

Patterns of early hominid site use at Olduvai Gorge

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Abstract: *Olduvai Gorge, Tanzania, preserves an almost unprecedented record of early hominid bio-behavioral evolution. As such, it provides a unique opportunity to document spatio-temporal variability in hominid behavior. New taphonomic data reveal that hominids played little or no role in the formation of the faunal assemblages from many of the sites excavated by Mary Leakey from Beds I and II. In fact, the faunas from only two sites, FLK 22 from Bed I and BK from Bed II, can be considered as largely the result of hominid subsistence activities. This finding has important implications for interpretations of the Olduvai lithics and for patterns of hominid subsistence in the paleo-Olduvai basin. Taphonomic proxies of competition also suggest that hominids concentrated their stone-tool-using activities in lower competition settings during Bed I times, while higher competition settings were exploited in greater frequency during Bed II times. The pattern that emerges is one of variability in site use by Plio-Pleistocene hominids in the Olduvai basin.*

Keywords: *Early hominids, Olduvai Gorge, Tanzania, Plio-Pleistocene, Subsistence strategies, Taphonomy, Site use*

Nutzungsmuster auf Fundplätzen früher Hominiden in der Olduvai-Schlucht

Zusammenfassung: Die Fundstellen in der Olduvai-Schlucht in Tansania gehören zu den bedeutendsten Referenzpunkten, wenn es um die Frage des Verhaltens früher Hominiden geht. Insbesondere ist zu fragen, inwieweit Hominiden in dieser Region vor bis zu 1,9 Millionen Jahren an der Bildung der Fundstellen beteiligt waren und wie sich ihre Strategien der Nahrungsbeschaffung in Konkurrenz zu den großen Fleischfressern wie Großkatzen und Hyänen entwickelt haben. Eine Vorreiterrolle kommt dabei den Arbeiten Mary Leakeys in den sogenannten Beds I und II von Olduvai zu. Ihre Interpretationen wurden in den letzten Jahren jedoch immer mehr kritisch hinterfragt und diskutiert. Eine Neubewertung des reichsten Fundinventars der Olduvai-Region, Schicht 22 der Fundstelle FLK (FLK 22), zog eine Neubewertung auch anderer Inventare dieser Region nach sich. Der vorliegende Beitrag verwendet aktualisierte Daten für eine Reihe von Leakeys Fundinventaren aus den als Bed I und Bed II bezeichneten ältesten Formationen von Olduvai, um einen neuen Blick auf die Variabilität bei der Platzwahl und Landschaftsnutzung im plio-pleistozänen Olduvai-Becken zu werfen. Dabei werden drei Fragenkomplexe behandelt. Zunächst geht es um eine Neubewertung der Rolle von Hominiden bei der Bildung der Knochenanhäufungen in den Fundstellen, weiterhin werden taphonomische Daten verwendet, um festzustellen, welche Aktivitäten die Hominiden an den verschiedenen Plätzen ausgeführt haben. Schließlich werden Parameter erarbeitet, die das Ausmaß der Konkurrenz zwischen Hominiden und Fleischfressern erkennen lassen und die Aussagen über die Habitatselektion der Hominiden innerhalb der Olduvai-Landschaft zulassen.

Der Verfasser hat mit seinen Kollegen insgesamt 19 Fundinventare aus neun Fundstellen in Bed I und II der Olduvai-Schlucht ausgewertet. Im Einzelnen sind es in Bed I die Inventare DK Level 1, DK Level 2 und DK Level 3, alle mit einem Alter von ca. 1,86 Millionen Jahre, FLK Level 15 (1,82 Millionen Jahre), FLK Level 22, FLK North North Level 2, FLK North North Level 3 (alle 1,85 Millionen Jahre), FLK North Levels 1-2, FLK North Level 3, FLK North Level 4, FLK North Level 5, FLK North Level 6 (alle 1,82 Millionen Jahre) und in Bed II die Inventare HWK East Levels 3-5 (1,6 Millionen Jahre), MNK Main, FC West (beide 1,4 Millionen Jahre), TK Lower Floor, TK Upper Floor, BK (alle 1,2 Millionen Jahre). Alle Inventare wurden hinsichtlich ihres Tierartenspektrums und der Häufigkeit einzelner Skeletteile, alle Knochen hinsichtlich ihrer Bruchmuster und Oberflächenmodifikationen wie Biss-, Schlag- und Schnittspuren analysiert.

Für den ersten Fragenkomplex hat die Detailanalyse ergeben, dass Hominiden nur eine geringe bzw. keine Rolle bei der Bildung der Faunenansammlungen in vielen der von Mary Leakey ergrabenen Fundstellen der Beds I und II in der Olduvai-Schlucht gespielt haben. Tatsächlich können lediglich die Faunenreste von zwei Inventaren, nämlich FLK 22 in Bed I und BK in Bed II, weitgehend als Ergebnis der Nahrungsbeschaffungsaktivitäten von Hominiden gelten. Dieser Befund hat wichtige Auswirkungen auf den zweiten Fragenkomplex, und zwar auf die Interpretation der Steinartefakte aus den Olduvai-Fundstellen und auf die Muster menschlicher Subsistenzstrategien im plio-pleistozänen Olduvai-Becken. Zwar ist es sehr wahrscheinlich, dass bereits die frühesten Steinartefakte zumindest teilweise für die Verarbeitung von Tierkörpern verwendet wurden. Da jedoch in Olduvai außer den Inventaren FLK 22 und BK die meisten analysierten Faunenansammlungen eher das Ergebnis der Aktivitäten von Fleischfressern als solcher von Hominiden sind, obwohl an jenen Fundstellen (mit einer Ausnahme) Steinartefakte regelhaft die Anwesenheit von Hominiden belegen, existiert offenbar in der Regel keine funktionale Beziehung zwischen den Knochen und den Steinen. An solchen Fundstellen sind die Artefakte zum größten Teil nicht das Ergebnis gezielter Grundformproduktion und -verwendung, sondern sie entstanden bei anderer Benutzung von Steinen als Hammer und auch Unterlieger. Denkbar wäre die Verarbeitung pflanzlicher Nahrung, z.B. das Knacken von Nüssen. Subsistenzstrategien jenseits der Nutzung von Tierkadavern regelten also bis zu einem gewissen Grad die Platzwahl plio-pleistozäner Hominiden in der Landschaft von Olduvai. Bei beiden Inventaren, bei denen Hominiden nennenswert zur Entstehung beigetragen haben, ist dagegen ein Zusammenhang zwischen gezielt hergestellten Abschlägen und ihrer Verwendung bei der Verarbeitung von Tierkörpern nachzuweisen. Hinsichtlich des dritten Fragenkomplexes ist erkennbar, dass die Hominiden zur Zeit der Ablagerungen von Bed I, also dem älteren Abschnitt der Folge, ihre Aktivitäten, die mit der Verwendung von Steinartefakten verbunden waren, unter Bedingungen geringerer Konkurrenz mit Fleischfressern ausübten, während sie dies im jüngeren Abschnitt der Folge, also zu Zeiten der Ablagerungen von Bed II, häufiger unter Bedingungen stärkerer Konkurrenz taten. Aus allen Analysen erwächst ein Muster der Variabilität in der Platzwahl durch plio-pleistozäne Hominiden im Olduvai-Becken, wie man es in dieser Komplexität erst durch die modernen Forschungsansätze sichtbar machen kann.

Schlagwörter: Frühe Hominiden, Olduvai-Schlucht, Tansania, Plio-Pleistozän, Subsistenzstrategien, Taphonomie, Fundplatznutzung

Introduction

The nature of hominid site use in the Plio-Pleistocene (here between 2.6 and 1.2 million years ago) is an issue of long-standing debate. While some envision the large stone and bone accumulations at places like Olduvai Gorge, Tanzania, and Koobi Fora, Kenya, as reflections of repeated transport and sharing of large mammal carcasses (Leakey 1971; Isaac 1978a, b; Bunn 2007), others have argued that the earliest archaeological sites represent competitive refugia (Blumenshine 1991) or simply picked-over carnivore kills (Binford 1981). Of particular importance to these debates is the significance of meat and marrow in the diets of Plio-Pleistocene hominids, as several researchers have suggested that a shift towards these nutrient-dense resources may have fueled encephalization, modifications in life history, and expanded range size (Kaplan et al. 2000; Aiello and Wells 2002; Antón et al. 2002; Leonard et al. 2007).

Assessing the role of hominids in the accumulation of many Plio-Pleistocene bone assemblages is often hindered by poor preservation, small sample sizes, and the difficulty of accessing materials for study. For these reasons, the large and well-preserved faunas from Mary Leakey's (1971) excavations in Beds I and II at Olduvai have traditionally played a pivotal role in discussions of hominid meat-eating and Plio-Pleistocene site function. Over the past fifteen years or so, however, the data from many of these sites has been treated with growing caution (e.g., Marean et al. 1992; Plummer 2004), and, in fact, recent syntheses have relied heavily (though not exclusively) on evidence from a single assemblage: Level 22 at the gorge's FLK locality (the "Zinjanthropus Floor") (Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003; Plummer

2004; Bunn 2007). The focus on FLK 22 is justified given that the site boasts a fauna with extraordinary taphonomic evidence for hominid behavior, all of it excavated from a high-integrity geological context. This nearly unique combination remains unmatched in all of Plio-Pleistocene Africa, even fifty years after the site's initial excavation. Ever since the ground-breaking work of Bunn (1982) and Potts (1982, 1988), FLK 22 has been the testing ground for state-of-the-art taphonomic techniques. In the fallout of all this important work comes the realization that interpretations of many other Olduvai sites, especially those from Bed I, are based on outdated or underdeveloped taphonomic frameworks that cannot answer many of the issues raised by recent theoretical and methodological developments.

