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## Research on Late Pliocene Oldowan Sites at Kanjera South, Kenya

The late Pliocene is notable for the appearance of two new hominid genera as well as the first archaeological sites, generally attributed to the Oldowan Industrial Complex. However, the behavioral ecology of Oldowan hominids has been little explored, particularly at sites older than 2.0 Ma. Moreover, debates on Oldowan hominid foraging ecology and behavior have centered on data from only two regions, and often from single site levels. Here we describe the preliminary results of our investigation of Oldowan occurrences at Kanjera South. These occurrences preserve the oldest known traces of hominid activity in southwestern Kenya, and unlike most of the Oldowan sites in the 2.0–2.5 Ma time interval, artefacts are found in spatial association with a well-preserved fauna.

In 1996 and 1997, this project initiated the first excavation program for Kanjera South. Magneto- and biostratigraphy indicate that deposition began approximately 2.2 Ma, substantially earlier than previously thought. At Excavation 1, artefacts were found in spatial association with a taxonomically diverse faunal assemblage in Beds KS-1 and KS-2. Excavation 2 yielded a partial hippopotamus axial skeleton with artefacts in KS-3. Cores from both sites were incidentally flaked and represent a Mode I lithic technology indistinguishable from the Oldowan. Approximately 15% of the artefacts were manufactured from non-local raw materials, indicating a flow of resources into the area.

Stable isotopic analysis of KS-1 and KS-2 pedogenic carbonates suggests that the Excavation 1 assemblages formed in a relatively open (>75% C<sub>4</sub> grass) habitat. The Excavation 1 and 2 faunas contain a high proportion of equids relative to Oldowan accumulations from Bed I Olduvai Gorge, Tanzania. Beds KS-1 and KS-2 thus preserve traces of Oldowan hominid activities in a more open setting than has been previously documented.

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### Introduction

The late Pliocene (c. 1.8–3.0 Ma) of Africa saw important developments in the evolu-

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tion of the Hominidae, including the extinction of the gracile australopithecines, the first appearances of the genera *Homo* (e.g., Hill *et al.*, 1992; Wood, 1992; Kimbel *et al.*, 1996) and *Paranthropus* (Grine, 1988) and the earliest archaeological traces (Harris *et al.*, 1987; Howell *et al.*, 1987; Roche, 1989; Kibunjia, 1994; Rogers *et al.*, 1994; Semaw *et al.*, 1997). Environmental change,

linked to both tectonic uplift (Partridge *et al.*, 1995) and global cooling (Vrba, 1985, 1995; Prentice & Denton, 1988; deMenocal & Bloemendal, 1995) appears to have transformed the densely wooded habitats favored by early Pliocene hominids to complex mosaics incorporating larger amounts of  $C_4$  grasses (Leakey *et al.*, 1995; WoldeGabriel *et al.*, 1994; Reed, 1997; Bonnefille, 1995; Wesselman, 1995). The appearance of the robust australopithecine morphology and the earliest archaeological sites (generally attributed to the genus *Homo*) may reflect novel hominid adaptive responses to both a changing resource base over geologic time as well as an increasingly seasonal distribution of food over the annual cycle (Foley, 1987).

While clearly a crucial time interval for understanding the origins of the earliest lithic technology, as well as the biological substrate for our ancestral species (*Homo ergaster*/early *Homo erectus*), paleoanthropological data from the Plio-Pleistocene of East Africa is largely derived from just two fluvial-lacustrine systems: Olduvai Gorge, Tanzania (Hay, 1976; Kappelman, 1984; Kappelman *et al.*, 1997; Cerling & Hay, 1986; Potts, 1988; Sikes, 1994; Tobias, 1991) and the Turkana basin deposits in Kenya and Ethiopia (Bonnefille, 1995; Brown & Fiebel, 1988; Cerling *et al.*, 1988; Coppens *et al.*, 1976; Harris *et al.*, 1988; Harris, 1991; Reed, 1997; Toth, 1987; Wood, 1991). These two basins have also provided most of the data used in reconstructing Plio-Pleistocene hominid behavioral ecology (e.g., Bunn *et al.*, 1980; Bunn & Kroll, 1986; Howell *et al.*, 1987; McHenry, 1994; Plummer & Bishop, 1994; Potts, 1988; Rogers *et al.*, 1994; Sikes, 1994). Debates on such important issues as Oldowan hominid ranging patterns and mode of faunal acquisition are largely centered on data from a few sites, or even from single site levels (e.g., FLK Zinj—Binford, 1988; Bunn & Kroll, 1986; Blumenschine,

1995; Capaldo, 1997; Oliver, 1994; Dominguez-Rodrigo, 1997).

One of the primary goals of the current project is to expand the investigation of Oldowan hominid activities to another geographic setting, the Homa Peninsula, southwestern Kenya. The Kanjera South Oldowan occurrences are among only a handful of sites older than 2.0 Ma, and unlike most of the Oldowan sites in the 2.0–2.5 Ma time interval, artefacts are found in spatial association with a well-preserved fauna. Moreover, Oldowan hominid traces are found in a previously unreported paleoenvironmental setting (>75%  $C_4$  grass), the first clear documentation of Oldowan hominid usage of an open paleohabitat. The ultimate goal of this project is to generate data on Oldowan hominid behavior directly comparable to data collected from better known sites at Olduvai and the Turkana basin. Only by investigating hominid activities in a variety of locales, each with its own unique configuration of resources and environmental settings, will it be possible to assess behavioral variability in our extinct relatives (see also Potts, 1994).

