Chapter 12 Origins and Adaptations of Early *Homo*: What Archeology Tells Us

Hélène Roche, Robert J. Blumenschine and John J. Shea

Keywords Oldowan • Acheulean • lithic technology • flake production • hammerstones • carnivory • scavenging • butchery • preservation bias

Introduction

Brain enlargement, reduction in molar tooth size, increased stature and other features of early Homo did not evolve in a vacuum. These evolutionary changes reflect shifts in a complex web of relationships among their populations, between early Homo and other hominin species, and between their biotic community and abiotic forces (i.e., climate change). Archeological evidence complements and balances inferences from hominin fossil remains, non-hominin vertebrate paleontology, geology, and other component fields of paleoanthropology. This paper represents an attempt to pull together the various strands of its authors' expertise to shed light on the origins and adaptations of early Homo. It is not intended to be a comprehensive review of Oldowan sites, their chronology, lithic typology, paleontological associations, and interpretive issues. For recent overviews of these subjects, see Plummer (2004), Schick and Toth (2006) as well as papers in Toth and Schick (2006), Ungar (2007) and Hovers and Braun (2009). The coincidence of knapped stone tools, butchery-marked bones and fossil remains of early Homo is usually linked to increased hominin carnivory. This paper

Directeur de recherches au CNRS, UMR 7055 du CNRS, Université Paris X – Nanterre, Maison de l'Archéologie et de l'Ethnologie, 21 allée de l'Université, 92023 – Nanterre, France e-mail: helene.roche@mae.u-paris10.fr reviews evidence for this hypothesis, and considers alternative hypotheses as well.

The Nature of the Earliest Oldowan

The scope of this paper is the Oldowan in Africa during the Late Pliocene and Early Pleistocene, roughly 2.7–1.6Ma. For convenience and clarity, we distinguish this as the "Earliest Oldowan." Since it was first proposed by Leakey (1936), the term Oldowan has gradually eclipsed "Chellean," "Pre-Acheulean" and similar local terms for Early and Middle Pleistocene Eurasian stone tool industries that lack evidence for Acheulean bifacial technology. Although the adoption of this name implies a comparable antiquity to the earliest Oldowan" industries have turned out to be much younger. The relationship, if any, between these younger Eurasian "Oldowan" assemblages and their Plio-Pleistocene counterparts in Africa lies beyond the scope of this paper.

The defining technological feature of the Oldowan Industry is the production of flakes from pebbles, cobbles, and angular rock fragments by hard hammer percussion, or knapping. The earliest evidence of stone knapping appears as early as 2.6 Ma in East Africa (Semaw et al., 1997, 2003). The end of the Oldowan is less clear. For the purposes of this paper, we shall fix it at ca. 1.6–1.7 Ma, prior to the wide-spread appearance of Acheulean assemblages throughout Africa. Lasting approximately 1 million years, the Oldowan is not the static entity as which it is sometimes portrayed (Semaw, 2000).

The Earliest Oldowan Occurrences

The known spatial and temporal distribution of earliest Oldowan sites suggests that the initial stages of stone knapping were isolated and sporadic. Whether the gaps among these early sites are real, or artifacts of preservation and discovery remains unclear. Insufficient field research in

H. Roche (🖂)

R.J. Blumenschine

Center for Human Evolutionary Studies, Department of Anthropology, Rutgers University, The State University of New Jersey, 131 George Street, New Brunswick, NJ 08901-1414, USA e-mail: rjb@rci.rutgers.edu

J.J. Shea

Department of Anthropology and Turkana Basin Institute, Stony Brook University, Stony Brook, NY 11794–4364, USA e-mail: John.Shea@sunysb.edu

appropriate deposits (which are rare) may play a major role in the sporadic aspect of the data. So far, the 2.6–2.5 Ma evidence is limited to four sites located at Gona in the Hadar Formation (Upper Awash, Ethiopia) (Roche and Tiercelin, 1980; Harris, 1983; Semaw et al., 1997, 2003). There is a great potential in the Gona area where more sites have been identified, and it is likely that still more sites – including older ones – may be found in the future. At 2.5 Ma, within the Hata Member of the Bouri Formation, bone fragments reported to bear cut marks and percussion marks have been found in the same general area as fossil remains of *Australopithecus garhi* (Asfaw et al., 1999; de Heinzelin et al., 1999). No stone tools were found with these bones, and they are not in close association with hominin remains. Thus, their bearing on stonetool production by *A. garhi* remains unresolved.

More sites are found between 2.4 and 2.3 Ma. In Hadar, there are two excavated sites, A.L. 666 and A.L. 184, (Kimbel et al., 1996; Hovers et al., 2002). De la Torre (2004) has reassessed the lithic assemblages from the Lower Omo Valley Shungura Formation Members E and F that were excavated in the 1970s (Howell et al., 1987). Only three sites qualified with good context and intentionally knapped lithic material (Omo 57, Omo 123 and FtJi 2), as well as two channel sites with unabraded stone tools recovered in situ (FtJi1 and FtJi5). All of these sites are from Member F, and are thus bracketed between 2.34 and 2.32 Ma. In the Nachukui Formation, in the western part of the Turkana Basin, the two Late Pliocene sites of Lokalalei 1 and Lokalalei 2C are dated at 2.3 Ma (Kibunjia et al., 1992; Kibunjia, 1994; Roche et al., 1999). Less than ten excavated archeological sites are thus recorded for the 2.4–2.3 Ma time period. Unlike the earlier sites, these are often characterized by association or at least spatial proximity between hominin remains and stone tools concentrations: Homo aff. H. habilis at site A.L. 666 in Hadar (Kimbel et al., 1996), and early Homo at Lokalalei 1 in West Turkana (Prat et al., 2005). There is presence but no proximity of Paranthropus boisei/aethiopicus for the Omo sites in the Shungura Formation (Member G, 2.32–1.9 Ma) and for Lokalalei sites in West Turkana (KNM-WT 17000, Lokalalei Member, 2.5 Ma) (Walker et al., 1986).

What is the nature of and basis for variation among the earliest Oldowan assemblages? Variation among Oldowan knapping sequences is thought to reflect cognitive and motor abilities, raw materials, and other situational variables. Oldowan knapping skills appear somewhat limited by lithic raw material properties in the earlier assemblages. Later Oldowan assemblages exhibit greater freedom from raw material constraints. This is illustrated, for instance, when knappers become able to rectify a knapping accident and thus to go on with the knapping process, showing a real improvement in decision making. To be able to create new striking platforms and to be less constrained by the shape of the original raw material is another example. This suggests the development of an ability to create morphology that is totally independent of the shape of the clast; an ability seen later, and somewhat more clearly, for shaped Acheulean handaxes.

The Leakeys (Leakey, 1936, 1971) originally treated the Oldowan as an undifferentiated entity, whose stability contrasted with both the Developed Oldowan and Acheulean. Following discoveries of very early occurrences of stone knapping (Roche and Tiercelin, 1977; Harris, 1983; Kibunjia et al., 1992), several researchers distinguished a break (ca. 2.0 Ma) between a "Pre-Oldowan" and an Oldowan based on technological patterns (Roche, 1989; Kibunjia, 1994; Roche and Kibunjia, 1996). Discoveries made in the mid 1990s, mainly in Gona (Semaw et al., 1997, 2003), Hadar (Kimbel et al., 1996) and West Turkana (Roche et al., 1999) challenged this distinction, and few researchers today retain it. At the very most, an "Early Oldowan" (prior to 2Ma) could be distinguished. However, the Oldowan lithic assemblages are not homogenous, whether one considers the raw material procurement strategies, the operational sequences (chaînes opératoires), or the by-products that are obtained. The Oldowan is not only marked by the emergence of a behavior which put into action skills never used by other animal species, it is also characterized by a wide range of techno-economic patterns, some of them being more productively efficient than others. There is no single explanation for this variability. Functional adaptation for food acquisition, response to environmental constraints (including raw material availability), and variations in inter- or intra-specific cognitive and motor abilities are all viable and non-exclusive hypotheses for Oldowan technological variability.

