'share a basis in more general human capacities for complex, goal-directed action' (Stout *et al.* 2008: 1939), although brain activation patterns in Mode 1 or Oldowan knapping indicate that it is not demanding in a cognitive sense (Stout 2005). Oldowan flaking showed no evidence of prefrontal involvement in problem solving or planning, but does indicate heightened visuomotor demands (Stout 2006). Some of these PET imaging studies have deliberately compared and contrasted brain activation in Oldowan toolmaking versus Acheulean toolmaking (Stout *et al.* 2006, 2008), with some indication that differences may be more quantitative in terms of intensity than qualitative in terms of the location of the neural circuits involved. There was, however, evidence of increased activity in the right hemisphere in Acheulean handaxe production relative to that observed in Oldowan flaking, possibly due to more manipulation of the Acheulean handaxe in the left hand, which is controlled by the right hemisphere (Stout *et al.* 2006).

Further investigation of Oldowan toolmaking through PET imaging involved a study of six novice knappers and detected that Oldowan flaking activated 'both primitive and derived parietofrontal perceptual motor systems' (Stout and Chaminade 2007: 1091), corroborating the observation that this simple mode of flaking was primarily a perceptual-motor adaptation, especially concerned with object manipulation and evaluation of core morphology. Its authors speculate that 'it may be acquisition of such sensorimotor capabilities, rather than executive capacities for strategic planning, that represent the critical bottleneck in the initial development of complex tool use and tool making abilities' (Stout and Chaminade 2007: 1098). In a subsequent study, Stout and Chaminade (2009) stressed the activation of brain circuits involved in co-ordinating manual grasping, starting with Oldowan toolmaking and with the addition of prefrontal and more right hemisphere activation in Acheulean toolmaking.

In a study designed to conduct experimental research into the 'likely neuroanatomical targets of natural selection' that might affect the ability to make stone tools (Hecht *et al.* 2015: 2315), MRI and DTI (diffusion tensor imaging, a type of MRI) scans identified brain areas activated during stone toolmaking. The toolmaking methods included Oldowan flaking, Acheulean biface production and prepared core techniques, such as Levallois. The activated areas involved the inferior frontoparietal regions, which are also involved in action panning and language. The findings of this study largely corroborated the PET studies reported previously (Stout and Chaminade 2007; Stout *et al.* 2008) 'that early hominin toolmaking was supported by evolutionary elaborations of a primitive ventral frontoparietal circuit for object manipulation that is shared with other primates' (Hecht *et al.* 2015: 2328).

Stout and his colleagues have led the way in more recent brain imaging studies, employing functional magnetic resonance imaging (fMRI) and other approaches to address a range of questions pertaining to stone artefact manufacture and cognition. One study explored aspects of cultural transmission of toolmaking using this brain imaging technique (Stout *et al.* 2011). Individuals in three groups, each at a different level of initiation or expertise in stone toolmaking — novices, trainees and expert knappers — observed videos of Oldowan knapping and Acheulean knapping. They found that the brain activation spurred by watching the videos differed between the groups, depending upon their level of knowledge and expertise of the knapping process, with implications regarding the shifting nature and location of the learning process in the course of adopting stone technological skills. Stout *et al.* (2011: 1) conclude that their 'findings support motor resonance hypotheses for the evolutionary origins of human social cognition and cumulative culture'. The implication is that learning toolmaking tasks may have relied to a good deal upon the developing ability to perceive others' actions and sensory experiences and to foster internal activation and understanding in the observer. A subsequent study (Stout *et al.* 2015) examined differences in brain activation in subjects who were trained in both Oldowan and Acheulean toolmaking, particularly with regard to when they were making judgments regarding planned, future technical actions. Heightened dorsal prefrontal cortex activity coincided with the timing of such judgments.

