Key, Alastair J. M. and Lycett, Stephen J. (2017) Form and function in the Lower Palaeolithic: history, progress, and continued relevance. Journal of Anthropological Sciences, 95 . pp. 67-108. ISSN 2037-0644.

DOI

https://doi.org/10.4436/jass.95017

doi 10.4436/jass.95017
e-pub ahead of print

JASs Invited Reviews
Journal of Anthropological Sciences
Vol. 95 (2017), pp. 1-42

Form and function in the Lower Palaeolithic: history, progress, and continued relevance

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Summary - *Percussively flaked stone artefacts constitute a major source of evidence relating to hominin behavioural strategies and are, essentially, a product or byproduct of a past individual's decision to create a tool with respect to some broader goal. Moreover, it has long been noted that both differences and recurrent regularities exist within and between Palaeolithic stone artefact forms. Accordingly, archaeologists have frequently drawn links between form and functionality, with functional objectives and performance often being regarded consequential to a stone tool's morphological properties. Despite these factors, extensive reviews of the related concepts of form and function with respect to the Lower Palaeolithic remain surprisingly sparse. We attempt to redress this issue. First we stress the historical place of form–function concepts, and their role in establishing basic ideas that echo to this day. We then highlight methodological and conceptual progress in determining artefactual function in more recent years. Thereafter, we evaluate four specific issues that are of direct consequence for evaluating the ongoing relevance of form–function concepts, especially with respect to their relevance for understanding human evolution more generally. Our discussion highlights specifically how recent developments have been able to build on a long historical legacy, and demonstrate that direct, indirect, experimental, and evolutionary perspectives intersect in crucial ways, with each providing specific but essential insights for ongoing questions. We conclude by emphasising that our understanding of these issues and their interaction, has been, and will be, essential to accurately interpret the Lower Palaeolithic archaeological record, tool-form related behaviours of Lower Palaeolithic hominins, and their consequences for (and relationship to) wider questions of human evolution.*

Keywords - *Lithic Artefacts, Morphology, Flake, Biface, Handaxe, Stone-tool Function.*

Functional concepts within Lower Palaeolithic archaeology

Palaeolithic stone artefacts are the product of a past individual's intention to modify a natural rock such that it is capable of performing a definable objective or activity. That is, they are a product of creating a tool capable of modifying an aspect of an individual's physical or social environment in respect to some broader goal. Hence, while many artefacts excavated from Palaeolithic sequences may have been considered a byproduct (i.e. waste), their production was nonetheless the result of flaking a stone object for functional purposes. Consequently, functional concepts have maintained a prominent position within studies of lithic artefacts (Semenov, 1964; Keeley, 1980; Odell 1981; Torrence, 1989a; Nelson, 1991; Kuhn, 1994; Shea, 2007; Roche *et al.*, 2009; Gowlett, 2011a; Braun, 2012; Key, 2016). Most notably, archaeologists have frequently drawn links between form and functionality, with functional objectives and performance often being regarded as consequential to a stone tool's morphological properties. In turn, 'function' is frequently presented as an explanatory hypothesis for the forms of stone artefacts recovered archaeologically.

In many respects, function may be considered a principal influence on stone tool form during the Lower Palaeolithic. Certainly, their role as tools raises important questions relating to the choices underlying their production and how this relates to their ability to be applied to utilitarian tasks and the wider behavioural strategies of hominin populations (Torrence, 1989b). Given the potentially contentious nature of implying 'function' to be a principal determinate of stone tool morphologies, it is important to stress that the term 'principal' need not imply that function is necessarily the most frequent cause of variation between artefactual forms, or even the variable with the strongest potential influence. Indeed, an important role of the present review is to highlight limitations to the explanatory power of form–function relationships and the fact that in many situations the application of functional models should not only be done with caution, but often leads directly to the need to consider other explanatory hypotheses.

The 'function' of a lithic artefact within Plio-Pleistocene contexts was potentially diverse and could accordingly be defined too narrowly. As noted by Schiffer & Skibo (1987), artefactual 'function' may be considered in either utilitarian (techno-function), social (socio-function) or ideological (ideo-function) terms. Functional discussions within an archaeological context do, then, imply the use of an artefact for a particular purpose. Most functional studies of lithic artefacts are concerned with the use of stone tools during cutting behaviours, where the forceful application of an object (usually with a clearly defined edge) to material results in fracturing and deformation of that material. The variability of potential cutting actions undertaken by stone technologies is diverse and includes slicing, cleaving, piercing, grinding, scraping and drilling, among others (Atkins, 2009; Key, 2016). Their possible role as percussive tools or as projectiles has also been discussed, as has their potential ability to influence the perception and behaviour of other individuals or groups within hominin social systems. Hence, in theory, change or stability in the formal properties (material, mass, size, shape, etc.) of artefacts through time can be explained, in part, by selective processes that increase or maintain a tool's *performance characteristics* within a given functional context (Meltzer 1981; Schiffer & Skibo 1987, 1997; O'Brien *et al.* 1994; Key & Lycett, in press; Lycett *et al*. 2016). Performance characteristics may be defined as "an interaction-and-activity-specific capability of a person or artefact" (Schiffer *et al*. 2001, p.731). In this way, a tool's performance characteristics describe its ability to undertake specific techno-, socio- and ideo-functions, based on its formal properties (Schiffer & Skibo 1997). Moreover, such various functional categories are not necessarily mutually exclusive and could be incorporated simultaneously into artefactual forms (Sackett, 1977). Accordingly, the interaction between a tool's formal attributes and performance could, in principle, lead to the exertion of selective pressure on artefactual form (O'Brien *et al*., 1994).

Despite these factors, extensive reviews of the related concepts of form and function with respect to the Lower Palaeolithic remain sparse. This could be considered surprising given that stone artefacts constitute one of the most important data sets relating to hominin behaviour and the central role that function may have played in forming that record. Here, we attempt to redress this issue. First we stress the historical place of form–function concepts, and their role in establishing basic ideas that echo to this day. However, we show how little progress beyond listing plausible functions was made in the early phases of the discipline. We next, therefore, highlight methodological and conceptual progress in determining artefactual function in more recent years. Thereafter, we evaluate four specific issues that are of direct relevance to determining whether form–function interactions were of relevance to Lower Palaeolithic hominin behaviour. In one sense, the notion of form and function with regard to the Lower Palaeolithic may seem quaint or even outdated entirely. In conclusion, therefore, and based directly on the issues raised, we attempt to untangle the extent to which form and function may have been entwined in Lower Palaeolithic stone technologies. Moreover, we assess the continued relevance of these concepts for Palaeolithic archaeology, especially with respect to their ongoing relevance for understanding human evolution more generally.

Lower Palaeolithic Stone Technology

The Lower Palaeolithic is characterised—at its most basic level—by the production of large (>10cm) or small flake (<10cm) tools (modified or unmodified) and bifacially flaked core tools, produced by means of direct percussion using hard (lithic) or soft (bone/antler/wood) hammers and/or through bipolar percussion or anvil (passive) techniques. The potentially oldest and deliberately flaked stone-tool industry (although see Proffitt *et al.*, 2016), are the recently described 3.3 million-year-old large flakes (and associated cores) from Lomekwi 3, West Turkana, Kenya (Harmand *et al.*, 2015). From 2.6 million years ago, the Palaeolithic record is characterised by 'Oldowan' assemblages and becomes more abundant in terms of the number of artefacts and sites (Hovers & Braun, 2009; Roche *et al.* 2009; Rogers & Semaw, 2009). Although 'Oldowan-like' (or Mode 1) flake and core industries are produced throughout the Lower Palaeolithic (and beyond), many archaeologists regard the 'Oldowan' to end around ~1.7–1.5 MYA coinciding with the appearance of Acheulean bifaces (Semaw *et al.*, 2009: 173; Diez-Martín *et al.*, 2015).

The Acheulean (or Mode 2) techno-complex is defined by the appearance of new manufacturing methods, including the ability to shape relatively large (> 10cm) flakes or nodules into an elongated, but broadly 'oval', 'tear-drop', or 'triangular', bifacial form (Clark, 1970; Gowlett 1988; Goren-Inbar & Saragusti, 1996; Lycett & Gowlett, 2008; Semaw *et al.*, 2009; Sharon, 2010; Diez-Martín & Eren, 2012). Cleavers, also characteristic of the Acheulean, were produced from large flakes and possess a sharp, straight edge at one end, which is left from the original flake surface (Isaac, 1977; Clark & Kleindienst, 2001). Many studies have focused on documenting and analysing size and shape variation within and between handaxe and cleaver assemblages distributed across Africa and Eurasia (e.g., Isacc, 1977; Roe, 1981; Wynn & Tierson, 1990; Saragusti *et al.*, 1998; McPherron, 1999; Vaughan, 2001; McNabb *et al.*, 2004; Sharon, 2007; Lycett & Gowlett, 2008; Lycett, 2008; Chauhan, 2010; Iovita & McPherron, 2011; Shipton & Petraglia, 2011; Wang *et al.*, 2012; Gowlett, 2011a, 2015), identifying both similarities and differences in artefactual forms. The appearance of 'Levallois' prepared-core (or Mode 3) technologies at least 300 KYA is often regarded to signify the end of the Lower Palaeolithic and beginning of the Middle Palaeolithic (Moncel *et al.*, 2011; Tryon & Faith, 2013).

While the above discussion is by no means a definitive account of Lower Palaeolithic technological or morphological variability (see e.g., Semaw *et al.*, 2009; Hovers, 2012; Gowlett, 2015; Harmand *et al.*, 2015 for discussion of broader and additional features), it is clear that there is considerable variation in the size and shape of stone tools that are being produced by hominins during the Lower Palaeolithic. As has long been recognised, an obvious question to address is, therefore, whether some of that variation might be influenced by—or have consequences for—functional issues.

A brief history of functional and morphological concepts within Lower Palaeolithic research: 1800–1950

John Frere (1800, p.204) is well known for providing the first suggestion for handaxe function, describing artefacts recovered from Hoxne (UK) as "evidently weapons of war, fabricated and used by a people who had not the use of metals". While the great antiquity of these tools went unrecognised and their form was not reported in detail, it appears that Frere (1800) viewed these objects as having been intentionally produced. Frere's discovery was, however, largely ignored at the time (Wymer, 1968; Sackett, 2000) and it was not until the second half of the 19th century and developments in other fields, most notably geology, that the deep antiquity of human origins and recognition of an 'Old Stone Age' came to be (Sackett, 2000). The emergence of Palaeolithic archaeology as an academic field during the 19th and early 20th centuries has been described in detail elsewhere (Dennell, 1990; Sackett, 2000; Davis, 2009; Gowlett, 2009a; Pettitt & White, 2011; Henke, 2015). Here, to set contemporary work and concepts in broader historical context, we are concerned specifically with the history and development of hypotheses and evidence surrounding potential functions of different Lower Palaeolithic stone tool forms.

The association between Palaeolithic implements and the remains of extinct animals was first reported in France and Belgium (Pettitt & White, 2011; Henke, 2015). Of particular note is Philippe-Charles Schmerling (1833) who published a detailed monograph on 40 Palaeolithic sites in Belgium documenting associations between stone artefacts and faunal remains. Boucher de Perthes (1847) similarly recognised an association between stone implements and extinct animals in the gravel terraces of Abbeville in the Somme Valley. Somewhat surprisingly, however, he characterised the handaxes recovered not as utilitarian tools, but instead as Sackett (2000, p.45) notes "symbolic items used for purposes of ritual, exchange, and trade". This is, as far as we know, the earliest suggestion for Lower Palaeolithic tools having a social function. de Perthes' work was followed by Jérôme Rigollot (1854) who supported the contemporaneity of stone tools and extinct animals in the Somme Valley, most notably at Saint-Acheul, which would eventually become the eponymous site for the 'Acheulean' techno-complex. In all instances, however, the claims associating stone tools and faunal remains were largely dismissed by their contemporaries (Sackett, 2000; Gowlett, 2009a).

Associations between faunal remains and stone tools began to be debated seriously by the late 1850s, particularly following excavations at Brixham Cave (UK) (Grayson, 1990). A notable moment in associating Palaeolithic stone tools and faunal remains came with the visit of Joseph Prestwich, Charles Lyell, and John Evans to Amiens and Abbeville in the Somme Valley, who having observed the terraces for themselves, "all came away convinced" of the lithic-faunal associations that had earlier been proposed by Boucher de Perthes & Rigollot (Grayson, 1990, p.10). Prestwich's (1860, pp.295-296) description of the flint implements from these sites is, however, particularly noteworthy:

> *"In these implements we find three principal types: one, lance-shaped; a second, almond shaped; and a third smaller form, a flattened ovoid … These forms are constant, and each type presents a nearly constant relation between the length and breadth of the specimens … [T]he cutting edge extends all round … it is to be observed that these cutting edges are always on one plane, and that they were produced by blows applied at the edge …and that the sides are equilateral."*

Prestwich (1860, p.296) was, of course, describing the variable forms among what would later be referred to as 'Acheulean handaxes' (Fig. 1). However, he went further, stating that: "one object is apparent throughout, that of giving to a hard durable substance a shape either sharp-pointed or cutting." It is the consideration given to the functional or potential 'design' elements that is notable for the time – certainly, the reader can be left in little doubt what Prestwich thought regarding the intent to produce specific forms, and that he considered their functional capacities to centre on their pointed shape and sharp edges.

Evans (1859; reproduced in Prestwich [1860]) had, however, slightly earlier alluded to functional implications when describing the Abbeville and Saint Acheul artefacts, noting the more "pointed weapons" (handaxes) to be analogous to "lance or spear heads", while the "oval or almond-shaped" handaxes were characterised by the presence of a cutting edge all around. No precise purpose for handaxes is given, with Evans

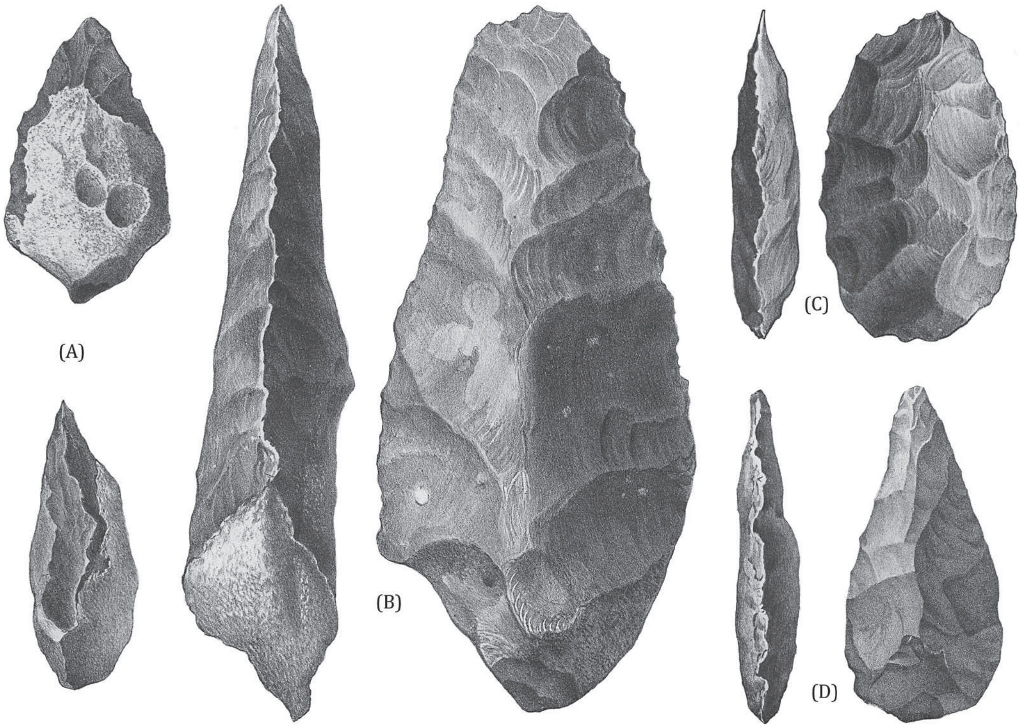

Fig. 1 - Selection of 'flint implements' described by Prestwich (1860) from Saint Acheul (a, b, d) and Abbeville (c). These artefacts clearly show what would later be commonly described as 'handaxes' and are representative of the variable forms often found in northern Europe. Length a = 7.8cm; length b = 19.4cm; length c = 9.1cm; length d = 12.9cm.

himself noting "it is impossible to say for what purpose they were intended" (reproduced in Prestwich, 1860, p.311), merely speculating that more pointed forms may be spear tips or for splitting wood or "grubbing in the ground", while the oval and almond-shaped forms may have been axes or "sling-stones". Evans also noted, however, that "flakes or splinters arising from the chipping of the flint, will of necessity present sharp cutting edges, and are certain in consequence to be utilized", potentially as "arrowheads or knives" (Prestwich, 1860, p.310). At the same time Lartet (1860) suggested cut marks on Pleistocene bones discovered north of Paris were caused by stone tools, and in a remarkably prescient example of experimentation, indicated that he had been able to produce similar marks with flint flakes on fresh bones. Contemporaries such as Desnoyers (1863) and Lyell (1863) also speculated that cut marks on fossil bones from northern France were produced through the use of flint tools (for discussion see Grayson, 1986).

A little later, Evans (1864) published evidence of "Reindeer-horn" having been cut and carved by "flint instruments" that were mixed with bones of other animals. While many have stressed (e.g. Clark, 1962; Henke, 2015) the importance of this as early evidence of the contemporaneity of humans and extinct animals, the modified antler is also among the first-documented examples of direct Palaeolithic stone tool use (albeit within an Upper Palaeolithic context). It is, however, a volume of combined works by Lartet & Christy (1865-75) that provides one of

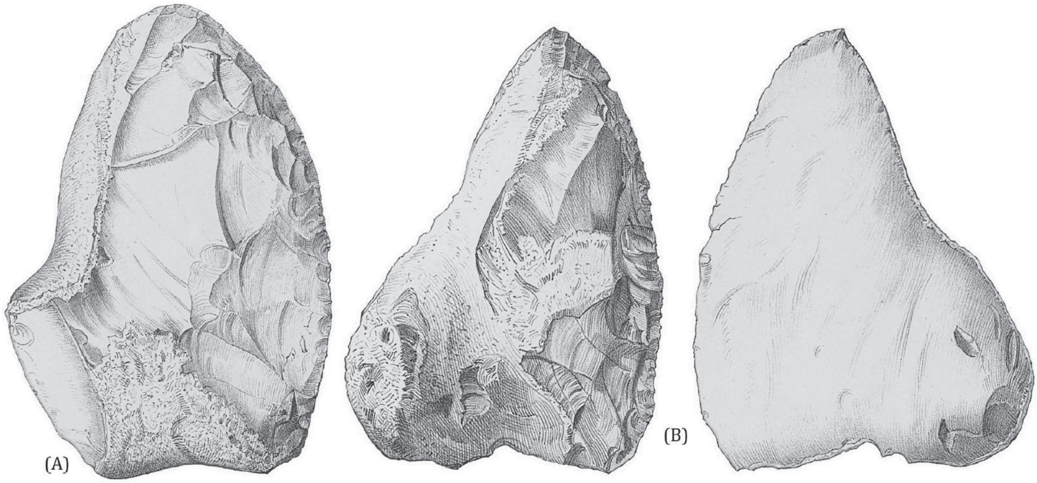

Fig. 2 - Reproduction of Lartet & Christy's (1865-75, p.17) figure detailing large flake cutting tools, with the larger tool (a) being described as "being one-edged cutting-instrument, or chopper…chipped on both faces along one margin, so as to produce a sharp cutting-edge". Length a = 12.7cm; length b = 9.5cm.

the clearest insights into emergent ideas concerning Palaeolithic tool function. In their discussion of handaxes (albeit Middle Palaeolithic) from Le Moustier they describe them as "cutting or chopping, hatchet-like implements", including one where "the but-end is blunt, so that the 'hatchet' can stand on end" (Lartet & Christy, 1865-1875, p. 78). Perhaps the most intriguing of items to be described by Lartet & Christy (at least given modern Acheulean literature) are two artefacts that would best be described today as large flake cutting tools (Fig. 2). One of which is described as being a "one-edged cutting-instrument, or chopper…finely chipped on both faces along one margin, so as to produce a sharp cutting-edge in the form of a segment of a circle. The other margin is left with the natural crust of the flint, and can be conveniently held in the hand" (Lartet & Christy, 1865-1875, p.17). Clearly, the potential functional applications of varying forms of handaxes and other artefacts in both the Lower and Middle Palaeolithic were not lost on these early pioneers of Palaeolithic archaeology.