### Geologic background

An overview of the history of research on the Homa Peninsula is provided in Ditchfield *et al.* (1999), Behrensmeyer *et al.* (1995), and Plummer & Potts (1989, 1995). The Kanjera Fm deposits outcrop in three areas, termed the Northern, Middle and Southern Exposures (Figure 1). Magneto- and biostratigraphy suggest that deposition of the Kanjera Fm (N) began in the mid to late early Pleistocene and continued into the middle Pleistocene (Behrensmeyer *et al.*, 1995). Sediments were deposited at the margin of a small playa or lake, in fluvial, lake flat and lacustrine settings. Magneto- and biostratigraphy indicate that Kanjera Fm (S) deposition occurred during the late Pliocene and that Beds KS-1 through KS-3 underlie the Reunion Subchron, dated

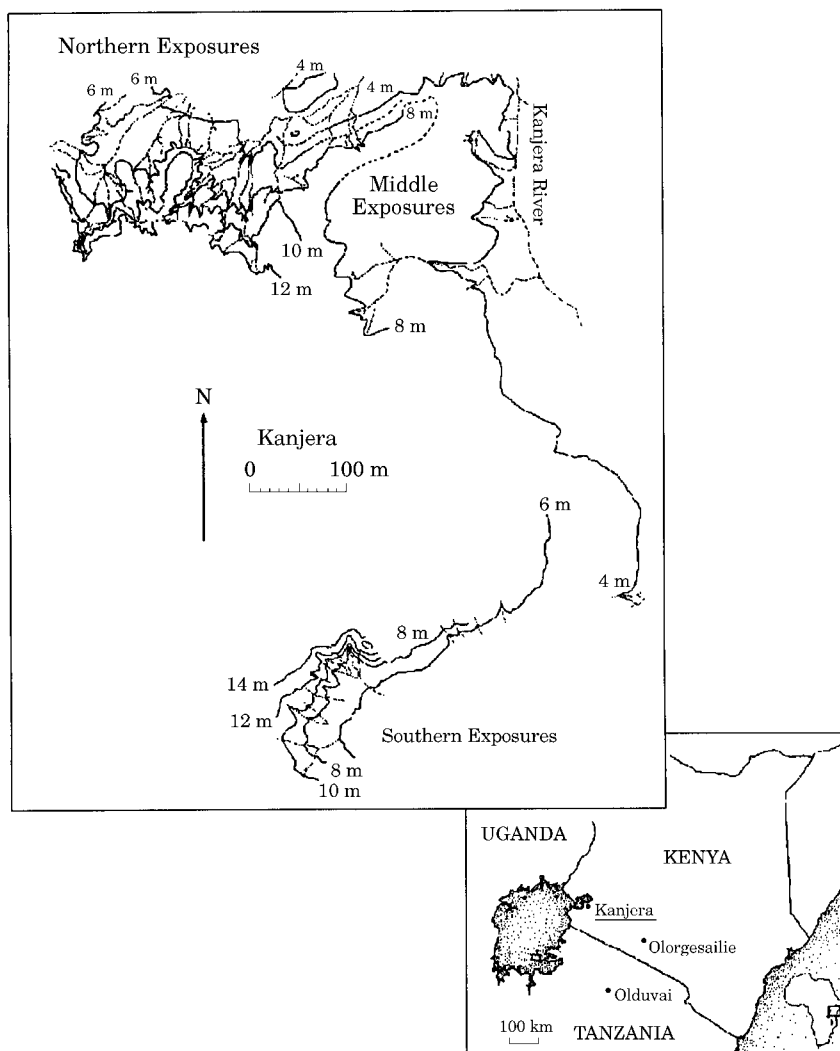


Figure 1. Location of Kanjera within Kenya and a partial topographic map showing the Northern, Middle and Southern Exposures. Unmapped areas between the exposures are mostly grassy flats and cultivated fields. After Behrensmeier *et al.*, 1995: Figure 2.

at 2.14–2.15 Ma (Figure 2) (Table 1) (Ditchfield *et al.*, 1999). A pending  $^{40}\text{Ar}/^{39}\text{Ar}$  date on biotites collected by A. Deino (Berkeley Geochronology Center) from an agglomerate capping the Kanjera Fm (S) should further refine this temporal framework. Deposition of the Kanjera Fm (S) is consistent with a lake margin setting, with paleoflow directed towards the depositional

low to the north. Fossils and artefacts were deposited under both low and high energy flow regimes in fluvial, swamp, lake flat and possibly lacustrine environments.

#### Recent excavations at Kanjera South

In 1987 and 1988, the Smithsonian Expedition to Kanjera documented abundant

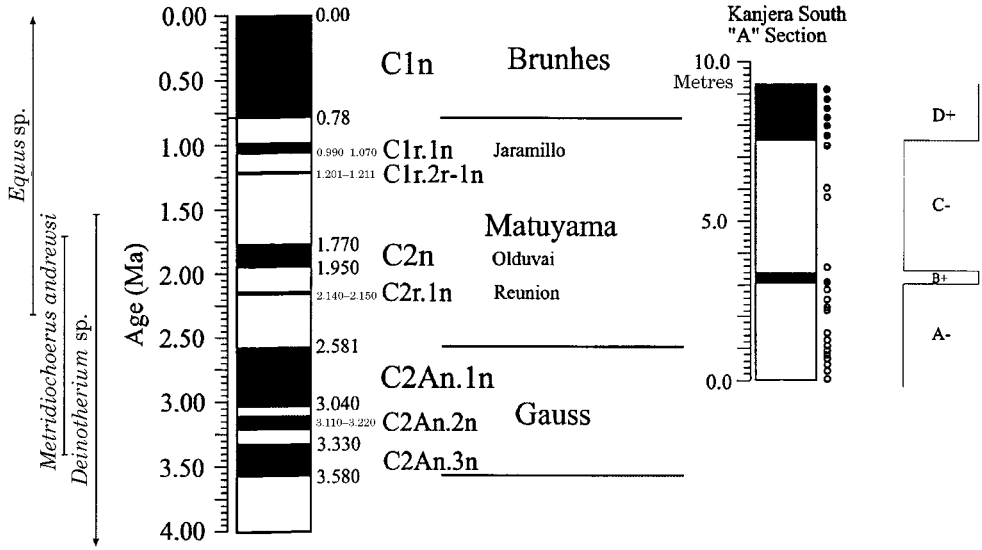


Figure 2. Summary plot of the magneto- and biostratigraphy of the Kanjera Fm (S). Filled circles and dark bands in the column represent normal intervals, open circles and light bands in the column represent intervals of reversed polarity. The interpreted magnetostratigraphic sequence of the Kanjera Fm (S) is labeled A – through D+. The best matches for normal bands B+ and D+ are the Reunion and Olduvai Subchrons, respectively. Beds KS-1 and KS-3 underlie B+, suggesting an age greater than 2.15 Ma. See Ditchfield *et al.* (1998) for details. Timescale after Cande & Kent (1995).

fossils, as well as Early Stone Age (ESA) artefacts on the surface of the Southern Exposures. One excavation, the SC (Stream Channel) Site, was begun to recover a hippopotamus pelvis eroding out of KS-3. However, this site was back-filled after a short time due to the expansion of excavations in the Northern Exposures.