In a recent study using the brain-imaging technique of functional near-infrared spectroscopy (fNIRS) by Putt *et al.* (2017), subjects were taught (roughly half verbally and half non-verbally) to make Oldowan and Acheulean artefact forms. Nonverbal instruction was used in one group to avoid the possible effect of internal verbalisation impinging on tasks and associated brain activation (as may have occurred, the authors suggest, in some previous brain imaging studies of toolmaking, which detected activation in areas involved with language processing). Interestingly, the cognitive network seen in Acheulean handaxe production was associated with the visual working memory network (of the middle and superior temporal cortex) and was almost identical to that of trained pianists playing the piano (as opposed to speech), leading the researchers to suggest that this cognitive network was critical in audiomotor integration (the Oldowan artefact production was much weaker in these regions). They go on to suggest that Oldowan toolmakers prior to 1.8 Mya may have had more ape-like cognitive abilities, primarily involving the co-ordination of visual attention and motor control, while Acheulean toolmakers (probably the larger-brained *Homo erectus*) had more human-like cognitive abilities, requiring 'the integration of higher-order motor planning, working memory and auditory feedback mechanisms' (Putt *et al.* 2017: 4). This experimental work supports a working memory hypothesis rather than a language area hypothesis.

Considerations: cognition, tools, memory and culture

Many researchers have theorised that toolmaking and tool-using were critical components of human cognitive evolution. In a recent overview of interest in cognitive evolution in Palaeolithic archaeology, Wynn and Coolidge (2016: 211) observed that 'much of hominin cognitive evolution was co-evolutionary with material culture. Artefacts played a critical scaffolding role from at least the beginning of stone knapping' and went on to posit that cognitive evolution basically required 'active engagement with artefacts'. They suggest that human technical cognition was developed on a neural foundation established in ape evolution that supported anthropoid 'object manipulation', as well as 'long-term procedural memories, the kind that are basic to the anthropoid object manipulation networks' (Wynn and Coolidge 2016: 201, 204). They do not, however, view language as a necessary component in the earlier phases of our technological evolution, suggesting that technical cognition 'remained largely nonverbal during the course of hominin evolution' (Wynn and Coolidge 2016: 204). In their view, Oldowan technology only required 'ape-like spatial cognition' and it was only much later, by late Acheulean times *c.* 500,000 years ago, that 'modern concepts of space were in place' and that they identify the earliest direct evidence of working memory component (Wynn and Coolidge 2016: 206, 209).

Some of the basic, underlying premises of much Palaeolithic research have recently been challenged, including the inference of planning and strategising in some stone tool-making procedures and even the question of whether stone toolmaking "traditions" are safely inferred to be "cultural" in a larger sense. One such study, by Moore and Perston (2016), conducted experiments to examine whether Oldowan core and Acheulean handaxe morphologies require higher order planning strategies, or can result from randomised flaking due to constraints imposed by nature of fracture mechanics. They argue that random selection of flaking platforms (from a set assessed by experienced knappers, judging appropriate places to strike to remove an optimal, maximum-sized flake) produce both simple Oldowan-like cores (as well as "proto-bifaces") with no predetermination or "intent" on the part of the knapper.

Some researchers have recently suggested that flaked stone technology may not be the product of long-term robust cultural transmission, but could instead be the product of numerous independent innovations over time. For instance, Tennie *et al.* (2016) have suggested that Oldowan and even Acheulean material culture may not, in fact, be truly "cultural" in the modern human sense (what they define as involving "high-fidelity social learning" such as imitation and teaching), but might rather be a much simpler system (what they call "low-fidelity social learning" or the "zone of latent solutions" or ZLS), such as stimulus enhancement and product emulation. (They define a latent solution as a 'behavior that lies "dormant" or "latent" in an individual until triggered by a particular set of social or environmental cues and sufficient motivation on the part of the learner'; Tennie *et al.* (2016: 125)).

Tennie *et al.* (2016) further argue that in primate societies many behaviours deemed "cultural" can be reinvented spontaneously by an individual without a teacher or model, do not require high-fidelity social learning and do not represent cumulative culture. Furthermore, they posit that much of the early Palaeolithic record contains tools that may fall in this realm and not require a model or teacher. The degree of culturally transmitted complexity, in an evolutionary perspective, is clearly a continuum, especially when one considers the eventual role of the evolution of language in the evolution of cultural transmission. Applying this ZLS test to the assessment of the Gona artefacts by Stout *et al.* (2005, 2010), Tennie *et al.* (2016: 129) suggest that the tool patterns may not have required 'high fidelity cultural transmission' and urge a reassessment of Early Stone Age patterns to put the assumption of cumulative culture (essentially requiring high-fidelity social learning) to the test.