This study uses updated taphonomic data from several of Mary Leakey's Bed I and II sites to provide new perspectives on variability in hominid site use in the paleo-Olduvai basin. Three issues will be explored. First, the roles of hominids and large carnivores in the formation of the faunal assemblages will be reviewed. Second, taphonomic data will be used to determine what sorts of activities were being carried out at each of the sites by hominids. Finally, taphonomic measures of competition will be used to assess hominid habitat selection across the Olduvai landscape.

Competition and paleoecology

Inter- and intra-specific competition are widely recognized as integral components of ecological communities and how they are structured, maintained, and transformed (Cody and Diamond 1975; Tilman 1982; Roughgarden 1983; Diamond and Case 1986). Two conditions are required for inter-specific competition to occur (Wallace 1987, 113-116): niche overlap and resource limitation. The importance of niche overlap suggests that competition should be most intense within a guild, which, according to Root (1967, 335), is "a group of species that exploit the same class of environmental resources in a similar way" and thus "...overlap significantly in their niche requirements" (see also Simberloff and Dayan 1991). Research substantiates the view that competition plays an important role in structuring the modern African large carnivore guild, with observations of high potential niche overlap (Caro and Stoner 2003), frequent intra-guild predation (Palomares and Caro 1999; Van Valkenburgh 2001), and evidence for superior competitors depressing the population sizes of inferior competitors (e.g., lions and hyenas versus wild dogs [Creel and Creel 1996]).

As hominids incorporated large mammal resources into their diets during the Plio-Pleistocene, they would have entered the large carnivore guild. Competition can be a valuable concept from a paleoecological standpoint because it varies with habitat type. In addition, the intensity and context of competition provides predictions about carcass availability and, to some extent, where on the landscape hominids and carnivores would have transported and consumed them. Finally, and most critically, actualistic studies of modern processes have demonstrated that competition leaves "specific and detectable zooarchaeological signatures" (Blumenschine et al. 1994, 208).

The documentation of leopard canine punctures on the SK 54 *Australopithecus robustus* calotte from Member 1 at Swartkrans (Brain 1970) demonstrates that hominids were not only potential competitors but occasional prey, just as modern apes (e.g., Boesch 1991;

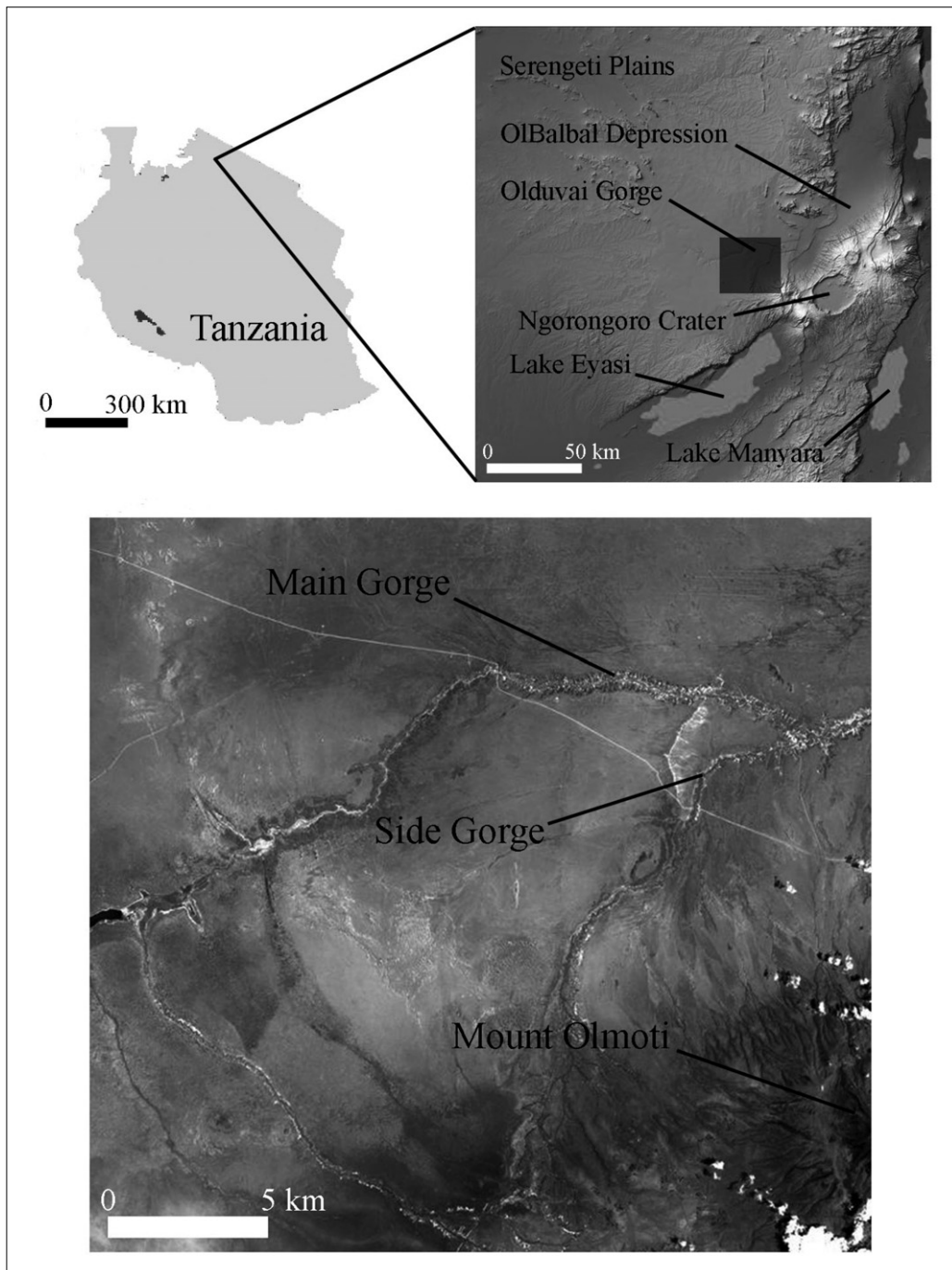


Fig. 1: Location of Olduvai Gorge and other significant landforms. Satellite images from http://en.wikipedia.org/wiki/Olduvai_Gorge.

Tsukahara 1993; D'Amour et al. 2006) and humans (e.g., Treves and Naughton-Treves 1999) are. Therefore, insights may be gained by considering hominid carcass foraging and site use within the broader context of a diverse and probably highly competitive large carnivore guild (cf. Turner 1988, 1992; Shipman and Walker 1989; Brantingham 1998a, b; Van Valkenburgh 2001; Stiner 2002; Pobiner and Blumenschine 2003).

Geology, dating, and Plio-Pleistocene environments in the Olduvai basin

Olduvai Gorge is located in northern Tanzania, between the western margin of the East African Rift Valley and the eastern edge of the Serengeti Plain (Fig. 1). Although the paleontological and archaeological importance of the gorge had long been recognized (summarized in Leakey 1951), it was not until after the discovery of OH 5 (Leakey 1959) that large-scale excavations began throughout the gorge. Under the direction of Mary Leakey (1967, 1971, 1975) a number of localities containing both stone tools and faunal material were uncovered.

What is known of the geology of Olduvai Gorge is due largely to the seminal work of the late Richard Hay (1963, 1967a, b, 1973, 1976). The Olduvai basin itself formed about 2.0 million years ago through the uplift of volcanic highlands to the east and south. The modern gorge, which splits into two fingers (the main and side gorges), was formed over the past 200,000 years by down-cutting stream activity. The basin is underlain by metamorphic basement rocks, some of which still outcrop today as inselbergs like Naibor Soit and Kelogi and served as important lithic raw material sources during the Plio-Pleistocene. Seven geological formations are recognized within the gorge, which are referred to, from oldest to youngest, as Beds I, II, III, IV, and the Masek, Ndotu, and Naisiusiu Beds (Hay 1976). The sediments overlying Beds I and II date to between 1.3–1.2 million years ago and 60,000—40,000 years ago (Hay 1976, 1990; Leakey and Hay 1982; Manega 1993; Skinner et al. 2003) and are not considered further here.

Bed I is composed of lava flows overlain by lake, lake-margin, alluvial fan, and alluvial plain deposits. The lavas and volcanic marker tuffs of Bed I are well-dated by potassium-argon and argon-argon methods (Fig. 2) (Walter et al. 1991, 1992; Manega 1993; Blumenschine et al. 2003). The first Bed I marker tuff, Tuff IA, overlays the basal lavas and dates to 1.99 million years ago. Capping Tuff IA are the Bed I lavas, which are dated to 1.87 million years ago. The Bed I lavas and the sedimentary rocks that underlie them were originally referred to by Hay (1967b) as the Basalt and Lower Members, respectively, of Bed I, although he later abandoned this classification (Hay 1976). It is significant, however, that the sediments below the "Basalt Member" are devoid of stone tools and fossils. Above the Bed I lavas are a series of well-dated marker tuffs. The first of these marker tuffs, Tuff IB, overlies the oldest archaeological occurrences in the gorge and is dated to 1.85 million years ago, while the last, Tuff IF, marks the boundary between Beds I and II and dates to 1.79 million years ago.