The appearance of the Oldowan also marks a drastic niche shift within the lineage of its makers. This shift involves not only expansion of the diet to include foods from larger mammals (>5 kg body mass), but also an expanded set of relationships with members of the larger carnivore guild they joined. The presence of stone tool cut marks (e.g., Bunn, 1981; Potts and Shipman, 1981) and percussion marks (e.g., Blumenschine and Selvaggio, 1988; Blumenschine, 1995) on bones of animals ranging in size up to elephants demonstrates that Oldowan hominins had become the first primate to consume meat, marrow and perhaps other edible tissues from animals greater than or equal to their own body weight. Cut-marked bones associated with stone artifacts from Gona, Ethiopia (Domínguez-Rodrigo et al., 2005) suggest that this dietary shift was coincident with the earliest stone artifacts at 2.6 Ma (Semaw et al., 1997). This dietary niche expansion placed Oldowan hominins as the only predominantly planteating members of the large carnivore guild of the East African Late Pliocene. This large carnivore guild included a richer range of medium to large-bodied felids, hyaenids, canids and crocodilians than are extant today (Werdelin and Lewis, 2005). While the Oldowan hominins likely remained prey for all of these carnivores, they also became direct or indirect food competitors for some of the carnivores. The nature of these intra-guild interactions is central to understanding the behavioral, technological and social capabilities of Oldowan hominins. Historically, these interactions have been conceptualized as the hunting vs. scavenging debate, and investigated in terms of co-occurrences of butchery marks and tooth marks in bone assemblages (and sometimes on the same bone). There is a growing recognition that framing such ecological relationships in terms of a simple dichotomy is an oversimplification that does justice neither to the evidence, nor to the behavioral variability of the species under consideration (cf. Washburn and Lancaster, 1968; Isaac, 1978; Shipman and Walker, 1989; Aiello and Wheeler, 1995; Foley, 2001; Blumenschine and Pobiner, 2007; Bunn, 2007).

Nature of the Oldowan-Acheulean Transition

Approximately 1.7 Ma can be considered the transition interval between the Oldowan and the Acheulean phases of technocultural evolution. This period is marked by the appearance of a new hominin species (Homo ergaster/erectus). In stone knapping, this period witnesses the beginnings of purposeful bifacial shaping (faconnage) of large core tools. A third major aspect of this transitional period is the apparent increase in hominin population size, as shown by the extension of the geographic range of Homo ergaster/erectus beyond Africa, and by the increase in the number of identifiable Acheulean archaeological sites throughout Africa. This population growth seems to start circa 1.8 Ma in East Africa, at least in certain favorable environments. The colonization of new lands and territories is another noteworthy fact of the post-Oldowan period. Because hominins fossils are rare or absent from these contexts, this expansion of the geographic range of Homo ergaster/erectus within Africa and beyond is traced primarily through the archaeological record.

After 2.0–1.9 Ma, the whole of the East African Rift Valley area is populated by greater numbers of archeological sites than was seen earlier. Similar increases in archeological "visibility" are apparent in South Africa (Kuman, 1994, 2003) and North Africa (Sahnouni, 2005, 2006). Beyond Africa, the two most secure occurrences of early hominins are Dmanisi in Georgia (Gabunia et al., 2001; Lordkipanidze et al., 2006) and Ubeidiya in Israel (Bar-Yosef and Goren-Inbar, 1993; Guérin et al., 2003). For recent overviews of other claimed Plio-Pleistocene sites in Eurasia, see Antón and Swisher (2004), Langbroek (2004), Dennell and Roebroeks (2005), and Wang et al. (2007).

Lithic Technology

Technical behavior is documented through analysis of the lithic component of the hominin's technical system. Technological

analysis takes us back to the cognitive abilities and motor skills of early hominins, from the individual performance of a single stone-knapper to the level of competence of a group at a given time. Studies of raw material sources and procurement/distribution also inform us about interactions with environment and land use (Blumenschine et al., 2008). Stone knapping is the earliest known technical behavior that strongly contrasts with technical behaviors of nonhuman primates observed in the wild (Roche, 2005). The ability to intentionally modify a natural homogenous, isotropic, hard and rigid mineral material (e.g., hard rock) is a technical behavior only shared by humans and their congeneric ancestors. It can be contrasted to the faculty of using unmodified mineral or organic natural elements, or to the faculty of altering natural soft or plastic organic material, both of which are shared by a number of animal species. Hundreds of well-known examples of stone-using by chimpanzees in the wild have been documented, including archeological evidence (Boesch and Boesch, 1984; McGrew, 1992; Mercader et al., 2002). A case of hunting with tools by Pan troglodytes verus confirms the ability of chimpanzees to transform soft vegetal material (Pruetz and Bertolani, 2007). Stone knapping by any animal species other than humans or their ancestrally-related forms has never been reported. Moreover, there is a fundamental shift in technical behavior between using natural stone tools and processing soft material, on the one hand, and knapping hard rocks on the other. Beyond the remarkable cognitive and motor abilities that stone knapping implies, it also results in drastic changes in the hominin's relation with their external milieu. From handling natural elements (stones, leaves, branches, etc.) to having direct access to nutrients or for defense, as is the case with the rest of tool using animal species, we shift to a technical system that implies an increasing number of steps (each step consisting in a chain of actions, underpinned by decision-making), the second step being a consequence of the first and allowing the third, and so on, until the anticipated goal is achieved.

From the very beginning, the aim of stone knapping was to create, and to infinitely reproduce a physical function which is absent, or extremely rare, in the natural world: the cutting function. This is obtained by collecting raw material (first step), extracting flakes bearing sharp cutting edges from a block of raw material (the second step), which in itself constitutes most of the innovation of this new behavior. Flake production is made with a natural intermediary tool, a stone hammer. These objects will, in turn (third step), act on the external milieu by cutting organic soft materials. Used on animal tissues, they give direct access to nutrients (the case of breaking bones is treated below). Used to process vegetal components, they can also give direct access to nutrients (edible plants, fruits, etc.), but they can also be used to build shelter with branches and foliage. Lastly, they can be used as intermediary tools to handcraft wooden weaponry (fourth step) or traps, which expand access to food, improve either self or group protection during encounters with predators (which can also involve natural stones), and many other individual or social behaviors (see below).

Generally speaking, Oldowan assemblages are comprised of pebbles and cobbles or blocks of raw material reduced by percussion-controlled conchoidal fracture. The knapping sequences result in flakes (the intended products) and cores (usually the waste), and sometimes chopper-cores, i.e. objects which could either be flake-producing cores and/or heavyduty cutting tools. Unworked cobbles are very often present at sites, sometimes in large amounts, and are considered as part of the lithic assemblage and as hammerstones. Hammerstones and any tools that could have been used for percussive activities, such as breaking bones (see below) indisputably play an important role in hominin activity (Mora and de la Torre, 2005). The status of the unmodified material is more subject to debate (de la Torre and Mora, 2005; Delagnes and Roche, 2005). Among the two unique knapping modes (percussion and pressure) used during prehistoric times (Inizan et al., 1999), only percussion was used during the Oldowan. Among the three specific knapping actions (flaking, shaping and retouching), flaking is most prominent. Retouching is found in limited occurrences, and only towards the end of the Oldowan do we find polyhedric shaping (see Fig. 3.1 in Roche, 2005). Among the dozens of techniques invented for modifying stones, only three of them were put to use during the Oldowan: (1) direct percussion with a hand held stone hammer, (2) direct percussion on an anvil (no hammerstone; the block of raw material is held in hand), and (3) bipolar percussion between a hand-held stone hammer and anvil, the raw material to be fractured being held with the second hand (analogous to the technique used to crack a hard-shelled nut). The first technique is by far the one most often employed; it can be precisely controlled and is, therefore, more efficient (Inizan et al., 1999; Pelegrin, 2005; Roche, 2005). It is not yet certain that any of the knapping sequence patterns in evidence for the Oldowan can be qualified as a method (that is, an "orderly sequence of actions carried out according to one or more techniques and guided by a rational plan" (Inizan et al., 1999: 145), such as the "Kombewa method" or the "Levallois method"), but it can be applied to some shaping operational sequences.

When stone knapping becomes visible in the archeological record, this behavior is no longer in its very earliest possible form – a stage that will be extremely difficult, if not impossible, to identify. To the contrary, the earliest record of Oldowan tool-making shows an already well-mastered technical behavior shared by small, possibly isolated groups of hominins. However, the mode, action, techniques and methods show a limited range of technological possibilities compared to what stone knapping would eventually become. What then accounts for the variability in Oldowan technical behavior? Some of the avenues for research on this question include the investigation of raw material procurement strategies and of stone tool production techniques.