Evans' (1872) volume *The Ancient Stone Implements, Weapons, and Ornaments, of Great Britain* not only reconfirms distinctions between the three implement forms that he described in 1859 (see above), but adds a number of additional forms, due in part to the fact that he frequently focuses on individual artefacts. Evans (1872, p.565) does, however, amend his earlier functional propositions and now considered it unlikely that pointed forms (handaxes) were spears tips, although he still regarded them as "weapons of offense [rather] than mere tools or implements". Evans (1872) also helpfully provides a review of potential handaxe functions proposed by his contemporaries, including their use as ice chisels, wedges for splitting wood, hatchets, axes to cut down trees, prepare firewood or carve out canoes, as well as their use as throwing implements, food-cutting tools and hunting implements. He even recited Lubbock's (1862, p.250) opinion that "almost as well might we ask to what would they not be applied". Notably, Evans did not repeat the social functions for handaxes proposed by de Perthes (1847). Regarding Acheulean flake tools, Evans (1872, p.562) suggests "their use appears to have been for cutting and scraping whatever required to be cut or scraped". In sum, there appears to be few cutting activities that Lower Palaeolithic stone tools were considered not to have been applied.

The association between extinct fauna and Palaeolithic artefacts continued to be noted from the 1870s onwards (e.g. Spurrell, 1880; Hughes, 1897), including by French prehistorian Gabriel de Mortillet (1867), who is perhaps better known for using tool typologies to differentiate between Palaeolithic industries in the late 1860s. Spurrell (1884) provides a perceptive account concerning the production of Palaeolithic stone tools; however, it is his distinction between the functional capabilities of modified and unmodified flake tools that is of particular interest. Indeed, Spurrell (1884, p.117) suggests "trimmed" flake edges with rounded sides would be less likely to pierce skin during skinning relative to an unmodified flake. The functional value Spurrell (1884) assigns flake tools, despite discussing other technologies such as handaxes, demonstrate that the relative simplicity of these artefacts did not result in him overlooking their functional potential.

Reports of Palaeolithic artefacts became more frequent and geographically widespread between 1870–1910 (Laing, 1892; Wymer, 1968). However, it would not go too far to state that few advances were made in terms of either broadening ideas about the potential uses of stone tools or providing more rigorous investigations of whether certain forms were preferentially suited to particular tasks. Davies (2009, p.130) describes this theoretical situation as a consequence of the typological distinctions constructed by de Mortillet and others proving a "straightjacket" to developments. The eolithic debate likely also distracted from functional considerations as it kept discussion focused on whether artefacts were of anthropogenic or geological origin, even though actualistic research sometimes formed part of this debate (Grayson, 1986). However, the relative lack of attention given to behavioural inferences is due also, in part, to the struggle to establish chronological and geographical frameworks for the artefacts being discovered. In other words, prehistorians were concerned with other fundamental questions that were deemed of greater importance at the time. Seton-Karr's (1896, 1909) descriptions of handaxes from Somaliland provides a useful example. These tools were among the first Lower Palaeolithic artefacts to be reported from sub-Saharan Africa (Seton-Karr, 1896), and as a result, it is the establishment of human prehistory in a new geographical context that is of upmost concern to the author, not their function. Certainly, Seton-Karr (1909, p.182) gives little consideration to their function beyond that they were "probably for barter and exchange".

The period between 1910 and ~1930 is notable for publications by French prehistorian Abbé Henri Breuil (Breuil, 1912, 1926; Breuil & Koslowski, 1934). Accordingly, Dennell (1990, p.553) contends that Breuil produced "arguably the most important Lower Palaeolithic study of the 1930s" with his work in the Lower Palaeolithic sequences in the Somme valley (Breuil & Koslowski, 1934). However, such works, although important in defining technological aspects of sequentially progressive periods (that would not be superseded until the 1960s), did little to further understanding of the use of Palaeolithic artefacts. For example, while discussing large flake assemblages ('Clactonian') in Britain, little comment is made regarding their potential function beyond "l'association à une faune chaude à Eléphant antique est certaine" (Breuil, 1926, p.225). The three chapters dedicated to the 'Chellean' and Acheulean periods in Arthur Keith's (1915) *The Antiquity of Man* are similarly sparse. Certainly, it is the geological context of artefacts, the way they were produced, and their relationship to the antiquity of 'man' that arguably continues to be of chief concern among prehistorians.

As is apparent, functional concepts during the 19th and early 20th century were predominantly informed by analogy with modern tools, considerations of intent regarding the production of sharp edges, and contextual associations with faunal remains. The influence of early ethnographic accounts of modern stone tool using populations must, however, also be noted. Certainly, indigenous peoples encountered in the Americas, Australia and other areas of the world came to influence ideas on the potential uses of Palaeolithic artefacts (Gosden, 1999; Pettitt &

White, 2011) and, on occasion, led early prehistorians to actively seek the opinion of (European) individuals who had spent time among such communities (e.g., Lartet & Christy, 1865-75). Despite these accounts being a product of their time (i.e. subjective, biased and subscribing to notions of 'primitive' populations), and in many instances being offensive to the populations described (e.g., Tylor, 1894), these basic ethnographic descriptions provided one of the few pieces of evidence relating to plausible uses for stone tools. Accordingly, ethnographic accounts formed a prominent contributor toward early ideas concerning Palaeolithic stone tool function (e.g., Lubbock, 1865; Tylor, 1894; Aiston, 1928).

Between World Wars I and II, Palaeolithic studies continued to be dominated by Breuil's evolutionary ideas regarding the (progressive) technological development of Lower Palaeolithic sequences (Dennell, 1990). For the first time, however, there is a substantial shift in focus towards Palaeolithic industries in Africa and Asia (e.g., Wayland, 1934; de Terra & Teilhard de Chardin, 1936; Movius 1944, 1948), including their associations with cut-marked faunal remains (Pei, 1933). Famously, this includes Louis Leakey's first visits to Olduvai Gorge (Leakey, 1931, 1951) and his assessment of functional hypotheses through experimentation. In *Adam's Ancestors* Leakey (1953, p.58) notes how "experiments suggest that the hand-axe was a kind of general utility tool rather than a weapon…with a hand-axe it is possible to dig up wild edible roots, to dig holes to serve as pit-traps, to dig along the burrows of rodents until the nest chamber is reached, to chop the smaller bones of animals when cutting up a beast, and, of course, to cut up meat". Leakey also describes the more limited ability of handaxes to sharpen wooden stakes or skin an animal relative to flake tools, and the potential functions of cleavers, scrapers and 'Clactonian' tools. A published lecture by Leakey in 1949 (Leakey, 1950) reaffirms these functional statements, but adds that handaxes "were certainly not missiles" but may have been used as "clubs or choppers". Regarding butchery behaviours, it is cleavers that Leakey assigns greatest value, noting that he was able to "cut up a large hartebeest in less than two hours, using only a cleaver" (Leakey, 1950, p.73). Indeed, after readily admitting failure to cut animal skin "with his hands, nails or even his teeth", Leakey (1950, p.71) appears convinced of the adaptive benefit of stone tools and their importance in animal food processing.

At this time more explicit statements concerning tool (form) attributes and function appear, with Barnes (1939, p.109), for instance, highlighting the need for "acute edges (less than 90°) for cutting and scraping" and so providing early commentary on edge angle, which would become increasingly discussed in later years. In 1948, Praus provides an early comparative examination of Palaeolithic and modern metal cutting tools and also suggested that modern engineering/mechanical theory might be used to shed light on prehistoric tools. Moreover, he indirectly confirms the novelty of Leakey's experiments by noting that functional inferences had previously been derived only through ethnographic analogy or general appeals based on shape. It is with Praus (1948, p.158) too, that there is early assertion that handaxes "cannot be considered a true ax[e]". However, evidence of the continued importance of ethnography in related debates also appear in works of the time (Mitchell, 1949).

Movius (1944, 1948) is widely known for his work around this time that would later lead to establishment of the famous 'Movius Line'. However, Movius (1948, p.349) also noted how the terminology he used in describing Asian assemblages was based entirely on artefactual forms and production techniques "rather than any hypothetical functions". Movius (1948) would not, however, be alone in highlighting the functional connotations inherent within many typological systems and the potential problems this can pose (Wymer, 1968; Clark, 1970; Odell 1981; Toth, 1985).

During the second half of the 20th century, however, functional concepts began to receive more earnest attention. Importantly, distinct analytical techniques focusing on the use of stone tools emerged, and empirical analyses of tool forms become more explicitly integrated with functional considerations. Advances in radiometric dating in the 1950s, the subsequent freeing from a purely typological–chronological perspective, and the increasing focus of archaeologists to specialise by technological period, also guided research away from generalised discussions of 'Palaeolithic' technologies. Ultimately, this shift also contributed toward the famous Bordes–Binford debate, whereupon it was argued that Mousterian variability might better be explained by functional parameters than culture-historic alternatives (Binford & Binford, 1966). However, these broader shifts also contributed toward greater focus on the Lower Palaeolithic as a distinct period, with greater awareness of the evolutionary context that inevitably contributes to debate on form and function during this timeframe. Consequently, a strictly chronological review, as has been undertaken thus far, may become unclear in terms of describing how different approaches have combined to form current perspectives. Moreover, current research builds directly on works from the 1960s-80s, and their inclusion in a historical review could misrepresent their continued importance. Hence, discussion continues in the following section first by means of current evidence surrounding the possible functions of Lower Palaeolithic artefacts, and then by means of current knowledge regarding relationships between stone tool forms and functional application.

The present state of research concerning the form and function of Lower Palaeolithic stone tools

What were Lower Palaeolithic stone tools used for?

Current ideas surrounding the possible functions of Lower Palaeolithic implements build on ~60 years of increasingly detailed and steadily cumulative research. This is not to say, however, that the number of *suggested* functions for these tools has changed considerably since the 19th century. Rather, the amount of *evidence* supporting or refuting the possible functional applications has increased.

The presence of sharp edges on flakes, handaxes, cleavers and other core forms has ensured that recent discussion has continued to focus primarily on their potential role as cutting implements (e.g., Posnansky, 1959; Toth, 1985; Shea, 2007; Roche *et al.*, 2009; Barsky *et al.*, 2011; Braun, 2012; Hovers, 2012; Key, 2016). It is, however, impossible to discuss the potential functions of Lower Palaeolithic technologies, as inferred from aspects of their form, without mentioning their potential utility within hominin social systems. Most prominently, Kohn & Mithen (1999, p.519) argued handaxes may have been "integral to the process of mate choice within socially complex and competitive [hominin] groups". Kohn & Mithen's (1999) argument hinges on the assumption that handaxes are over-engineered for functional purposes alone and, given that they have potential to be costly (time and energy) to produce, may, therefore, have acted as viable indicators of mate quality. That is, "fine symmetrical handaxe[s]" may have acted as an indicator of "good genes", demonstrating their producers had knowledge of resource distributions, an ability to complete complex tasks and social awareness (Kohn & Mithen, 1999, p.521). While the sexual selection hypothesis is an intriguing one (Currie, 2014), it has received credible criticism (Machin, 2008; Nowell & Chang, 2009). Similarly, Spikins (2012) and Hiscock (2014) have proposed that because handaxes may go beyond the immediate need to produce a viable tool this might indicate roles extending beyond strictly techno-functional applications. Pope *et al.* (2006) meanwhile contended that discarded handaxes may have acted as signals and behavioural cues to other hominin individuals or groups. As intriguing and inventive as they are, few of these hypotheses, however, are currently supported by direct evidence or through formal analyses of data independent of that from which they are built.

Shea (2006) has also highlighted that a considerable portion of the stone artefacts recovered from Palaeolithic contexts may have been the product of imitative behaviours by juveniles or bouts of knapping practice by unskilled individuals. If this supposition is correct, the function of these 'training pieces' would strictly be for increasing knapping proficiency (be this motor-processes, technological capabilities, etc.). Theoretically, artefacts resulting from such learning bouts might be discernible through a greater number of mistakes (step fractures, breakages, mauled platforms, etc.); however, as Shea (2006) notes, there are many challenges to identifying these activities reliably.

Ethnographic accounts have continued to provide important information relating to the potential functions of Lower Palaeolithic tools over the past 60 years. Accounts from a variety of populations have detailed the use of unmodified flakes when producing spears, digging sticks, clothing, bone needles, arrow shafts, knife handles, and more generally during numerous scraping and cutting actions on wooden, shell and bone objects, as well as butchery (White & Thomas, 1972; Binford, 1986; Hampton, 1999; Sillitoe & Hardy, 2003; Shott & Sillitoe, 2005; Holdaway & Douglass, 2012; Hayden, 2015). As noted by Shott and Sillitoe (2005, p.654) when describing tool use in New Guinea, flakes "were ubiquitous and mundane. They served in all tasks for which stone was required and ground-stone axes could not be or were not used" (see also, Holdaway & Douglas, 2012). Ethnographic accounts describing the use of bifacial/core tools are notably rarer than for flakes (Kelly, 1988). However, Gould (1980) recorded use of hand-held choppers (cobbles with few flakes removed) for woodworking tasks, including the cutting of spear-throwers and spear shafts. Hayden (2015) similarly noted the use of handaxe-like implements in Papunya (Australia) for the manufacture of wooden winnowing troughs. As has long been noted, however, while ethnography can demonstrate a range of plausible tool applications (Skibo, 2009; McCall, 2012), it does not mean that Palaeolithic populations necessarily used them in these ways, nor that there are not additional uses that have no modern analogue (Wobst, 1978).

Experimental archaeology developed as a distinct methodological approach during the 1960s and 70s (Ingersoll *et al.*, 1977; Coles, 1979; Outram, 2008) and from this point the functional utility of Lower Palaeolithic artefacts began to be addressed more earnestly through experimental means. These early functional experiments were described by some of their practitioners as largely "freewheeling" (informal and qualitative) in nature, often conceived with the objective of increasing "understanding, from an archaeologist's point of view, of the serviceability of various items of a diversified lithic tool kit" (Crabtree & Davis, 1968, p.426). Although few experiments were quite so openly explorative as those of Crabtree & Davis (1968), similar experiments utilised broad, investigative methodologies to assess the suitability of specific tool forms to undertake functional tasks (e.g., Sonnenfeld, 1962; Swauger & Wallace, 1964; Huckell, 1979; Jones, 1980).

Since the 1980s, experimental archaeology has flourished to the extent that it contributes a substantial proportion of new information concerning Palaeolithic technologies (Eren *et al.*, 2016). The effective capabilities of unmodified flakes for butchery has now been confirmed by numerous experimental studies (Toth, 1985; Jones, 1994; McCall, 2005; Dewbury & Russell, 2007; Braun *et al.*, 2008a; Merritt, 2012, 2015). Similarly, handaxes and cleavers have demonstrated efficacy during butchery activities (Jones, 1980; Toth, 1985; Mitchell, 1995; Machin *et al.*, 2007; McCall, 2005; Bello *et al.*, 2009; Toth & Schick, 2009; Galán & Domínguez-Rodrigo, 2014). Such studies have even demonstrated the ability of both flakes and bifaces to butcher megafaunal pachyderms such as elephants (Frison, 1989; Jones, 1994; Toth & Schick, 2009, p.333; Gingerich & Stanford, in press). It is notable that experiments examining the suitability of Lower Palaeolithic technologies for plant processing tasks are relatively rare. Those that have been undertaken, however, indicate that flakes and bifaces are capable of numerous woodworking activities, including amongst others, the production of spears, bamboo knives, and digging sticks (Toth, 1985; McNabb, 1989; Jones, 1994; Hardy & Garufi, 1998; Toth & Schick, 2009;

Bar-Yosef *et al.*, 2012). Experiments examining the suitability of handaxes for digging appear to have been largely overlooked (although see, Toth & Schick, 2009). The suitability of handaxes as projectile tools/weapons has also been tested experimentally. While the conclusions of these experiments have at times been inconsistent, generally, they have been shown to make unreliable projectiles (O'Brien, 1981; Whittaker & McCall, 2001; Samson, 2006; McCall & Whittaker, 2007).

One novel source of evidence emerged in the 1960s from studies of tool use by wild great apes, most notably chimpanzees (*Pan troglodytes*) (e.g., Lawick-Goodall, 1968; Struhsaker & Hunkeler, 1971). Through phylogenetic parsimony, these studies provided evidence that early hominin stone-tool behaviours were likely to have emerged during subsistence-related strategies (McGrew, 1992; Panger *et al.*, 2002). Indeed, following decades provided widespread evidence that other nonhuman primates, including bonobos (*Pan paniscus*), capuchins (*Cebus* sp.) and macaques (*Macaca* sp.) are capable of using tools for food acquisition and processing (Gumert *et al.*, 2009; Visalberghi *et al.*, 2009; Shumaker *et al.*, 2011). Such evidence further bolsters suggestions that food-related tool use in hominins has deep roots.

Studies of faunal remains and cut-marks by Shipman, Bunn and Potts in the 1980s were instrumental in providing further evidence of stone-tool-assisted butchery in Lower Palaeolithic contexts. In particular, their work at Olduvai Gorge provided some of the first unequivocal (direct) evidence that early stone tools were used for butchery (Bunn, 1981; Potts & Shipman, 1981; Shipman & Rose, 1984; Bunn & Kroll, 1986; Potts, 1988). Although their work more widely across the Old World should also be noted (e.g., Shipman *et al.*, 1981; Shipman & Rose, 1983a,b; Bunn, 1986, 1994). The species identified as having been butchered included numerous bovid, giraffid, hippopotamus, antelope and equid species through to primates such as geladas and even mid-to-late Pleistocene *Homo* (Bunn, 1981; Potts & Shipman, 1981; Shipman *et al.*, 1981; White, 1986; Potts, 1988; Bunn, 1994).

In subsequent years, evidence for stone-tool related bone modification has become more chronologically and geographically widespread. Currently, the earliest examples may be as old as 3.4 MYRs (McPherron *et al.*, 2010), although, notably, these are contentious (Domínguez-Rodrigo *et al.*, 2012). In sites dating from 2.5 MYRs through to the Middle Palaeolithic transition such evidence is, however, more regularly recorded (e.g., de Heinzelin *et al.*, 1999; Domínguez-Rodrigo *et al.*, 2005; Choi & Driwantoro, 2007; Bello *et al.*, 2009; Stiner *et al.*, 2009; Ferraro *et al.*, 2013; Diez-Martín *et al.*, 2015; Starkovich & Conard, 2015; Landeck & Garriga, 2016). The number of species butchered by Lower Palaeolithic hominins has also increased since the 1980s and now includes catfish, perch, turtle, crocodile (Braun *et al.*, 2010; Archer *et al.*, 2014), beaver (Lebreton *et al.* 2017), bear (Gaudzinski, 2004), monkeys (Pobiner *et al.*, 2008), bison (Landeck & Garriga, 2016), rhinoceros (Landeck & Garriga, 2016), elephants (Yravedra *et al.*, 2010), deer (Rabinovich *et al.*, 2008; Stiner *et al.*, 2009), felids (Kolfschoten *et al.*, 2015) and additional hominin species (Saladié *et al.*, 2012). The age, context and form of cut-marks found has sometimes been used to suggest that either flakes or bifaces were specifically used (e.g., Bunn, 1994; de Heinzelin *et al.*, 1999; Domínguez-Rodrigo *et al.*, 2005; Pobiner *et al.*, 2008; Bello *et al.*, 2009; Yravedra *et al.*, 2010), indicating that in at least some instances both tools were used for butchery. Cut marks present on the ~300 KYA Schöningen wooden spears from Germany also indicate that flint tools were used during their production (Schoch *et al.*, 2015). Similarly, the wooden Clacton (spear) point (~400 Kya) displays striations consistent with having been worked by flint tools (Oakley *et al.*, 1977). Hominin-imposed modifications on faunal remains and wooden artefacts, therefore, unequivocally indicate that Lower Palaeolithic stone tools were used to butcher animal carcasses and make wooden spears.