Bed II is generally characterized by higher-energy fluvio-lacustrine deposits, although three separate units can be distinguished in the sequence. Lower Bed II, which contains significant lake, lake-margin, and alluvial fan deposits, is broadly similar to Bed I in terms of sedimentology and paleogeography (see below). Just above this occurs a widespread sequence of eolian tuffs known as the Lemuta Member. These eolian tuffs inter-

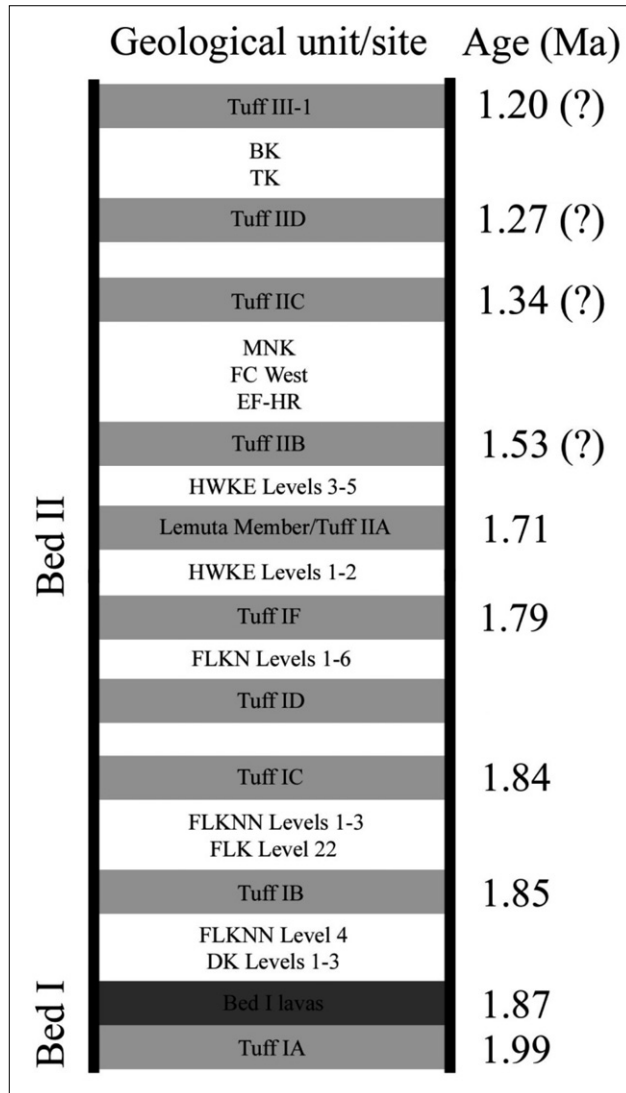


Fig. 2: Simplified composite stratigraphic sequence for Beds I and II. Dates based on Curtis and Hay (1972), Walter et al. (1991, 1992), Manega (1993), Hay and Kyser (2001), and Blumenschine et al. (2003).

finger with lake-margin sediments and mark a period of significant aridification and lake regression. A disconformity caused by basin-wide faulting denotes the boundary between the Lemuta Member and the deposits of middle and upper Bed II, which are largely of fluvio-lacustrine origin. The chronostratigraphy of Bed II is less straightforward than that of Bed I due to the reworked nature of many of the marker tuffs. However, radiometric dates from the bottom (Tuff IF) and top (Tuff III-1) of Bed II suggest an age range of about 1.79–1.20 million years ago (Fig. 2) (Curtis and Hay 1972; Walter et al. 1991, 1992; Manega 1993).

During Bed I and lower Bed II times Olduvai Gorge was a shallow basin dominated by a saline and alkaline paleolake of fluctuating size (Hay 1976; Peters and Blumenschine 1995; Hay and Kyser 2001). Intermittent streams draining the volcanic highlands to the south and east of the lake formed an alluvial fan and plain on the eastern margin of the basin. A majority of the Bed I archaeological occurrences, and all of those considered in this study, occur in what Hay (1976) termed the Eastern Lake Margin lithofacies. This pattern of site location is likely linked to the presence of fresh water along the eastern edge of the basin (Hay 1976; Peters and Blumenschine 1995; Deocampo et al. 2002). The lake expanded and contracted several times until, during Upper Bed II times (after about 1.3 million years ago), the perennial lake disappeared and was replaced by small ponds and marshlands that developed along a large drainage running east to west. Archaeological sites are found in a wider variety of settings in Bed II, including along stream channels and within both the eastern and western lake margin areas. Figure 3 shows both the paleogeographic evolution of the Olduvai basin during Bed I and Bed II times and the location of each of the study sites.

Like the rest of East Africa, the Olduvai basin experienced a general shift towards drier and more open habitats throughout the Pleistocene. Data from pedogenic carbonates suggest an increase in C4 ecosystems over time at Olduvai, from closed wooded grasslands (Bed I and lower Bed II) to more open grassy woodlands (middle and upper Bed II) and, eventually, to open grasslands (post-Bed II) (Sikes 1994, 1999). Cerling and Hay's (1986) isotopic data indicate annual rainfall on the order of 800 mm and average temperatures of 16°C during Bed I and II times, which are wetter and cooler than the Olduvai basin is today (modern mean annual rainfall = 566 mm; average temperature = 22°C).

Five major environmental episodes can be distinguished during Bed I and II times. The first episode occurred before the deposition of Tuff ID about 1.8 million years ago. Lake levels were high early in this period and fluctuated thereafter (Hay and Kyser 2001). The presence of urocyclid slugs (Verdcourt 1963) and closed habitat rodents (Jaeger 1976; Fernández-Jalvo et al. 1998) in the lowermost deposits of Bed I indicate that densely vegetated and humid habitats were common (Kappelman 1986). Although the bovid data are more equivocal, closed and mixed habitat taxa are more common below Tuff ID than they are in any other stratigraphic interval (Gentry and Gentry 1978a, b; Kappelman 1984; Potts 1988; Shipman and Harris 1988; Plummer and Bishop 1994; Kappelman et al. 1997). Isotopic data from FLK 22 suggest a riparian or grassy woodland setting during this period (Sikes 1994). The second environmental episode occurred between the deposition of Tuffs ID and IF. The climate became very arid and, based on pollen evidence, annual rainfall may have been as low as 350 mm (Bonnefille 1984). The lake level dropped during this period and open habitat rodents and bovinds became prevalent. The evidence from lower Bed II (1.79–1.71 million years ago) indicates a return to moister conditions, as the lake expanded and appears to have supported relatively closed habitats like riparian and grassy woodlands (Sikes 1994). As discussed above, the 1.7-million-year-old Lemuta Member of Bed II represents a hyper-arid period, and isotopic data indicate a spike in C4 vegetation at this time in addition to increased temperature and/or decreased rainfall (Cerling and Hay 1986). The final environmental episode (after 1.7 million years ago) was characterized by additional C4 expansion and increasing aridity at about 1.5 million years ago (Cerling and Hay 1986). The perennial lake also disappeared by about 1.3 million years ago (Hay 1976).