In 1995, a rich concentration of fossils and artefacts was noted on a gentle slope of KS-1 and KS-2 sediment trending west to east away from the main Kanjera Fm (S) embankment. Surface sediment from a 5 m × 8 m area was swept and sieved with 1 mm mesh. A total of 1438 fossils including bovid, equid (*Equus* sp.), suid, hippopotamid, proboscidean (*Deinotherium* sp.), crocodile and fish remains were collected, along with 19 flakes and a scraper. A 2.0 m × 4.0 m test square (Test Square 1) was excavated in 5 cm spits in this slope with awls and dental picks. The coordinates of 92

fossils and 96 lithics were recorded with a laser transit, and hundreds of additional fossils and artefacts were recovered in spit bags and sieving through 1 mm mesh.

Fieldwork in 1996 and 1997 focused on clarifying the context, age and nature of the archaeological occurrences in the Southern Exposures. Two large excavations (Excavations 1 and 2; 41 m<sup>2</sup> and 15 m<sup>2</sup>, respectively) and three small excavations (Excavations 5, 6 and 7, 4 m<sup>2</sup> each) were carried out (Figure 3). Excavation again proceeded in 5 cm spits and all sediment was sieved through 1 mm mesh. Excavation 1 incorporated Test Square 1, and Excavation 2 incorporated the SC Site. Each of the excavations recovered Oldowan artefacts and fossils in spatial association, though object density was highest in Excavations 1 and 2. Our preliminary findings from these two excavations are described below.

**Table 1** Macromammalian fauna from the Kanjera Fm (S)

	KS-1/KS-2	KS-3	KS-4	KS-5
Cercopithecidae	X			
<i>Theropithecus</i> sp.	X			
Felidae, large	X			
<i>Metridiochoerus</i> sp.	X		X	
<i>M. andrewsi</i>	X			
<i>Kolpochoerus</i> sp.	X		X	
Hippopotamidae, large	X	X	X	
Bovidae, indeterminate				X
<i>Tragelaphus</i> cf. <i>scriptus</i>	X			
<i>Tragelaphus</i> , medium	X			
Tragelaphini, large			X	
Bovini	X		X	
Reduncini, small	X			
Reduncini, medium	X			
<i>Kobus</i> sp.	X			
Hippotragini	X			
Alcelaphini, medium	X	X	X	
<i>Megalotragus</i> sp.			X	
Antilopini	X			
<i>Gazella</i> sp.	X			
Equidae		X	X	
<i>Equus</i> sp.	X			X
<i>Hipparion</i> sp.	X			
Elephantidae, indeterminate	X			
<i>Elephas recki</i>			X	
<i>Deinotherium</i> sp.	X		X	

The KS-1 and KS-2 fossil samples are combined because surface sampling often cannot resolve between the two units.

### Excavation 1

Excavation 1 documented rich concentrations of ESA artefacts and well preserved fossils in both KS-1 and KS-2 (Figure 4). Work was conducted in two rectangular areas separated by a 0.5 m balk, designated Excavation 1 and the Excavation 1 Extension, respectively. KS-1 here was a fine sand to sandy silt with granule patches and occasional pebbles. No channel features have been found in this unit, and it appears that deposition occurred through diffuse flow, perhaps on a floodplain.

KS-2 sediments at Excavation 1 were deposited by a small channel cutting into the top of KS-1. Two KS-2 facies were documented; a 5–10 cm thick, discontinuous conglomerate in a calcareous matrix lining the channel base (KS-2 CP) overlain by a

pebbly, fine to medium sand (KS-2 PS). KS-1 and KS-2 sediment samples from within and below Excavation 1 contained small pedogenic carbonate nodules and associated organic matter as well as petrographic evidence of weakly to moderately developed soils. Water flow was transient and soils formed during depositional hiatuses. KS-3 consisted of a sandy silt, deposited in low aspect channels under a low energy flow regime.

A substantial number of artefacts and fossils were collected after their three-dimensional coordinates had been recorded with a laser transit. Four hundred and thirty one artefacts as well as 367 fossils were recovered from KS-1, 262 artefacts and 74 fossils were collected from KS-2 CP and 730 artefacts and 362 fossils were collected

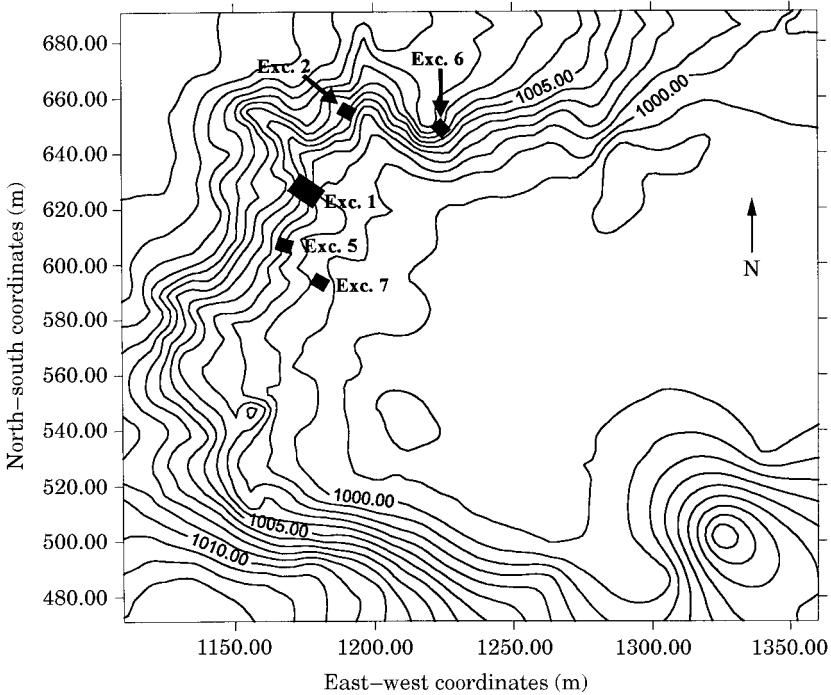


Figure 3. Contour map of the Southern Exposures, showing the relative positions of Excavations 1, 2, 5–7.

from KS-2 PS. Finally, 12 flakes and 12 fossils were recovered from KS-3. Many additional fossils and artefacts were collected in spit bags and sieving from each of these units.