Additional direct methods of identifying Palaeolithic tool functions were also being attempted by the early 1980s, namely lithic microwear (use-wear) and residue analyses (Semenov, 1964; Stemp *et al.*, 2015). Keeley's pioneering work in the early 1980s specifically attempted to apply microwear analysis to Lower Palaeolithic artefacts (Keeley, 1980; Keeley & Toth, 1981). Indeed, Keeley & Toth (1981) identified wear traces on nine Oldowan artefacts from Koobi Fora (dating to 1.5 MYRs) and determined that these tools had been used to cut both animal and plant tissue. Similarly, Keeley's (1980) analysis of British Lower Palaeolithic artefacts resulted in diverse functional assignments for flake and core tools, including their use during plant processing and butchery behaviours. These publications had a substantial impact on Lower Palaeolithic research, and in combination with the early analyses of cut-marked bones by Shipman, Bunn & Potts, purportedly provided the first direct evidence relating to the function of Lower Palaeolithic stone tools. Isaac (1983, p.18) noted the impact of these works at the time, stating that prior to this point "we could and did speculate [about the function of early stone tools], but we had no direct evidence".

In the ~20 years immediately following Keeley's publications there were only a small number of microwear studies examining Lower Palaeolithic stone tools, most of which are limited in artefact numbers and methodological detail (Roberts *et al.*, 1986; Beyries, 1990; Mitchell, 1998; White *et al.*, 1998). In part, this has been assigned to problems such as the naturally rough surfaces of volcanic rocks commonly used, taphonomic damage (Beyries, 1990) and questions over the replicability and precision of Keeley's methods (Unger-Hamilton, 1984; Levi-Sala, 1996; Newcomer *et al.*, 1986; Shea, 1987).

In 1999 Carbonell *et al.* published the first substantial analysis of Lower Palaeolithic microwear traces since the early 80s. Their work on the ~780 Kya lithic artefacts from Gran Dolina, Atapuerca (Spain), resulted in the identification of 24 flake tools displaying wear traces suggested to indicate they were primarily used to cut wood and meat. Lemorini *et al.* (2006) similarly suggested the primary function of Lower–Middle Palaeolithic (382-152 Kya) flakes at Qesem Cave (Israel) was butchery, alongside occasional gathering of herbaceous or woody plants. Others have since interpreted microwear on Lower Palaeolithic handaxes and flakes to indicate their use for plant/animal processing (e.g., Ollé *et al.*, 2012; Sahnouni *et al.*, 2013; Lemorini *et al.*, 2014; Viallet, 2016). It is notable that there is still (Shea, 2011) a lack of Lower Palaeolithic microwear analysts employing the use of high-powered 3D microscopy techniques widely advocated in other areas of lithic microwear research (e.g., Stevens *et al.*, 2010; MacDonald, 2014; Stemp *et al.*, 2015). Nonetheless, taken at face value, current literature indicates that microwear traces have potential to yield important evidence directly relating to the functions of Lower Palaeolithic tools, and according to existing studies, both meat and plant-processing tasks may have been undertaken with flakes and handaxes.

Other analysts have combined microwear and residue analyses, which has potential to provide greater security of conclusion. However to date, it has only been utilised on three occasions within Lower Palaeolithic contexts. Rots and colleagues' (2015) analysis of flakes from Schöningen (~300Kya, Germany) identified residues and wear indicating woodworking and meat/hide processing. More recently, flint artefacts dating to ~300 Kya from Qesem Cave (Israel) revealed collagen and bone residue in association with microwear indicating longitudinal cutting motions (Zupancich *et al.*, 2016). Combined with the recovery of a deer bone showing signs of having been worked by a flint tool, this indicates that at least some of these artefacts were used to deliberately modify bone. Solodenko *et al.* (2015) also combined microwear and residue analysis of a biface, flake and scraper from Revadim Quarry (Israel), finding fat residue (likely elephant) on the biface and scraper.

There have been additional studies of residues on tools from Lower Palaeolithic contexts. Domínguez-Rodrigo *et al.* (2001) is perhaps the best known, having identified wood phytoliths on three handaxes dating to ~1.7–1.5 Mya at Peninj, Tanzania. Use of Lower Palaeolithic tools for woodworking has also been supported

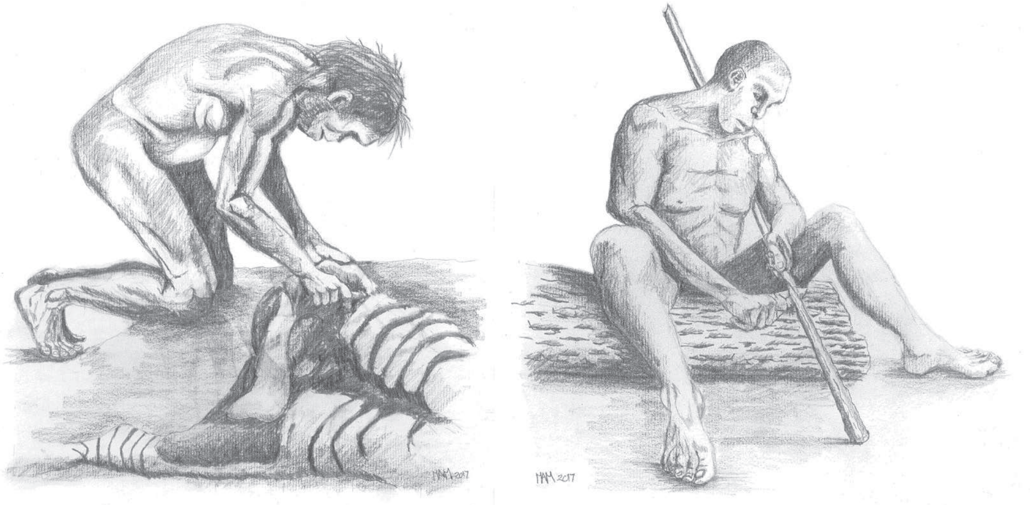

Fig. 3 - Illustrations depicting two hypothesised stone tool functions that have been a mainstay of Lower Palaeolithic archaeology for over 150 years. Depicted here is the butchery of a large mammal (left) and the production of a wooden implement (right), both of which are supported by direct evidence. However, these specific actions potentially form only part of the functional repertoire of Lower Palaeolithic stone tools.

through residue analyses by Loy (1998). The relative importance of Loy's (1998) discovery was, however, in the purported identification of animal proteins on Oldowan tools dating to 2 Mya from Sterkfontein, South Africa. More recently Nowell *et al*. (2016) identified 17 artefacts (15 flake artefacts and two handaxes) from the late Acheulean site of Azraq (Jordan) displaying traces of horse, rhinoceros, camel and duck antiserum. This study is particularly important in substantiating the use of tools on a diverse range of species, including the processing of waterfowl. Moreover, it is worth noting that the two handaxes were identified as having been used to process horse and rhinoceros, both larger animals among those represented.

In sum, prior to the 1980s functional inference continued to rely heavily on interpretations of tool forms, analogy with modern or ethnographic tools, and contextual associations with faunal remains. The expansion of experimental archaeology and primatological studies in the 1960s and 70s provided new and important sources of evidence, however, it is nonetheless the case that evidence continued to be indirect. As Desmond Clark (1970, pp.99-100) stated at the time: "unfortunately, we have, as yet, no direct means of knowing what many of these tools were used for". Following the introduction of microwear, residue and cut-mark analyses from the 1980s onwards, workers have been exploring potential direct links between artefacts and their use, providing evidence that at least some Lower Palaeolithic artefacts were used for plant and animal processing. Despite these advances, however, general consensus regarding the primary functions of Lower Palaeolithic stone tools has not changed considerably in the past 60 years (Wymer, 1968; Clark, 1970; Isaac 1971, 1981; Roe, 1981; Villa, 2001; Shea, 2007; Roche *et al*., 2009; Diez-Martín & Eren, 2012; Plummer & Bishop, 2016). Certainly, there has long been consensus that Lower Palaeolithic stone tools were not only likely to have been multifunctional tools, but were used to butcher a variety of sized animals and cut and modify plant materials (Fig. 3). Discussion regarding the adaptive significance of these behaviours and how they may have come to influence the tool forms found in the artefact record is, however, not only more contentious, but less frequently addressed. It is to these issues which we turn in the following section.

Potential relationships between stone-tool forms, functional utility and hominin behaviour

Suggestions of functionally related intentionality and selectivity (either cultural or natural) during the production and use of Lower Palaeolithic stone tools raises four important considerations. The first is whether variation in artefact form has the potential to influence their effectiveness in functional tasks. Secondly, whether there was an adaptive benefit to the preferential use or production of particular tool forms. Thirdly, in the case of more cognizant selection, the extent to which hominins were capable of preferentially 'selecting' or recognizing more effective tool forms. Finally, there is a need to identify whether Lower Palaeolithic artefacts provide evidence that hominins were producing or using certain tool forms dependent on their functional performance characteristics.

Would the form of a Lower Palaeolithic stone tool have influenced its functional abilities?

As we have noted, the primary function of Lower Palaeolithic stone tools would likely have been to cut plant and animal materials. Accordingly, it is logical to question whether the form of a stone tool could impact its cutting capabilities. Certainly, mechanical and ergonomic investigations of modern hand-held tools often detail how the form of cutting edges and manual contact areas (e.g., handles) are important in determining their effectiveness (e.g., Hall, 1997; McGorry *et al.*, 2005; Atkins, 2009; Rossi *et al.*, 2014; Schuldt *et al.*, 2016), and the value of this literature to Palaeolithic archaeology has recently been reviewed elsewhere (Key, 2016). Here, we are concerned specifically with evidence from lithic-centric sources that detail what impact, if any, a Lower Palaeolithic stone tool's form may have on its functional performance.

As noted previously, ethnographic accounts have the potential to provide important functional information. Across a wide range of studies it has been observed that the form of a flake's cutting edge is an important morphological feature for individuals when choosing potential tools (White & Thomas, 1972; Gould, 1980; Sillitoe & Hardy, 2003; Hiscock, 2004; Holdaway & Douglass, 2012). Most notably, edge angle in flakes has been described as consequential to the type of task undertaken. For example, Gould (1980, p.119) noted that among Western Desert Aborigines "flakes with edge angles of 40-89 degrees … were called *purpunpa* and were consistently used for wood scraping and chopping tasks in procuring and shaping … hard woods", while those with more acute angles of 15–59 degrees "were called *tjimari* and were used as knives for cutting flesh, sinew, and fibrous materials". Such accounts alone raise the question of whether Plio-Pleistocene hominins made similar functional distinctions, although of course, cannot prove it.

It is from experimental research, however, that arguably the greatest detail regarding the potential influence of morphological variation on stone-tool performance has been provided. Here, we deliberately focus on three sets of experimental research that are specifically relevant to the utilitarian impact of form in Lower Palaeolithic artefacts. The first is concerned with the comparative utility of differing flake forms, the second examines differing biface forms, while the third investigates the comparative use of flakes and bifaces directly.

Flakes

Three studies have examined the impact of flake size on their cutting abilities. Jobson (1986) identified a significant relationship between increased flake length and greater efficiency (cut-stroke count) during the butchery of rabbits (n = 24 flakes and rabbits), most likely due to their longer cutting edges, greater penetration, and manipulability. When flake size was examined in terms of mass, however, this appeared to have limited impact on performance. In turn, Jobson (1986, p.15) suggested that "flake geometry supersedes sheer mass with respect to how well a tool performs". Prasciunas (2007) similarly investigated the impact of flake size (n = 30 flakes) on cutting but used a standardised material (denim) during the experiment. Her results suggested a relationship between increasing flake size and the amount of material cut in 10 minutes, with a drop in efficiency once tools dropped below 5g or had a surface area below 7cm² (Prasciunas, 2007). In each of these studies, however, the size variation examined was limited, with only one and two flakes (respectively) in each assemblage weighing over 50g. Key & Lycett (2014) recently addressed this issue by examining cutting efficiency in 342 flakes ranging between 27–105 mm length and 3–408 g in mass. Their results indicated that there is not an absolute relationship between increased flake size and efficiency; rather, results indicated that once flake sizes reach a specific 'threshold', increased size has limited influence on effectiveness. Below this threshold, however, the use of smaller flakes reduces performance.

The remaining flake-specific studies have investigated the impact of edge form on cutting efficiency. Walker (1978) investigated the comparative effectiveness of 20 flakes with unmodified edges and 25 flakes with bifacial edges. Through butchery of a variety of large mammals, Walker (1978) concluded that both edge forms were effective, but bifacially flaked edges were less effective in most tasks, except skinning. Collins (2008) undertook a more controlled experiment, examining the impact of edge curvature and angle on flake effectiveness during wood scraping. Collins (2008) identified that convex edges resulted in significantly greater amounts of material being removed relative to straight edges. Edge angle was also determined to have a statistically significant impact on scraping, with more acute-edged tools removing material at greater rates (Collins, 2008). Jobson (1986) also examined the impact of flake edge angles on butchery efficiency. Contrary to Collins (2008), his results suggested no relationship between these two variables, however, it should be noted that the range of variability examined was limited (10°–47°) (Jobson, 1986). Key & Lycett (2015) also examined the influence of edge angle, but investigated its influence during a more standardised cutting task, using a greater range of edge angles (12°–67°) and specifically recorded loading levels applied across flakes of varying size. Their results highlight the potentially complex relationships that can exist between different aspects of a tool's form and its performance. Specifically, although there is a relationship between edge angle and increased cutting efficiency in smaller flakes, as tool size increases, the potential for greater working load also increases. Consequently, larger flakes with more obtuse edge angles can cut as effectively as smaller ones with acute angles (Key & Lycett, 2015).

Bifaces

The number of studies that have systematically examined the functional performance characteristics of bifaces varying in form is more limited than for flakes. Diez-Martín & Eren (2012, p.341) highlighted this, noting that experimental use of handaxes has principally been limited to demonstrating "what a hand ax[e] could have been used for and the experimental falsification of those potential uses". To our knowledge, only Machin *et al*. (2005, 2007) and Key, Lycett and colleagues (Key & Lycett, 2017a; Key *et al*., 2016) have specifically investigated how the cutting performance of handaxes might co-vary with variation in form. However, it should be noted that Whittaker & McCall (2001) experimentally examined whether handaxes can be used as projectiles, comparing both a large and small handaxe in terms of ease of use and distance thrown. Distinctions between tool forms were noted, with the smaller tool capable of being thrown further, but less stable in flight.

Machin and colleagues (2005, 2007) looked at the potential influence of handaxe symmetry on efficiency during the experimental butchery of deer. Their first study was limited in scale (eight deer), but led to an initial conclusion that "there is not a strong correlation between either frontal or side symmetry and the effectiveness of a handaxe for butchery" (Machin *et al.*, 2005, p.28). The second study was more extensive, comparing 60 handaxes varying in frontal and side symmetry during the butchery of 60 deer carcasses (Machin *et al.* 2007). Despite the larger sample, a relationship between symmetry and butchery efficiency was still not firmly established, with results suggesting "at the very most, frontal symmetry has a small role to play" (Machin *et al.*, 2007, p.891). Indeed, the two participants undertaking the butchery provided contrasting results, and any positive relationships were dependent on subjective scorings or the removal of an outlier.

More recently, Key & Lycett (2017a) compared cutting efficiency (time) across 500 handaxes in a standardised experimental task. The replica tools displayed considerable variation in size (4–30 cm in length and 8–4484 g) and morphometric shape properties, which deliberately exceeded those typically found archaeologically in order to push the range of variability examined. Results showed that variation in handaxe shape had little effect on cutting efficiency. Moreover, comparison of efficiency and mass across all 500 handaxes also revealed a statistically insignificant effect (Key & Lycett, 2017a). However, their results did demonstrate evidence for a 'threshold' effect at the lower end of size variation, beyond which, as handaxes reduced in size, their functional performance decreased accordingly (Key & Lycett, 2017a). This suggests 'minimal size' may be a pertinent consideration in handaxe cutting effectiveness.

In a follow-up study, Key *et al.* (2016) examined edge angles in these replica handaxes and investigated their effect on cutting effectiveness. Variation was investigated at a whole handaxe level (mean angles) and more localised levels (individual points around the edge). Somewhat counterintuitively, results at a whole-tool level showed that more obtuse edges actually increased cutting efficiency. However, this effect was observed only up to a threshold of around 70°, beyond which, increased angles resulted in decreased efficiency. Key *et al.* (2016) were further able to show that angles in the proximal (butt) portion of handaxes showed the strongest relationship to efficiency. These results are consistent with suggestions that more obtuse angles in the butt of the handaxe facilitate greater application of force during use and, in turn, increase cutting efficiency.

Flakes vs. Bifaces

Direct comparison of flakes and bifaces has received greater attention than the influence of variation within a single tool type. Jones (1980, 1994) undertook a series of well-known experiments at Olduvai Gorge functionally comparing flakes with handaxes. One of his main conclusions was that relatively larger tools (ideally with a bifacial edge) were preferable butchery tools compared to smaller tools. Jones (1980) attributed this to their increased mass, edge length, ease of gripping and applying force, and capacity for prolonged use. Serrated edges were also suggested to be the "sharpest and longest lasting", although retouched edges were considered less efficient than fresh edges (Jones, 1994, p.293). For woodworking, Jones (1994) suggested that unmodified edges, such as those found on flakes, were unsuitable and that more robust, modified edges with thicker profiles were preferable due to reduced fracturing.

A series of experiments comparing flakes and bifaces was summarised recently by Toth & Schick (2009). This work stresses the advantages provided by larger tool forms for chopping or shaping wood, although lighter woodworking can be undertaken using flakes. Based on experiments comparing efficiency during disarticulation of pork ribs, Toth & Schick (2009) also suggested that although "refined and crude handaxes had similar cutting efficiency", flakes dulled quicker than handaxes. They concluded that "Early Stone Age groups that habitually butchered medium to large mammals would likely develop either large bifacial handaxe/cleaver technologies like the Acheulean or flake denticulate technologies" (Toth & Schick, 2009, p.277). Based on other experiments, McCall (2005), however, argued that flakes could be more efficient than core tools due to their acute angles. Galán &

Domínguez-Rodrigo (2014), meanwhile, compared the efficiency of eight basic (unmodified) flakes, seven retouched flakes, two small handaxes and one large handaxe during butchery. They concluded that "small-sized handaxes can be more efficiently used … than flakes" and that "large handaxes typical of the ESA Acheulian do not seem to be as efficient for butchery as the small handaxes" (Galán & Domínguez-Rodrigo, 2014, p.1071). Their reasons for this suggestion include the larger handaxe being more difficult to handle and its more obtuse edges. Somewhat conversely, Merritt's (2012, 2016) experiments using flake and core tools led him to suggest these might be of equal value during butchery tasks. A butcher involved in one of these tasks did, however, describe personal preference for the longer, straighter edge of flakes compared with bifaces (*contra* Jones, 1980, 1994). Merritt (2016) also examined the influence of tool mass and edge angle on butchery time, with neither displaying significant relationships.

Key & Lycett (2017b) have recently highlighted that the form–function disparities observed across these studies may be due to the differing tasks undertaken in each case. Indeed, when Key and Lycett (2017b) compared the efficiency of flakes, handaxes, and flakes of equal size to handaxes (n = 60 in each instance), they observed that the relative utility of each tool was dependent on the type of cutting activity undertaken. 'Basic' flakes were significantly more effective than handaxes during tasks requiring greater precision and where the amount of material was relatively limited. Conversely, handaxes were significantly more efficient than 'basic' flakes when cutting more substantial portions of resistant material. This suggests the adoption and use of each tool type by Palaeolithic hominins were likely linked to the material contexts in which they were used. Interestingly, the comparative efficiencies of handaxes and flakes of equal size were less pronounced. This prompted these authors to reiterate the value of considering additional factors motivating handaxe production, such as their potential use as cores, capacity for resharpening, greater length of cutting edge, and that the scalloped edges would likely increase their efficiency compared to straight-edged tools when blunt (Key & Lycett, 2017b).