Raw Material Procurement Strategies

For the few Early Oldowan sites at 2.7–2.6 and 2.4–2.3 Ma, there is no evidence of long distance transport of raw material from source to the place of use, loss and/or discard. To the contrary, it has been shown that raw materials were collected from immediate-to-local sources less than a few hundreds meters distant (Harmand, 2005; Stout et al., 2005; Goldman and Hovers, 2009). In some instances, comparisons of raw materials at potential sources and the material recovered from archeological sites has shown an obvious selection for particular rock types. Selection criteria appear to have included different rock types and petrographic, structural and granular patterns (Harmand, 2004, 2005, 2009a,b; Stout et al., 2005), as well as morphology and size of the clasts. Systematic knapping experiments confirm the superior knapping properties of the selected vs. non-selected raw material (Harmand, 2005; Stout et al., 2005). Rock type selection varies according to the petrographic substratum of each region. All these substrates are dominated by lavas, but of variable quality. Archeological assemblages feature conspicuously high proportions of the rare, high-quality raw materials from the surrounding environment. When it is possible to conduct a diachronic study within a single area, as in West Turkana, which yields archeological sites through a sequence from 2.3 to 0.7 Ma (Roche et al., 2003), the sourceto-site distance remains the same, but there is more selection in term of rock type, granularity and size of clasts during later Oldowan (1.8-1.7 Ma) (Harmand, 2005, 2009a). Within the Oldowan, from 2.0Ma onwards, and with an increasing number of sites, there is evidence for transport of raw materials from sources to places of use over longer distances (up to 15–20km). This applies, for instance, to Koobi Fora (Isaac et al., 1997), Olduvai (Hay, 1976; Blumenschine et al., 2003, 2008), and Kanjera (Plummer et al., 1999; Braun et al., 2009). Where studied, the same patterns of raw material selectivity are indicated.

Stone Tool Production Techniques

Oldowan stone tool production techniques show a range of different patterns. The more common of these include the following:

• Very limited production of flakes by blow-after-blow random flaking of a cobble

- Very limited production of flakes by one to several contiguous or alternating removals on a side of a core, creating a strong cutting edge (chopper-core or core tool)
- More abundant production of flakes with simple and non-organized *débitage* of an ordinary core (i.e., a core for which there was no morphological selection of the original clast)
- Elevated production of flakes with an organized *débitage*, with successive, multiple and orderly series of removals on a specific core (i.e., a core whose form indicates morphological selection of the original clast)

These patterns might be too similar to be differentiated from one another. This is true in terms of general tendency, and when compared with later stages of stone knapping. However, a careful examination of the Oldowan lithic assemblages shows these different knapping sequences vary according to raw material availability and, more importantly, are linked to the level of the abilities implied in the technical actions. Most of the hominin groups chose only one knapping process or, when two or (seldom) more were chosen, one predominates. This is the case in the two late Pliocene sites of Lokalalei in West Turkana, dated at 2.3 Ma.

At Lokalalei 1 (Kibunjia, 1998) flakes were produced by simple and non-organized débitage of globular cores, while at Lokalalei 2C (Delagnes and Roche, 2005) an organized débitage predominated. Moreover, the simple débitage at Lokalalei 1 was inadequately implemented, considering the petrographic organization of the raw material (which, by the way, is of good knapping quality and has been selected for this purpose). The result is low productivity, with a majority of accidentally broken flakes, and with cores bearing many scars of knapping accidents. In contrast, at Lokalalei 2C, controlled débitage has been conducted, following constant rules applied to a good quality raw material. Blocks and cobbles were also chosen with peculiar natural angular morphologies (i.e., cobbles with a flat surface as opposed to a convex one), thus providing directly serviceable striking angles (<90°). Sometimes, the flat surface was obtained by splitting a rounded cobble or was formed on the ventral face of large flakes. This flat surface was then exploited as a flaking surface, by means of successive and multidirectional series of invasive and sub-parallel flakes, a practice that maintained the flaking surface flat and allowed the production of large numbers of flakes (Roche et al., 1999; Delagnes and Roche, 2005). This very specific reduction sequence, and the ensuing high productivity have been documented by dynamic reconstruction of entire cobbles on the basis of particularly informative refitting sets (where 12% of a total of 2,614 artifacts may refit to one another). On average, 18 flakes were knapped from each core, and up to 73 flakes were removed from a single block of raw material. The production of such a large number of flakes shows foresight and anticipation

while the whole operational sequence is in progress. This cognitive ability goes with a controlled motor skill, shown by the high control of percussion gestures, which can be seen on flakes and cores, and with a very circumscribed and limited area bearing percussion marks on the hammerstones (Delagnes and Roche, 2005).

It has not yet been demonstrated that a similar level of raw material management, anticipation, and manual dexterity exists elsewhere during Oldowan times. At A.L. 666 in Hadar, which is penecontemporaneous to the Lokalalei sites, the same morphotype of clast (a flat surface opposed to a convex one) was flaked, but with much stronger blows such that each flake removed was thick, and the flaking surface was not maintained flat (Hovers, 2001). This stopped the flaking process and curtailed core productivity. At Gona, flaking appears to have been more simple, at least to judge from the published descriptions (Semaw, 2000; Semaw et al., 2003). At Olduvai, production is mainly from core tools, and there are few, if any, examples of real débitage (i.e., systematic flake production, as opposed to the purposeful shaping [faconnage] involved in chopper-core or core-tool flaking) (Leakey, 1971; Stiles et al., 1974).

Although they are not always easy to decipher, the different knapping sequences allow us to characterize the competence of group or individual performance, and it is through the whole operational sequence that planning and foresight can be evaluated. Several hypotheses can be proposed to explain the diversity of Oldowan technical behaviors. At present, variation in cognitive and motor abilities as implied by the knapping action seems more likely than any other factor. This is not to say that other factors (e.g., raw material, function), lack explanatory power; rather, they are relatively difficult to investigate. In the near absence of use-wear evidence, almost nothing is known about the functionality of the lithic artifacts, apart from the indisputable cutting quality of the sharp edges of the flakes, and the pounding qualities of cobble and core forms. Nevertheless, as discussed in the next section, it is precisely these cutting and pounding aspects of the lithic artifacts that link them meaningfully to the faunal remains with which they are associated in archeological sites.

Larger Mammal Carnivory

Blumenschine and Pobiner (2007) recently reviewed the zooarchaeological evidence for large mammal carnivory in Oldowan hominins, which we summarize below. Although assemblages of larger mammal bones have been reported from almost 20 Oldowan localities (Blumenschine and Pobiner, 2007: Table 10.1), most of what is known about Oldowan hominin carnivory derives from a single site, FLK Level 22 (*Zinjanthropus* level), in Bed I of Olduvai Gorge,

dated to approximately 1.8 Ma. (Bunn and Kroll, 1986; Potts, 1988; Oliver, 1994; Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al., 2007b; Bunn, 2007).

The animal species and tissue types consumed define a basic parameter of the Oldowan hominin carnivorous niche. Butchery marks on bone surfaces provide direct evidence for hominins extracting flesh using sharp-edged stone flakes (cut marks), and marrow using rounded hammerstones and infrequently choppers (percussion marks). To the extent that the butchery-marked bone can be identified taxonomically, traces of hominin feeding provide paleoanthropology with a more specific itemization of dietary elements than is currently possible from other lines of evidence (e.g., tooth morphology and wear, stable isotopes). Blumenschine and Pobiner (2007) compiled comprehensive lists of both published occurrences of butchery-marked bone from Oldowan assemblages, as well as the larger mammalian species (≥5kg live body weight) in these assemblages that have been reported to be butchery marked. Two remarkable features of Oldowan hominin carnivory highlight the results of these compilations.

First, of the 16 Oldowan localities from which butcherymarking has been reported, only two, FLK Level 22 and FLK N Levels 1-2 from Bed I, Olduvai Gorge, show substantial proportions of cut-marked and/or percussion-marked bone: approximately 9% of analyzed (non-dental) larger mammal specimens from FLK Level 22 are reported to be cut-marked (Bunn and Kroll, 1986), while approximately 27% and 28% of analyzed long bone specimens from FLK Level 22 and FLK N Levels 1-2, respectively, are reported to be percussion-marked (Blumenschine, 1995; Capaldo in Blumenschine et al., 2007a). Fewer than nine butchery-marked specimens, and often only one or two, have been reported from 11 other localities, including the Olduvai assemblages from FLK N Level 6, FLK NN Level 2, HWK E Levels 1-2, and OLAPP Trench 57 (Bunn, 1982; Monahan, 1996; Blumenschine et al., 2003); the West Turkana assemblage from Lokalalei 1A (Kibunjia, 1994); the Gona localities of DAN2, EG13, OGS-6, and WG9 (Semaw et al., 2003; Domínguez-Rodrigo et al., 2005); Bouri (de Heinzelin et al., 1999); and Sterkfontein Member 5 (Pickering, 1999; Pickering et al., 2000). No butchery marks were identified on the poorly preserved bones from the three KBS Industry localities of FxJj1, 3, and 10 (Bunn, 1997; Isaac and Harris, 1997).