*Preliminary analysis of site formation.* The recovery of Oldowan artefacts from KS-1, KS-2 and KS-3 confirm that hominids were active in the vicinity of the Southern Exposures during the deposition of these beds. Cores recovered from the excavations include forms common at Bed I Olduvai (e.g., choppers, polyhedrons; Leakey, 1971) as well as incidentally flaked blocks of stone. Flakes from both early and late stages of Toth's (1987) reduction sequence have been noted.

Field observations of bone and artefact orientations, skeletal part representation and artefact and fossil spatial association suggest that the influence of hydraulic activity on

assemblage formation varied among the different stratigraphic units in Excavation 1. Water flow frequently aligns objects with long axes either parallel or perpendicular to the direction of flow (Lyman, 1994). A nonrandom orientation distribution may indicate that water flow influenced object alignment and potentially played an important role in forming or modifying an assemblage. Because randomness yields an essentially uniform distribution, it is possible to use a chi-square test to compare the expected frequency of object orientations in  $10^\circ$  intervals to the observed frequency (Swan & Sandilands, 1995). The KS-1 distribution of object orientations is indistinguishable from a random sample drawn from a uniform data set (chi square value = 37.51; critical value of 49.80 with d.f. = 35,  $\alpha = 0.05$ ). The KS-2 PS and KS-2 CP samples, however, both have orientation distributions significantly different from

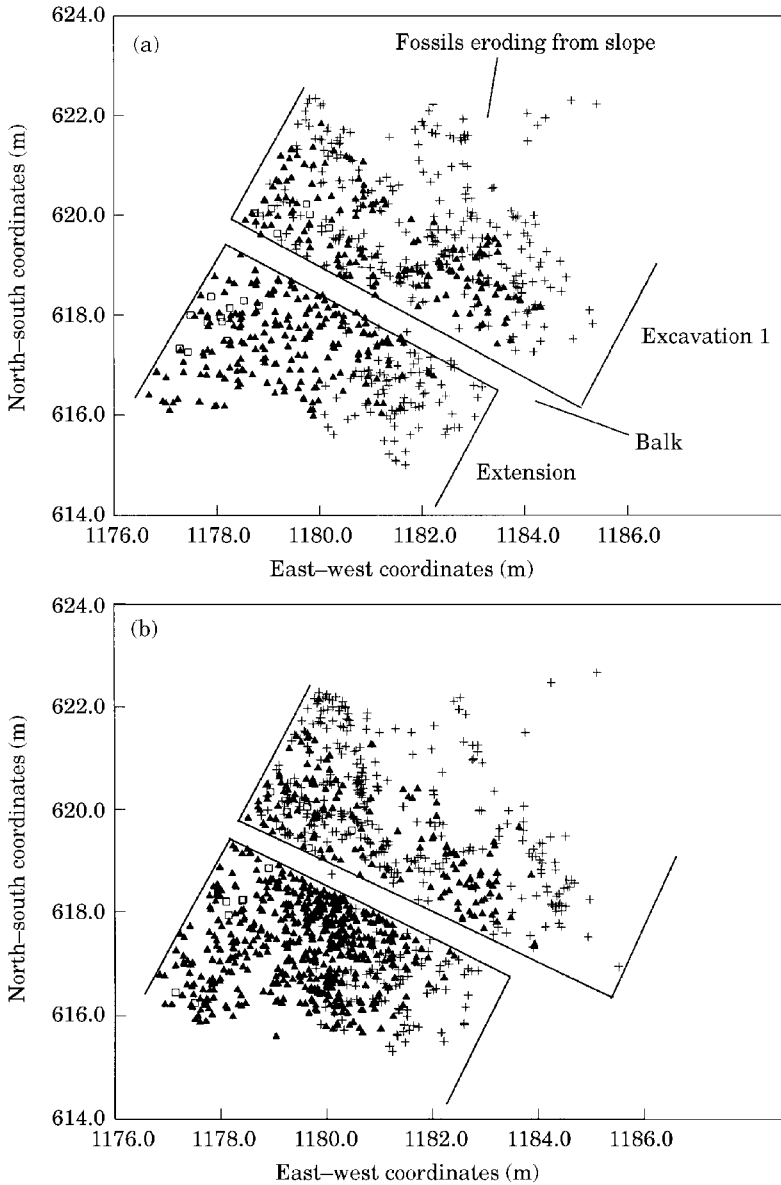


Figure 4. (a) and (b) .

random (chi square values of 52.60 and 85.00, respectively). Rayleigh's test indicates that the KS-2 CP sample has a significant mean direction of  $6.45^\circ$  ( $R\text{-bar}=0.54$ ; critical value of 0.21 with  $n=72$ ,  $\alpha=0.05$ ), indicating relatively rapid flow towards the depositional low to the north.

There was not a single prevailing current direction during KS-2 PS deposition ( $R\text{-bar}=0.13$ ; critical value of 0.18 with  $n=91$ ,  $\alpha=0.05$ ) (Swan & Sandilands, 1995).