Would there potentially have been an adaptive benefit in preferring specific tool forms?

Flaked stone technology is generally considered to have conveyed an adaptive benefit to hominins, in turn, facilitating their widespread production among populations across the Old World (Ambrose, 2001; Shea, 2007; Roche *et al.*, 2009; Plummer & Bishop, 2016). Indeed, as Braun (2012, p.223) notes, "it seems unlikely that hominins invested time and energy in the development of a complex series of behaviors that had no impact on their eventual genetic fitness". Typically, the purported adaptive benefits of stone technology centre on the ability to effectively process animal and plant foods. However, the use of stone tools to procure other items (e.g., shelter, firewood, spears) might also have been important. The extent to which it would have been beneficial for Lower Palaeolithic hominins to modify or produce specific tool forms to optimise their utilitarian value, however, has received less attention.

The underlying assumption of specifically adaptive arguments in behavioural models is that energetic efficiency would have been of concern to individuals, and selective pressures contributed toward optimising this (Codding & Bird, 2015). Although the ecological niche of Lower Palaeolithic hominins would have been highly variable due to the broad geographical and chronological boundaries of the period, the optimisation of energetic expenditure relative to gain would have been a prevailing selective force across populations. Indeed, optimal foraging modelling (or more broadly, human behavioural ecology) demonstrates that in situations where energy resources are constrained and/or costly to procure, there are adaptive benefits to increasing the efficiency of energy procurement behaviours (Smith & Winterhalder, 1992; Bird & O'Connell, 2006; Codding & Bird, 2015). Hence, given that stone-tool use is hypothesised to have been an essential component in Lower

Palaeolithic subsistence strategies, the efficiency with which these technologies undertook cutting activities is likely to be of evolutionary consequence. Accordingly, it is frequently stated that energetic efficiency is a driving force of tool production and selection decisions undertaken by hunter-gatherer populations (Bamforth, 1986; Bleed & Bleed, 1987; Fitzhugh, 2001; Bird & O'Connell, 2006; Kelly, 2013; Plummer & Bishop, 2016). At a broad level, then, it would have been adaptive for hominins to have preferentially produced and selected tool forms that reduced costs and were functionally efficient.

The extent to which more energetically optimised stone tool forms would always have been produced by Lower Palaeolithic hominins is, however, more complex than this generalised model. Indeed, the costs and benefits associated with using stone technology cannot be solely measured through the direct utilitarian application of the tool, but must take into account raw materials costs, investment of time, body stress, mobility patterns, risk, tool reliability and maintainability, among other considerations (Bamforth, 1986; Bleed, 1986; Torrence, 1989a,b; Jeske, 1992; Kuhn, 1994; Bamforth & Bleed, 1997; Beck *et al.*, 2002; Brantingham, 2003, 2010; Bousman, 2005; Bettinger *et al.*, 2006). As Ugan *et al.* (2003, p.1323) put it, "the costs of technology are every bit as important as their benefits when trying to assess investment decisions". Accordingly, stone-tool production and selection choices could represent solutions shaped by multiple selective pressures (Bleed & Bleed, 1987).

Moreover, Lower Palaeolithic stone tools were likely utilised in a variety of situations, suggesting a further need to consider trade-offs between using a greater number of specialised tools versus more generalised tools (Bleed, 1986; Nelson, 1991). Stevens & McElreath (2015) have recently modelled such considerations in Holocene ground stone tools, which have attendant implications for Palaeolithic technologies. Their results again highlight that tool form production and selection decisions are not only underpinned by the relative efficiency with which a tool may complete a task, or the relative duration of a tool-use activity, but also by how regularly a specific task is likely to be undertaken (Stevens & McElreath, 2015). Indeed, "if a multifunctional tool is cheaper [less costly] to make, and has a decent return rate across multiple tasks, it can outcompete more specialized tools", however, "specialized tools, even if they are more expensive to manufacture, can outcompete multifunctional tools, but only when the tasks they are designed for are performed often enough, or occur with enough certainty, to make it worthwhile" (Stevens & McElreath, 2015, p.108). More broadly, however, this implies that if a hominin cannot reliably predict a tool's functional context at the point of production, or there is a likelihood that it will be used in multiple functional contexts, then a multifunctional tool would be optimal.

Finally, it is important to emphasise that these studies specifically refer to energetic considerations in anatomically modern humans. While such models might reasonably be applied to hominins associated with Acheulean technologies (e.g., *Homo erectus s.l.*) (Bird & O'Connell, 2006), greater caution is necessary for the producers of Lomekwian and Oldowan technologies. Certainly, differences in anatomy likely preclude direct energy-consumption comparisons for some behaviours (e.g., raw-material transportation costs), and thus may convey additional/reduced energy requirements relative to modern humans. This does not alter underlying requirements to optimise energetic expenditure relative to gains and the adaptive benefits of using more efficient tool forms. Indeed, this emphasizes that understanding the relative efficiencies of varying tools forms might provide an important 'anchor' variable within a wider range of complex and potentially unknowable considerations.

Were Lower Palaeolithic hominins capable of intentionally selecting or producing functionally preferable tool forms?

The tool selection and modification behaviours of nonhuman primates provide important insights into the potential capabilities that were likely displayed by Lower Palaeolithic hominins. Indeed, parsimony suggests that if extant nonhuman primates can preferentially select and produce different tool forms, then early humans may similarly have been capable of doing so. Accordingly, it is often argued that chimpanzee tool use is an effective model for understanding the technological and behavioural capabilities from which Lower Palaeolithic tools emerged (McGrew, 1992; Ambrose, 2001; Wynn *et al.*, 2011; Carvalho & McGrew, 2012). Moreover, if such capabilities are not only displayed in our closest relations within the genus *Pan*, but more widely across the primate order, then such claims are strengthened.

In some chimpanzee communities, termite fishing involves the forceful opening of a mound's exterior with a sturdy 'perforating twig' (Sanz *et al.*, 2004), followed by use of more slender stems to extract termites (Sanz *et al.*, 2009). Sanz *et al.* (2009) examined the design of termite-fishing tools from chimpanzees in the Goualougo Triangle (Republic of Congo) and identified specific tool modifications by chimpanzees, including the fraying of probe ends, splitting the probe, separating plant fibres, and modifying the length (Sanz *et al.*, 2009). Experimental data indicated that those with modifications were "significantly more effective in gathering termites" (Sanz *et al.*, 2009, p.295). Intentional tool-modification processes are further noted in chimpanzees that hunt for prosimians (*Galago senegalensis*) with 'spear like' probes. Up to five modification behaviours are sometimes undertaken prior to use of these tools (Pruetz & Bertolani, 2007). In ~50% of cases, they are used before all steps of modification have been undertaken, implying that individuals are assessing the effectiveness of partially modified tools and only continue with further modification if necessary (Pruetz & Bertolani, 2007).

Boesch *et al.* (2009) have observed chimpanzees in Loango National Park, Gabon, undertaking sequential tool choice and modification procedures, producing several different tools used together for honey extraction. These 'tool-sets' consistently contain of a number of branches of distinct forms and raw materials that are employed in different stages of the honey extraction process. Hence, Boesch *et al.* (2009) note that chimpanzees are displaying an appreciation of tool raw-material quality prior to undertaking a task, selectively transporting certain tool types to a food resource, modifying tools prior to use, and repeatedly producing tools of specific proportions and morphologies, an inference further supported experimentally (Manrique *et al.*, 2010).

Wild chimpanzees have also been observed preferentially selecting nut-cracking hammers depending on their material and form properties (Sirianni *et al.*, 2015), which is a behaviour only previously having been noted in captive populations (Schrauf *et al.*, 2012). Specifically, Sirianni *et al.* (2015) observed chimpanzees of the Taï National Park (Côte d'lvoire) preferring stone hammers over wooden alternatives, heavier stone hammers relative to light stone ones, increasingly heavier hammer stones the closer they are to an anvil, and the preferential selection of lighter hammer stones when cracking nuts on a wooden anvil. This demonstrates a complex, multidimensional tool-selection strategy that may be considered representative of foraging optimisation through appropriate tool-form selection (Sirianni *et al.*, 2015) similar to that discussed above for humans. Schrauf *et al.* (2012) further demonstrated that captive chimpanzees are not only capable of selecting the most effective hammerstones for nut cracking, but that they can identify tool mass as central to the effectiveness of the tool. Schrauf *et al.* (2012, p.12) conclude that "encoding the requirements that a nut-cracking tool should meet (in terms of weight) to be effective therefore lies within chimpanzees' capabilities". Chimpanzees are, then, not only capable of preferentially altering the form of a tool so that it may better undertake a functional task, but are able to assess the relative performance attributes of varying tool forms and, accordingly, make informed choices.

Insights into the stone-tool modification and selection capabilities of *Pan* also come from experiments with captive apes. Famously, the bonobo Kanzi was shown how to knap sharp stone flakes (Toth *et al.*, 1993; Schick *et al.*, 1999). Kanzi was then encouraged to use these flakes to cut pieces of cordage and gain access to a food reward. Notably, Kanzi preferentially selected the largest flakes and then tested their sharpness using his tongue (Schick *et al.*, 1999). Although this is only a single individual, it is indicative of a capability to assess both the ergonomic benefits of a larger flake and the necessity of a sharp edge when undertaking cutting tasks.

Old World monkeys also preferentially select tools based on their functional capabilities. Gumert *et al.* (2009) presented evidence that wild long-tailed macaques (*Macaca fascicularis*) select and use different stone tools depending on the type of food-processing activity undertaken. Specifically, macaques used smaller stones and their pointed ends when detaching oysters, whereas tools found at anvils (for processing larger molluscs and nuts) tended to be larger and displayed evidence of broader surfaces having been utilised (Gumert *et al.*, 2009; Gumert & Malaivijitnond, 2013). Some New World monkeys have similarly displayed such abilities. Fragaszy *et al.* (2010), for example, experimentally demonstrated that wild bearded capuchins (*Sapajus libidinosus*) can discriminate between the differing resistance of nut species and the mass of different hammerstones, in turn selecting combinations of tools and nuts that minimise the number of hammerstone strikes. It has also been noted that both visual and manual cues are used by capuchins when assessing the functional suitability of hammerstones, prompting Visalberghi *et al.* (2009, p.215) to conclude that they "consistently and immediately selected functional tools, regardless of the condition intricacies".

Evidence from the fossil record indicates that the encephalization quotients of likely Lomekwian and Oldowan stone-tool producers were only marginally larger—if at all— compared with *Pan* (Antón *et al.*, 2014). It may, therefore, be suggested that the earliest stone-tool producing hominins would likely have been as capable of the tool-choice proficiencies displayed by the living nonhuman primates discussed. Evidence of raw material selectivity based on cutting-edge durability further suggests that Oldowan hominins were capable of relevant tool selection decisions (Harmand, 2008; Braun *et al.* 2009), as does their ability to selectively transport specific flake forms dependent on their lack of cortex, edge durability, size and completeness (Stiles, 1991; Reti, 2016). The demonstrable understanding of stone fracturing and knapping skills by Oldowan hominins (Roche *et al.* 1999; Delagnes & Roche, 2005; Stout *et al.*, 2010), which exceeds even those of Kanzi (Toth *et al.*, 2006), and their ability to display differential tool-production strategies depending on the relative costs of raw materials (Blumenshine *et al.*, 2008; Gurtov & Eren, 2014; Reti, 2016) may further underline the selective capabilities of Oldowan hominins. A conscious awareness of the feedback mechanisms relating to tool performance (ease of use, effectiveness, etc.) that underpin tool production decisions and inform individuals of the consequences of technological choices (Schiffer & Skibo, 1997) may, then, have been within the cognitive capabilities of these Lower Palaeolithic hominins.

After ~1.8 MYA, some hominin species begin to display substantially increased cranial capacities relative to *Pan* and on the order of twice those (upwards of ~800cc) of earlier hominins (Antón *et al.*, 2014). Consequently, the sophisticated tool selection and modification processes displayed by chimpanzees are arguably going to have been exceeded by Acheulean hominins. This is potentially further supported by the tool production strategies displayed by Acheulean hominins (Wynn, 2002; Goren-Inbar, 2011; Stout *et al.*, 2014). The extent to which Acheulean hominins could exceed the tool selectivity and functionally related modification processes displayed by *Pan* is, however, a point that requires further attention in the future. Although, as the following discussion highlights, work with relevance to this discussion is beginning to be undertaken.

Do Lower Palaeolithic artefacts indicate that relatively more effective tool forms were being intentionally produced or selected by hominins?

To some extent, the evidence for hominin tool selectivity and their likely capabilities to do so will have changed over the course of time engulfed by the 'Lower Palaeolithic' (i.e. *c.*3.3 MYRs to ~300 KYRs). Accordingly, we consider these issues on a chronological and technological basis.

The Lomekwian

The 3.3 million-year-old stone tools found at Lomekwi 3 (West Turkana, Kenya) have only recently been described, although evidence to date suggests that relatively large flake tools were being intentionally produced (Harmand *et al*., 2015). Indeed, the mean length and mass of published Lomekwian flakes (n = 26) is 120mm and 842g (Harmand *et al*., 2015). Key & Lycett (2014) demonstrated that flakes just under this size (103mm in mean length) are not only effective cutting tools, but are as effective flakes 88–58mm in length and are more efficient than flakes below ~43mm in length. Moreover, flakes of similar size (mean length = 145mm, mean mass = 677g) to the Lomekwian material have been shown experimentally to be effective cutting tools during a variety of different tasks (Key & Lycett, 2017b). On the basis of such results, there appears little to reason to suggest that the large 'Lomekwian' flakes were necessarily ineffective if ever used as cutting tools. Key & Lycett (2014) also demonstrated that the loading capabilities of flake tools increases with size. Whether this indicates that loading potential was important to the hominins at Lomekwi is currently unclear. However, if the makers of these flakes were restricted in their physical ability to exert downwards momentum during use (Schick *et al*., 1999; Domalain *et al*., in press), the greater load potential afforded by large flakes may have been of value (Key & Lycett, 2017b).

The Oldowan

Oldowan flake artefacts are highly variable in shape and size. Across broad chronological and geographic ranges, however, mean flake lengths of individual assemblages are typically between 35–50mm (Semaw, 2000; de la Torre, 2003; Delagnes & Roche, 2005; Stout *et al*., 2010; Harmand *et al*., 2015). Broadly, this coincides with the more efficient flakes utilised by Jobson (1986) and is above the minimum size-efficiency thresholds identified by Prasciunas (2007) and Key & Lycett (2014). Arguably, flakes of this size may correspond to an optimisation between maximising functional performance and minimising material costs associated with producing larger (but fewer) flakes per unit of raw material (Brantingham, 2010; Surovell, 2009). Given the controlled reduction strategies exhibited in many of these assemblages (e.g., Semaw, 2000; de la Torre, 2003; Delagnes & Roche, 2005), there is reason to predict that Oldowan hominins were preferentially producing flakes above experimentally described functional thresholds to produce flake tools that could be efficiently used as a hand- or finger-held cutting tools. Of course, the form of Oldowan flakes may depend on multiple factors (Kimura, 1999; Braun *et al*., 2008b; Blumenshine *et al*., 2008; Roche *et al*., 2009; Stout *et al*., 2010; Reti, 2016), many flakes within excavated assemblages may not been used (Roche *et al*., 1999; Lemorini *et al*., 2014) and hominins may have displayed only limited selectivity once flakes met minimum thresholds (Hiscock, 2004; Holdaway & Douglass, 2012). Nonetheless, flake data does indicate that—on average—Oldowan hominins were producing functionally efficient flake sizes. Some Oldowan sites, however, exhibit disproportionally high numbers of small flakes, at times with mean lengths of ≤25mm (de la Torre, 2004; Zaidner, 2013; Gallotti & Mussi, 2015). Experimental evidence would, then, seem to indicate that these flakes displayed somewhat restricted functional potential (Jobson, 1986; Key & Lycett, 2014), perhaps being particularly suited to tasks requiring limited force, restricted use times, or involving relatively small amounts of material. However, while additional factors require consideration (e.g., the availability of differently-sized raw materials [de le Torre, 2004]), the presence of such assemblages suggests some uncertainty regarding the extent to which hominins were always capable of optimising flake size, at least on the basis of experimental data.

Edge morphology data are rarely reported from Oldowan assemblages, with discussion tending to centre on the value and intentional production of 'sharp' cutting edges (e.g., Toth, 1985; Semaw, 2000; Barsky *et al*., 2011). Lemorini *et al*. (2014) provide one of the few studies of edge angles for Oldowan flake tools at Kanjera South, Kenya. For the 39 artefacts described, edge angles ranged between 29–90°, although little other morphological or methodological information is provided making it difficult to definitively relate such variation to functional issues. Zaidner's (2013) description of small flakes from the Early Pleistocene site of Bizat Ruhama (Israel), however, reported a mean angle of 37° across the assemblage. Experimental and ethnographic evidence indicates that flakes with acute edges typically display increased efficiency (e.g., White & Thomas, 1972; McCall, 2005; Collins, 2008) but that small flake tools, in particular, require more acute edges due to their reduced loading capabilities (Key & Lycett, 2015). Hence, this is consistent with hominins at Bizat Ruhama preferentially producing small flakes with relatively acute edges in order to facilitate their more effective use as cutting tools. Retouched flakes are often rare in Oldowan assemblages (e.g., Roche *et al.*, 1999, 2009). It may, therefore, be the case that Oldowan hominins were often not modifying edges to exploit any potential benefits provided by increased scalloping/serration or sinuosity (Walker, 1978; Atkins, 2009; Key, 2016).

There have been a few suggestions of Oldowan hominins preferentially selecting flake tools based on their form. Stiles (1991, pp.10-13) suggested a bias in the selection and transportation of "whole flakes" from Bed II at Olduvai Gorge and that there was a "distinct selection for medium-sized, thin flakes". Kuman & Field (2009) similarly suggest the preferential transportation of medium-sized Oldowan quartzite flakes at Sterkfontein (South Africa), in turn suggesting the preferential transportation of functionally efficient tool sizes (Jobson, 1986; Key & Lycett, 2014). More recently, Reti (2016) undertook a replication experiment indicating Oldowan hominins at Olduvai Gorge selectively transported quartzite flakes dependent on their form, most likely due to levels of cortex retention, more durable edges and, in turn, increased functional potential. This is arguably demonstrative of an ability by hominins to appreciate the increased utility of certain flake forms and to subsequently make appropriate selective decisions. Blumenshine (2008) similarly determined that tool transportation distances at Olduvai may have been related to durability of cutting edges. Braun (2008c), Harmand (2008) and Kuman & Field (2009) also demonstrated that raw-material selection at Kanjera South and Lokalaei in Kenya, and Stekfontein in South Africa (respectively), was likely dependent on durability. These latter four studies do not directly relate to the selection of specific tool forms, but they highlight the importance of maintaining functionally efficient tool forms (sharp edges) over extended periods in hominin tool production-related decisions.

The Acheulean

Acheulean assemblages may contain flakes, bifaces, or a combination of the two. Among other hypotheses, this has sometimes been taken to indicate that hominins may have been producing each tool in response to varying utilitarian (behavioural) demands (Domínguez-Rodrigo *et al.*, 2014; Diez-Martín *et al.*, 2015; Moncel *et al.*, 2015). Certainly, it has been repeatedly demonstrated that these two tool types can (depending on the task being undertaken) display divergent performance capabilities (Jones, 1980; Toth & Schick, 2009; Galán & Domínguez-Rodrigo, 2014; Key & Lycett, 2017b), and may accordingly have underlain the decision-making processes that resulted in either tool form being produced.