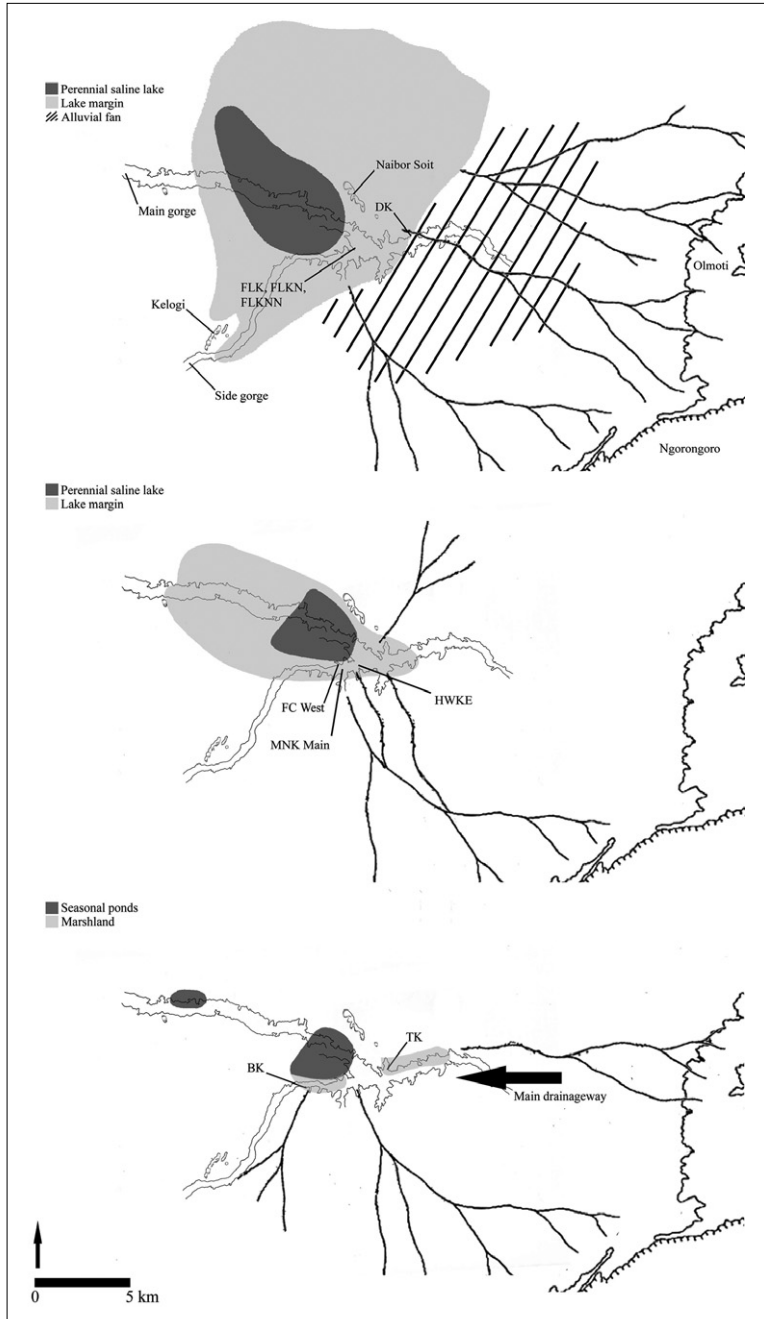


Fig. 3: Paleogeographic reconstructions of the paleo-Olduvai basin during Bed I (1.79 million years ago; top), middle Bed II (1.50 million years ago; middle) and upper Bed II (1.30 million years ago; bottom) times based on Hay (1976). Base map modified from Hay (1976, Figure 18) and Peters and Blumenschine (1995, Figure 4).

Environments in the Olduvai basin during Bed I and II times were therefore characterized by increasing aridification over time. However, at any one moment, the savanna-mosaic ecosystem of the Plio-Pleistocene Olduvai basin would have supported a wide variety of microhabitats, including open grassland, marshland, and riparian woodland (Peters and Blumenschine 1995). This habitat heterogeneity has important implications for understanding patterns of hominid site use (Blumenschine and Peters 1998).

The Olduvai sample and taphonomic methods

The faunal assemblages from 19 levels at nine Bed I and II Olduvai localities were analyzed by the author and colleagues (Domínguez-Rodrigo et al. 2007a; Egeland 2007; Egeland and Domínguez-Rodrigo in press). Table 1 summarizes pertinent information for each assemblage. A brief summary of the zooarchaeological and taphonomic methods is provided here. More comprehensive discussions can be found in Domínguez-Rodrigo et al. (2007a, 23-32), Egeland (2007, 36-64), and Egeland and Domínguez-Rodrigo (in press). Data were collected on skeletal part frequencies, bone surface modifications, and bone breakage. Minimum number of element (MNE) estimates were made using a manual overlap approach and took into account overlapping landmarks, element side, ontogenetic age, and overall size. Following Bunn (1982, 1986) and others (Watson 1979; Todd and Rapson 1988; Morlan 1994; Pickering et al. 2003), shaft fragments were included in all long bone MNEs. Cortical surfaces were examined for cutmarks, percussion marks, and carnivore tooth marks with the aid of 10X magnification and a strong oblique light source (Bunn 1981; Blumenschine et al. 1996). Bone breakage was also analyzed to distinguish fragmentation characteristic of hammerstone-wielding hominids from that of large carnivores (see Bunn 1982, 1989; Johnson 1985; Capaldo and Blumenschine 1994; Pickering et al. 2005; Alcántara García et al. 2006).

Site	Bed	Age (Ma)	Number of bones	Number of stones	Hominid involvement in fauna
DK Level 1	I	1.86	217	1021*	Almost none
DK Level 2	I	1.86	1686		Marginal
DK Level 3	I	1.86	1249		Marginal
FLK Level 15	I	1.82	211	9	None
FLK Level 22	I	1.85	>40,000	2664	Extensive
FLK North North Level 2	I	1.85	426	0	None
FLK North North Level 3	I	1.85	1254	42	None
FLK North Levels 1-2	I	1.82	2873	1456	Almost none
FLK North Level 3	I	1.82	1254	214	Almost none
FLK North Level 4	I	1.82	929	83	Almost none
FLK North Level 5	I	1.82	1580	132	Almost none
FLK North Level 6	I	1.82	616	129	None
HWK East Levels 3-5	II	1.6	207	3173	Almost none
MNK Main	II	1.4	814	5315	Almost none
FC West	II	1.4	95	1162	Cannot be determined
TK Lower Floor	II	1.2	80	2325	Cannot be determined
TK Upper Floor	II	1.2	135	5140	Cannot be determined
BK	II	1.2	2479	7220	Extensive

Table 1: Basic characteristics and taphonomic interpretations of the Olduvai sites. Note: "Number of bones" includes macrofauna only. *Includes all three DK levels combined. References: Leakey (1971), Bunn (1982), de la Torre (2004), Domínguez-Rodrigo et al. (2007a), Egeland (2007).

Hominids, carnivores, and the formation of the Olduvai faunas

New taphonomic data reveal that among the Bed I assemblages, only FLK 22 is largely the result of hominid carcass transport and processing behavior (see Table 1) (Domínguez-Rodrigo et al. 2007a). Cutmarks are located on areas of the skeleton that are defleshed by carnivores early in their consumption sequence (Domínguez-Rodrigo et al. 2007a), which indicates that hominids enjoyed early and almost exclusive access to fully fleshed carcasses (Bunn 1982, 2001; Bunn and Kroll 1986). Patterns of skeletal element representation suggest that at least 18 complete bovid carcasses were transported to the site for butchery (Domínguez-Rodrigo et al. 2007a). Percussion mark frequencies and bone breakage demonstrate that hominids also participated substantially in marrow extraction (Oliver 1994; Blumenschine 1995; Domínguez-Rodrigo et al. 2007a). Hominids were therefore the primary accumulator at FLK 22 while carnivores were limited to secondary scavenging of hominid food refuse.

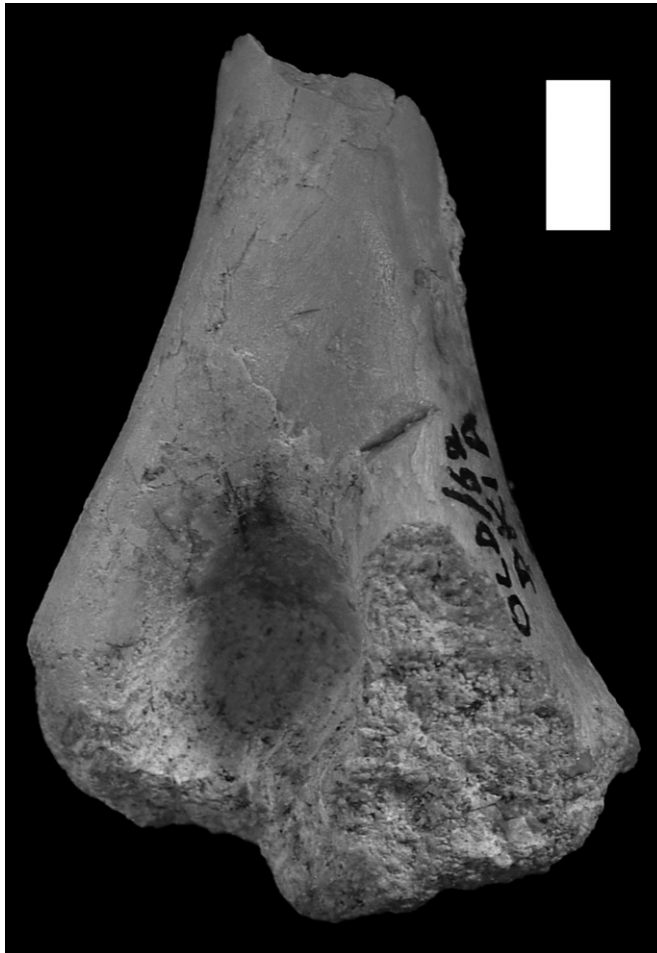


Fig. 4: Caudal view of a distal bovid humerus from DK showing cutmarks. Scale bar = 1 cm.

Surprisingly, the faunas from the other Bed I sites are nearly as deficient in evidence for hominid involvement as the fauna from FLK 22 is brimming with it. FLKNN 3 and DK 3 stand out in particular, as both sites, like FLK 22, preserve co-occurring fauna and stone tools within thin paleosols. Hominid surface modifications (e.g., Fig. 4) were identified on only 14 bone fragments from all three DK levels combined, most of them ($n = 12$) from Level 2 (Egeland 2007). Bone breakage data do indicate that hominid marrow extraction accounts for some of the bone fragmentation, and information from skeletal part frequencies and the lithic assemblage suggest that some transport of carcass parts for off-site processing may also have occurred (see below). Nevertheless, carnivore damage is much more abundant at DK, which indicates that carnivores were more active carcass accumulators than were hominids. A total of 38 bone fragments were found with hominid surface modifications in the remaining nine Bed I faunas, 33 of which come from the ca. 2,800-piece assemblage of FLKN 1–2 (Domínguez-Rodrigo et al. 2007a). In addition, breakage data demonstrate that hominids participated little or not at all in bone fragmentation. Carnivores therefore appear to be the dominant behavioral agent in the formation of the FLKN, FLKNN, and FLK 15 faunas.