In some cases, the low numbers of butchery-marked specimens can be attributed to small assemblage size, poor bone-surface preservation, or incomplete analysis. Alternatively, the paucity of butchery-marking outside of the two abundantly-marked Olduvai assemblages might be a signal that large mammal carnivory was infrequent during the early stages of this adaptation, and/or that localized carcass processing leading to concentrations of butcherymarked specimens took place only in specific landscape settings such as those exposed at FLK Level 22 and FLK N Level 1-2. These landscape settings theoretically afforded hominins a long-lived grove of refuge trees adjacent to places where carcasses could be found regularly (Blumenschine and Peters, 1998). No known method can determine the frequency of large mammal carnivory by hominins. However, one relevant consideration is that the large amounts of flesh, marrow or brain from even small, gazelle-sized carcasses, and the very high rates of nutrient return from processing these tissues with Oldowan stone tools, suggest that available carcass foods should have been taken whenever encountered (for discussion, see Blumenschine and Pobiner, 2007). Nonetheless, the possibility that Oldowan hominin carnivory was uncommon appears to stand in contrast to at least some immediate post-Oldowan assemblages such as those recently described from Okote Member occurrences at East Turkana, where butchery-marking is common (Pobiner, 2007).

A second remarkable feature of Oldowan hominin carnivory is the large body size range and broad ecological range of butchery-marked ungulates that have been identified to the genus or species level (Blumenschine and Pobiner, 2007). Fourteen taxa reported to be butchery-marked encompass the full size range of larger mammals, from the small gazelle Antidorcas recki through Hippopotamus gorgops and possibly Elephas recki, and include seven bovids, two suids, one equid, two giraffids, one hippopotamid, and one elephantid. Among bovids for which femoral ecomorphology was measured by Kappelman et al. (1997), butchery-marked taxa are associated with open to light cover through light to heavy cover. Although they are present in the assemblages, bovids that represent open, heavy cover or forest settings have not been reported to be butchery-marked. Butchery-marked specimens derive from species identified as either grazers or browsers on the basis of carbon stable isotopes (Cerling et al., 1999, 2003; Harris and Cerling, 1999) and jaw ecomorphology (Spencer, 1997). Given that the vast majority of butchery marks occur on specimens identifiable only to the family level or above, the series of butchery-marked taxa was probably broader, including some or all of the 14 other taxa present at the Oldowan localities. Most of the butcherymarked taxa are reported only from FLK Level 22, but it is clear that here, Oldowan hominins at least occasionally fed on taxa that were prey for a full size range of predator/ scavengers in the larger carnivore guild of the East African Plio-Pleistocene.

Whether Oldowan hominins acquired food from larger mammals through hunting and/or scavenging can be cast more broadly as the emerging role of hominins in the larger carnivore guild (cf. Blumenschine and Pobiner, 2007). It is during the Oldowan that members of presumably one hominin lineage expanded their range of interactions with large carnivores from sole status as prey, to include indirect and/or direct competition with at least some species for larger mammal carcasses and/or live prey, eventually leading to modern humans' status as the top predators in most ecosystems.

Passive scavenging, or the acquisition of foods from carcasses unattended by large carnivores, is an evolutionarily conservative hypothesis, requiring few derived behavioral and technological capabilities of Oldowan hominins over their direct ancestor. Many forms of passive scavenging have been hypothesized on the basis of observations of scavenging opportunities in modern settings and the inferred habits of extinct carnivores (e.g., Blumenschine, 1987; Cavallo and Blumenschine, 1989; Marean, 1989). Those hypothesized to have provided opportunities that were most frequent, moderate to high-yielding, predictably located, and of low risk from predation, disease or toxicity are scavenging from abandoned lion kills, temporarily or finally abandoned treestored leopard kills, and abandoned saber-tooth cat kills. Passive scavenging from abandoned felid kills can account for many aspects of Oldowan bone assemblage composition and condition, including head and limb-dominated skeletal part profiles, most of the extreme body size and ecological ranges of carcass taxa, the frequency and anatomical distribution of cut and percussion marks, and the high frequency of carnivore tooth marking on long bone midshafts from FLK Level 22 (e.g., Blumenschine, 1987, 1995; Marean et al., 1992; Capaldo, 1997; Selvaggio, 1998; Blumenschine and Pobiner, 2007). A recent claim that passive scavenging from felid kills at FLK Level 22 has been falsified (Domínguez-Rodrigo and Barba, 2006) has been invalidated on the basis of serious methodological and conceptual flaws (Blumenschine et al., 2007b).

Passive scavenging, in its most opportunistic form, involving encounters with abandoned carcasses during plant food foraging or other daily activities, requires only that Oldowan hominins carry stone for butchery-tool production and/or transport carcass parts to tool locations. Involving no direct interactions with large carnivores, it would represent conservation of the presumed predator avoidance of ancestral hominins, while allowing for the acquisition of calorie- and protein-rich foods linked to brain expansion and gut reduction (Aiello and Wheeler, 1995), among other developments.

Confrontational scavenging, or kleptoparasitism of kills from feeding large social or solitary predators, denotes more advanced behavioral and technological capabilities for Oldowan hominins. By usurping complete or nearly complete carcasses from carnivores, confrontational scavenging would yield extremely large quantities of food. For example, an adult wildebeest, the size of the animals most commonly represented at the Oldowan sites, bears approximately 70 kg of flesh, implying large hominin group sizes and/or a high proportionate contribution of meat to the diet. The presence of cut marks on "meaty" upper limb bones is often cited in support of confrontational scavenging (e.g., DomínguezRodrigo, 1997; Bunn, 2001). However, the relationships between the location and frequency of cut-marking, on the one hand, and the amounts of flesh removed, on the other, are currently uncertain, remaining as one of the most important issues in the early hominin hunting and scavenging debate. Unlike the predator avoidance of passive scavenging, confrontational scavenging implies that Oldowan hominins were dominant members of the larger carnivore guild, presumably achieving this status through coordinated group tactics, such as "power scavenging" (Bunn, 2001) and/or the use of effective offensive weaponry.

Like confrontational scavenging, hunting by Oldowan hominins would yield extremely large quantities of food from complete carcasses. As such, the two types of carcass acquisition would be largely indistinguishable on the basis of skeletal part profiles or patterns of cut-marking. If hunting can be shown to account for the full size and ecological range of prey species at Oldowan sites, top predator status likely involving effective projectile weaponry would be implied for Oldowan hominins, conditions that appear incongruent with their small body size and simple stone technology.

The Other Uses of Oldowan Tools

For what purposes were Oldowan tools used? The two irrefutable answers are, for stone tool production and for butchering animal carcasses (see above). But were Oldowan tools used for other cutting tasks? In trying to answer this question, one must remember that Oldowan tool use involves one of the most problematic and conjectural aspects of stone tool technology at the extreme limits of the archeological record. This record has to be augmented by middle-range theoretical principles derived from actualistic-experimental studies, from ethnoarcheology, and from studies of tool use by non-human species. Lastly, it also has to be understood that preservation bias strongly influences our perceptions of the evolutionary forces that shaped Oldowan stone tool technology.

Percussion-marked hammerstones are most clearly implicated in stone tool production. However, the kind of comminution and crushing that identifies a stone object as having been used to knap stone forms cumulatively. Stones used briefly as percussors may not preserve diagnostic traces of use. The artifact category of manuports may preserve superficially-utilized hammerstones.

We do not know which of the particular categories of sharp-edged Oldowan tools created cut marks on animal bones. Pebble cores, flakes, and retouched flake-tools all work reasonably well as butchery aids in experiments (Jones, 1980, 1994; Toth, 1987, 1997). Stone tools knapped and used for ad hoc butchery by recent mobile human groups show little attention to imposition of design beyond assuring the presence of a sharp cutting edge (e.g., Gould et al., 1971). Thus there is no compelling reason to reject the hypothesis that any or all Oldowan stone tools could have been used as butchery aids by early hominins. Whether the performance differences some experimenters have noted among different classes of replicated Oldowan tools in butchery experiments (Toth et al., 1996; Tactikos, 2005; Shea, 2007) were sufficient to influence the decisions of Oldowan tool-users remains an open question.

The use of stone tools as butchery aids is likely to have generated large numbers of flaked stone artifacts, for several reasons.