Limited research has been published regarding the comparative forms of Acheulean flake tools, particularly in relation to their possible functions (Gowlett, 2015). The presence of large 'Clactonian' flakes in Britain has often been noted (Pettitt & White, 2012) and, at times, has been linked to their use in specific contexts (Ashton *et al.*, 1994), such as associations with large mammal butchery sites (Wenban-Smith *et al.*, 2006), which may suggest heavy-duty cutting tasks (Jones, 1980, 1994; Key & Lycett, 2014, 2017b). However, it is at Iberian sites that the most detailed functional analyses of Acheulean flake-tool forms have been attempted. Terradillos-Bernal & Rodríguez (2012, 2017) examined the mass, edge form, raw-material properties and functional capabilities of flakes from several sites. They proposed three distinct categories of flake tools were being produced based on edge form (particularly edge angle) and tool mass (Terradillos-Bernal & Rodríguez, 2012). Furthermore, they contended that use of different raw materials affected flake-edge form and utility and, in turn, influenced the forms produced and raw materials selected (Terradillos-Bernal & Rodríguez-Álvarez, 2017). These works are important as two of the first Lower Palaeolithic artefact studies to incorporate mechanical principles when considering tool form choices and form–function relationships. However, and as noted by Key & Lycett (2015), the complex interdependent relationships between flake size, loading, edge angle and the amount of work (energy) required to cut materials, need also to be considered. Further research is, therefore, needed to clarify the extent that Acheulean hominins were selectively producing different flake tool forms with respect to use.

Handaxes and cleavers have received considerable attention regarding variation and standardisation in their form. However, functional considerations have not always been considered as a leading explanatory hypothesis for such variation. Wynn & Tierson (1990, p.81), for example, surmised that "no one has ever made a convincing argument that mechanical function is responsible for the general shape of the biface, let along the differences in shape". Conversely, others have proposed that biface form might have particular functional relevance (e.g., Roe, 1981; Grosman *et al.*, 2011; Beyene *et al.*, 2013; Diez-Martín *et al.*, 2014; Gowlett, 2011a, 2013, 2015; Moncel *et al.*, 2015). Two studies by Gowlett & Crompton (1994; Crompton & Gowlett, 1993), for example, demonstrated that size attributes in handaxe assemblages may display allometric scaling, meaning that an increase in the absolute length of a handaxe does not necessarily lead to a linearly scaled increase in its thickness. They interpret these scaling relationships in terms of the need to maintain functionally effective tool-mass ranges in larger artefacts. Gowlett (2009b, 2015) has since provided further evidence that handaxe mass was likely controlled for functional reasons, including links between recurrent average tool mass (~0.5kg) and biomechanical limitations. Although Key and Lycett (2017a) failed to find a significant drop in biface efficiency levels in tools greater than 0.5kg in mass, their experiment did not examine tool use over extended (i.e. >10 minutes) periods, where mass may have greater influence (Jones, 1980, 1994). These authors did, however, find an effectiveness threshold at the lower end of handaxe variation (Key & Lycett, 2017a). Given that handaxes frequently appear to have been abandoned with further reductive potential remaining (Pitts & Roberts, 1997; Goren-Inbar & Sharon, 2006; Petraglia & Shipton, 2008; Shipton & Clarkson, 2015; Gowlett, 2015; Moncel *et al.*, 2015) it is plausible that hominins managed reduction and discard behaviours with regard for such a threshold (Key & Lycett, 2017a).

Examinations of handaxe edge form have generally been limited to Middle Palaeolithic bifaces, where edge-angle variation has been linked with use in differing functional contexts (Soressi & Hays, 2003) and a possible need to maintain effective angles following resharpening (Iovita, 2014). However, Key *et al.* (2016) showed that Acheulean handaxes tend to display increasingly obtuse edge-angles from tip to base and that mean angles in the base rarely exceeded 70°. Both trends were suggested to be functionally derived, with the former resulting in an effective cutting edge toward the tip, while simultaneously facilitating the exertion of high loading by the hand at its base. The latter meanwhile may represent a need to, at least occasionally, utilise the base as a functional (cutting) edge (Key *et al.*, 2016). Recurrent thickness measurements in the proximal portion of handaxes at Nahal Zihor (Israel) further suggest artefact forms may be linked to functional and ergonomic constraints (Grosman *et al.*, 2011). Such factors can also be connected to previous suggestions linking the presence of a 'globular butt' and dimensional properties of handaxes to an increased ability to stabilise, grip and balance a handaxe during use (Gowlett, 2006, 2011b, 2013).

Cultural evolutionary approaches to handaxe variability have also stressed the role that selective factors may have played. Simão (2002, p.419), for example, proposed that symmetry may have been influenced by functional pressures, or as he put it, “the selective recreation of tools depending on how well they fitted their target function(s)”. He specifically argued that symmetry potentially reduces torque and maximises power by putting a handaxe’s centre-of-mass in line with motion during use (Simão, 2002). Subsequently, using principles drawn from population genetics, Lycett (2008) argued that symmetry variation in handaxes does not conform to a null model of neutral variation but, rather, displays evidence of having been subject to selective forces, with techno-functional, socio-functional and aesthetic selection all being possible candidate mechanisms. More recently, Kempe *et al.* (2012) explicitly modelled size variation resulting from copying error and compared this to variation in 2061 archaeological handaxes from 21 different sites. Their results demonstrated that artefacts displayed limited size variation compared to the model, indicating functionally-related cultural selection was likely operating, particularly the need to grip a handaxe comfortably in the hand (Kempe *et al.*, 2012, p.6). This conclusion has further been supported by experimental work examining the impact of tool-user handsize on the effectiveness of handaxes during cutting (Key & Lycett, in press). Vaughan (2001) similarly used evolutionary theory to examine variation in 251 handaxes covering some 1.5 MYRs. Following Dunnell (1978), Vaughan reasoned that traits displaying a relatively high level of variation were likely more ‘stylistic’ and subject to random evolutionary changes (drift, transmission error), while ‘functional’ traits would be less variable due to selection. Accordingly, Vaughan (2001) argued that handaxe length may have been under less selection than other attributes such as breadth. However, as noted by Lycett (2013, p.118), Vaughan’s (2001) characterisation of ‘stylistic’ versus ‘functional’ traits does not adequately account for the idea that cultural selection can operate outside of purely utilitarian parameters, and in this sense, even ‘stylistic’ parameters can be subject to selection. Indeed, Key & Lycett’s (2017a) study suggests there would have been little direct functional benefit to specific handaxe shapes, which is in line with recent studies stressing the role of cultural drift in creating shape differences within and among different handaxe assemblages, even if there were some selected limits to overall form (Lycett 2008; Lycett *et al.*, 2016).

Conclusions: untangling form and function in Lower Palaeolithic technologies and their continued analytical relevance

A range of nonhuman primates have now been observed using unmodified stone tools for percussion activities in the wild (Gumert *et al.*, 2009; Fragaszy *et al.*, 2010; Carvalho & McGrew, 2012). However, even though such behaviour sometimes results in the breakage of lithic matter (e.g., Mercader *et al.*, 2007; Proffitt *et al.*, 2016), crucially, no living nonhuman primate has ever been observed using a stone cutting tool in the wild, nor deliberately flaking lithic material for subsequent use as a tool. This contrasts with evidence that occurs alongside some of the earliest appearances of knapped material in the archaeological record, showing hominins were using stone tools for cutting activities (e.g., Semaw, 2006); a focussed tool-use pattern that continued for millennia thereafter. Accordingly, as others have noted, the appearance of stone cutting technology seems to be a uniquely hominin invention, motivated by particular needs (Roux & Bril, 2005). Consequently, considerations of whether stone-tool form relates to functional matters has deep historical roots in the discipline. Current perspectives clearly draw on and directly build upon this historical legacy. However, it has long been recognised that distinctions between tool forms, including those used to create categorical types, are not necessarily tantamount to differences in the activities to which they can be applied (Odell, 1981). In turn, contemporary concerns exhibit a focus on more precisely identifying how indirect and direct evidence might shed light on form–function relationships. Debate concerning the comparative performance characteristics of different tool forms, and the extent to which lithic artefacts may have been optimized with respect to these characteristics, has also grown in consequence. Here, we have reviewed evidence regarding these issues in Lower Palaeolithic flaked-stone-technology against this historical backdrop. We have proposed that four broad questions may be used to address whether Lower Palaeolithic hominins were producing and/or selecting different stone tool forms with specific regard to their performance capabilities. Current evidence in response to these four questions may be summarised as follows:

- Experimental evidence has repeatedly shown that morphological attributes in flakes and bifaces have the potential to significantly influence their cutting performance in a variety of material contexts. This includes evidence suggesting that determining whether a flake or handaxe will be the more effective tool, depends on the physical properties of the task. In turn, there is potential for functionally derived selective pressures to have influenced the form of stone tools during the Lower Palaeolithic. This may be in the form of directional, disruptive or stabilising selection. As significant as these findings are, research indicating that artefactual variation may occur independently of functional performance is just as important. Indeed, in several instances it has been identified that once tool forms are above or below form-dependent performance thresholds, there is potential for a substantial area of 'free play' where tools may vary without functional consequence (Crompton & Gowlett, 1993; Lycett *et al*., 2016). A logical consequence of this is that it is often necessary to test a wide range of tool forms (that often go beyond those observed in the artefact record) to adequately test their performance limits. Furthermore, in recent years it has become increasingly clear that complex relationships exist between a stone tool's form, the material being worked and the individual tool user − all of which interact to influence efficiency. Moreover, multiple performance characteristics (e.g., loading, manipulability, cutting stress created) may interact to influence the final form of a tool (Schiffer & Skibo, 1987). This does not necessarily detract from our ability to identify important implications regarding form–function relationships and the decisions underlying hominin tool-production choices, but rather, suggests that anyone modelling these relationships needs to be measured in their approach.
- In general terms, the potentially adaptive value of stone technology for Lower Palaeolithic hominins can be assumed with some security. Questions relating to the adaptive significance of specific stone tool forms has, however, rarely been discussed (although for examples see: Bamforth, 1986; Bleed, 1986; Jeske, 1992; Torrence, 1989a), particularly within a Lower Palaeolithic context. As discussed, it is reasonable to infer that optimising energetic expenditure relative to gain would have been consequential to hominins. Certainly, within Lower Palaeolithic contexts there would likely have been strong selective mechanisms in place favouring not only the use of stone tools to aid in the procurement of energy resources, but also minimizing the costs associated with manufacturing and using these tools. This indicates that more detailed examinations of these issues in Lower Palaeolithic contexts is desirable.
- Studies of extant nonhuman primates demonstrate relatively complex tool production and selection decisions by species with relative brain sizes equal to, or less than, those of Lower Palaeolithic hominins. Importantly, such decisions are often based on a tool's form or material properties and often increase performance within functional contexts. Parsimony, then, allows us to infer that Lower Palaeolithic hominins were

likely capable of intentionally selecting different stone tool forms depending on their basic attributes and performance feedback during use, as speculated half a century ago by David Clarke (1968, p.182, pp.217-218). Further, there is evidence that some Acheulean hominins may have exhibited functionally related tool selection and production capabilities in excess of those exhibited by extant nonhuman primates (Wynn, 2002; Key *et al.*, 2016; Stout *et al.*, 2014). In sum, there is evidence to suggest that hominins would have been able to recognise basic relative performance capabilities of different Lower Palaeolithic tool forms and appropriately modify related behaviours in response. Indeed, based on data from chimpanzees suggesting they manufacture 'tool sets' comprised of tools with differing performance attributes, there seems reason to suspect Lower Palaeolithic hominins may also have combined stone tools with different functional benefits. Most notably, given recent data highlighting the functional benefits of flakes and handaxes are potentially specific, the beneficial combination of both tools as a 'tool set', is set in new light.

- Multiple variables interact to influence a tool's efficiency (Fig. 4). Discussed here are a range of artefact analyses indicating that Lower Palaeolithic hominins were potentially producing stone tool forms with respect to their functional capabilities. In some instances, evidence is as straightforward as the identification that flakes and bifaces were recurrently produced within functionally efficient size ranges and meeting minimum thresholds. In other cases, and often with regards to bifaces, there are specific aspects of assemblage variability that are suggestive of tool forms being produced that increase their functional performance. When combined, there is convincing evidence to suggest that at least in regards to a number of key morphological attributes, Lower Palaeolithic hominins were producing specific stone tool forms with respect to their functional performance. However, better understanding how evolving cognitive, anatomical and social capacities to manipulate these variables relate to archaeological patterns (within and beyond the Lower Palaeolithic) clearly emphasizes the role form–function considerations must play in further investigation of these broader components of human evolution.

Based on current evidence we can, therefore, contend that the comparative performance capabilities of differing tool forms could theoretically have influenced stone tool production and selection decisions during the Lower Palaeolithic period. Moreover, hominins likely had both the cognitive capacity and adaptive stimulus to respond to such pressures and, additionally, the artefact record has the potential to inform us about how functionally related production and selection behaviours came to shape the stone tool forms recovered. Being explicit about this is important, if stone tools are to live up to their potential to inform us about important aspects of human evolution (Gowlett, 2010; Shea, 2011; Lycett, 2013).

'Function' should not, of course, be considered a lone influence on Palaeolithic tool forms (Roe, 2003; Gowlett, 2011a, 2011b). There is near consensus that no single behaviour or variable satisfactorily accounts for the variation observed within or between artefact types during the Lower Palaeolithic (Noll & Petraglia, 2003; McNabb *et al.*, 2004; Machin, 2009; Gowlett, 2009b; Archer & Braun, 2010; Diez-Martín *et al.*, 2014; Eren *et al.*, 2014; Lycett & von Cramon-Taubadel, 2015; Moncel *et al.*, 2015). The discussion presented here reflects this and emphasises the importance of considering multiple explanatory hypotheses when interpreting variation and standardisation in artefact forms. Recent experiments identifying areas of 'free play' in handaxe shape and cutting performance highlight this point (Key & Lycett, 2017a) and stress the role that additional factors play in influencing aspects of assemblage variation (McPherron, 1999; Archer & Braun, 2010; Lycett & von

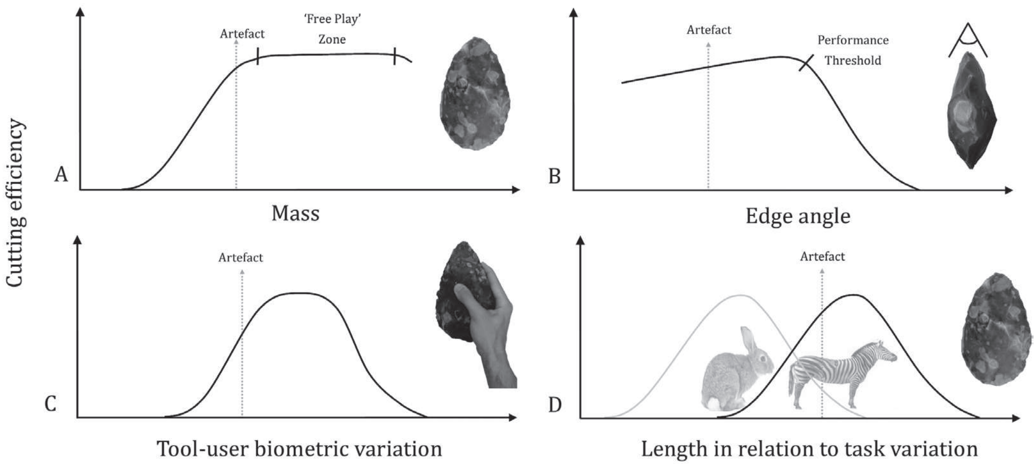

Fig. 4 - Schematic illustrating how several variables intrinsic to the artefact (e.g., a and b) as well as external to the artefact (e.g., c and d) may conspire to determine an artefact's efficiency with respect to a task such as cutting. A single variable such as mass (a) may have a notable effect on cutting efficiency, but then efficiency may be independently influenced by a second morphometric property such as edge angle (b). However, in some attributes, considerable morphological variation ('free play' zone in a) may be permissible with little discernible implications for efficiency except when specific morphological 'thresholds' are reached. The same artefact may also perform differently depending on the biometric attributes of the tool user (c). The same artefact may perform differently in two similar types of task with variable environmental properties (d), whereupon it is close to optimal in respect to one task (e.g., butchering large fauna) but relatively poorer in a similar task (e.g., butchering smaller fauna). The colour version of this figure is available at the JASs website.

Cramon-Taubadel, 2015; Schillinger *et al.*, 2017). Certainly, if experiments cannot identify a strong relationship between aspects of a tool's form and its performance characteristics across broad ranges of variation (i.e. the attribute is influence-neutral to functional performance) or within task-dependent 'thresholds', then there must be alternative mechanisms influencing the forms of tool produced.

It could, however, equally be stressed that stone tools are functional objects and must have met basic morphological criteria enabling their use to at least minimum performance thresholds (Meltzer, 1981; Schiffer & Skibo, 1997). Specifically, stone tools must have facilitated the provisioning of returns that exceed their respective accumulated costs, especially in the case of recurring tool forms. As demonstrated in experimental studies (Prasciunas, 2007; Key & Lycett, 2014, 2015, 2017a), these minimum performance levels may be modelled as task-dependent thresholds. In turn, functional concerns interacting with other factors are likely reflected in some of the strong and deep-rooted regularities observed within and between Lower Palaeolithic artefact assemblages (Goren-Inbar & Saragusti, 1996; Lycett & Gowlett, 2008; Hovers, 2012; Gowlett, 2015). Moreover, the ability to experimentally discern compromises in tool performance, as exhibited by artefactual deviations away from more 'optimised' tool forms, facilitates investigation into other causal factors underlying variability (Schiffer & Skibo, 1997). Hence, further experiments examining our relative ability to identify mechanically and ergonomically optimised tool forms are vital to not only understanding any influence of functionally selective mechanisms on artefact forms, but may profitably be used to identify the relative influence of other causal factors. Moreover, the importance of direct evidence to more securely infer the context of tool applications in archaeological settings is reemphasized.

A functional perspective when interpreting artefacts forms is, therefore, vital to our ability to accurately interpret the tool-form related behaviours of Lower Palaeolithic hominins, and their consequences for (and relationship to) wider factors of human evolution. Moreover, direct, indirect, experimental, and evolutionary perspectives intersect in crucial ways. Given that many basic statements about the functions of Lower Palaeolithic stone tools have changed little over more than a century, the recognition of this interaction, and methodological improvements to investigate it, are arguably the most outstanding contribution that developments in more recent decades have made. Moreover, they hint that methodological innovations that more rigorously allow each of these factors to be investigated, will also be where the greatest contributions can be made in the future.

Acknowledgements

AK's research is funded by a British Academy Postdoctoral Fellowship. SJL's work is supported by the Research Foundation for the State University of New York. We are grateful to the editorial board for their invitation to undertake this review and the anonymous reviewers for their constructive and detailed comments. We are indebted to Morag Masters for the illustrations provided in Figure 3.

References

Aiston G. 1928. Chipped stone tools of the Aboriginal tribes east and north-east of Lake Eyre, South Australia. *Papers and Proceedings of the Royal Society of Tasmania*, pp. 123-131.

Ambrose S.H. 2001. Paleolithic technology and human evolution. *Science,* 291: 1748-1753

Antón S.C., Potts R. & Aiello L.C. 2014. Evolution of early *Homo*: An integrated biological perspective. *Science,* 345: 1236828.

Archer W. & Braun D.R. 2010. Variability in bifacial technology at Elandsfontein, Western cape, South Africa: a geometric morphometric approach. *J. Archaeol. Sci.,* 37: 201-209.

Archer W., Braun D.R., Harris, J.W.K., McCoy J.T. & Richmond B.G. 2014. Early Pleistocene aquatic resource use in the Turkana Basin. *J. Hum. Evol.,* 77: 74-87.

Ashton N., McNabb J., Irving B., Lewis S. & Parfitt S. 1994. Contemporaneity of Clactonian and Acheulian flint industries at Barnham, Suffolk. *Antiquity,* 68: 585-589.

Atkins T. 2009. *The Science and Engineering of Cutting*. Butterworth-Heinemann, Oxford

Bamforth D.B. 1986. Technological efficiency and tool curation. *Am. Ant.,* 51: 38-50.

Bamforth D.B. & Bleed P. 1997. Technology, flaked stone technology, and risk. *Archaeol. Papers Am. Anthropol. Ass.,* 7: 109-139.

Barnes A.S. 1939. The differences between natural and human flaking on prehistoric flint implements. *Am. Anthropol.,* 41: 99-112.

Barsky D., Chapon-Sao C., Bahain J.-J., Beyene Y., Cauche D., Celiberti V., Desclaux E., de Lumley H., de Lumley M.-A., Marchal F., Moullé P.-E. & Pleurdeau D. 2011. The early Oldowan stone-tool assemblage from Fejej FJ-1a, Ethiopia. *J. Afr. Archaeol.,* 9: 207-224.