There are several reasons to suspect that felids were the carnivore type largely responsible for accumulating the carcasses at these Bed I sites. First, felids have been shown to tooth-mark bones at lower frequencies than hyenas (Domínguez-Rodrigo et al. 2007b), and many of the Bed I bone assemblages have tooth mark frequencies that fall below those attained in experiments that use hyenas as the major carcass modifier (e.g., Blumenshine 1988, 1995; Capaldo 1997). In addition, complete or nearly complete long bones are relatively well-represented. Finally, patterns of bone modification characteristic of felid feeding have been identified at several sites (Domínguez-Rodrigo et al. 2007a, b). Hyena activity is certainly documented at all the Bed I sites as well (e.g., Fig. 5), although it appears to be limited mainly to ravaging carcasses after they were deposited by felids.

A similar pattern is seen among the Bed II assemblages, with BK standing alone in preserving a strong hominid signal. Like FLK 22, the frequency and anatomical placement of cutmarks at BK demonstrate that hominids were butchering fully fleshed carcasses (see also Monahan 1996a, b). Much of the bone breakage at the site can also be attributed to hominids. The bone fragmentation that was the result of carnivore activity was carried out after hominids had processed and abandoned the carcasses (Monahan 1996a, b; Egeland 2007; Egeland and Domínguez-Rodrigo in press). No hominid surface modifications were identified in the HWKE 3–5 assemblage, and only four were present at MNK Main. Tooth mark frequencies at MNK Main are the highest of any of the Olduvai bone assemblages, and little or no evidence for hominid bone breakage is preserved at either HWKE 3–5 or MNK Main. Unfortunately, FC West and TK are among the few Olduvai assemblages that have poorly preserved bone surfaces. Any surface modifications that were once present cannot now be identified, which makes it very difficult to determine the agent responsible for the formation of these small faunal assemblages.

Overall, there is a much stronger hyena signal in the Bed II assemblages relative to their Bed I counterparts. This taphonomic shift is no doubt due to a number of factors, but it does broadly coincide with the expansion of drier, more open habitats and the extinction in East Africa of two felid genera, *Megantereon* and *Homotherium* (Werdelin and Lewis 2005; Egeland and Domínguez-Rodrigo in press).

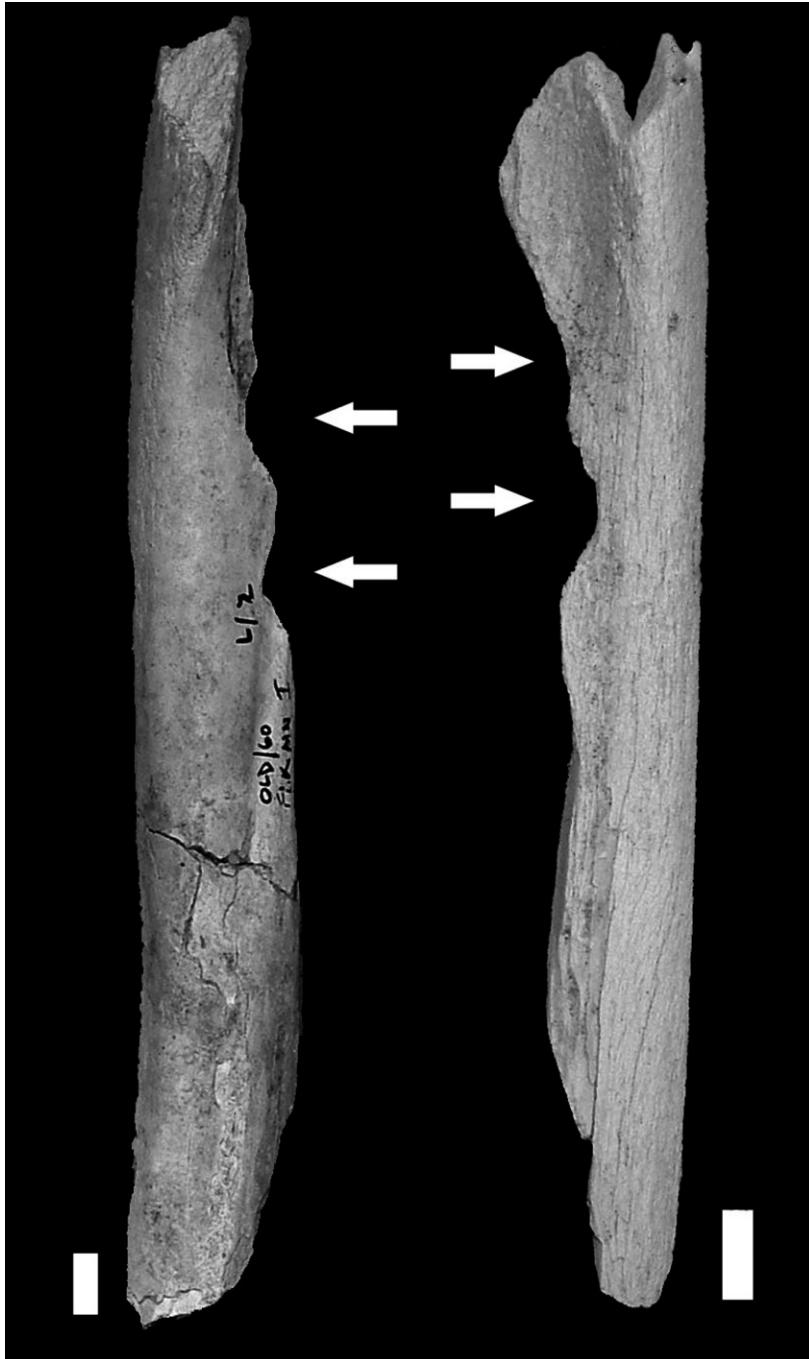


Fig. 5: Cranial view of tibiae from FLKNN 2 (left) and a spotted hyena den in the Masai Mara (right) showing similar patterns of notching (arrows). Scale bars = 1 cm.

Hominid subsistence activities and the function of the Olduvai lithics

Toth (1985) demonstrated that sharp-edged flakes, rather than the better-known "heavy duty" core forms, were often the desired goal of early stone knappers. Experimental work (Jones 1981, 1994; Toth 1985; Schick and Toth 1993) and use-wear analysis (Keeley and Toth 1981) confirmed the effectiveness of flakes (along with other tool types) as carcass butchery tools. Although it was long assumed that the co-occurrence of stone tools with fossil bones linked early technology to carcass processing (e.g., Clark and Haynes 1970; Leakey 1971), it was not until the discovery of cutmarks at Plio-Pleistocene sites that this relationship was confirmed (Bunn 1981; Potts and Shipman 1981). Percussion marks and other fracture features have demonstrated the use of stone artifacts as marrow-processing implements as well (Bunn 1981; Oliver 1994; Blumenshine 1995). That butchered bones have been excavated at the earliest archaeological sites (de Heinzelin et al. 1999; Domínguez-Rodrigo et al. 2005) in addition to many other Plio-Pleistocene localities leaves no doubt that, from its inception, early stone technology was used at least in part for processing carcasses.

However, apart from FLK 22 and BK, most of the Olduvai faunal assemblages discussed here are largely the result of carnivore, rather than hominid, behavior. This means that no functional association exists between the lithics and fauna from many of the Olduvai sites. Nevertheless, the presence of stone tools at every site (except for FLKNN 2) signals the use of these areas by hominids. What, then, were the stone tools at these sites being used for? A possible answer comes from Mora and de la Torre's (2005) reexamination of the idea that percussive activities unrelated to knapping sharp-edged flakes may have been an important component of the stone technology at Olduvai during Bed I and II times (see also Schick and Toth [1994] and Willoughby [1987]). They document the presence of what are termed "active hammerstones with fracture angles" (Mora and de la Torre 2005, 181), which are characterized by ridges with stepped and hinged fractures. According to Mora and de la Torre (2005), the angularity of these pieces would have made them unsuitable as hammerstones for inducing predictable conchoidal fracture. They also identified anvils, which, following Leakey (1971), are described as cuboid blocks with battering along the edges. Finally, they argue that many of the pieces originally described by Leakey (1971) as broken flakes and chips are in fact chunks detached from anvils during percussion. Many of these pieces show extensive battering and all lack most of the morphological features of flakes.