First, the energetic costs involved in gathering locallyavailable rocks and knapping a few flakes to be carried as "personal gear" would have been miniscule compared to the potential windfall energetic gain from meat- and fat-bearing animal carcasses encountered in daily foraging. Stone tools are durable resources that, once knapped, could have persisted on the landscape for decades or more. (Nearly every known ethnographic stone-tool-using human population treats abandoned campsites and known archaeological sites as sources of raw material for their immediate needs.) Assuming that there was some degree of local-scale continuity among Oldowan toolmakers, a strategy of returning unused flakes to central places/residential sites (Isaac, 1978) and/or one involving in-bulk stockpiling of raw materials at strategic points on the landscape (Potts, 1988) would be, in effect, a strategy with direct benefits to the knappers themselves and to their immediate descendants.

Secondly, while butchery is not necessarily a task that involves high rates of edge attrition on stone tools, it is a task that can have low thresholds for tool discard (and correspondingly high rates for tool provisioning). Prolonged and forceful contact between a stone tool and bone causes numerous minute fractures on the tool edge. These fracture scars scoop up fat, meat, and periosteum, lubricating the edge, and reducing its cutting effectiveness. Microtopographic irregularities on the surface of coarse-grained rocks function in the same way, even in the absence of microfracturing damage. The functionality of such a lubricated stone tool edge declines rapidly, requiring that the tool either be resharpened or replaced. Knapping razor-sharp stone whilst one's hands are caked in blood, dirt, hair and grease is never a good idea (JS has the scar tissue to prove it!). A far safer option would have been to simply replace the tool with a fresh one from a previously-knapped supply. It is possible that the vast quantities of knapped stone at Oldowan sites reflect the accurate perception by their makers that butchery episodes require frequent replacements of stone tools.

Lastly, in human hunter-gatherer societies, control over the distribution of meat may confer social status and significant social and reproductive advantages (Kaplan and Hill, 1985; Hill and Kaplan, 1993). The benefits of meat-sharing among chimpanzees are less clear (Mitani and Watts, 2001; Stanford and Bunn, 2001; Gilby, 2006). If, as the forgoing discussion suggests, early hominin carnivory involved regular interactions with larger carcasses than those consumed by chimpanzees, it follows that being able to knap and use stone tools as aids to butchery would have been a skill with positive fitness consequences. Knapping is a learned skill, and it further follows that there would also have been strong selective pressure for hominins to start knapping at an early age and to practice (particularly with unfamiliar materials) throughout the course of their lives. The virtually indestructible lithic byproducts of such practice knapping may form a significant portion of the stone tools at Plio-Pleistocene sites (Shea, 2006).

In textbook accounts of human origins, the inception of knapped stone technology is usually linked to increased hominin carnivory. This limited view of Oldowan tool use ignores contrary arguments in favor of a more functionally diversified early hominin stone tool technology.

First, the edges of ethnographically documented knapped stone tools are used for many other purposes than butchery, including woodworking, preparing leather from animal hides, and processing soft plant matter. Inasmuch as chimpanzees regularly shape tools out of wood and soft plant matter, it seems reasonable to suppose that early hominins would have appreciated the benefits of carving wood with stone tools, rather than with their teeth and fingernails. Experiments suggest that even simple stone tools would have dramatically increased the rate at which hominins would have been able to shape wood into useful subsistence aids, such as digging sticks, spears, clubs, or throwing sticks (Crabtree and Davis, 1968). Such increased work rates would have substantially lowered the costs involved in technologically-assisted foraging, potentially leading in turn to a broadening of early hominin subsistence strategies.

Second, the prominence of the link between stone tools and butchery is plainly a function of preservation bias. Cutmarked bones are more likely to fossilize than wooden implements. Archaeologists have not discovered preserved wooden tools in Plio-Pleistocene contexts, but this may as much reflect the absence of waterlogged contexts of this antiquity in tropical Africa. Middle Pleistocene waterlogged contexts associated with lithic traces of hominin activity, including Gesher Benot Ya'acov (Israel), Kalambo Falls (Zambia), and Schöningen (Germany) have yielded rich evidence of hominin woodworking skills (Theime, 1997; Clark, 2001; Goren-Inbar et al., 2002). This evidence includes clubs, spears, possible fragments of trays, and, especially from Kalambo Falls, objects whose purposes remain enigmatic. In view of the wide range of uses our near primate relatives make of wooden implements, stone-tool-assisted Plio-Pleistocene carpentry is difficult to dismiss out of hand. Evidence for Plio-Pleistocene woodworking comes from

microwear and residue studies. Keeley and Toth (1981) report microwear polishes interpreted as woodworking traces on flake tools from Developed Oldowan (Karari Industry) contexts in East Turkana, Kenya. Domínguez-Rodrigo et al. (2001) have identified wood phytoliths preserved on the edges of early Acheulean stone tools from Peninj, Tanzania.

The only evidence we have for Plio-Pleistocene hominin use of osseous tissues as tool material are a series of bone fragments from Swartkrans (South Africa) whose ends have been abraded and polished from use as digging instruments (Brain and Shipman, 1993; D'Errico and Backwell, 2003). Working bone with stone tools is an immensely timeconsuming activity. It is possible that early hominins inattention to the potential of carved bone tools may reflect either (1) that they could be rendered into useful shapes without carving, or (2) that carving them into shapes other than those in which they naturally occurred was prohibitively costly in terms of time and energy.

Of the use of stone tools to process hide or soft plant matter, the only evidence is from a small sample of tools that has been examined for lithic microwear. The scarcity of evidence for these activities, on the other hand, cannot be taken at face value. Microwear traces form slowly in most activities that involve soft materials, such as animal hide or non-lignous plant matter. If Oldowan tool use was relatively brief, a hypothesis consistent with other indications of minimal effort in tool design (i.e., retouch), there may have been insufficient time for diagnostic wear traces to form. Furthermore, many of the rocks of which Oldowan tools are made are of a friable nature, such that their edges do not preserve wear traces. Hide-working is today a uniquely human technology, and so absence of such wear traces may legitimately indicate its recent origin. Processing wood and soft plant matter, on the other hand, are activities abundantly documented among nonhuman primates. In the case of these activities, it would be foolish to equate absence of evidence with evidence of absence.

What difference does it make whether Oldowan flaked stone production was specialized, linked primarily to butchery (and thus to carnivory), or was instead a more generalized, functionally-diverse technology of which the carnivoryrelated dimensions are simply the best preserved remains?

The hypothesis linking stone tool production to carnivory predicts that changes in hominin predatory strategies ought to be correlated with significant variation in stone tool technology. Bramble and Lieberman (2004) have argued that the evolution of a more modern-looking postcranial skeletal form by *Homo ergaster/erectus* reflects increasing dependence on hunting strategies that involve endurance running. It is possible that the large, purposefully-shaped, bifacial core tools (handaxes, cleaver, etc.) that appear around the same time, *ca.* 1.7–1.6 Ma, are related to increasing demands for highly-portable tools that are simultaneously efficient

butchery tools and (when recycled as cores) effective sources for smaller flakes (Shea, 2007).

One of us, (Shea, 2007) has proposed that we should view Oldowan stone tool production as a lithic strategy for optimizing stone tool versatility, rather than simply a response to the need for butchery tools. If this model of a functionally differentiated Oldowan is correct, then the period over which Oldowan assemblages are distributed may have witnessed not just increased carnivory among one or more hominin species, but also the emergence of a broader pattern of technologically-assisted subsistence (again, among one or more hominin species). The particular focus of Oldowan technology may have varied widely through time, across space, and among the one or more hominin species responsible for it. Some sets of Oldowan tools may reflect increasing emphasis on carnivory, others increased production of wooden tools, others both these things, and still others combinations of tool uses whose nature remains unknown. Oldowan stone tools are found over such a long period of time, and in so wide a range of contexts that any hypothesis linking their appearance to a one-time-only behavioral shift among a single hominin species is almost certainly wrong.

Conclusions

This paper has explored some of the interpretive issues surrounding early hominin stone tool production, stone tool use, and carnivory. These are the questions that most interest archeologists working on the early phases of human evolution. We have saved for last the question that we archeologists are most often asked by our physical anthropologist colleagues, "who (i.e., which hominins) made the Oldowan tools?"

If one bases an assessment of the identity of the Oldowan toolmakers strictly on chronostratigraphic associations between hominin fossils and the earliest Oldowan lithic assemblages, the putative authors include Australopithecus garhi, Paranthropus aethiopicus, P. boisei, P. robustus, Homo habilis, H. rudolfensis, and H. ergaster/erectus. The most repetitive pattern of association between hominin taxa and Oldowan tools is with "early Homo" (H. habilis and H. ergaster/erectus) and various species of Paranthropus. The claim that Paranthropus made stone tools rests upon two arguments. The first is Susman's (1991) observation that the thumb attributed to P. robustus exhibits morphological adaptations to a precision grasp associated with tool use. The second is the fact that Paranthropus fossils are stratigraphically associated with stone tools at many Plio-Pleistocene localities. The claim that Homo was the principal tool author rests primarily with similar repetitive stratigraphic association, and with evolutionary changes in cranial shape (brain

enlargement) and dentition (molar reduction) *thought to reflect increased carnivory*, and thus greater dependence on tool use. No such trends are apparent in the *Paranthropus* lineage and, indeed, its extinction leaves not the slightest trace in the pattern of African Early Paleolithic industrial variability. Therefore, while we cannot rule out stone tool production and use by australopiths and *Paranthropus*, the principal beneficiaries of knapped stone tool technology appear to have been early representatives of the genus *Homo*.