Bar-Yosef O., Eren M.I., Yuan J., Cohen D.J. & Li Y. 2012. Were bamboo tools made in prehistoric Southeast Asia? An experimental view form South China. *Quat. Int.,* 269: 9-21.

Beck C., Taylor A.K., Jones G.T., Fadem C.M., Cook C.R. & Millward S.A. 2002. Rocks are heavy: transport costs and Paleoarchaic quarry behaviour in the Great Basin. *J. Anthropol. Archaeol.,* 21: 481-507

Bello S.M., Parfitt S.A. & Stringer C. 2009. Quantitative micromorphological analysis of cut marks produced by ancient and modern handaxes. *J. Archaeol. Sci.,* 36: 1869-1880.

Bettinger R.L., Winterhalder B., McElreath R., 2006. A simple model of technological intensification. *J. Archaeol. Sci.,* 33: 538-545.

Beyene Y., Katoh S., WoldeGabriel G., Hart W.K., Uto K., Sudo M., Kondo M., Hyodo M., Renne P.R., Suwa G. & Asfaw B. 2013. The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. *Proc. Natl. Acad. Sci. U.S.A.,* 110: 1584-1591.

Beyries S. 1990. Problems of interpreting the functional results for ancient periods. In K.

Knutsson, B. Graslund, H. Knuttsson & J. Taffinder (eds): *The Interpretative Possibilities of Microwear Studies*, pp. 71-76. Societas-Archaeological Upsaliensis, Uppsala.

Binford L.R. 1986. An Alyawara day: making men's knives and beyond. *Am. Ant.,* 51: 547-562

Binford L.R. & Binford S.R. 1966. A preliminary analysis of functional variability in the Mousterian of Levallois facies. *Am. Anthropol.,* 68: 238-295.

Bird D.W. & O'Connell J.F. 2006. Behavioral ecology and archaeology. *J. Archaeol. Res.,*14: 143-188.

Bleed P. 1986. The optimal design of hunting weapons: maintainability and reliability. *Am. Ant.,* 51: 737-747.

Bleed P. & Bleed A. 1987. Energetic efficiency and hand tool design: a performance comparison of push and pull stroke saws. *J. Anthropol. Archaeol.,* 6: 189-197.

Blumenshine R.J., Masao F.T., Tactikos J.C. & Ebert J.I. 2008. Effects of distance from stone source on landscape-scale variation in Oldowan artifact assemblages in the Paleo-Olduvai Basin, Tanzania. *J. Archaeol. Sci.,* 35: 76-86.

Boesch C., Head J. & Robbins M.M. 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *J. Hum. Evol.,* 56: 560-569.

Bousman C.B. 2005. Coping with risk: Later Stone Age technological strategies at Blydefontein Rock Shelter, South Africa. *J. Anthropol. Archaeol.,* 24: 193-226.

Brantingham P.J. 2003. A neutral model of stone raw material procurement. *Am. Ant.,* 63: 487-509

Brantingham P.J. 2010. The mathematics of chaînes opératoires. In S.J. Lycett & P.R. Chauhan (eds): *New Perspectives on Old Stones: Analytical Approaches to Palaeolithic Technologies*, pp. 183-206. Springer, New York.

Braun D.R. 2012. What does Oldowan technology represent in terms of hominin behaviour? In M. Domínguez-Rodrigo (ed): *Stone Tools and Fossil Bones: Debates in the Archaeology of Human Origins*, pp. 222-244. Cambridge University Press, Cambridge.

Braun D.R., Pobiner B.L. & Thompson J.C. 2008a. An experimental investigation of cut mark production and stone tool attrition. *J. Archaeol. Sci.,* 35: 1216-1223.

Braun D.R., Tactikos J.C., Ferraro J.V., Arnow S.L. & Harris J.W.K. 2008b. Oldowan reduction sequences: methodological considerations. *J. Archaeol. Sci.,* 35: 2153-2163.

Braun D.R., Plummer T., Ditchfield P., Ferraro J.V., Maina D., Bishop L.C. & Potts R. 2008c. Oldowan behaviour and raw material transport: perspectives from the Kanjera Formation. *J. Archaeol. Sci.,* 35: 2329-2345.

Braun D.R., Plummer T., Ferraro J.V., Ditchfield P. & Bishop L.C. 2009. Raw material quality and Oldowan hominin toolstone preferences: evidence from Kanjera South, Kenya. *J. Archaeol. Sci.,* 36: 1605-1604.

Braun D.R., Harris J.W.K., Levin N.E., McCoy J.T., Herries A.I.R., Bamford M.K., Bishop L.C., Richmond B.G. & Kibunjia M. 2010. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proc. Natl. Acad. Sci. U.S.A.,* 107: 10002-10007.

Breuil H. 1912. Les Subdivisions du Paléolithique Supérieur et leur Signification. *Congrès International d'Anthropologie et d'Archéologie Préhistoriques - Compte-rendu de la XIVème Session, Genève*, pp.165-238.

Breuil H. 1926. Palaeolithic industries from the beginning of the Rissian to the beginning of the Wurmian Glaciation. *Man,* 26: 176-179.

Breuil H. & Koslowski L. 1934. *Etude de stratigraphie paleolithique dans le nord de la france, la belguque et l'Angletrre. La Vallee de la Somme*. Masson, Paris.

Boucher de Perthes J. 1847. *Antiquités Celtiques at Antédiluviennes*. Treuttel and Wurtz, Paris.

Bunn H.T. 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature,* 291: 574-577.

Bunn H.T. 1986. Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.,* 15: 673-690.

Bunn H. T. 1994. Early Pleistocene hominin foraging strategies along the ancestral Omo River at Koobi Fora, Kenya. *J. Hum. Evol.,* 27: 247-266.

Bunn H.T. & Kroll E.M. 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthropol.,* 431-452.

Carbonell E, García-Anton M.D., Mosquera M., Ollé A., Rodríguez X.P., Sahnouni M., Sla R., Vergès M. 1999. The TD6 level lithic industry from Gran Dolina, Atapuerca (Burgos, Spain): production and use. *J. Hum. Evol.,* 37: 653-693.

Carvalho S. & McGrew W. 2012. The origins of the Oldowan: why chimpanzees (*Pan troglodytes*) still are good models for technological evolution in Africa. In M. Domínguez-Rodrigo (ed): *Stone Tools and Fossil Bones: Debates in the Archaeology of Human Origins,* pp. 201-221. Cambridge University Press, Cambridge.

Chauhan P.R. 2010. Metrical variability between South Asian handaxe assemblages: preliminary observations. In S.J Lycett & P.R. Chauhan (eds): *New Perspectives on Old Stones: Analytical Approaches to Paleolithic Technologies*, pp. 119-166. Springer, Dordrecht.

Choi K & Driwantoro D. 2007. Shell tool use by early members of *Homo erectus* in Sangiran, central Java, Indonesia: cut mark evidence. *J. Archaeol. Sci.,* 32: 48-58.

Clark G. 1962. *World Prehistory: An Outline*. Cambridge University Press, Cambridge.

Clark J.D. 1970. *The Prehistory of Africa*. Thames and Hudson, London.

Clark J.D. & Kleindienst M.R. 2001. The Stone Age cultural sequence: terminology, typology and raw material. In J.D. Clark (ed): *Kalambo Falls Prehistoric Site: Volume III*, pp. 34-65 Cambridge University Press, Cambridge.

Clark J.D., de Heinzelin J., Schick K.D., Hart W.K., White T.D., WoldeGabriel G., Walter R.C., Suwa G., Asfaw B., Vrba E. & H.-Selassie Y. 1994. African *Homo erectus*: old radiometric ages and young Oldowan assemblages in the Middle Awash Valley, Ethiopia. *Science,* 264: 1907-1910.

Clarke D.L. 1968. *Analytical Archaeology*. Methuen, London.

Codding B.F. & Bird D.W. 2015. Behavioral ecology and the future of archaeological science. *J. Archaeol. Sci.,* 56: 9-20.

Coles J. 1979. *Experimental Archaeology*. Academic Press, London.

Collins S. 2008. Experimental investigations into edge performance and its implications for stone artefact reduction modelling. *J. Archaeol. Sci.,* 35: 2164-2170.

Crabtree D.E. & Davis E.L. 1968. Experimental manufacture of wooden implements with tools of flaked stone. *Science,* 159: 426-428.

Crompton R.H. & Gowlett J.A.J. 1993. Allometry and multidimensional form in Acheulean bifaces from Kilombe, Kenya. *J. Hum. Evol.,* 25: 175-199.

Currie G. 2014. The Master of the Masek Beds: Aesthetics and the evolution of mind. In P. Goldie & E. Schellekens (eds): *The Aesthetic Mind: Philosophy and Psychology*, pp. 9-31. Oxford University Press, Oxford.

Davies W. 2009. The Abbé Henri Breuil (1877-1961). *Lithics,* 30: 127-141.

Delagnes A. & Roche H. 2005. Late Pliocene hominid knapping skills: the case of Lokalakei 2c, West Turkana, Kenya. *J. Hum. Evol.,* 48: 435-472.

Dennell R. 1990. Progressive gradualism, imperialism and academic fashion: Lower Palaeolithic archaeology in the 20th century. *Antiquity,* 64: 549-58.

Desnoyers J. 1863. Libro Note sur des indices matériels de la coexistence de l'homme avec l'Elephas meridionalis dans un terrain des environs de Chartres, plus ancien que les terrains de transport quaternaires des vallées de la Somme et de la Seine. *Comptes Rendus Hebdomadaires de l'Académie des Sciences,* 56: 1073-1083.

Dewbury A.G. & Russell N. 2007. Relative frequency of butchering cutmarks produced by obsidian and flint: an experimental approach. *J. Archaeol. Sci.,* 32: 354-357.

Diez-Martín F. & Eren M.I. 2012. The early Acheulean in Africa: past paradigms, current ideas, and future directions. In Domínguez-Rodrigo M. (ed): *Stone Tools and Fossil Bones: Debates in the Archaeology of Human Origins,* pp. 201-221. Cambridge University Press, Cambridge.

Diez-Martín F., Yustos P.S., de la Rúa D.G., González J.A.G., de Luque L. & Barba R. 2014. Early Acheulean technology at Es2-Lepolosi (ancient MHS-Bayasi) in Peninj (Lake Natron, Tanzania). *Quat. Int.,* 322-323: 209-236.

Diez-Martín F., Yustos P.S., Uribelarrea D., Baquedano E., Mark D.F., Mabulla A., Fraile C., Duque J., Díaz I., Pérez-González A. *et al.* 2015. The origin of the Acheulean: the 1.7 million-year-old site of FLK West, Olduvai Gorge (Tanzania). *Sci. Rep.,* 5: 17839.

Domalain M., Bertin A. & Daver G. (in press). Was *Australopithecus afarensis* able to make the Lomekwian stone tools? Towards a realistic biomechanical simulation of hand force capability in fossil hominins and new insights on the role of the fifth digit. *Comp. Ren. Pal.,* DOI: 10.1016/j.crpv.2016.09.003.

Domínguez-Rodrigo M., Serrallonga J., Juan-Tresserras J., Alcala L. & Luque L. 2001. Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). *J. Hum. Evol.,* 40: 289-299.

Domínguez-Rodrigo M., Pickering T.R., Semaw S. & Rogers M.J. 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *J. Hum. Evol.,* 48: 109-121.

Domínguez-Rodrigo M., Pickering T.R. & Bunn H.T. 2012. Experimental study of cut marks made with rocks unmodified by human flaking and its bearing on claims of 3.4-million-year-old butchery evidence from Dikika, Ethiopia. *J. Archaeol. Sci.,* 39: 205-214.

Domínguez-Rodrigo M., Diez-Martín F., Mabulla A., Baquedano E., Bunn H.T. & Musiba C. 2014. The evolution of hominin behavior during the Oldowan–Acheulean transition: Recent evidence from Olduvai Gorge and Peninj (Tanzania). *Quat. Int.,* 322-323: 1-6.

Dunnell R.C. 1978. Style and function: a fundamental dichotomy. *Am. Ant.,* 43: 192-202.

Eren M.I., Roos C.I., Story B.A., von Cramon-Taubadel N. & Lycett S.J. 2014. The role of raw material differences in stone tool shape variation: an experimental assessment. *J. Archaeol. Sci.,* 49: 472-487.

Eren M.I., Lycett S.J., Pattern R.J., Buchanan B., Pargeter J. & O'Brien M.J. 2016. Test, model, and method validation: the role of experimental stone artefact replication in hypothesis-driven archaeology. *Ethnoarch.,* 8: 103-136.

Evans J. 1864. On some bone- and cave-deposits of the Reindeer-period in the South of France. *Quart. J. Geolog. Soc.,* 20: 444.

Evans J. 1872. *The Ancient Stone Implements, Weapons and Ornaments of Great Britain*. Longmans, Green and Co., London.

Ferraro J.V., Plummer T.W., Pobiner B.L., Oliver J.S., Bishop L.C., Braun D.R., Ditchfield P.W., Seaman III J.W., Binetti K.M., Seaman Jr J.W. *et al.* 2013. Earliest archaeological evidence of persistent hominin carnivory. *PLoS One,* 8: e62174.

Fitzhugh B. 2001. Risk and invention in human technological evolution. *J. Anthropol. Archaeol.,* 20: 125-167.

Fragaszy D.M., Greenberg R., Visalberghi E., Ottoni E.B., Izar P. & Liu Q. 2010. How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Anim. Behav.,* 80: 205-214.

Frere J. 1800. Account of flint weapons discovered at Hoxne in Suffolk. *Archaeologia,* 13: 204-205.

Frison G.C. 1989. Experimental use of Clovis weaponry and tools on African elephants. *Am. Ant.,* 54: 766-784.

Galán A.B. & Domínguez-Rodrigo M. 2014. Testing the efficiency of simple flakes, retouched flakes and small handaxes during butchery. *Archaeom.,* 56: 1054-1074.

Gallotti R. & Mussi M. 2015. The unknown Oldowan: ~1.7-Million-Year-Old standardized obsidian small tools from Garba IV, Melka Kunture, Ethiopia. *PLoS One,* 10: e0145101.

Garcia J., Martínez K. & Carbonell E. 2013. The early Pleistocene stone tools from Vallparadís (Barcelona, Spain): rethinking the European mode 1. *Quat. Int.,* 316: 94-114.

Gaudzinski S. 2004. Subsistence patterns of Early Pleistocene hominids in the

Levant—taphonomic evidence from the ‘Ubeidiya Formation (Israel). *J. Archaeol. Sci.,* 31: 65-75.

Gingerich J.A.M. & Stanford D.J. (in press). Lessons from Ginsberg: an analysis of elephant butchery tools. *Quat. Int.,* doi: 10.1016/j.quaint.2016.03.025.

Goren-Inbar N. 2011. Culture and cognition in the Acheulian industry: a case study from Gesher Benot Ya'aquo. *Phil. Trans. R. Soc. B,* 366: 1038-1049.

Goren-Inbar N. & Saragusti I 1996. An Acheulian biface assemblage from Gesher Benot Ya'aqov, Israel: indications of African affinities. *J. Field Archaeol.,* 23: 15-30.

Goren-Inbar N. & Sharon G. 2006. Invisible handaxes and visible Acheulian biface technology at Gesher Benot Ya'aqov, Israel. In N. Goren-Inbar & G. Sharon (eds): *Axe Age: Acheulian Tool-Making From Quarry to Discard,* pp. 111-135. Equinox, London.

Gosden C. 1999. *Archaeology and Anthropology: A Changing Relationship*. Routledge, London.

Gould R.A. 1980. *Living Archaeology*. Cambridge University Press, Oxford.

Gowlett J.A.J. 1988. A case of Developed Oldowan in the Acheulean? *World Archaeol.,* 20: 13-26.

Gowlett J.A.J. 2006. The elements of design form in Acheulean bifaces: modes, modalities, rules and language. In N. Goren-Inbar & G. Sharon (eds): A*xe Age: Acheulian Tool-Making From Quarry to Discard*, pp. 203-221. Equinox, London.

Gowlett J.A.J. 2009a. Boucher de Perthes: pioneer of Palaeolithic prehistory. *Lithics,* 30: 13-24.

Gowlett J.A.J. 2009b. Artefacts of apes, humans, and others: towards comparative assessment and analysis. *J. Hum. Evol.,* 57: 401-410.

Gowlett J.A.J. 2010. The future of lithic analysis in Palaeolithic archaeology: a view from the Old World. In S.J Lycett. & P.R. Chauhan (eds): *New Perspectives on Old Stones: Analytical Approaches to Paleolithic Technologies*, pp. 295-309. Springer, New York.

Gowlett J.A.J. 2011a. The Vital Sense of Proportion: Transformation, Golden Section, and 1:2 Preference in Acheulean Bifaces. *PaleoAnthropol.,* 2011: 174-187.

Gowlett J.A.J. 2011b. The empire of the Acheulean strikes back. In Sept J. & Pilbeam D. (eds): *Casting the Net Wide: Papers in Honor of Glynn Isaac and His Approach to Human Origins Research*, pp. 93-114. Oxbox, Oakville.

Gowlett J.A.J. 2013. Elongation as a factor in artefacts of humans and other animals: an Acheulean example in comparative context. *Phil. Trans. R. Soc. B.,* 368: 20130114.

Gowlett J.A.J. 2015. Variability in an early hominin percussive tradition: the Acheulean versus cultural variation in modern chimpanzee artefacts. *Phil. Trans. R. Soc. B,* 370: 20140358.

Gowlett J.A.J. & Crompton R.H. 1994. Kariandusi: Acheulean morphology and the question of allometry. *Afr. Archaeol. Review,* 12: 3-42.

Grayson D. 1986. Eoliths, archaeological ambiguity, and the generation of “middle-range” research. In D. Meltzer, D. Fowler & J. Sabloff (eds): *American Archaeology Past and Future: A Celebration of the Society for American Archaeology 1935–1985,* pp. 77–133. Smithsonian Institution Press, Washington, D.C..

Grayson D.K. 1990. The provision of time depth for paleoanthropology. In L.F Laporte (ed): *Establishment of a Geological Framework for Paleoanthropology*, pp. 1-14. GSA Books, Boulder.

Grosman L., Goldsmith Y. & Smilansky U. 2011. Morphological analysis of Nahal Zihor handaxes: a chronological perspective. *Paleoanthropology,* 2011: 203-215.

Gumert M.D., Kluck M. & Malaivijitnond S. 2009. The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. *Am. J. Primatol.,* 71: 594-608.

Gumert M.D. & Malaivijitnond S. 2013. Long-tailed macaques select mass of stone tools according to food type. *Phil. Trans. R. Soc. B.,* 368: 20120413.

Gurtov A.N. & Eren M.I. 2014. Lower Paleolithic bipolar reduction and hominin selection of quartz at Olduvai Gorge, Tanzania: what's the connection? *Quat. Int.,* 322-323: 285-291.

Hall C. 1997. External pressure at the hand during object handling and work with tools. *Int. J. Indus. Ergonom.,* 20: 191-206.

Hampton O.W. 1999. *Culture of Stone: Sacred and Profane Uses of Stone among the Dani*. Texas A&M University Press, College Station.

Hardy B.L. & Garufi G.T. 1998. Identification of woodworking on stone tools through residue and use-wear analyses: experimental results. *J. Archaeol. Sci.,* 25: 177-184.

Harmand S. 2008. Variability in raw material selectivity at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In E. Hovers & D.R. Braun (eds): *Interdisciplinary Approaches to the Oldowan*, pp. 85-98. Springer, Dordrecht.

Harmand S., Lewis J.E., Feibel C.S., Lepre C.J., Prat S., Lenoble A., Boes X., Quinn R.L., Brenet M., Arroyo A. *et al.* 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature,* 521: 310-315.

Hayden B. 2015. Insights into early lithic technologies from ethnography. *Phil. Trans. R. Soc. B,* 370: 20140356.

de Heinzelin J. Clark J.D., White T., Hart W., Renne P., WoldeGabriel G., Beyene Y. & Vrba E. 1999. Environment and behaviour of 2.5-million-year-old Bouri hominids. *Science,* 284: 625-629.