If sharp-edged flakes are considered the major butchery tool in the lithic toolkit, then they should be associated with butchered faunas. Table 2 lists the artifact categories for those Olduvai sites recently reanalyzed by de la Torre (de la Torre 2004; Mora and de la Torre 2005). There is a notable paucity of flakes from the assemblages that lack evidence for butchery. At FLKN, for example, the lithic assemblages from Levels 3–6 have a total of only 39 complete or retouched flakes. FLKN 1–2, which has the highest frequency of cutmarked fragments (though still only 1.1% of the total faunal assemblage), also has the highest number of flakes ($n = 92$). Both anvils and hammerstones with fracture angles are present throughout the FLKN deposit, and the fact that some smaller fragments show evidence of battering suggests that most of the angular fragments were detached from anvils during non-flake-producing percussion activities. In terms of weight, almost 44% of the FLKN lithic material can be linked to non-knapping percussion (de la Torre

	DK	FLKNN 3	FLK 22	FLKN 1-2	FLKN 3	FLKN 4	FLKN 5	FLKN 6	FC West	TK LF	TK UF
Test cores	7 (0.7)	5 (11.9)	19 (0.7)	16 (1.1)	5 (2.3)	0 (0.0)	1 (0.7)	0 (0.0)	4 (0.3)	2 (0.1)	5 (0.1)
Cores	69 (6.8)	3 (7.1)	49 (1.8)	85 (5.9)	11 (5.1)	8 (9.6)	15 (11.4)	4 (3.1)	39 (3.4)	8 (0.3)	19 (0.3)
Core fragments	0 (0.0)	8(19.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2 (0.2)	0 (0.0)	0 (0.0)
Hammerstones	37 (3.6)	0 (0.0)	21 (0.8)	76 (5.2)	26 (12.1)	13 (15.7)	17 (12.9)	11 (8.6)	84 (7.2)	2 (0.1)	24 (0.4)
Hammerstone with fracture angles	0 (0.0)	0 (0.0)	0 (0.0)	13 (0.8)	4 (1.9)	0 (0.0)	5 (3.8)	0 (0.0)	31 (2.7)	9 (0.4)	28 (0.5)
Hammerstone fragments	2 (0.2)	0 (0.0)	5 (0.2)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	30 (2.6)	12 (0.5)	3 (0.1)
Fractured hammerstones	2 (0.2)	0 (0.0)	6 (0.2)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Anvils	0 (0.0)	0 (0.0)	2 (0.1)	25 (1.7)	9 (4.2)	1 (1.2)	9 (6.8)	10 (7.8)	8 (0.7)	18 (0.7)	33 (0.6)
Flakes	115 (11.3)	7 (16.7)	125 (4.7)	84 (5.7)	16 (7.5)	4 (4.8)	5 (3.8)	9 (7.0)	69 (5.9)	42 (1.8)	42 (0.7)
Flake fragments	511 (50.0)	19 (45.2)	865 (32.5)	543 (37.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	425 (36.6)	296 (12.7)	1430 (27.1)
Possible flake fragments	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	59 (27.6)	10 (12.0)	48 (36.4)	18 (14.0)	0 (0.0)	0 (0.0)	0 (0.0)
Retouched flakes	10 (1.0)	0 (0.0)	15 (0.6)	8 (0.5)	3 (1.4)	0 (0.0)	1 (0.7)	1 (0.8)	15 (1.3)	30 (1.3)	42 (0.7)
Debitage	140 (13.7)	0 (0.0)	1320 (49.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Chips (<20 mm)	0 (0.0)	0 (0.0)	0 (0.0)	222 (15.2)	18 (8.4)	5 (6.0)	4 (3.0)	35 (27.1)	230 (19.8)	0 (0.0)	3122 (59.2)
Angular fragments	132 (12.9)	0 (0.0)	131 (4.9)	117 (8.0)	19 (8.9)	14 (16.9)	23 (17.4)	9 (7.0)	225 (19.4)	1891 (81.3)	171 (3.2)
Spheroids/subspheroids	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (0.2)	48 (0.9)
Battered fragments	0 (0.0)	0 (0.0)	0 (0.0)	20 (1.4)	0 (0.0)	0 (0.0)	2 (1.5)	30 (23.6)	0 (0.0)	0 (0.0)	222 (4.2)
Unmodified stones	0 (0.0)	0 (0.0)	107 (4.0)	246 (16.9)	44 (20.6)	28 (33.7)	2 (1.5)	2 (1.6)	0 (0.0)	11 (0.5)	79 (1.4)
Total	1021 (100.0)	42 (100.0)	2664 (100.0)	1456 (100.0)	214 (100.0)	83 (100.0)	132 (100.0)	129 (100.0)	1162 (100.0)	2325 (100.0)	5268 (100.0)

Table 2: Frequency of lithic categories from selected Olduvai sites. References: de la Torre (2004), Domínguez-Rodrigo et al. (2007a).

2004; Mora and de la Torre 2005). The small lithic assemblages from FLKNN 1 and 3 are deficient in flakes, which is consistent with a general lack of butchery damage at that locality. The very low frequency of butchery marks at DK is surprising given that flakes are relatively well-represented at the site. It is possible that the flakes present at the site were used to skin and/or disarticulate carcass parts that were then transported off-site for further butchery (thus butchery marks were imparted elsewhere) (Egeland 2007). Flake discard rates during skinning and disarticulation would have been high, as the dulling of stone tool edges proceeds quickly when performing these activities (Braun et al. 2008). The flake-rich lithic assemblage from FLK 22 was clearly geared towards carcass butchery, which is confirmed by the high frequencies of butchery marks.

In Bed II, the low frequency of lava (basalt and phonolite) flakes relative to the number of cores at HWKE suggests that flake production in this raw material was not the major goal of the Olduvai tool-makers there (Kimura 1999). Although quartz and chert flakes are relatively common at the site, many of the quartz cores show evidence of battering (Kimura 1999), which may indicate that they were subsequently used for percussion activities unrelated to carcass butchery. The lack of butchery marks at MNK Main is somewhat unexpected considering complete flakes are common in the lithic assemblage; however, battered pieces make up significant portions of the assemblages as well, especially in terms of weight (Leakey 1971). Kimura (2002) and Mora and de la Torre (2005) have documented a high incidence of battered pieces at both FC West and TK, which again could indicate that activities other than (or in addition to) carcass butchery were carried out at these sites. Like FLK 22, the lithic assemblage from BK is rich in flakes (Leakey 1971) and, given the abundance of butchery marks, was also used largely for butchering carcasses.

Mora and de la Torre (2005; see also Toth 1985; Schick and Toth 1993) suggest that the battered components of the Olduvai assemblages could have been used to break open bones or process nuts and other plant material. The lack of percussion marks or other evidence for hominid-induced fragmentation at most of the Olduvai sites rules out bone-breaking, but the undeniable importance of plant foods in early hominid diets (Peters 1987; Sept 1992) makes it likely that these resources dictated when and where hominids chose to concentrate their tool-using activities at Olduvai (Peters and Blumenschine 1995). Use-wear and phytolith analysis in addition to renewed excavations should shed light on the exact resource(s) these tools were used to process.

Competition and habitat selection

Taphonomic proxies of competitive intensity can aid in reconstructing habitats at a relatively fine-grained scale. While other paleoecological indicators offer critical information, it is often at scales too broad to infer the microhabitat and level of competition at specific sites. A taphonomic perspective allows these factors to be deduced at the same scale at which hominid and carnivore behavior is taking place (i.e., at a very specific locality). The level of competition is largely determined by carnivore-to-prey ratios and habitat type (Blumenschine et al. 1994). Open habitats tend towards high levels of competition because visibility is good and cues to carcass location (e.g., vultures) are common (Blumenschine 1986a, 1987; Creel and Creel 1996, 1998; Domínguez-Rodrigo

2001). Both Binford (1981) and Domínguez-Rodrigo (1994) have demonstrated that interspecific competition can determine the nature and extent of carcass part transport by carnivores. More importantly, several studies show that competition directly impacts carcass persistence and the completeness of skeletal parts (Haynes 1982; Blumenschine 1986a, b, 1989; Blumenschine et al. 1994; Domínguez-Rodrigo 1996, 1999, 2001; Selva et al. 2003; Faith and Behrensmeyer 2006). Given these observations, several taphonomic variables can be used to estimate levels of competition.

Complete long bones represent untapped within-bone resources. Potts (1982, 1984, 343-344; 1988, 353-355) argued that a high frequency of complete limb bones at many Bed I Olduvai sites reflects hurried and incomplete carcass processing by hominids and thus high levels of on-site competition. However, in high competition settings, incompletely processed carcasses would be quickly consumed by other carnivores subsequent to their abandonment by hominids. Therefore, the presence of many complete long bones probably reflects low levels of on-site competition (cf. Capaldo 1997, 589-590). In landscape taphonomic studies, both Blumenschine (1989) and Domínguez-Rodrigo (1996) encountered higher frequencies of complete long bones in lower competition settings such as riparian woodlands. Faith and Behrensmeyer (2006) documented a decline in the frequency of complete long bones at Amboseli National Park (Kenya) from the 1970s to the 2000s, which they linked to the gradual increase of carnivore populations (and thus competition) during that time interval.

It is also well-known that carnivores, especially hyenas, preferentially consume and thus delete less-dense, grease-laden axial bones and long bone epiphyses (Brain 1967, 1969, 1981; Richardson 1980; Marean et al. 1992; Capaldo 1998; Pickering et al. 2003). Therefore, the extent to which these bones or bone portions are deleted should reflect differing levels of competition. Blumenschine (1989), Domínguez-Rodrigo (1996), and Haynes (1982) have shown that these bones and bone portions survive at higher rates in areas of low competition. The representation of axial bones and long bone epiphyses has also fallen dramatically with increased competition at Amboseli over the past 30 years (Faith and Behrensmeyer 2006). Levels of epiphyseal destruction have also been shown to increase as the number of carnivores feeding on a carcass increases (Selvaggio 1994a, b).