Since skeletal parts vary in their susceptibility to water transport based on differences



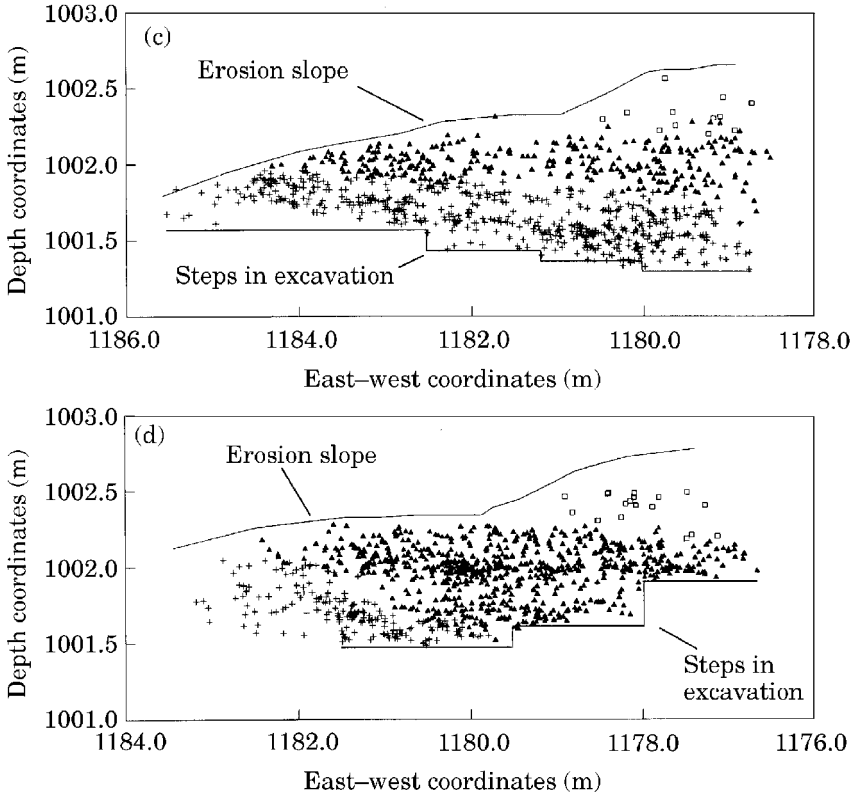


Figure 4. (c) and (d).

Figure 4. Horizontal distribution of (a) fossils and (b) artefacts and vertical distributions of (c) artefacts and fossils from Excavation 1 and (d) artefacts and fossils from Excavation 1 Extension. Plotting symbols are as follows: plus signs=KS-1, filled triangles=KS-2 PS, open squares=KS-3. For clarity, objects from KS-2 CP are not plotted.

in density, weight and shape (Voorhies, 1969; Behrensmeyer, 1975; Lyman, 1994), analysis of the skeletal part representation of an assemblage can assist in determining the significance of fluvial processes in site formation. Many studies have sorted skeletal parts into one of three transport groups: easily transported (e.g., axial bones), intermediate (e.g., most long bones), or lag (e.g., isolated teeth and jaws) (Voorhies, 1969; Behrensmeyer, 1975). Table 2 presents the field identifications of the sub-sample of piece-plotted fossils from Excavation 1 identifiable to skeletal part. The KS-1 sample is clearly not dominated by lag elements and contains a higher proportion of axial bones

and a lower proportion of skull fragments than either KS-2 facies.

Deposition of the KS-2 CP conglomerate probably occurred over a relatively short period of time, under a high energy flow regime. The preferred orientation of objects from this unit, as well as the higher concentration of lag elements relative to the KS-1 assemblage suggests that hydraulic activity played the dominant role in assemblage formation.

Objects from KS-2 PS also exhibit non-random orientations, but the largest artefacts and fossils appear to be oversized clasts relative to grain size. This suggests that fossil and artefact deposition was not simply the



**Table 2** Field identifications of bones recovered with coordinates from Excavations 1 and 2, presented as number of identifiable specimens (NISP)

Anatomical part	Excavation 1				Excavation 2			
	KS-1	KS-2 CP	KS-2 PS	KS-3	KS-1	KS-2 CP	KS-2 PS	KS-3
Cranial fragments	1	1	3	0	1	0	0	0
Mandibular/maxillary	8	3	3	0	1	0	0	0
Isolated teeth	48	9	80	4	5	9	11	4
Vertebrae	15	2	5	0	6	0	4	6
Ribs	39	5	12	0	2	4	6	3
Scapulae	5	2	2	0	1	0	0	0
Innomimates	5	0	2	0	0	0	0	3
Girdle indeterminate	0	0	0	0	0	2	0	0
Humeri	5	1	0	0	0	0	0	0
Radii	3	0	1	0	0	1	1	0
Ulnae	3	0	2	0	0	0	0	0
Metapodials	6	1	5	0	2	0	2	0
Femora	3	0	1	0	0	0	1	0
Tibiae	4	0	2	0	0	1	0	0
Long bone indeterminate	43	6	22	0	3	7	5	0
Podials	3	1	2	0	2	0	1	0
Phalanges	1	1	3	0	1	0	0	0
<b>Total bones</b>	192	32	145	4	24	24	31	16
Percent cranial	30%	41%	59%	100%	29%	38%	35%	25%
Percent axial	28%	22%	12%	0%	33%	17%	32%	56%
Percent girdle	5%	6%	3%	0%	4%	8%	0%	19%
Percent limb	37%	31%	26%	0%	33%	38%	32%	0%

Percentages of bones by anatomical region are also provided. Cranial refers to cranial, mandibular and maxillary fragments and isolated teeth, axial refers to vertebrae and ribs, girdle refers to scapulae and innomimates and limb refers to long bones, podials and phalanges.

result of hydraulic activity. However, the fossil assemblage from this unit contains the highest concentration of lag elements (e.g., isolated teeth; Table 2). Hydraulic activity might thus have had two roles, both contributing material to the KS-2 PS fossil and artefact assemblages, as well as winnowing materials accumulated attritionally or through the activity of hominids and/or carnivores.

Lithic raw material type has been documented for a subset of the Excavation 1 artefacts in order to begin assessing hominid resource transport. For both KS-1 and KS-2 PS, the raw materials used in artefact manufacture were predominantly local, fine-grained igneous rocks derived from the Homa Mountain Carbonatite Complex (Table 3). The KS-2 CP conglomerate is

also dominated by local igneous rocks. In contrast, 14% of the KS-1 artefact sample and 17% of the KS-2 PS artefact sample are made from materials (quartzite, chert, vein quartz, quartz porphyry) either not present or only rarely present as clasts in the formations north of Homa Mountain (Ditchfield *et al.*, 1998). Given our current understanding of the regional stratigraphy, it seems possible that these imported raw materials were transported over distances greater than other sites of this age.