Henke W. 2015. Historical overview of paleoanthropological research. In W. Henke & I. Tattersall (eds): *Handbook of Paleoanthropology*, pp. 3-95. Springer, Heidelberg.

Hiscock P. 2004. Slippery and Billy: intention, selection and equifinality in lithic artefacts. *Cam. Archaeol. J.,* 14: 71-77.

Hiscock P. 2014. Learning in lithic landscapes: a reconsideration of the hominid "toolmaking" niche. *Biological Theory,* 9: 27-41.

Holdaway S. & Douglass M. 2012. A twenty-first century archaeology of stone artifacts. *J. Archaeol. Meth. Theory,* 19: 101-131

Hovers E. 2012. Invention, reinvention and innovation: the makings of Oldowan lithic technology. In S. Elias (ed): *Origins of Human Innovation and Creativity*, pp. 51-68. Developments in Quaternary Science, vol 16. Elsevier, Amsterdam.

Hovers E. & Braun D.R. 2009. *Interdisciplinary Approaches to the Oldowan*. Springer, Dordrecht

Huckell B.B. 1979. Of chipped stone tools, elephants, and the Clovis hunters: an experiment. *Plains Anthropol.,* 24: 177-189.

Hughes T.M. 1897. On the evidence bearing upon the early history of man which is derived from the form, condition of surface, and mode of occurrence of dressed flints. *Archaeol. J.,* 54: 363-376.

Ingersoll D., Yellen J.E. & Macdonald W. 1977 *Experimental Archaeology*. Columbia University Press, New York.

Iovita R. 2014. The role of edge angle maintenance in explaining technological variation in the production of Late Middle Paleolithic bifacial and unifacial tools. *Quat. Int.,* 350: 105-115.

Iovita R. & McPherron S.P. 2011. The handaxe reloaded: A morphometric reassessment of Acheulian and Middle Paleolithic handaxes. *J. Hum. Evol.,* 61: 61-74.

Isaac G. 1971. The diet of early man: aspects of archaeological evidence from lower and Middle Pleistocene sites in Africa. *World Archaeol.,* 2: 278-299.

Isaac G. 1977. *Olorgesailie: Archeological Studies of a Middle Pleistocene Lake Basin in Kenya*. University of Chicago Press, Chicago.

Isaac G. 1981. Emergence of human behaviour patterns. *Phil. Trans. R. Soc. Lond. B,* 292: 177-188.

Isaac G. 1983. *Early stages in the evolution of human behaviour: the adaptive significance of stone tools*. Joh. Enschedé en Zonen, Haarlem.

Jeske R.J. 1992. Energetic efficiency and lithic technology: an Upper Mississippian example. *Am. Ant.,* 57: 467-481.

Jobson R.W. 1986. Stone tool morphology and rabbit butchering. *Lithic Tech.,* 15: 9-20.

Jones P. 1980. Experimental butchery with modern stone tools and its relevance for Palaeolithic archaeology. *World Archaeol.,* 12: 153-165.

Jones P. 1994. Results of experimental work in relation to the stone industries of Olduvai Gorge. In M.D. Leakey & D.A. Roe (eds): *Olduvai*

Gorge: Excavations in Beds III, IV, and the Masek Beds 1968-1971, pp. 235-253. Cambridge University Press, Cambridge.

Keeley L.H. 1980. *Experimental Determination of Stone Tool Uses: a Microwear Analysis*. Uniiversity of Chicago Press, Chicago.

Keeley L.H. & Toth N. 1981. Microwear polishes on early stone tools from Koobi Fora, Kenya. *Nature,* 293: 464-465.

Keith A. 1915. *The Antiquity of Man*. Williams and Norgate, London.

Kelly R.L. 1988. The three sides of a biface. *Am. Ant.,* 53: 717-734.

Kelly R.L. 2013. *The Lifeways of Hunter-Gatherers: The Foraging Spectrum*. Cambridge, University Press.

Kempe M., Lycett S. & Mesoudi A. 2012. An experimental test of the accumulated copying error model of cultural mutation for Acheulean handaxe size. *PLoS One,* 7: e48333.

Key A.J.M. 2016. Integrating mechanical and ergonomic research within functional and morphological analyses of lithic cutting technology: key principles and future experimental directions. *Ethnoarch.,* 8: 69-89.

Key A.J.M. & Lycett S.J. 2014. Are bigger flakes always better? An experimental assessment of flake size variation on cutting efficiency and loading. *J. Archaeol. Sci.,* 41: 140-146.

Key A.J.M. & Lycett S.J. 2015. Edge angle as a variably influential factor in flake cutting efficiency: an experimental investigation of its relationship with tool size and loading. *Archaeom.,* 57: 911-927.

Key A.J.M. & Lycett S.J. 2017a. Influence of handaxe size and shape on cutting efficiency: a large-scale experiment and morphometric analysis. *J. Archaeol. Meth. Theory*, 22: 514-541.

Key A.J.M. & Lycett S.J. 2017b. Reassessing the production of handaxes versus flakes from a functional perspective. *Archaeol. Anthropol. Sci.*, 9: 737-753.

Key A.J.M. & Lycett S.J. (in press). Investigating interrelationships between Lower Palaeolithic stone tool effectiveness and tool user biometric variation: implications for technological and evolutionary changes. *Archaeol. Anthropol. Sci.*, doi:10.1007/s12520-016-0433-x.

Key A.J.M., Proffitt T., Stefani E. & Lycett S.J. 2016. Looking at handaxes from another angle: assessing the ergonomic and functional importance of edge form in Acheulean bifaces. *J. Anthropol. Archaeol.,* 44: 43-55.

Kimura Y. 1999. Tool-using strategies by early hominids at Bed II, Olduvai Gorge, Tanzania. *J. Hum. Evol.,* 37: 807-831.

Kohn M. & Mithen S. 1999. Handaxes: products of sexual selection? *Antiquity,* 73: 518-526.

Kolfschoten T.V., Parfitt S.A., Serangeli J. & Bello S.M. 2015. Lower Paleolithic bone tools from the 'Spear Horizon' at Schöningen (Germany). *J. Hum. Evol.,* 89: 226-263.

Kuhn S.L. 1994. A formal approach to the design and assembly of mobile toolkits. *Am. Ant.,* 59: 426-442.

Kuman K. & Field A.S. 2009. The Oldowan industry from Sterkfontein Caves, South Africa. In K. Schick & N. Toth (eds): *The Cutting Edge: New Approaches to the Archaeology of Human Origins*, pp. 151-169. Stone Age Institute Press, Gosport.

Laing S. 1892. *Human Origins*. Chapman and Hall, London.

Landeck G. & Garriga J.G. 2016. The oldest hominin butchery in European mid-latitudes at the Jaramillo site of Untermassfeld (Thuringia, Germany). *J. Hum. Evol.,* 94: 53-71.

Lartet M.E. 1860. On the existence of man with certain extinct quadrupeds, proved by fossil bones, from various Pleistocene deposits, bearing incisions made by sharp instruments. *Quart. J. Geolog. Soc.,* 16: 471-479.

Lartet E. & Christy H. 1865-75. *Reliquiae Aquitanicae; Being Contributions to the Archaeology and Palaeontology of Perigord and the Adjoining Provinces of Southern France*. Williams & Norgate, London.

Lawick-Goodall J.V. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Beh. Monographs,* 1: 61IN1-311IN12.

Leakey L.S.B. 1931. *The Stone Age Cultures of Kenya Colony*. Cambridge University Press, Cambridge.

Leakey L.S.B. 1950. Stone implements: how they were made and used. *S. Afr. Archaeol. Bull.,* 5: 71-74.

Leakey L.S.B. 1951. *Olduvai Gorge: A Report on the Evolution of the Hand-axe Culture in Beds I-IV. With Chapters on the Geology and Fauna*. Cambridge University Press, Cambridge.

Leakey L.S.B. 1953. *Adam's Ancestors: The Evolution of Man and his Culture*. Fourth Edition. Methuen & Co, London.

Lebreton L., Moigne A-M., Filoux A. & Perrenoud C. 2017. A specific small game exploitation for Lower Paleolithic: The beaver (*Castor fiber*) exploitation at the Caune de l'Arago (Pyrénées-Orientales, France). *J. Archaeol. Sci.,* 11: 53-58.

Lemorini C., Stiner M.C., Gopher A., Shimelmitz R. & Barkai R. 2006. Use-wear analysis of an Amudian laminar assemblage from the Acheuleo-Yabrudian of Qesem Cave, Israel. *J. Archaeol. Sci.,* 33: 921-934.

Lemorini C., Plummer T.W., Braun D.R., Crittenden A.N., Ditchfield P.W., Bishop L.C., Hertel F., Oliver J.S., Marlowe F.W., Schoeninger M.J. & Potts R. 2014. Old stones' song: Use-wear experiments and analysis of the Oldowan quartz and quartzite assemblage from Kanjera South (Kenya). *J. Hum. Evol.,* 72: 10-25.

Levi-Sala I. 1996. *A Study of Microscopic Polish on Flint Implements*. BAR International Series, Oxford.

Loy T.H. 1998. Organic residues on Oldowan tools from Sterkfontein Cave, South Africa. *Abstracts of Contributions to the Dual Congress,* pp.74-77.

Lubbock J. 1862. On the evidence of the antiquity of man afforded by the physical structure of the Somme Valley. *Nat. Hist. Rev.,* 2: 144–169.

Lubbock J. 1865. *Prehistoric Times*. Williams and Norgate, London.

Lycett S.J. 2008. Acheulean variation and selection: does handaxe symmetry fit neutral expectations? *J. Archaeol. Sci.,* 35: 2640-2648.

Lycett S.J. 2013. Cultural transmission theory and fossil hominin behaviour a discussion of epistemological and methodological strengths. In S. Ellen, S.J. Lycett & S.E. Johns (eds): *Understanding Cultural Transmission in Anthropology: a Critical Synthesis*, pp. 102-130. Berghahn Books, New York.

Lycett S.J. & Gowlett J.A.J. 2008. On questions surrounding the Acheulean 'tradition'. *World Archaeol.,* 40: 295-315.

Lycett S.J. & von Cramon-Taubadel N. 2015. Toward a "quantitative genetic" approach to lithic variation. *J. Archaeol. Meth. Theory,* 22: 646-674.

Lycett S.J., Schillinger K., Eren M.I., von Cramon-Taubadel N. & Mesoudi A. 2016. Factors affecting Acheulean handaxe variation: Experimental insights, microevolutionary processes, and macroevolutionary outcomes. *Quat. Int.,* 411: 386-401.

Lyell C. 1863. *The Geological Evidences of the Antiquity of Man with Remarks on Theories of the Origin of Species by Variation*. Third Edition. John Murray, London.

Macdonald D.A. 2014. The application of focus variation microscopy for lithic use-wear quantification. *J. Archaeol. Sci.,* 48: 26-33.

Machin A.J. 2008. Why handaxes just aren't that sexy: a response to Kohn & Mithen (1999). *Antiquity,* 82: 761-766.

Machin A. 2009. The role of the individual agent in Acheulean biface variability. *J. Soc. Archaeol.,* 9: 35-58.

Machin A.J., Hosfield R. & Mithen S.J. 2005. Testing the functional utility of handaxe symmetry: fallow deer butchery with replica handaxes. *Lithics,* 26: 23-37.

Machin A.J., Hosfield R. & Mithen S.J. 2007. Why are some handaxes symmetrical? Testing the influence of handaxe morphology on butchery effectiveness. *J. Archaeol. Sci.,* 34: 883-893.

Manrique H.M., Gross A.N.-M. & Call J. 2010. Great apes select tools on the basis of their rigidity. *J. Exp. Psych.,* 36:409-422.

McCall G.S. 2005. An experimental examination of the potential function of Early Stone Age tool technology and implications for subsistence behaviour. *Lithic Tech.,* 30: 29-43.

McCall G.S. 2012. Ethnoarchaeology and the organization of lithic technology. *J. Archaeol. Res.,* 20: 157-203.

McCall G.S. & Whittaker J. 2007. Handaxes still don't fly. *Lithic Techn.,* 32: 195-202.

McGorry R.W., Dowd P.C. & Dempsey P.G. 2005. The effect of blade finish and blade edge angle on forces used in meat cutting operations. *App. Ergonom.,* 36: 71-77.

McGrew W.C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press, Cambridge.

McNabb J. 1989. Sticks and stones: a possible experimental solution to the question of how the Clacton spear point was made. *Proc. Prehistoric Soc.,* 55: 251-257.

McNabb J., Binyon F. & Hazelwood L. 2004. The large cutting tools from the South African Acheulean and the question of social traditions. *Curr. Anthropol.,* 45: 653-677.

McPherron S.P. 1999. Ovate and pointed handaxe assemblages: two points make a line. *Préhistoire Européenne*, 14: 9-32.

McPherron S.P., Alemseged Z., Marean C.W., Wynn J.G., Reed D., Geraads D., Bobe R. & Béarat H.A. 2010. Evidence for stone-tool-assisted consumption of animal tissue before 3.39 million years ago at Dikika, Ethiopia. *Nature,* 466: 857-860.

Meltzer D.J. 1981. A study of style and function in a class of tools. *J. Field Archaeol.,* 8: 313-326.

Mercader J., Barton H., Gillespie J.D., Harris J.W.K., Kuhn S.L., Tyler R. & Boesch C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proc. Natl. Acad. Sci. USA*, 104: 3043-3048

Merritt S.R. 2012. Factors affecting Early Stone Age cut mark cross-sectional size: implications from actualistic butchery trials. *J. Archaeol. Sci.,* 39: 2984-2994.

Merritt S.R. 2016. Cut mark cluster geometry and equifinality in replicated Early Stone Age butchery. *Int. J. Osteoarchaeol.,* 26: 585-598.

Mitchell S.R. 1949. *Stone-Age craftsmen: Stone Tools and Camping Places of the Australian Aborigines*. Tait Book Co., Melbourne.

Mitchell J.C. 1995. Studying biface utilisation at Boxgrove: Roe deer butchery with replica handaxes. *Lithics,* 16: 64-69.

Mitchell J.C. 1998. *A Use-Wear Analysis of Selected British Lower Palaeolithic Handaxes with Special Reference to the Site of Boxgrove (West Sussex): a Study Incorporating Optical Microscopy, Computer Aided Image Analysis and Experimental Archaeology*. Unpublished PhD Thesis, University of Oxford.

Moncel M.-H., Moigne A.-M., Sam Y. & Combier, J. 2011. The emergence of Neanderthal technical behavior: new evidence from Orgnac 3 (Level 1, MIS 8), southeastern France. *Curr. Anthropol.,* 52: 37-75.

Moncel M.-H., Ashton N., Lamotte A., Tuffreau A., Cliquet D. & Despriée J. 2015. The early Acheulian of north-western Europe. *J. Anthropol. Archaeol.,* 40: 302-331.

de Mortillet G. 1867. *Promenades Préhistoriques. L'Exposition Universelle*. C. Reinwald, Paris.

Movius H.L. 1944. Early Man and Pleistocene Stratigraphy in Southern and Eastern Asia. *Papers of the Peabody Museum of American Archaeology and Ethnology*, vol. 19. Cambridge.

Movius H.L. 1948. The Lower Palaeolithic cultures of southern and eastern Asia. *Transactions of the American Philosophical Society,* 38: 329-420.

Nelson M.C. 1991. The study of technological organization. *Archaeol. Meth. Theory,* 3: 57-100.

Newcomer M., Grace R. & Unger-Hamilton R. 1986. Investigating microwear polishes with blind tests. *J. Archaeol. Sci.,* 13: 203-217.

Noll M.P. & Petraglia M.D. 2003. Acheulean bifaces and early human behavioural patterns in East Africa and South India. In M. Soressi & H.L. Dibble (eds): *Multiple Approaches to the Study of Bifacial Technologies,* pp. 31-54. University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia.

Nowell A. & Chang M.L. 2009. The case against sexual selection as an explanation of handaxe morphology. *Paleoanth.,* 2009: 77-88.

Nowell A., Walker C., Cordova C.E., Ames C.J.H., Pokines J.T., Stueber D., DeWitt R. & al-Souliman A.S.S. 2016. Middle Pleistocene subsistence in the Azraq Oasis, Jordan: protein residue and other proxies. *J. Archaeol. Sci.,* 73: 36-44.

Oakley K.P., Andrews P., Keeley L.H. & Clark J.D. 1977. A reappraisal of the Clacton spearpoint. *Proc. Prehist. Soc.,* 43: 13-30.

O'Brien E.M. 1981. The projectile capabilities of an Acheulian handaxe form Olorgesailie. *Curr. Anthopol.,* 22: 76-79.

O'Brien M.J., Holland T.D., Hoard R.J. & Fox G.L. 1994. Evolutionary implications of design and performance characteristics of prehistoric pottery. *J. Archaeol. Meth. Theory,* 1 : 259-304.

Odell G.H. 1981. The morphological express at function junction: searching for meaning in lithic tool types. *J. Anthropol. Res.,* 37: 319-342.

Ollé A., Verges J.M., Pena L., Aranda V., Canals A., & Carbonell E. 2012. A microwear analysis of handaxes from Santa Ana Cave (Cáceres, Extremadura, Spain). In J. Marreiros, N. Bicho & J.F. Gibaja (eds): *International Conference on Use-Wear Analysis*, pp. 270-278. Cambridge Scholar Publishing, Newcastle upon Tyne.

Outram A.K. 2008. Introduction to experimental archaeology. *World Archaeol.,* 40: 1-6.

Panger M.A., Brooks A.S., Richmond B.G. & Wood B. 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol. Anthropol.,*11: 235-245.

Pei W.C. 1933. Preliminary note on some incised, cut and broken bones found in association with *Sinanthropus* remains and lithic artifacts from Choukoutien. *Bull. Geolog. Soc. China,* 12: 105-112.

Petraglia M.D. & Shipton C. 2008. Large cutting tool variation west and east of the Movius Line. *J. Hum. Evol.,* 55: 962-966.

Pettitt P.B. & White M.J. 2011. Cave men: stone tools, Victorian science, and the 'primitive mind' of deep time. *Notes Records R. Soc.,* 65: 25-42.

Pettitt P. & White M. 2012. *The British Palaeolithic: Human Societies at the Edge of the Pleistocene World*. Routledge, London.

Pitts M. & Roberts M. 1997. *Fairweather Eden: Life in Britain Half a Million Years Ago as Revealed by the Excavations at Boxgrove*. Century, London.

Plummer T.W. & Bishop L.C. 2016. Oldowan hominin behaviour and ecology at Kanjera South, Kenya. *J. Anthropol. Sci.,* 94: 29-40.

Pobiner B.L., Rogers M.J., Monahan C.M., & Harris J.W.K. 2008. New evidence for hominin carcass processing strategies at 1.5 Ma, Koobi Fora, Kenya. *J. Hum. Evol.*, 55: 103-130.

Pope M., Russel K. & Watson K. 2006. Biface form and structured behaviour in the Acheulean. *Lithics,* 27: 44-57.

Posnansky M. 1959. Some functional considerations on the handaxe. *Man,* 61: 42-44.

Potts R. 1988. *Early hominid activities at Olduvai*. Aldine de Gruyter, New York.

Potts R. & Shipman P. 1981. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature,* 291: 577-580.

Praciunas M.M. 2007. Bifacial cores and flake production efficiency: an experimental test of technological assumptions. *Am. Ant.,* 72: 334-348.

Praus A.A. 1948. Mechanical principles involved in primitive tools and those of the machine age. *Isis,* 38: 157-160.

Prestwich J. 1860. On the occurrence of flint-implements, associated with the remains of animals of extinct species in beds of a later geological period, in France at Amiens and Abbeville, and in England at Hoxne. *Phil. Trans. R. Soc. London,* 150: 277-317.

Proffitt T., Luncz L.V., Falótico T., Ottoni E.B., de la Torre I. & Haslam M. 2016. Wild monkeys flake stone tools. *Nature,* doi:10.1038/nature20112.

Pruetz J.D. & Bertolani P. 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Curr. Biol.,* 17: 412-417.