Based on these observations, a number of indices can be used to measure competition. For example, based on actualistic samples modified by hyenas, Blumenschine and Marean (1993, 286-287) suggest that low ratios of epiphyseal fragments to shaft fragments accompanied by high tooth mark frequencies characterize low competition settings. This is because under conditions of low competition, carcass consumption (and thus tooth-marking) and epiphyseal destruction occur on-site. On the other hand, when competitors, including conspecifics, are present, hyenas remove skeletal parts elsewhere for undisturbed consumption (Kruuk 1972, 125; Marean et al. 1992, 112; Behrensmeyer 2007, 157). Although epiphyseal loss often remains high in settings of elevated competition, on-site tooth-marking decreases because carcass consumption takes place off-site. Domínguez-Rodrigo and Organista (2007) propose that the intensity of ravaging can be measured using three ratios (as measured by MNE): (1) the ratio of ribs and vertebrae to major long bones; (2) the ratio of femora to tibiae; and (3) the ratio of proximal humeri + distal radii to distal humeri + proximal radii. Each of these ratios presents as the numerator bones or bone portions that are less dense and therefore extremely suscepti-

ble to carnivore ravaging, while the denominator represents more dense bones or bone portions. No ravaging is characterized by ratios that are more or less equal relative to the proportion of skeletal parts in a complete skeleton, while more intense ravaging yields lower ratios. Finally, Faith and Behrensmeyer (2006, 1727) and Faith et al. (2007) argue that high correlations between density and skeletal part abundances signal lower competition because carnivores under little or no competitive pressure will choose to consume only the most greasy (and lowest density) bones and bone portions. Under conditions of intense competition, carnivores will consume both low (high grease yield) and high (low grease yield) density bones and bone portions, resulting in low or insignificant correlations.

Figure 6 provides a theoretical model for competition based on two taphonomic measures: the ratio of axial (vertebrae + ribs) bones to major long bones (in terms of MNE) and the ratio of long bone epiphyseal fragments to long bone shaft fragments. This model is similar to Domínguez-Rodrigo and Organista's (2007) "ravaging stages" approach, which draws upon actualistic research on carnivore ravaging. Sites in low competition areas (i.e., little or no carcass consumption) will show high axial-to-limb ratios and epiphysis-to-shaft ratios (upper right portion of graph). Once carcass consumption begins, carnivores choose to consume vertebrae first, as they have the lowest structural density

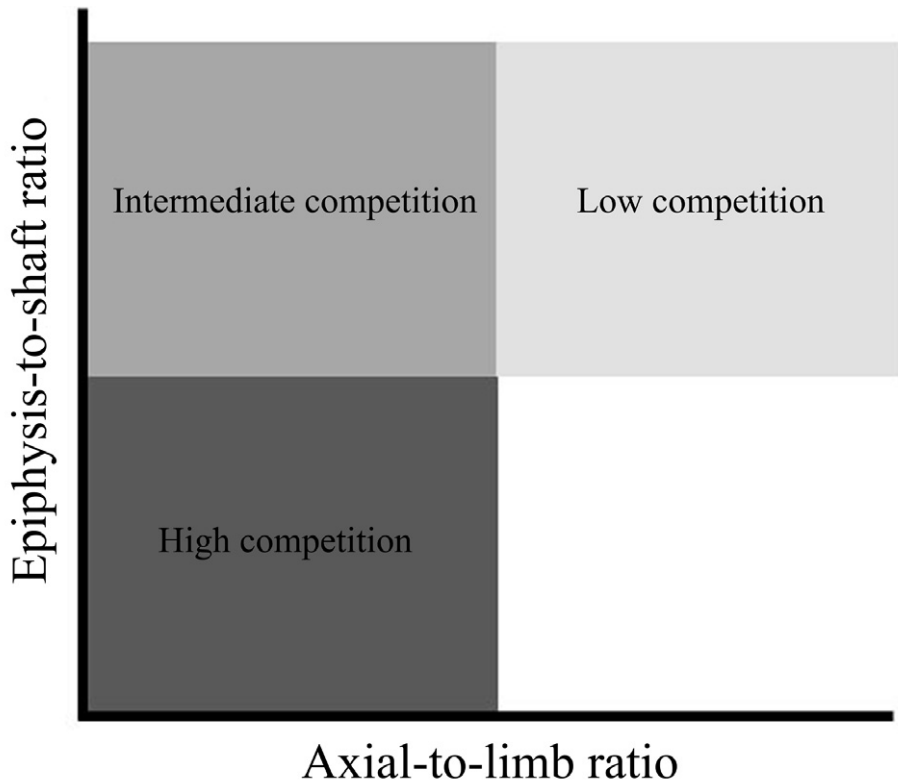


Fig. 6: Theoretical model of competition based on axial-to-limb and epiphysis-to-shaft ratios. See text for explanation.

	EP:SH	% Complete	Axial: Long	Femur: Tibia	HM PR + RD DS HM DS + RD PR
Olduvai Bed I					
DK Level 1	0.31	0.0	1.00	0.25	3.00
DK Level 2	0.46	8.5	0.42	0.74	0.46
DK Level 3	0.50	8.7	0.35	0.76	0.23
FLKNN 2	0.88	23.3	0.24	0.55	0.23
FLKNN 3	0.37	40.0	1.00	1.25	0.54
FLKN 1-2	0.46	13.8	0.35	0.58	0.31
FLKN 3	0.58	14.9	0.63	0.60	0.13
FLKN 4	0.89	10.1	0.36	0.90	0.22
FLKN 5	0.60	16.3	0.36	0.67	0.24
FLKN 6	4.80	32.0	1.40	0.60	0.83
FLK 15	0.34	2.7	0.14	0.66	0.18
FLK 22	0.10	11.8	0.80	0.71	0.30
Olduvai Bed II					
HWK E 1-2	1.70	–	0.71	–	–
HWK E 3-5	1.60	–	0.73	–	–
MNK (Main)	0.21	–	0.33	–	–
FC West	0.23	0.0	0.33	2.00	0.00
TK LF	0.14	0.0	0.40	1.70	0.00
TK UF	0.13	0.0	0.36	0.50	–
BK	0.14	4.4	0.31	0.88	0.26
Experimental					
Solitary consumer (low competition)	0.70	–	–	–	–
Small consumer group (intermediate competition)	0.78	–	–	–	–
Large consumer group (high competition)	0.28	–	–	–	–
Heavily ravaged (high competition)	0.02	0.0	0.67	–	–
Serengeti/Ngorongoro (Tanzania) landscape					
Serengeti riparian woodlands (low competition)	–	68.8	5.90	0.33	–
Serengeti open woodlands/plains (intermediate competition)	–	41.3	1.70	0.76	–
Ngorongoro (high competition)	–	13.6	1.60	0.86	–
Amboseli (Kenya) landscape					
1970s (low competition)	–	56.9	3.08	0.97	39.28
2000s (high competition)	–	18.4	0.75	0.92	17.95
Galana/Kulalu (Kenya) landscape					
Riparian woodland (low competition)	–	60.9	2.65	1.41	–
Bushland (intermediate competition)	–	25.0	3.52	1.25	–
Open grassland (high competition)	–	27.5	2.55	1.20	–
Carnivore dens					
Spotted hyena den (low competition)	0.63	–	–	–	–

Table 3: Taphonomic measures of competition for the Olduvai sites and several actualistic samples. References: Bunn (1982), Blumenschine (1989), Selvaggio (1994b), Domínguez-Rodrigo (1996), Capaldo (1998), Faith and Behrensmeyer (2006), Domínguez-Rodrigo et al. (2007a), Egeland (2007).

and highest grease yield (Marean et al. 1992). Sites in intermediate competition areas, therefore, will show depressed axial-to-limb ratios but will retain high ratios of epiphyses to shafts (upper left portion of graph). As competition increases, carnivores that are still hungry then move on to the long bones, which they will consume beginning with the softer epiphyses. Therefore, high levels of competition will be reflected in both low axial-to-limb ratios and low epiphysis-to-shaft ratios (lower left portion of graph). Table 3 provides these and other measures of competition for the Olduvai sites and several modern actualistic samples.

Before proceeding, some caveats should be kept in mind. It is important to first realize that no modern ecosystem provides a perfect analog for the Plio-Pleistocene Olduvai basin and that each of the modern and fossil assemblages is the result of unique combinations of ecological parameters. Consequently, "low" or "high" competition will differ by ecosystem and the taphonomic signatures will vary accordingly (cf. Tappen 2001). Even comparisons among the fossil assemblages themselves, all of which derive from the same general area, may be slightly problematic given the depth of time sampled by the Bed I and II sites. Therefore, what is identified taphonomically from each assemblage as a single "level" of competition is in fact an aggregation of competitive interactions reflecting the continuous shift in microhabitats that occurred over time at each site. It is also important to realize that competition in general and for carcasses in particular is not a stable, continuous phenomenon. In fact, "[t]he degree of competitive interaction between species will vary according to the rate of fluctuations in the environment and the degree of overlap between their requirements" (Foley 1987, 192). This is especially true in seasonal environments (Schoener 1983; Foley 1987). It is expected, therefore, that the effects of carnivore competition on largely vegetarian hominids foraging within a seasonal savanna-mosaic environment fluctuated between intense and almost non-existent.

If comparisons are made within the framework of these caveats, the general uniformitarian principles that govern the utilization of carcasses (Blumenschine et al. 1994) validate the use of taphonomic data for reconstructing competition. For example, whether discovered in the modern Amboseli Basin or at Plio-Pleistocene Olduvai, complete limb bones represent untapped within-bone resources and signal lower consumer-to-carcass ratios and a lack of carcass visibility: that is, lower competition. Thus, when used in combination with other lines of data, taphonomic variables can provide a proxy measure for the relative level of on-site competition for carcass resources and thus microhabitat.