Holloway (1969, 1981) has cogently emphasised the unique elements of culture and use of symbols in human cognitive evolution, while Davidson (2016) has provided a very useful consideration of the question on culture in nonhuman animals and in early hominins and of whether there is something between "culture" and "cumulative culture." In doing this he considers such elements as learned behaviour, the place of material culture in culture writ large and models of cultural transmission and the role of social transfer. He models a gradation from socially transmitted information to traditions to culture to cumulative culture and, eventually, discrete "cultures." He speculates that there may be transitional phases that are ill-defined, with different hominin groups making transitions from one level to another at different times in different places.

Aspects of memory, particularly long-term memory, as well as problem solving and reasoning, are repeatedly addressed by various researchers who address human cognitive evolution. In a paper reviewing the invention of technology in our lineage, De Beaune (2004: 142) suggests that 'apes can produce a cutting edge' but that 'this is because humans have taught them how to do so, which amounts to saying that the mental breakthrough is beyond their reach'. She has argued that analogic reasoning (transferring 'a familiar procedure from one situation or class of situations to a new situation that is similar but not identical' (De Beaune 2004: 150)), which is important in problem-solving, is deficient in apes and prevents or obstructs breakthrough reasoning, while our own toolmaking ancestors were able to apply principles learned in one context, say cracking open fruits or nuts, to another, say cracking open stones or bones. De Beaune argues that advances in long-term memory may have been the critical change advantaging our lineage, as they involved accessing analogue behaviour from past events.

In an attempt to assess the behavioural and cognitive complexity evidenced in lithic reduction strategies, Muller *et al.* (2017) used "problem-solution distance modelling" as applied to experimental core replications. To analyse the complexity of the technological operations, they produced "hierarchical diagrams" that distinguish specific phases of focus in the knapping process, as well as components or sub-foci within that phase, with "hierarchical depth" represented by how many phases are involved in the reduction and "hierarchical breadth" by how many sub-foci are within the longest phase. Together, this provides what are regarded as quantifiable measure of hierarchical complexity. All these components are retained in the knapper's memory, and so hierarchical complexity is deemed to be a measure of the cognitive complexity required by the task (Muller *et al.* 2017: 176). Not surprisingly, the assessment of hierarchical complexity in their schema is relatively low in Oldowan tool operations, but increases substantially with later technologies.

Haidle (2010) has presented a comparative view of tool behaviour in the larger animal world to that observable in the early archaeological record in respect of the working-memory components in various tool behaviours. She found that problem-solving through tool use in other, nonhuman, species developed solutions within a relatively narrow 'spatial and temporal vicinity' (Haidle 2010: S149), while human technological evolution, starting with Oldowan tool behaviour (making and using), shows an increased complexity regarding the number of elements in focus, an increasing number and diversity of steps involved and an enlargement in the time frame and spatial environment for the overall tool behaviour (procuring and transporting stone, manufacture and sometimes refurbishing of the tool and application to a task). Haidle (2010: S162) posits that the Oldowan evidence supports use of 'sequential memory' by early toolmakers, with problems 'no longer perceived or solved only in the immediate or extended present but beyond, with a cognitive time depth … growing at least in the future direction and probably also to the past'.

Many researchers, however, hold that human technological evolution has played a crucial, even pivotal role in human cognitive evolution. Davidson and McGrew (2005), for example, have suggested that stone knapping areas themselves created a new niche and that when revisiting knapping areas hominins could have potentially applied past behaviours to new uses. They suggest that stone tools may have had a role in the 'the emergence of this creativity' (Davidson and McGrew 2005: 793). Stout and Hecht (2017: 7861) have posited a uniquely human technological niche built on 'a shared primate heritage of visuomotor coordination and dexterous manipulation' and also emphasise the important, crucial role of social learning in the development and maintenance of technological traditions in human technological evolution. With regard to more specific cognitive evolutionary changes in human evolution, Hecht *et al.* (2015: 2329) consider that remodelling of the frontoparietal regions 'in response to Palaeolithic toolmaking is consistent with longstanding models of the mutually reinforcing interaction between technological, social, communicative, and neural complexity in human evolution' and furthermore that these frontoparietal circuits, remodelled for toolmaking, were ultimate co-opted or exapted 'to support proto-linguistic communication and then subsequently altered by secondary adaptations specific to language.'