Rabinovich R., Gaudzinski-Windheuser S. & Goren-Inbar N. 2008. Systematic butchering of fallow deer (Dama) at the early middle Pleistocene Acheulian site of Gesher Benot Ya'aqov (Israel). *J. Hum. Evol.,* 54: 134-149.

Reti J.S. 2016. Quantifying Oldowan stone tool production at Olduvai Gorge, Tanzania. *PLoS One,* 11: e0147352.

Rigollot J. 1854. *Mémoire sur des Instruments en Silex Trouvés à St. Acheul près d'Amiens et Considérés sous les Rapports Géologique et Archéologique*. Duval et Herment, Amiens.

Roberts M.B., Bates, M.R., Bergman C., Currant A.P., Haynes J.R., Macphail R., McConnell A., Scaife R., Unger-Hamilton R. & Whatley R.C. 1986. Excavation of the Lower Palaeolithic site at Amey's Eartham Pit, Boxgrove, West Sussex: a preliminary report. *Proc. Prehist. Soc.,* 52: 215-245.

Roche H., Delagnes A., Brugal J.-P., Fiebel C., Kibunjia M., Mourrell V. & Texier P.-J. 1999.

Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. *Nature,* 399: 57-60.

Roche H., Blumenshine R.J. & Shea J.J. 2009. Origins and adaptations of early *Homo*: what archaeology tells us. In F.E. Grine, J.G. Fleagle & R.E. Leakey (eds): *The First Humans – Origin and Early Evolution of the* Genus Homo*,* pp. 135-147. Springer, Dordrecht.

Roe D.A. 1981. *The Lower and Middle Palaeolithic Periods in Britain*. Routledge & Kegan Paul, London.

Roe D.A. 2003. An overview, with some thoughts on the study of bifaces. In M. Soressi & H.L. Dibble (eds): *Multiple Approaches to the Study of Bifacial Technologies*, pp. 273-285. University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia.

Rogers M.J. & Semwa S. 2009. From nothing to something: the appearance and context of the earliest archaeological record. In M. Camps & P. Chauhan (eds): *Sourcebook of Paleolithic Transitions*, pp. 155-171. Springer, New York.

Roux V. & Bril B. 2005. *Stone Knapping: The Necessary Conditions for a Uniquely Hominin Behaviour*. Oxbow Books, Oxford.

Rossi J., Goislard de Monsabert B., Berton E. & Vigouroux L. 2014. Does handle shape influence prehensile capabilities and muscle coordination? *Comp. Meth. Biomech. Biomed. Eng.,* 17: 172-173.

Rots V., Hardy B.L., Serangeli J. & Conard N.J. 2015. Residue and microwear analyses of the stone artefacts from Schöningen. *J. Hum. Evol.,* 89: 298-308.

Sackett J.R. 1977. The meaning of style in archaeology: a general model. *Am. Ant.,* 42: 369-380.

Sackett J.R. 1982. Approaches to style in lithic archaeology. *J. Anthropol. Archaeol.,* 1: 59-112.

Sackett J.R. 2000. Human antiquity and the Old Stone Age: the Nineteenth century background to paleoanthropology. *Evol. Anthropol.,* 9: 37-49.

Sahnouni M., Rosell J., van der Made J., Vergès J.M., Ollé A., Kandi N., Harichane Z., Derradji A. & Medig M. 2013. The first evidence of cut marks and usewear traces from the Plio-Pleistocene locality of El-Kherba (Ain Hanech), Algeria: implications for early hominin subsistence activities circa 1.8 Ma. *J. Hum. Evol.,* 64: 137-150.

Saladié P., Huguet R., Rodríguez-Hidalgo A., Cáceres I., Esteban-Nadal M., Arsuaga J.L., de Castro J.M.B. & Carbonell E. 2012. Intergroup cannibalism in the European Early Pleistocene: The range expansion and imbalance of power hypotheses. *J. Hum. Evol.,* 63: 682-695.

Samson D.R. 2006. Stone of contention: the Acheulean handaxe lethal projectile controversy. *Lithic Tech.,* 31: 127-135.

Sanz C., Morgan D. & Gulick S. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *Am. Nat.,* 164: 567-581.

Sanz C., Call J. & Morgan D. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Bio. Letters,* 5: 293-296.

Saragusti I., Sharon I., Katzenelson O. & Avnir D. 1998. Quantitative analysis of the symmetry of artefacts: Lower Paleolithic handaxes. *J. Archaeol. Sci.,* 25: 817-825.

Schick K.D., Toth N., Garufi G., Savage-Rumbaugh E.S., Rumbaugh D. & Sevcik R. 1999. Continuing investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *J. Archaeol. Sci.,* 26: 821-832.

Schiffer M.B. & Skibo J.M. 1987. Theory and experiment in the study of technological change. *Curr. Anthropol.,* 28: 595-622.

Schiffer M.B., Skibo J.M., Griffitts J.T., Hollenback K.L. & Longacre W.A. 2001. Behavioural archaeology and the study of technology. *Am. Ant.,* 66: 729-737.

Schillinger K., Mesoudi A. & Lycett S.J. (2017). Differences in manufacturing traditions and assemblage-level patterns: the origins of cultural differences in archaeological data. *J. Archaeol. Meth. Theory,* 24: 640-658.

Schmerling P.C. 1833. *Recherches sur les Ossemens Fossiles Découverts dans les Cavernes de la Province de Liège*. P-J. Collardin, Liège

Schoch W.H., Bigga G., Böhner U., Richter P. & Terberger T. 2015. New insights on the wooden weapons from the Paleolithic site of Schöningen. *J. Hum. Evol.,* 89: 214-225.

Schrauf C., Call J., Fuwa K. & Hirata S. 2012. Do chimpanzees use weight to select hammer tools? *PLoS One,* 7: e41044.

Schuldt S., Arnold G., Kowalewski Y., Schneider H. & Rohm H. 2016. Analysis of the sharpness of blades for food cutting. *J. Food Eng.,* 188: 13-20.

Semaw S. 2000. The world's oldest stone artefacts from Gona, Ethiopia: their implications for understanding stone technology and patterns of human evolution between 2·6–1·5 million years ago. *J. Archaeol. Sci.,* 27: 1197-1214.

Semaw, S. 2006. The oldest stone artifacts from Gona (2.6–2.5 Ma), Afar, Ethiopia: Implications for understanding the earliest stages of stone knapping. In N.Toth & K.D. Schick (eds): *The Oldowan: Case Studies into the Earliest Stone Age*, pp. 43–75. Stone Age Institute Press, Bloomington.

Semaw S., Rogers M. & Stout D. 2009. The Oldowan-Acheulian transition: Is there a "Developed Oldowan" artifact tradition?. In M. Camps & P. Chauhan (eds): *Sourcebook of Paleolithic Transitions*, pp. 173-193. Springer, New York.

Semenov S.A. 1964. *Prehistoric Technology: an Experimental Study of the Oldest Tools and Artefacts from traces of Manufacture and Wear*. Cory, Adams and Mackay, London.

Seton-Karr H.W. 1896. Discovery of Evidences of the Palaeolithic Stone Age in Somaliland (Tropical Africa). *J. R. Anthropol. Inst.,* 25: 271-275.

Seton-Karr H.W. 1909. Prehistoric implements from Somaliland. *Man,* 9: 182-183.

Sharon G. 2007. *Acheulian Large Flake Industries: Technology, Chronology, and Significance*. Archaeopress (BAR International Series), Oxford.

Sharon G. 2010. Large flake Acheulian. *Quat. Int.,* 223-224: 226-233.

Shea J.J. 1987. On accuracy and revelance in lithic use-wear analysis. *Lithic Tech.,* 16: 44-50.

Shea J.J. 2006. Child's play: reflections on the invisibility of children in the Palaeolithic record. *Evol. Anthropol.,* 15: 212-216.

Shea J.J. 2007. Lithic technology, or, what stone tools can (and can't) tell us about early hominin diets. In P.S. Ungar (ed): *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*, pp. 212-229. Oxford University Press, Oxford.

Shea J.J. 2011. Stone tool analysis and human origins research: some advice from uncle screwtape. *Evol. Anthropol.,* 20: 48-53.

Shipman P., Bosler W. & Davis K.L. 1981. Butchering of giant Geladas at an Acheulian site. *Curr. Anthropol.,* 22: 257-268.

Shipman P. & Rose J. 1983a. Evidence of butchery and hominid activities at Torralba and Ambrona; an evaluation using microscopic techniques. *J. Archaeol. Sci.,* 10: 465-474.

Shipman P. & Rose J. 1983b. Early hominid hunting, butchering, and carcass-processing behaviors: approaches to the fossil record. *J. Anthropol. Archaeol.,* 2: 57-98.

Shipman P. & Rose J. 1984. Cutmark mimics on modern and fossil bovid bones. *Curr. Anthropol.,* 25: 116-117.

Shipton C. & Petraglia M.D. 2011. Inter-continental variation in Acheulean bifaces. In C.J. Norton & D.R. Braun (eds): *Asian Paleoanthropology: From Africa to China and Beyond*, pp. 49-55. Springer, Dordrecht.

Shipton C. & Clarkson C. 2015. Handaxe reduction and its influence on shape: an experimental test and archaeological case study. *J. Archaeol. Sci.,* 3: 408-419.

Shott M.J. & Sillitoe P. 2005. Use life and curation in New Guinea experimental used flakes. *J. Archaeol. Sci.,* 32: 653-663.

Shumaker R.W., Walkup K.R. & Beck B.B. 2011. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. John Hopkins University Press, Baltimore.

Sillitoe P. and Hardy K. 2003. Living lithics: ethnoarchaeology in Highland Papua New Guinea. *Antiquity,* 77: 555-566.

Simão J. 2002. Tools evolve: the artificial selection and evolution of Paleolithic stone tools. *Behav. Brain Sci.,* 25: 419.

Sirianni G., Mundry R. & Boesch C. 2015. When to choose which tool: multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. *Anim. Behav.,* 100: 152-165.

Skibo J. 2009. Archaeological theory and snake-oil peddling: the role of ethnoarchaeology in archaeology. *Ethanoarch.,* 1: 27-56.

Smith E.A. & Winterhalder B. 1992. *Evolutionary Ecology and Human Behavior*. Transaction Publishers, New Brunswick.

Solodenko N., Zupancich A., Cesaro S.N., Marder O., Lemorini C. & Barkai R. 2015. Fat residue and Use-Wear Found on Acheulian Biface and Scraper Associated with Butchered Elephant Remains at the Site of Revadim, Israel. *PLoS One,* 10: e0118572.

Sonnenfeld J. 1962. Interpreting the function of primitive implements. *Am. Ant.,* 28: 56-65.

Soressi M. & Hays M.A. 2003. Manufacture, transport, and use of Mousterian bifaces: a case study from the Périgord (France). In M. Soressi & H.L. Dibble (eds): *Multiple Approaches to the Study of Bifacial Technologies*, pp. 125-148. University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia.

Spikins P. 2012. Goodwill hunting? Debates over the 'meaning' of Lower Palaeolithic handaxe form revisited. *World Archaeol.,* 44: 378-392.

Spurrell F.C.J. 1880. On implements and chips from the floor of a Palaeolithic workshop. *Archaeol. J.,* 37: 294-299.

Spurrell F.C.J. 1884. On some Palaeolithic knapping tools and modes of using them. *J. R. Anthropol. Inst.,* 13: 109-118.

Starkovich B.M. & Conard N.J. 2015. Bone taphonomy of the Schöningen "Spear Horizon South" and its implications for site formation and hominin meat provisioning. *J. Hum. Evol.,* 89: 154-171.

Stiles D. 1991. Early hominid behaviour and culture tradition: raw material studies in Bed II, Olduvai Gorge. *Afr. Archaeol. Rev.,* 9: 1-19.

Stemp W.J., Watson A.S. & Evans A. 2015a. Surface analysis of stone and bone tools. *Surf. Topog. Metrol. Prop.,* 4: 013001.

Stevens N.E., Harro D.R. & Hicklin A. 2010. Practical quantitative lithic use-wear analysis using multiple classifiers. *J. Archaeol. Sci.,* 37: 2671-2678.

Stevens N.E. & McElreath R. 2015. When are two tools better than one? Mortars, milllingslabs, and the California acorn economy. *J. Anthropol. Archaeol.,* 37: 100-111.

Stiner M.C., Barkai R. & Gopher A. 2009. Cooperative hunting and meat sharing 400-200 Kya at Qesem Cave, Israel. *Proc. Natl. Acad. Sci.,* 106: 13207-13212.

Stout D., Semaw S., Rogers M.J. & Cauche D. 2010. Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *J. Hum. Evol.*, 58: 474-491.

Stout D., Apel J., Commander J. & Roberts M. 2014. Late Acheulean technology and cognition at Boxgrove, UK. *J. Archaeol. Sci.,* 41: 576-590.

Struhsaker T.T. & Hunkeler P. 1971. Evidence of tool-using by chimpanzees in the Ivory Coast. *Folia Primatolog.,* 15: 212-219.

Surovell T.A. 2009. *Toward a Behavioural Ecology of Lithic Technology: Cases from Paleoindian Archaeology*. University of Arizona Press, Tucson.

Swauger J. & Wallace B.L. 1964. An experiment in skinning with Egyptian Paleolithic and Neolithic stone implements. *Pennsylvania Archaeol.,* 34: 1-7.

de Terra H & Teilhard de Chardin P 1936. Observations on the Upper Siwalik Formation and Later Pleistocene deposits in India. *Proc. Am. Phil. Soc.,* 76: 791-822.

Terradillos-Bernal M. & Rodríguez X.-P. 2012. The Lower Palaeolithic on the northern plateau of the Iberian Peninsula (Sierra de Atapuerca, Ambrona and La Maya I): a technological analysis of the cutting edge and weight of artefacts. Developing an hypothetical model. *J. Archaeol. Sci.,* 39: 1467-1479.

Terradillos-Bernal M. & Rodríguez-Álvarez X.-P. (2017). The influence of raw material quality on the characteristics of the lithic tool edges from the Atapuerca sites (Burgos, Spain). *Quat. Int.,* 433 (part A): 211-223.

de la Torre I. 2003. The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of Lower Pleistocene hominids. *J. Hum. Evol.,* 44: 203-224.

de la Torre I. 2004. Omo revisited: evaluating the technological skills of Pliocene hominids. *Curr. Anthopol.,* 45: 439-465.

Torrence R. 1989a. Tools as optimal solutions. In R.Torrence (ed): *Time, Energy and Stone tools*, pp. 1-6. Cambridge University Press, Cambridge.

Torrence R. 1989b. *Time, Energy and Stone Tools*. Cambridge University Press, Cambridge.

Toth N. 1985. The Oldowan reassessed: a close look at early stone artifacts. *J. Archaeol. Sci.,* 12: 101-120.

Toth N., Schick K.D., Savage-Rumbaugh E.S., Sevcik R.A. & Rumbaugh D.M. 1993. *Pan* the tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *J. Archaeol. Sci.,* 20: 81-91.

Toth N., Schick K. & Semaw S. 2006. A comparative study of the stone tool-making skills of *Pan*, *Australopithecus*, and *Homo sapiens*. In N.Toth & K. Schick (eds): *The Oldowan: Case Studies into the Earliest Stone Age*, pp. 155-222. Stone Age Institute Press, Gosport.

Toth N. & Schick K. 2009. The importance of actualistic studies in early stone age research: some personal reflections. In K. Schick & N.Toth (eds): *The Cutting Edge: New Approaches to the Archaeology of Human Origins*, pp. 267–344. Stone Age Institute Press, Gosport.

Tryon C. A. & Faith J. T. 2013. Variability in the Middle Stone Age of eastern Africa. *Curr. Anthropol.,* 54: S234–S254.

Tylor E.B. 1894. On the Tasmanians as representatives of Palaeolithic man. *J. R. Anthropol. Inst.,* 23: 141-152.

Unger-Hamilton R. 1984. The formation of use-wear polish on flint: beyond the "deposit versus abrasion" controversy. *J. Archaeol. Sci.,* 11: 91-98.

Ugan A., Bright J. & Rogers A., 2003. When is technology worth the trouble? *J. Archaeol. Sci.,* 30: 1315-1329.

Vaughan C.D. 2001. A million years of style and function: regional and temporal variation in Acheulean handaxes. In T.D. Hurt & F.M. Rakita (eds): *Style and Function: Conceptual Issues in Evolutionary Archaeology*, pp. 141-164. Bergin & Garvey, Westport.

Viallet C. 2016. Bifaces used for percussion? Experimental approach to percussion marks and functional analysis of the bifaces from Terra Amata (Nice, France). *Quat. Int.,* 409: 174-181.

Villa P. 2001. Early Italy and the Colonization of Western Europe. *Quat. Int.,* 75: 113-130.

Visalberghi E., Addessi E., Truppa V., Spagnoletti N., Ottoni E., Izar P. & Fragaszy D. 2009. Selection of effective stone tools by wild bearded capuchin monkeys. *Curr. Biol.,* 19: 213-217.

Walker P.L. 1978. Butchering and stone tool function. *Am. Ant.,* 43: 710–715.

Wang W., Lycett S.J., von Cramon-Taubadel N., Jin J.J.H. & Bae C.J. 2012. Comparison of handaxes from Bose Basin (China) and the western Acheulean indicates convergence of form, not cognitive differences. *PLoS One,* 7: e35804.

Wayland E.J. 1934. Rifts, rivers, rains and early man in Uganda. *J. R. Anthropol. Inst.,* 64: 333-352.

Wenban-Smith F.F., Allen P., Bates M.R., Parfitt S.A., Preese R.C., Stewart J.R., Turner C. & Whittaker J.E. 2006. The Clactonian elephant butchery site at Southfleet Road, Ebbsfleet, UK. *J. Quat. Sci.,* 21: 471-483.

White J.P. & Thomas D.H. 1972. What mean these stones? Ethnotaxonomic models and archaeological interpretations in the New Guinea Highlands. In D.E. Clarke (ed): *Models in Archaeology*, pp. 275-308. Routledge, London.

White M., Mitchell J., Bridgland D. & McNabb J. 1998. Rescue excavations at an Acheulean site at Southend road, South Woodford, London Borough of Redbridge, E18 (TQ 407905). *Archaeol. J.,* 155: 1-21.

White T.D. 1986. Cut marks on the Bodo cranium: a case of prehistoric defleshing. *Am. J. Phys. Anthropol.,* 69: 503-509.

Whittaker J.C. & McCall G. 2001. Handaxe hurling hominids: an unlikely story. *Curr. Anthropol.,* 42: 566-572.

Wobst H.M. 1978. The archaeo-ethnology of hunter-gatherers or the tyranny of the ethnographic record in archaeology. *Am. Ant.,* 43: 303-309.

Wymer J. 1968. *Lower Palaeolithic Archaeology in Britain: As Represented by the Thames Valley*. John Baker, London.

Wynn T. 2002. Archaeology and cognitive evolution. *Behav. Brain Sci.,* 25: 389-438.
Wynn T. & Tierson F. 1990. Regional comparison of the shapes of later Acheulean handaxes. *Am. Anthropol.,* 92: 73-84.
Wynn T., Hernandez-Aguilar A., Marchant L.F. & McGrew W.C. 2011. "An ape's view of the Oldowan" revisited. *Evol. Anthropol.,* 20: 181-197.
Yravedra J., Domínguez-Rodrigo M., Santonja M., Pérez-González A., Panera J., Rubio-Jara S. & Baquedano E. 2010. Cut marks on the Middle Pleistocene elephant carcass of Áridos 2 (Madrid, Spain). *J. Archaeol. Sci.,* 37: 2469-2476.
Zaidner Y. 2013. Adaptive flexibility of Oldowan hominins: secondary use of flakes at Bizat Ruhama, Israel. *PLoS One,* 8: e66851.
Zupancich A., Nunziante-Cesaro S., Blasco R., Rosell J., Cristiani E., Venditti F., Lemorini C., Barkai R. & Gopher A. 2016. Early evidence of stone tool use in bone working activities at Qesem Cave, Israel. *Sci. Rep.,* 6: 37686.

Associate Editor, Noreen Von Cramon-Taubadel