With these issues in mind, Figure 7 plots the axial-to-limb and epiphysis-to-shaft ratios for the Olduvai sites. Although the Olduvai sites do appear to cluster in areas of the graph, the separation of competition levels in Figure 7 is somewhat arbitrary and, thus, artificially sets boundaries on what is in fact a continuum. If habitat type does predict competition, then FLK 22 and the FLKNN sites, all of which are reconstructed as forested habitats, should show the lowest levels of competition. These should be followed by the dense woodland habitats of the lower levels of FLKN (4–6) and riparian woodlands of HWKE, the mixed habitats of DK, the open bushlands of the upper levels of FLKN (1–3) and, finally, the open habitats of the remaining Bed II sites (for paleoecological data see Leakey 1971; Hay 1976; Jaeger 1976; Gentry and Gentry 1978a, b; Bunn 1982; Potts 1982, 1988; Kappelman 1984, 1986; Shipman and Harris 1988; Plummer and Bishop 1994; Sikes 1994, 1999; Peters and Blumenschine 1995; Kappelman et al. 1997; Fernández-Jalvo et al. 1998; Albert et al. 2006; Bamford et al. 2006, 2008; Blumenschine et al. 2007).

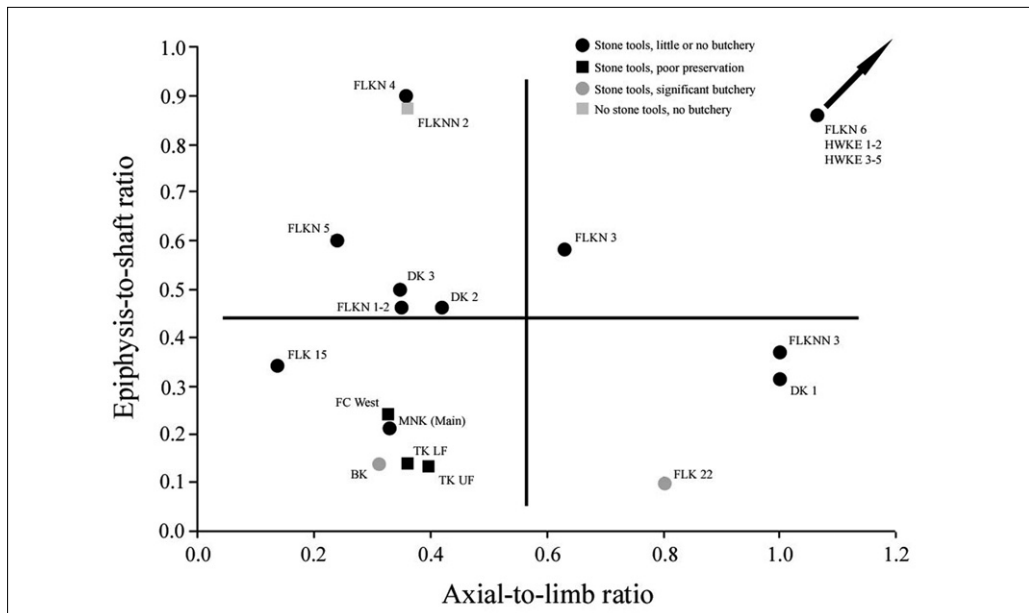


Fig. 7: Measures of competition for the Olduvai sites. Note: "stone tools" = presence of stone artifacts; "no stone tools" = complete lack of stone artifacts; "little or no butchery" = assemblage with well-preserved cortices and a virtual (i.e. a few modified specimens) or complete lack of butchered bone; "poor preservation" = assemblage with poorly preserved cortices where butchery marks cannot be identified; "no butchery" = assemblage with well-preserved cortices and a complete lack of butchered bone; "significant butchery" = assemblage with well-preserved cortices and substantial evidence (i.e. dozens of fragments with hominid-induced surface modifications and other lines of evidence for hominid involvement in carcass modification) for butchery.

According to the taphonomic data, FLKN 6 and HWKE plot off the graph in the area of very low competition. FLKN 3 also reflects a relatively low competition setting. FLKNN 2 and FLKN 4 plot in the low to intermediate area, showing higher levels of axial bone destruction but high epiphysis-to-shaft ratios. These are followed by DK 2 and 3 and FLKN 1–2 and FLKN 5, which fall into the intermediate area. The remaining Bed II sites and FLK 15 all fall into the high competition area. FLK 22, FLKNN 3 and DK 1 appear as outliers at the bottom right portion of the graph.

Other taphonomic measures of competition can be used to further refine these results. For example, the high axial-to-limb ratios at FLK 22 and FLKNN 3 are consistent with a setting of lower competition. Intensive fragmentation by hammerstone-wielding hominids at FLK 22 (Oliver 1994; Blumenshine 1995; Domínguez-Rodrigo and Barba 2006) likely accounts for the anomalously low epiphysis-to-shaft ratio, as hammerstone breakage produces disproportionately high frequencies of shaft fragments (Bunn 1989; Pickering and Egeland 2006). A low competition setting for FLK 22 is further supported by the fact that almost 12% of the limb bones are complete. Although FLKNN 3 shows an anomalous combination of axial and epiphyseal survival, the fact that 40% of the limb bones at this site are complete suggests a low competition setting as well. Other inconsistencies are more difficult to explain. For instance, at FC West and TK LF (presumably high competition settings), the femur-to-tibia ratios are the highest of any of the Olduvai sites.

The paleoecological and taphonomic data are generally consistent with each other, although the taphonomic variables can contribute to refined interpretations of paleohabitat. For example, although FLKN 3 is reconstructed as a broken woodland or bushland habitat (Fernández-Jalvo et al. 1998), the taphonomic data point to low levels of competition and perhaps a more closed habitat (e.g., a dense clump of trees) directly on-site. One pattern that does emerge is that many of the Bed I sites seem to cluster in the low to intermediate competition area, while nearly all the Bed II sites appear to reflect highly competitive environments.

Conclusions: patterns of hominid site use at Olduvai

It is now apparent that hominids played little or no role in the formation of the faunal assemblages from many of Mary Leakey's sites from Beds I and II. However, rather than marginalizing these assemblages in discussions of hominid behavior, the new interpretations simply add a new dimension to our understanding of hominid site use. For example, the faunas from these sites tend to be associated with lithic toolkits that were probably used for percussion activities unrelated to carcass butchery. This suggests that subsistence behaviors other than carcass transport and butchery determined to some extent where these bipedal primates used and discarded their stone tools across the Olduvai landscape. At the few sites where hominids were significantly involved with the formation of the faunal assemblages (FLK 22 and BK) there is strong evidence to suggest that they acquired and butchered fully fleshed carcasses.

Nearly all the artifact-bearing Bed I localities occurred in intermediate or low competition settings, while most of the Bed II sites were formed in higher competition settings. The use of lower competition settings by hominids does not necessarily mean that carnivore avoidance played a significant role in conditioning tool use and discard at these locations. At sites like FLKNN, FLKN, or HWKE, where hominids were not involved with the faunal assemblages, site usage by hominids and carnivores probably occurred in largely unrelated depositional events (Egeland 2007; Egeland and Domínguez-Rodrigo in press). Because hominid and carnivore visitations may have been separated by months, years, or even decades, it was not necessarily lower levels of competition that drew hominids to these locations but the resources that such settings provided, such as water, shade, and especially vegetal foods. Isaac (1983, 9; see also Isaac and Crader 1981; Binford 1983) made just such an argument a quarter century ago in his "common amenity" model of site formation, which suggested that water, food, and other "amenities" attracted both hominids and carnivores independently to the same locations on the landscape over many years.

The potential for ecological overlap between hominids and carnivores was much more pronounced at FLK 22 and BK, where large-scale carcass butchery would have attracted local carnivore populations. It is therefore possible that carnivore avoidance (in addition to other factors) encouraged the transport of carcass parts to a lower competition habitat at FLK 22. Indeed, the high carcass yields and concomitant need for processing equipment predicts carcass transport to a central place like FLK 22 (Blumenshine et al. 1994). Whether social factors like offspring/mate provisioning (e.g., Oliver 1994) or a sexual division of labor (e.g., Isaac 1978b) further mediated carcass transport behavior

is currently impossible to test directly. However, the large food surpluses created by the transport of so many fully fleshed carcasses strongly suggests that at least food-sharing was practiced (Bunn 1982, 2007; Domínguez-Rodrigo et al. 2007a). That BK is located in a high competition environment supports Monahan's (1996a, 118) argument that hominids during upper Bed II times could control high competition locations and carry out carcass processing. The ability of hominids to monopolize carcasses under such circumstances may signal changes in body and/or group size or perhaps the control of fire, for which there is (provisional) evidence at Koobi Fora, Kenya, by 1.6 million years ago (Belomo 1994) and Swartkrans Member 3, South Africa, by ca. 1.0 million years ago (Brain and Sillen 1988). Unfortunately, the BK bone assemblage was excavated from over a meter of deposit and the geological context indicates that the material is probably not in primary context (Leakey 1971; CPE personal observations). Therefore, it is perhaps premature to categorize BK socio-economically as a "central place" like FLK 22 or FxJj 50 from Koobi Fora (Bunn et al. 1980, 1997).

In preserving one of world's richest records of human evolution, Olduvai Gorge provides an excellent opportunity to examine spatio-temporal variability in hominid behavior. As hominids utilized space in the paleo-Olduvai basin they produced a variety of site "types", from central places like FLK 22 to locations for possible vegetal processing like FLKNN or FLKN. This pattern makes sense from a behavioral ecological standpoint, as hominids should have varied their behavior across the Olduvai landscape in response to an ever-changing eco-cultural milieu.

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