Acknowledgments We thank Fred Grine, Richard Leakey and John Fleagle for organizing the meeting out of which this paper developed. We also thank John Fleagle, Patricia Crawford, and two anonymous reviewers for their comments on earlier versions of this paper.

References

- Aiello, L.C., Wheeler, P., 1995. The expensive-tissue hypothesis: the brain and digestive system in human and primate evolution. Current Anthropology 36, 199–221.
- Antón, S., Swisher, C.C., 2004. Early dispersals of *Homo* from Africa. Annual Review of Anthropology 33, 271–296.
- Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., Suwa, G., 1999. Australopithecus garhi: a new species of early hominid from Ethiopia. Science 284, 629–635.
- Bar-Yosef, O., Goren-Inbar, N., 1993. The Lithic Assemblages of 'Ubeidiya. Hebrew University Institute of Archaeology, Jerusalem.
- Blumenschine, R.J., 1987. Characteristics of an early hominid scavenging niche. Current Anthropology 28, 383–407.
- Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. Journal of Human Evolution 29, 21–51.
- Blumenschine, R.J., Peters, C.R., 1998. Archaeological predictions for hominid land use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times. Journal of Human Evolution 34, 565–607.
- Blumenschine, R.J., Pobiner, B.L., 2007. Zooarchaeology and the ecology of early hominin carnivory. In: Ungar, P. (Ed.), Evolution of the Human Diet: The Known, the Unknown, and the Unknowable. Oxford University Press, Oxford, pp. 167–190.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behavior. Nature 333, 763–765.
- Blumenschine, R.J., Peters, C.R., Masao, F.T., Clarke, R.J., Deino, A.L., Hay, R.L., Swisher, C.C., Stanistreet, I.G., Ashley, G.M., McHenry, L.J., Sikes, N.E., van der Merwe, N.J., Tactikos, J.C., Cushing, A.E., Deocampo, D.M., Njau, J.K.,Ebert, J.I., 2003. Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. Science 299, 1217–1221.
- Blumenschine, R.J., Peters, C.R., Capaldo, S.D., Andrews, P., Njau, J.K., Pobiner, B.L., 2007a. Vertebrate taphonomic perspectives on Oldowan hominin land use in the Plio-Pleistocene Olduvai Basin, Tanzania. In: Pickering, T.R., Toth, N., Schick, K, (Eds.), Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain. Stone Age Institute Press, Gosport, Indiana, pp. 161–179.
- Blumenschine, R.J., Prassack, K.A., Kreger, C.D., Pante, M.C., 2007b. Carnivore tooth marking, microbial bioerosion, and the invalidation of Domínguez-Rodrigo and Barba's (2006) test of Oldowan hominin scavenging behavior. Journal of Human Evolution 53, 420–426.

- Blumenschine, R.J., Masao, F., Tactikos, J., Ebert, J., 2008. Effects of distance from stone source on landscape-scale variation in Oldowan artifact assemblages in the Paleo-Olduvai Basin, Tanzania. Journal of Archaeological Science, 35, 76–86.
- Boesch, C., Boesch, H., 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. Primates 25, 160–170.
- Brain, C.K., Shipman, P., 1993. The Swartkrans Bone Tools. Transvaal Museum Monograph 8, Transvaal Museum, Pretoria.
- Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. Nature 432, 354–352.
- Braun, D.R., Plummer, T.W., Ditchfield, P.W., Bishop, L.C., Ferraro, J.V., 2009. Oldowan technology and raw material variability at Kanjera South. In: Hovers, E., Braun, D. (Eds.), Interdisciplinary Approaches to the Oldowan. Springer, Dordrecht, pp. 99–110.
- 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., 1982. Meat-eating and human evolution: studies of the diet and subsistence patterns of Plio-Pleistocene hominids. Ph.D. dissertation, University of California, Berkeley.
- Bunn, H.T., 1997. The bone assemblages from the excavated sites. In: Isaac, G., Isaac, assisted by Isaac, B. (Eds.), Koobi Fora Research Project, Volume 5. Plio-Pleistocene Archaeology. Clarendon, Oxford, pp. 402–458.
- Bunn, H.T., 2001. Hunting, power scavenging, and butchery by Hadza foragers and by Plio-Pleistocene *Homo*. In: Stanford, C.B., Bunn, H.T. (Eds.), Meat Eating and Human Evolution. Oxford University Press, New York, pp. 199–218.
- Bunn, H.T., 2007. Meat made us human. In: Ungar, P.S. (Ed.), Evolution of the Human Diet: The Known, the Unknown, and the Unknowable. Oxford University Press, Oxford, pp. 191–211.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. Current Anthropology 27, 431–452.
- Capaldo, S., 1997. Experimental determinations of carcass processing by Plio-pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. Journal of Human Evolution 33, 555–597.
- Cavallo, J.A., Blumenschine, R.J., 1989. Tree-stored leopard kills: expanding the hominid scavenging niche. Journal of Human Evolution 18, 393–399.
- Cerling, T.E., Harris, J.M., Leakey, M.G., 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia 120, 364–374.
- Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of East African bovids based on stable isotope analysis. Journal of Mammalogy 84, 456–470.
- Clark, J.D., 2001. Modified, used and other wood and plant specimens fro Bwalya Industry Acheulean horizons. In: Clark, J.D. (Ed.), Kalambo Falls Prehistoric Site, Volume III, The Earlier Cultures: Middle and Earlier Stone Age. Cambridge University Press, Cambridge, pp. 481–491.
- Crabtree, D.E., Davis, E.L., 1968. Experimental manufacture of wooden implements with tools of flaked stone. Science 159, 426–428.
- d'Errico, F., Backwell, L., 2003. Possible evidence of bone tool shaping by Swartkrans early hominids. Journal of Archaeological Science 30, 1559–1576.
- de Heinzelin, J., Clark, D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-millionyear-old Bouri hominids. Science 284, 625–629.
- Delagnes, A., Roche, H., 2005. Late Pliocene hominid knapping skills: the case of Lokalalei 2C, West Turkana, Kenya. Journal of Human Evolution 48, 435–472.
- de la Torre, I., 2004. Omo revisited: evaluating the technological skills of Pliocene hominids. Current Anthropology 45, 439–467.