Summary

Hominins contemporary with Oldowan sites diverge from the biological, behavioural and ecological patterns seen in extant great apes in the following major features.

Biological trends

Increase in brain size

Although the earliest Oldowan sites appear to be contemporaneous with australopithecine hominins with ape-sized brains, later Oldowan sites are contemporary with early *Homo* with brains that were significantly larger. Judged by the Encephalisation Quotient (EQ, i.e. the ratio of the actual brain mass to the predicted brain mass for a given mammalian body size), by *Homo erectus* times the brain had essentially doubled in size from the situation found in its australopithecine ancestors (Table 2).

Brain reorganisation

As Holloway *et al.* (2004) and Schoenemann (2006, 2012, 2013) have pointed out, early *Homo* brain endocasts show greater asymmetries in terms of petalias (left occipital/right frontal) and the development of a prominence ("cap") in Broca's area in the left hemisphere, something that in modern humans is associated with such tasks as the processing of information responsible for speech production and processing syntax, linguistic and non-linguistic sequential processing, imaging hand motions and the detection of tone changes.

Increase in body size and modern-like limb proportions

By *Homo erectus* times, hominins show a general increase in body size, closer to the modern human range, as well as body proportions closer to those seen in modern humans compared to earlier hominins (longer legs relative to arm length, probably more habitual bipedalism and a greater potential for long-distance running (Bramble and Lieberman 2004). Although not evident in the fossil record, it is likely that these hominins had also evolved bodies with less surface hair, allowing sweating (and cooling of the body) during long-distance walking/running and other energetic activities.

Decrease in the size of jaws and teeth

A general trend in the evolution of the genus *Homo* is a general reduction in tooth size and jaw robusticity over time (Cartmill and Smith 2009: 263). The decrease in canine size in hominin evolution is interpreted by many palaeoanthropologists as evidence of reduced agonistic behaviour between males (Lovejoy 2009), while the reduction in tooth size and jaw robusticity in the genus *Homo* is seen as evidence for an increased reliance on tools and technology and a reduced emphasis on using large jaws and teeth for food consumption (Schick and Toth 1993).

More modern human-like hands

Even early australopithecines appear to have had hands reminiscent of modern human morphology (elongated thumb compared to apes), though still retaining some primitive traits such as curved, ape-like phalanges and less spatulate terminal phalanges. Later hominins of the genus *Homo* (and possible the later robust australopithecines as well) had more spatulate terminal phalanges, like modern humans, plus more profound markings (of, for example, the flexor pollicus muscle) that may indicate selection for more manipulative and tool-using behaviour (Tocheri *et al.* 2008).

Behavioural trends

Flaked stone technology

Production of intentionally-flaked stone artefacts by a range of techniques (hard-hammer percussion, bipolar technique, anvil ("block on block") technique, possibly throwing).

Deliberate edge modification

Deliberate modification of flake edges through retouch for resharpening (e.g. acute-edged denticulate "scrapers") or for reshaping (e.g. pointed awls).

Partial reduction sequences/movement of partially flaked materials

At some sites, only partial reduction histories of cores are present, indicating that partially flaked lithic materials were often carried from one behavioural locality to another on the landscape.

Curation of some stone tools

This is suggested by evidence of long-term, repeated use of some stone tools, for example well-battered and symmetrical spheroids, which may have been used for hours of use (Schick and Toth 1994, 2009b) either by habitual caching of items at locations to which hominins returned later or by habitual carrying of artefacts from locality to locality.

Long-distance transport of stone

Transport of (sometimes large amounts) of lithic raw materials, sometimes over more than ten kilometres, from their primary (outcrop) or secondary (gravel) sources to the archaeological occurrences.

Increased technological complexity over time

This is indicated by a temporal sequence moving from simple cores and flakes with little retouch to a trend for more heavily flaked cores (including discoids), more heavily battered spheroids, more retouched flakes and the striking of larger flakes from larger cores, a harbinger of the Acheulean technology to come.