Comparison of object densities (Table 4) demonstrates that Excavations 1, 2 and (for KS-2 PS) 6 have higher concentrations of artefacts and fossils than Excavations 5 and 7. This suggests that the fossils and artefacts recovered from the former excavations represent concentrations above the normal

**Table 3** Lithological breakdown of a subsample of artefacts from Excavations 1 and 2

	Exc. 1				Exc. 2
	KS-1	KS-2 CP	KS-2 PS	KS-3	KS-2 PS
Local fine-grained igneous	77	31	72	0	11
Local miscellaneous igneous	4	4	17	1	5
Sedimentary	4	1	0	0	0
Volcanic glass	0	0	0	0	1
<i>Quartz porphyry</i>	0	0	1	0	0
<i>Quartzite</i>	9	0	10	0	1
<i>Vein quartz</i>	0	0	3	0	0
<i>Chert</i>	5	0	4	0	0
<b>Total</b>	99	36	107	1	18
<i>Percent nonlocal</i>	14%	0%	17%	0%	6%

Italicized lithologies are not locally available and must have been transported to Kanjera South from elsewhere. Local igneous rocks refer to lithologies derived from the Homa Mountain Carbonatite Complex. Sedimentary refers to limestone and lithified sandstone.

**Table 4** Density of artefacts and fossils with coordinates from the Kanjera South excavations

Sample	Bone density (#/m <sup>2</sup> )	Artefact density (#/m <sup>2</sup> )
<b>Excavation 1</b>		
KS-1	9.0	10.5
KS-2 CP	2.6	9.2
KS-2 PS	10.1	20.5
KS-3	2.1	1.6
<b>Excavation 2</b>		
KS-1	8.7	6.2
KS-2 CP	10.4	16.7
KS-2 PS	9.6	9.6
KS-3	4.9	2.4
<b>Excavation 5</b>		
KS-1	10.00	2.75
KS-2 PS	1.50	2.00
KS-3	0.00	0.25
<b>Excavation 6</b>		
KS-1	4.00	1.50
KS-2 CP	1.50	1.00
KS-2 PS	17.00	11.00
KS-3	0.00	0.25
<b>Excavation 7</b>		
KS-1	2.50	0.50
KS-2 PS	1.50	0.00
KS-3	0.50	0.00

background scatter of material. While hydraulic activity may have modified the Excavation 1 assemblages, it seems unlikely to have been the primary agent of accumu-

lation of KS-1. Excavation recovered fossils and artefacts ranging in size from small fragments less than 1 cm long to complete long bones of wildebeest-sized animals and 15 cm long cores. Many of the bones and artefacts are outsized clasts relative to grain size and are unlikely to have been water transported. Bones potentially belonging to single individuals (e.g., small antelope cranial and postcranial fragments found within a 10 cm interval over a 6 m<sup>2</sup> area) are associated with artefacts. Stone flakes were found in direct contact with several fossils.

Thus, there is a strong possibility that hominids were involved in forming the KS-1 assemblages at Excavation 1, given the clear spatial association between artefacts and fauna, the presence of non-local artefact raw materials, the lack of evidence for hydraulic accumulation and the relatively high concentrations of both artefacts and fauna. Bone surface preservation in general is good and it should be possible to discern surface modifications (stone tool cutmarks/percussion marks, carnivore toothmarks, sedimentary abrasion) once the bones are fully prepared. Moreover, Excavation 1 can be profitably extended, as the concen-

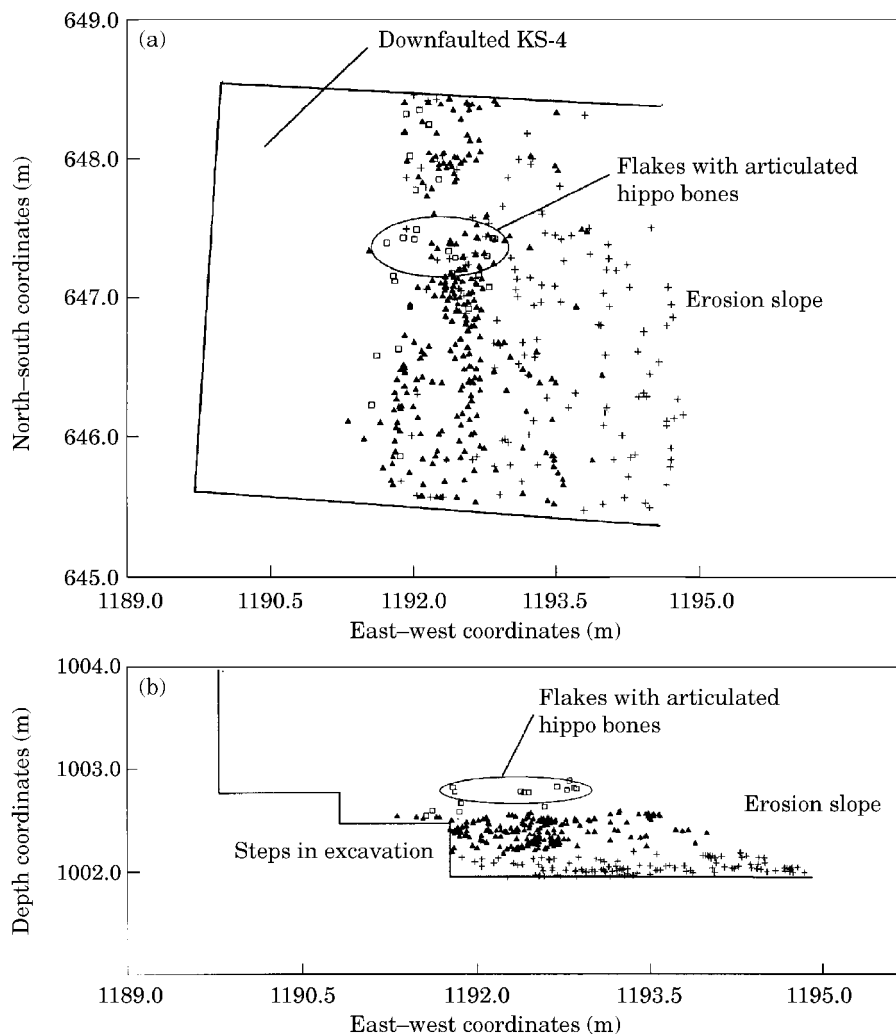


Figure 5. Horizontal (a) and vertical (b) distribution of fossils and artefacts from Excavation 2. Articulated hippo bones and associated flakes in KS-3 found within the elliptical area. Plotting symbols as in Figure 4.

trations of objects in both KS-1 and KS-2 PS did not taper off at the excavation margins.