- de la Torre, I., Mora, R., 2005. Unmodified lithic material at Olduvai Bed I: manuports or ecofacts? Journal of Archaeological Science 32, 273–285.
- Dennell, R., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. Nature 438, 1099–1104.
- Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. Journal of Human Evolution 33, 669–690.
- Domínguez-Rodrigo, M., Barba, R., 2006. New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivorehominid-carnivore hypothesis falsified. Journal of Human Evolution 50, 170–194.
- Domínguez-Rodrigo, M., Serralonga, 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). Journal of Human Evolution 40, 289–299.
- Domínguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, M.J., 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Ethiopia: implications for the function of the world's oldest stone tools. Journal of Human Evolution 48, 109–121.
- Foley, R.A., 2001. The evolutionary consequences of increased carnivory in hominids. In: Stanford, C.B., Bunn, H.T. (Eds.), Meat Eating and Human Evolution. Oxford University Press, New York, pp. 305–331.
- Gabunia, L., Antón, S.C., Lordkipanidze, D., Vekua, A., Justus, A., Swisher, C.C., 2001. Dmanisi and dispersal. Evolutionary Anthropology 10, 158–170.
- Gilby, I.C., 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. Animal Behaviour 71, 953–963.
- Goldman, T., Hovers, E., 2009. Methodological issues in the study of Oldowan raw material selectivity: insights from A.L. 894 (Hadar, Ethiopia). In: Hovers, E., Braun, D. (Eds.), Interdisciplinary Approaches to the Oldowan. Springer, Dordrecht, pp. 71–89.
- Goren-Inbar, N., Werker, E., Feibel, C.S. (Eds.), 2002. The Acheulian Site of Gesher Benot Ya'acov, Israel: The Wood Assemblage. Oxbow Books, Oxford.
- Gould, R.A., Koster, D.A., Sontz, A., 1971. The lithic assemblage of the Western Desert Aborigines of Australia. American Antiquity 36, 149–168.
- Guérin, C., Bar-Yosef, O., Debard, E., Faure, M., Shea, J., Tchernov, E., 2003. Oubeidiyeh, carrefour biogéographique et culturel entre l'Afrique et l'Eurasie au paléolithique ancien. In: Vandermeersch, B. (Ed.), Echanges et Diffusion dans la Préhistoire Méditerranéenne. Editions du Comité des travaux historiques et scientifiques, Paris, pp. 131–146.
- Harmand, S., 2004. Raw material and economic behaviour of late Pliocene hominids: the case of Lokalalei 2C and Lokalalei 1 sites, West Turkana (Kenya). Paper presented at the Paleoanthropological Society Annual Meeting, Montreal, Canada.
- Harmand, S., 2005. Matières premières lithiques et comportements techno-économiques des homininés plio-pleistocènes. Ph.D. dissertation, Université Paris X-Nanterre.
- Harmand, S., 2009a. Raw materials and techno-economic at Oldowan and Acheulean sites in the West Turkana region, Kenya. In: Blades, B. (Ed.), Lithic Materials and Palaeolithic Societies. Blackwell, Oxford, pp. 3–14.
- Harmand, S., 2009b. Variability in raw material selectivity at the late Pliocene sites of Lokalalei, West Turkana, Kenya. In: Hovers, E., Braun, D. (Eds.), Interdisciplinary Approaches to the Oldowan. Springer, Dordrecht, pp. 85–98.
- Harris, J.M., Cerling, T.E., 1999. Dietary adaptations of extant and Neogene African suids. Journal of Zoology, London 256, 45–54.
- Harris, J.W.K., 1983. Cultural beginnings: Plio-Pleistocene archaeological occurrences from the Afar, Ethiopia. African Archaeological Review 1, 3–31.

- Hay, R.L., 1976. The Geology of Olduvai Gorge: a Study of Sedimentation in a Semi-arid Basin. University of California Press, Berkeley.
- Hill, K., Kaplan, H., 1993. On why male foragers hunt and share food. Current Anthropology 34, 701–706.
- Hovers, E., 2001. Stone knapping in the Late Pliocene of Hadar, Ethiopia. Abstract of paper presented at: Knapping Stone: A Uniquely Human Behavior? web.mae.u-paris10.fr/knappingstone/ participant.htm
- Hovers, E., Schollmeyer, K., Goldman, T., Eck, G., Reed, K., Johanson, D., Kimbel, W., 2002. Late Pliocene archaeological sites in Hadar, Ethiopia. Journal of Human Evolution 42, A17.
- Howell, F.C., Haesaerts, P., de Heinzelin, J., 1987. Depositional environments, archeological occurrences, and hominids from Members E and F of the Shungura Formation (Omo Basin, Ethiopia). Journal of Human Evolution 16, 665–700.
- Inizan, M.-L., Reduron-Ballinger, M., Roche, H., Tixier, J., Féblot-Augustins, 1999. Technology and Terminology of Knapped Stone. Cercle de Recherches et d'Etudes Préhistoriques (CNRS), Meudon.
- Isaac, G., Harris, J.W.K., 1997. Sites stratified within the KBS Tuff: reports. In: Isaac, G. assisted by Isaac, B. (Eds.), Koobi Fora Research Project, Volume 5: Plio-Pleistocene Archaeology. Clarendon, Oxford, pp. 71–114.
- Isaac, G., Harris, J.W.K., Kroll, E.M., 1997. The stone artefact assemblages: a comparative study. In: Isaac, G., assisted by Isaac, B. (Eds.), Koobi Fora Research Project, Volume 5: Plio-Pleistocene Archaeology. Clarendon, Oxford, pp. 262–362.
- Isaac, G.L., 1978. The food sharing behavior of protohuman hominids. Scientific American 238, 90–109.
- Jones, P.R., 1980. Experimental butchery with modern stone tools and its relevance for palaeolithic archaeology. World Archaeology 12, 153–165.
- Jones, P.R., 1994. Results of experimental work in relation to the stone industries of Olduvai Gorge. In: Leakey, M.D., Roe, D.A. (Eds.), Olduvai Gorge, Volume 5: Excavations in Beds III, IV and the Masek Beds, 1968–1971. Cambridge University Press, Cambridge, pp. 254–298.
- Kaplan, H., Hill, K., 1985. Hunting ability and reproductive success among male Ache foragers: preliminary results. Current Anthropology 26, 131–133.
- Kappelman, J., Plummer, T., Bishop, L., Duncan, A., Appleton, S., 1997. Bovids as indicators of paleoenvironments in East Africa. Journal of Human Evolution 32, 229–256.
- Keeley, L.H., Toth, N.P., 1981. Microwear polishes on early stone tools from Koobi Fora, Kenya. Nature 293, 464–465.
- Kibunjia, M., 1994. Pliocene archaeological occurrences in the Lake Turkana basin. Journal of Human Evolution 27, 159–171.
- Kibunjia, M., 1998. Archaeological investigations of Lokalalei 1 (GaJh5): a Late Pliocene site, west of Lake Turkana, Kenya. Ph.D. dissertation, Rutgers University.
- Kibunjia, M., Roche, H., Brown, F.H., Leakey, R.E.F., 1992. Pliocene and Pleistocene archaeological sites west of Lake Turkana, Kenya. Journal of Human Evolution 23, 431–438.
- Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L, Assefa, Z., Marean, C.W., Eck, G.G., Bobe-Quinteros, R., Hovers, E., Rak, Y., Vondra, C., Yemane, T., York, D., Chen, Y., Evenson, N.M., Smith, P.E., 1996. Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. Journal of Human Evolution 31, 549–561.
- Kuman, K., 1994. The archaeology of Sterkfontein, past and present. Journal of Human Evolution 27, 471–495.
- Kuman, K., 2003. Site formation in the early South African stone age sites and its influence on the archaeological record. South African Journal of Science 99, 251–254.
- Langbroek, M., 2004. Out of Africa: An Investigation into the Earliest Occupation of the Old World. Archaeopress (British Archaeological Reports International Series 1244), Oxford.

- Leakey, L.S.B., 1936. Stone Age Africa. Oxford University Press, London.
- Leakey, M.D., 1971. Olduvai Gorge: Excavations in Beds I and II, 1960–1963. Cambridge University Press, Cambridge.
- Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, P.G., Zollikofer, C.P.E., Ponce de Leon, M.S., Agusti, J., Kiladze, G., Mouskhelishvili, A., Nioradze, M., Tappen, M., 2006. A fourth hominin skull from Dmanisi, Georgia. Anatomical Record 288A, 1146–1157.
- Marean, C.W., 1989. Sabertooth cats and their relevance for early hominid diet and evolution. Journal of Human Evolution 18, 559–582.
- Marean, C.W., Spencer, L.M., Blumenschine, R.J., Capaldo, S.D., 1992. Captive hyaena bone choice and destruction, the schlepp effect and Olduvai archaeofaunas. Journal of Archaeological Science 19, 101–121.
- McGrew, W.C., 1992. Chimpanzee Material Culture: Implications for Human Evolution. Cambridge University Press, Cambridge.
- Mercader, J., Panger, M., Boesch, C., 2002. Excavation of a chimpanzee stone tool site in the African rain forest. Science 296, 1452–1455.
- Mitani, J.C., Watts, D.P., 2001. Why do chimpanzees hunt and share meat? Animal Behaviour 61, 915–924.
- Monahan, C.M., 1996. New zooarchaeological data from Bed II, Olduvai Gorge, Tanzania: implications for hominid behavior in the Early Pleistocene. Journal of Human Evolution 31, 93–128.
- Mora, R., de la Torre, I., 2005. Percussion tools in Olduvai Beds I and II (Tanzania): implications for early human activities. Journal of Anthropological Archaeology 24, 179–192.
- O'Brien, E.M., 1981. The projectile capabilities of an Acheulean handaxe from Olorgesailie. Current Anthropology 22, 76–79.
- Oliver, J.S., 1994. Estimates of hominid and carnivore involvement in the FLK *Zinjanthropus* fossil assemblage: some socioecological implications. Journal of Human Evolution 27, 267–294.
- Pelegrin, J., 2005. Remarks about archaeological technics and methods of knapping: elements of cognitive approach to stone knapping. In: Brill, B., Roux, V. (Eds.), Stone Knapping: the Necessary Conditions for a Uniquely Hominid Behaviour. Cambridge University Press, Cambridge, pp. 23–34.
- Pickering, T.R., 1999. Taphonomic interpretations of the Sterkfontein early hominid site (Gauteng, South Africa) reconsidered in light of recent evidence. Ph.D. dissertation, University of Wisconsin, MI.
- Pickering, T.R., White, T.D., Toth, N., 2000. Cutmarks on a Plio-Pleistocene hominid from Sterkfontein, South Africa. American Journal of Physical Anthropology 111, 579–584.
- Plummer, T., 2004. Flaked stone and old bones: biological and cultural evolution at the dawn of technology. Yearbook of Physical Anthropology 47, 118–164.
- Plummer, T., Bishop, L.C., Ditchfield, P., Hicks, J., 1999. Research on Late Pliocene Oldowan sites at Kanjera South, Kenya. Journal of Human Evolution 36, 151–170.
- Pobiner, B.L., 2007. Hominin-carnivore interactions: evidence from modern carnivore bone modification and Early Pleistocene archaeofaunas (Koobi Fora, Kenya; Olduvai Gorge, Tanzania). Ph.D. dissertation, Rutgers University.
- Potts, R., 1988. Early Hominid Activities at Olduvai. Aldine de Gruyter, New York.
- Potts, R., Shipman, P., 1981. Cut-marks made by stone tools on bones from Olduvai Gorge, Tanzania. Nature 291, 577–580.
- Prat, S., Brugal, J.-P., Tiercelin, J.-J., Barrat, J.-A., Bohn, M., Delagnes, A., Harmand, S., Kimeu, K., Kibunjia, M., Texier, P.-J., Roche, H., 2005. First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3–2.4 Myr. Journal of Human Evolution 49, 230–240.
- Pruetz, J.D., Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Current Biology 17, 412–417.
- Roche, H., 1989. Technological evolution in early hominids. Ossa 14, 97–98.