The acquisition and processing of large mammalian carcasses

At some sites, notably FLK 22 (Zinj) at Olduvai Gorge *c.* 1.84 Mya, there is clear evidence of large animal carcasses having been processed with the aid of stone tools after having been obtained either by scavenging (Binford 1981, 1983; Blumenschine 1995) or by hunting/early access (Bunn and Kroll 1986; Domínguez-Rodrigo *et al.* 2007) or a combination of the two (Pante *et al.* 2012). As this behaviour became habitual in hominin evolution it would have produced a significant addition of quantities of protein (meat) and fat (fat, marrow, and brains) in the diet. This increase in diet breadth and possible increase in caloric intake could have helped fuel a larger brain (cf. Aiello and Wheeler 1995).

The accumulation of large quantities of flaked stone artefacts, percussors and unmodified stones, and sometimes also large quantities of animal bones

Some prehistorians have interpreted these accumulations as evidence of "home bases" or "central foraging places," essentially camps to which hominins regularly returned after completing foraging rounds in their vicinity (M. Leakey 1971; G. Isaac 1976b; Rose and Marshall 1996). Glynn Isaac (1976) emphasised food sharing and also a sexual division of labour as important components of this model, which would suggest that early hominins delayed consumption through inhibition to bring food resources to a favoured place for redistribution and consumption. Rose and Marshall (1996) subsequently revisited the home base model, suggesting that sites represented places where groups concentrated animal parts that they could defend through co-operative defence, although they dismissed pair bonding or sexual division of labour as intrinsic components of this model. Binford (1983) argued to the contrary that these early sites were not home bases, but rather locations where hominins scavenged available carcasses near water sources, while Sept (1992) observed that the spatial distribution of debris from chimpanzee feeding and nesting behaviours has strong parallels with the distribution of materials produced by hominins on the palaeolandscape. Potts (1988, 1991), on the other hand, suggested that Oldowan sites represent stone caches where stone raw materials were deliberately concentrated by hominins for future tool-making and tool-using activities, while Schick (1987) proposed that sites showing accumulations of stone artefacts and animal bones represent "favoured places" where hominins sought amenities such as water, trees (offering shade, nesting areas or refuge from predators) or other food resources, resulting in the accretion over time of the stone tools that they brought with them, as well as any animal parts brought to the locality for consumption in a safer space. In any case, many Oldowan sites appear to have had significant quantities of stone and animal resources brought to them, indicating at least periodic localisation of activities on the landscape.

Fire?

Although it has been argued that early hominins may have made/used fire to increase nutritional quality (Wrangham 2009; Herculano-Houzel 2016), there is little evidence (e.g. reddened sediment patches, hearths, thermally altered stone artefacts or burnt bones) for long-term, habitual use of fire until much more recent times in Africa. Sporadic evidence of fire has been found at a few Oldowan sites, for instance at Koobi Fora and GnJi 1/6E (Chesowanja), Kenya, and at Swartkrans Cave, South Africa (Gowlett 2016). However, natural causes for such fires, or rare opportunistic use of naturally occurring fire, cannot be ruled out. A recent study by Hlubil *et al.* (2017) of the evidence for fire at FxJj 20AB at Koobi Fora, in the form of thermally altered stone tools, burnt bone and altered soil, seems to have documented evidence that fire did act on these materials, but does not substantiate that this was through intentional, hominin-produced or hominin-maintained fires rather than those occurring naturally on the landscape. Nevertheless, even without the advantage of fire and cooking, stone technology (as well as tools of other materials such as wood, horn, bone and tusk) could have greatly enhanced the procurement, processing and digestion of foods, and could have played a major role in the encephalisation of hominins over time (Aiello and Wheeler 1995).

Ecological trends

Occupation of a range of environments, including grasslands.

In contrast to the African great apes, which are primarily found in more closed, forested habitats, Oldowan hominins appear to have occupied a range of environments, from woodlands to open grasslands (Plummer *et al.* 2009). No remains of fossil great apes have been found at localities where Oldowan hominins or Oldowan artefacts have been recovered. The climatic evidence suggests a general pattern of cooling and drying during the time period of the Oldowan and the spread of grasslands replacing woodlands over time. Especially profound arid/open time periods occurred at 2.8 Mya, 1.7 Mya and 1.0 Mya (deMenocal 1995). The likely emergence of the genus *Paranthropus* and the genus *Homo* occurred around the time of the first arid phase at 2.8 Mya.