#### Excavation 2

Excavation 2 was a 5 m × 3 m excavation approximately 30 m north of Excavation 1 (Figure 3). The excavation was stepped to sample KS-1 to KS-4 (Figure 5). KS-2 exhibits both pebbly sand (PS) and

conglomerate (CP) facies similar to those sampled in Excavation 1, and KS-3 is a sandy silt with rare pebbles. KS-4 is a silty clay, downfaulted along the western side of the excavation. KS-4 was largely sterile here, so excavation focused on a 3 m × 3 m area sampling KS-1 to KS-3.

Oldowan artefacts and fossils were again found spatially associated in Beds KS-1, KS-2 and KS-3. KS-3 yielded a complete

hippopotamus pelvis with at least five articulated lumbar vertebrae, as well as a canine and two ribs, in spatial association with five flakes (Figure 5). The flakes were recovered from the sediment adhering to the pelvis and vertebrae, suggesting that they were behaviorally linked to these bones. A core, two flakes, three possible artefacts and several additional fossils (Table 2) were also recovered from this unit. The relatively fine grain size of KS-3 and the articulated hippo bones suggest minimal disturbance during burial. The KS-3 concentration of fossils and artefacts is not very dense and it seems that our excavation partially uncovered the death site of a hippopotamus, which may have been butchered by hominids. This reconstruction of site formation will be evaluated once the hippo bones are cleaned of matrix and assessed for hominid and carnivore damage.

Seventy-two artefacts were recovered with coordinates from KS-2 PS. Both local and nonlocal raw materials were used in artefact manufacture (Table 3). KS-2 CP yielded 75 artefacts and 56 artefacts were collected from KS-1. The small samples of identifiable bones recovered thus far from each unit (Table 2) are not dominated by lag elements, though KS-2 CP has the lowest proportion of axial bones.

In summary, traces of hominid activity were found *in situ* in KS-1, KS-2 and KS-3 in the Southern Exposures at Kanjera. Based on magneto- and biostratigraphy, these beds are older than 2.15 Ma. They were deposited within a small basin, probably by low aspect channels with diffuse flow of variable velocity. Poor to moderate paleosol formation indicates that stable landsurfaces formed during depositional hiatuses. The contexts of the fossil and artefact assemblages varies from primary context (e.g., the KS-3 hippo axial bones and flakes at Excavation 2) to strongly influenced by fluvial processes (artefacts and fossils found within KS-2 CP).

Randomly-oriented artefacts and fossils, skeletal elements with a variety of transport potentials and the presence of both artefact and fossil outsized clasts suggests that the KS-1 assemblages were not formed primarily through hydraulic activity, though they may have been modified by water flow. The relatively high concentrations of objects at Excavations 1 and 2 versus 5, 6 and 7 suggests that behavioral processes may have concentrated objects at the former sites. A detailed reconstruction of site formation processes will be carried out following the preparation of excavated materials. One hypothesis to be tested is that hominids played a primary role in accumulating materials in KS-1, and possibly KS-2 PS, at Excavation 1.

#### **Preliminary paleoecological analysis**

The presence of archaeological materials in Beds KS-1 through KS-3 provides clear evidence that hominids were active at the Southern Exposures over a long period of time. Documentation of the specific habitats present on-site, as well as of the broader macromammalian paleocommunity, provides a valuable insight into the range of habitats utilized by Oldowan hominids during deposition of the Kanjera Fm (S).

The paleoecology of the Kanjera Fm (S) is currently being interpreted through analysis of the stable isotopic composition of the pedogenic carbonates and taxon-based faunal analysis. In addition to these methods, we intend to employ taxon-free analysis of ungulate postcrania (cf. Bishop, 1994; Plummer & Bishop, 1994; Kappelman *et al.*, 1997) and stable isotopic analysis of soil organics and fossil tooth enamel in the future (cf. Sikes, 1994; Morgan *et al.*, 1994).

Preliminary results of stable isotopic analysis of pedogenic carbonates from four of the six beds of the Kanjera Fm (S) are presented in Table 5 and Figure 6. Delta

**Table 5 Preliminary stable isotopic data from the Kanjera Fm (S)**

Sample description	Sample number	Delta <sup>13</sup> C per mil	Delta <sup>18</sup> O per mil
KS-5 pedogenic carbonate nodule samples	HP-95-37a	-0.63	2.22
	HP-95-37b	-6.61	0.39
KS-4 pedogenic carbonate nodule samples	HP-95-38a	-6.16	-2.58
	HP-95-39	3.60	-4.84
	HP-95-40c	2.47	-2.97
	HP-95-40b	-1.97	-4.72
	HP-95-40a	-1.87	-3.06
KS-2 PS pedogenic carbonate nodules in Exc. 1	HP-95-58	-1.24	-5.80
KS-2 CP carbonate cement in Exc. 1	KJS-96-2/1	-0.65	-2.11
KS-1 pedogenic carbonate nodules in Exc. 1	KJS-96-6b	0.23	-4.40
KS-1 pedogenic carbonate nodules below Exc. 1	HP-95-46	-0.52	-7.19

Samples are listed in stratigraphic sequence from the base (KS-1) to the top (KS-5) of the formation. Results are not yet available for Beds KS-3 and KS-6.

<sup>13</sup>C values for pedogenic carbonates formed in 100% C<sub>3</sub> (closed canopy forest) and 100% C<sub>4</sub> (open grassland) habitats range between -14 to -9 per mil and +1 to +4 per mil, respectively (Cerling, 1984; Cerling *et al.*, 1989; Sikes, 1994). Intermediate delta <sup>13</sup>C values indicate a mix of C<sub>3</sub> and C<sub>4</sub> vegetation. All of the KS-1 and KS-2 samples from within the excavation, as well as a KS-1 sample from below the excavation are indicative of habitats with a significant fraction (>75%) of C<sub>4</sub> plant biomass. These values are consistent with wooded grassland, dwarf shrub grassland or open grassland habitats (Figure 6), indicating that the Excavation 1 assemblage accumulated in a relatively open setting. Delta <sup>13</sup>C values from KS-4 are suggestive of open grassland during much of the deposition of this bed. However, the proportion of C<sub>3</sub> vegetation seems much greater near the top of KS-4 and at the base of KS-5, suggesting deposition under grassy woodland conditions. Pedogenic carbonates at the top of KS-5 are again suggestive of a C<sub>4</sub>-dominated plant community.