- Roche, H., 2005. From simple flaking to shaping: stone knapping evolution among early hominins. In: Brill, B., Roux, V. (Eds.), Stone Knapping: the Necessary Conditions for a Uniquely Hominid Behaviour. Cambridge University Press, Cambridge, pp. 35–52.
- Roche, H., Kibunjia, M., 1996. Contribution of the West Turkana Plio-Pleistocene sites to the archaeology of the lower Omo Turkana Basin. Kaupia 6, 27–30.
- Roche, H., Tiercelin, J.-J., 1977. Découverte d'une industrie lithique ancienne in situ dans la Formation d'Hadar. Comptes Rendus de l'Acadamie des Sciences Paris, 284, série D, 1871–1874.
- Roche, H., Tiercelin, J.-J., 1980. Industries lithiques de la Formation plio-pléistocène de Hadar, Ethiopie (campagne 1976). In: Leakey, R.E.F., Ogot, B.A. (Eds.), Proceedings of the Seventh Panafrican Congress of Prehistory and Quaternary Studies (Nairobi 1977). The International Louis Leakey Memorial Institute for African Prehistory, Nairobi, Kenya, pp. 194–199.
- Roche, H., Delagnes, A., Brugal, J.-P., Feibel, C.S., Kibunja, M., Mourre, V., Texier, P.-J., 1999. Early hominid stone tool production and technical skill 2.34 Myr ago, in West Turkana, Kenya. Nature 399, 57–90.
- Roche, H., Brugal, J.-P., Delagnes, A., Feibel, C., Harmand, S., Kibunjia, M., Prat, S., Texier, P.-J., 2003. Les sites archeologiques plio-pleistocenes de la formation de Nachukui, Ouest-Turkana, Kenya: bilan synthétique 1997–2001. Comptes Rendus Palevol 2, 663–673.
- Sahnouni, M., 2005. Point des connaissances du Paléolithique ancien d'Afrique du Nord et la question de la première occupation humaine au Maghreb. In: Sahnouni, M. (Ed.), Les cultures paléolithique en Afrique. ArtCom-Errance, Paris, pp. 99–128.
- Sahnouni, M., 2006. The North African Early Stone Age and the sites at Ain Hanech, Algeria. In: Toth, N.P., Schick, K. (Eds.), The Oldowan: Case Studies Into the Earliest Stone Age. Stone Age Institute Press, Bloomington, pp. 77–112.
- Schick, K., Toth, N.P., 2006. An overview of the Oldowan industrial complex: the sites and the nature of the evidence. In: Toth, N.P., Schick, K. (Eds.), The Oldowan: Case Studies Into the Earliest Stone Age. Stone Age Institute Press, Bloomington, pp. 3–42.
- Selvaggio, M.M., 1998. Evidence for a three-stage sequence of hominid and carnivore involvement with long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. Journal of Archaeological Science 25, 191–202.
- 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. Journal of Archaeological Science 27, 1197–1214.
- Semaw, S., Renne, P., Harris, J.W.K., Feibel, C.S., Bernor, R.L., Fesseha, N., Mowbray, K., 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. Science 284, 625–629.
- Semaw, S., Rogers, M.J., Quade, J., Renne, P.R., Butler, R.F., Dominguez-Rodrigo, M., Stout, D., Hart, W.S., Pickering, T., Simpson, S.W., 2003. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. Journal of Human Evolution 45, 169–177.
- Shea, J.J., 2006. Child's play: reflections on the invisibility of children in the paleolithic record. Evolutionary Anthropology 15, 212–216.
- Shea, J.J., 2007. Lithic archaeology, or, what stone tools can (and can't) tell us about early hominin diets. In: Ungar, P.S. (Ed.), Evolution of the Human Diet: The Known, the Unknown and the Unknowable. Oxford University Press, Oxford, pp. 321–351.
- Shipman, P., Walker, A., 1989. The costs of becoming a predator. Journal of Human Evolution 18, 373–392.
- Spencer, L.M., 1997. Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. Journal of Human Evolution 32, 201–228.
- Stanford, C.B., Bunn, H.T. (Eds.), 2001. Meat Eating and Human Evolution. Oxford University Press, New York.

- Stiles, D.N., Hay, R.L., Oneil, J.R., 1974. The MNK chert factory site, Olduvai Gorge, Tanzania. World Archaeology 5, 285–308.
- Stout, D., Quade, J., Semaw, S., Rogers, M.J., Levin, N.E., 2005. Raw material selectivity of the earliest stone toolmakers at Gona, Afar, Ethiopia. Journal of Human Evolution 48, 365–380.
- Susman, R.L., 1991. Who made the Oldowan tools? Fossil evidence for tool behavior in Plio-Pleistocene hominids. Journal of Anthropological Research 47, 129–151.
- Tactikos, J.C., 2005. A Landscape Perspective on the Oldowan from Olduvai Gorge, Tanzania. Ph.D. dissertation, Rutgers University.
- Theime, H., 1997. Lower Paleolithic hunting spears from Germany. Nature 385, 807–810.
- Toth, N., Schick, K., Semaw, S., 1996. Further investigations of the Oldowan: lessons from the prehistoric record, experimental archaeology, and apes. In: Braun D., Hovers, E. (Orgs), Symposium: Interdisciplinary Approaches to Understanding the Oldowan, Annual Meeting of the Society for American Archaeology, San Juan, Puerto Rico.
- Toth, N.P., 1987. Behavioral inferences from early stone artifact assemblages: an experimental model. Journal of Human Evolution 16, 763–787.

- Toth, N.P., 1997. The artifact assemblages in the light of experimental studies. In: Isaac, G.L., Isaac, assisted by Isaac, B. (Eds.), Koobi Fora Research Project, Volume 5: Plio-Pleistocene Archaeology. Clarendon, Oxford, pp. 363–402.
- Toth, N.P., Schick, K. (Eds.), 2006. The Oldowan: Case Studies Into the Earliest Stone Age. Stone Age Institute Press, Bloomington, IN.
- Ungar, P. (Ed.), 2007. Evolution of the Human Diet: The Known, the Unknown, and the Unknowable. Oxford University Press, New York.
- Walker, A., Leakey, R.E., Harris, J.M., Brown, F., 1986. 2.5-myr Australopithecus boisei from west of Lake Turkana, Kenya. Nature 322, 517–522.
- Wang, W., Potts, R., Baoyin, Y., Huang, W., Cheng, H., Edwards, R.L., Ditchfield, P., 2007. Sequence of mammalian fossils, including hominoid teeth, from the Bubing Basin caves, South China. Journal of Human Evolution 52, 370–379.
- Washburn, S.L., Lancaster, C.S., 1968. The evolution of hunting. In: Lee, R.B., DeVore, I. (Eds.), Man the Hunter. Aldine, Chicago, IL, pp. 293–303.
- Werdelin, L., Lewis, M., 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. Zoological Journal of the Linnean Society 144, 121–144.