Spread out of Africa into Eurasia

The emergence of Acheulean technology and *Homo erectus*, and the spread of hominins out of Africa into Eurasia roughly correspond to the second of these arid phases. Acheulean technology appears in Africa by at least 1.76 Mya. The spread of hominins out of the African continent was accomplished by 1.8 Mya by an early form of *Homo erectus* equipped with an Oldowan technology, as evidenced by the site of Dmanisi in the Georgian Caucasus (Lordkipanidze *et al.* 2013). Subsequent sites are evident in East Asia in China's Nihewan Basin by about 1.7 Mya (Ao *et al.* 2013), and in western Europe at Orce, Spain, by about 1.2 Mya (de Lumley *et al.*, 2009; Fajardo, 2009). By the third arid phase, around 1 Mya, later *Homo erectus* appears to have established populations in many parts of tropical and temperate Africa and Eurasia.

Conclusion

There is clearly a wide variety of opinions regarding the cognitive abilities of early hominins, ranging from the view that hominins were essentially like modern apes to that which sees them as having evolved to a new, more human-like threshold of cognitive abilities. It has sometimes been said that primatologists tend to emphasise the *similarities* between modern apes and humans (modern and fossil), stressing commonality shared between these genera, while many anthropologists tend to emphasise the *differences*, trying to identify uniquely human characteristics. It is our opinion that the hominins responsible for Oldowan sites herald a new and more complex form of cognition and behaviour, starting with an australopithecine grade of hominin that slowly evolved into the significantly larger-brained (and probably even more cognitively and behaviourally complex) forms of early *Homo* by 1.9 Mya, if not sooner. The difference in brain size between early *Homo* (650 cm^3) and chimpanzees/bonobos and early australopithecines (~400 cm^3) shows an increase in *Homo* of about 60 percent within one million years. There must have been strong selective forces for this to happen, and that selection was almost certainly involving higher cognitive abilities in foraging, social interaction and communication. This was probably accompanied by the evolution of a smaller gut over time and the incorporation of a higher quality diet, with consumption of higher amounts of meat and marrow (Aiello and Wheeler 1995), the presence of larger social group sizes (Dunbar 1993, 2017; Schoenemann 2006; Dunbar *et al.* 2014) and a more efficient search/processing/consumption pattern (Herculano-Houzel 2016). Dunbar (2017) argues that, prior to language, laughter and singing were probably important means of vocal grooming in the hominin social group, laying the foundations for the development of language *per se*.

After 2 Mya, Oldowan sites become much more pervasive in the archaeological record, with many more localities documenting Oldowan hominin presence over more and more parts of Africa and then Eurasia. Many of these sites also persist over time, with occupation debris documenting occupation by tool-wielding hominins over long periods, sometimes hundreds of thousands of years. It is our opinion that this record documents a substantial immersion of hominins into a culturally mediated, tool-centred adaptation, one that entered into complex interplay with our cognitive evolution. This adaptation eventually allowed our ancestors to compete successfully in the changing palaeoenvironments of the Pleistocene and to substantially expand their territorial and environmental range throughout much of Africa and then into Eurasia.

By 1.76 Mya some of these early hominin populations had started to produce Acheulean handaxes and cleavers, contemporaneous with other hominin populations that produced later Oldowan, non-handaxe sites. Although there is very sporadic evidence of fire at a few Oldowan localities, we cannot rule out use of natural brushfires and lightning strikes, although we do not see a habitual use of fire (in the form of hearths, fire-altered lithics, burnt bone or charcoal) until fairly recent prehistoric times, especially in the last 250,000 years. Although the controlled production and use of fire would admittedly have been an enormous advantage to our evolving lineage, opening up a myriad of opportunities regarding protection from predators, preparation and conservation of foodstuffs, extraction of more nutrients from foods, extension of activities after sundown and more comfortable habitation of higher elevation and higher latitude environments, definitive evidence of this technological innovation is currently lacking during the Oldowan.

The technological niche into which we had entered, however slowly and with whatever common features initially shared with our closest living relatives among the apes, gradually became our domain. As many of the studies mentioned here suggest, the cognitive foundations for this new evolutionary direction seem firmly grounded in our ape ancestry, but the ramifications of this have had profound effects on our brain evolution and laid a critical foundation for the ensuing evolution of our species.

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