Preliminary analysis of the faunal samples from Excavations 1 and 2 suggests that these occurrences were not being formed in an

isolated patch of C<sub>4</sub>-rich vegetation, but that grass was a significant component of the regional plant paleocommunity. The three most common macromammalian families in many modern East African, grass-dominated ecosystems are (from greatest to least abundant) the Bovidae, the Equidae and the Suidae (Table 6) (Potts, 1988). Bovids typically comprise at least 70%, equids between 10% and 25% and suids less than 5% of the fauna in game reserves with a large C<sub>4</sub> grass component (Houston, 1979; Turner & Watson, 1964; Lamprey, 1964; Foster & McLaughlin, 1968; Kruuk, 1972; Schaller, 1972). Central and West African game reserves with heavy tree and/or bush cover also exhibit high proportions of bovids, but generally have few (or no) equids and variable numbers (2% to 37%) of suids (Table 6) (Milligan *et al.*, 1982). The proportions of bovids, equids and suids recovered from the surface of Excavation 1 and *in situ* in KS-1 and KS-2 is similar to the proportions of these families in modern, C<sub>4</sub>-dominated game reserves (Table 6). Moreover, even where samples are small, these families consistently have abundance rankings of bovids>equids>suids. The relatively high proportion of equids

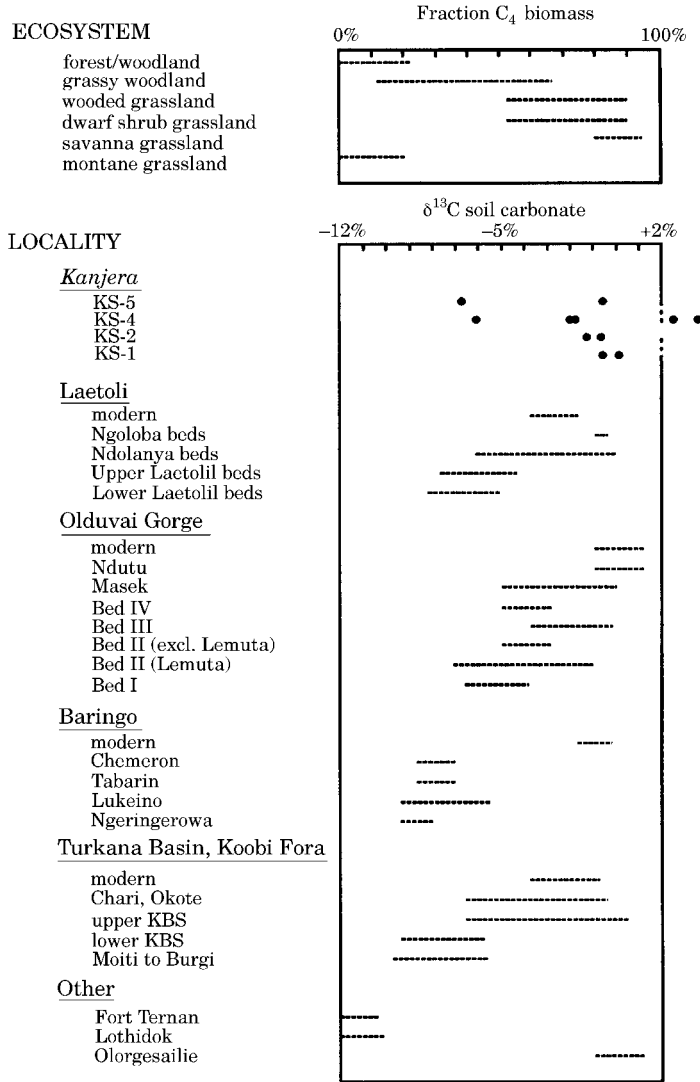


Figure 6. Estimated C<sub>4</sub> biomass for the Kanjera Fm (S) based on the carbon isotopic composition of paleosol carbonates, compared to data from modern East African ecosystems and fossil localities (after Cerling, 1992: Figure 3).

complements our stable isotopic analysis of pedogenic carbonates in suggesting that a significant amount of C<sub>4</sub> vegetation existed in the vicinity of Southern Exposures during Kanjera Fm (S) deposition. It thus seems likely that excavations at Kanjera preserve traces of Plio-Pleistocene hominid activity in a relatively open setting.

**Discussion**

The goal of our research at Kanjera South is to investigate the paleoecology and behavior of late Pliocene hominids. Technological analysis of the artefacts and detailed reconstructions of site formation will follow laboratory analysis in the near future. Here

Table 6 Proportion representation of bovids, equids and suids in a sample of modern African game reserves, Excavations 1 and 2 from Kanjera and Bed I Olduvai archeological levels

Modern samples	Annual rainfall	Dominant vegetation types	% Bovids	% Equids	% Suids
<b>Wildlife preserves with high proportions of C4 grass</b>					
Serengeti, Tanzania	800	Bushland, grassland	87	10	2
Ngorongoro Crater, Tanzania	750	Bushland, grassland and montane	77	23	<0.5
Nairobi Park, Kenya	500	Bushland, grassland	79	14	4
<b>Wildlife preserves with high proportions of C3 vegetation</b>					
Comoe, Ivory Coast	1200	Woodland, forest/grassland	97	0	3
Arl, Burkina Faso	1000	Woodland	88	0	12
Yankari, Nigeria	1000	Woodland	63	0	35
<b>East African paleoanthropological samples</b>					
<b>Excavation 1</b>					
Surface (5 m × 8 m area) ( <i>n</i> =89; 70 bovid, 10 equid, 2 suid, 5 hippo, 2 proboscidean)			79	11	2
<i>In situ</i> in KS-2 PS ( <i>n</i> =55; 40 bovid, 10 equid, 3 cercopithecoid, 2 hippopotamid)			73	18	0
<i>In situ</i> in KS-2 CP ( <i>n</i> =13; 12 bovid, 1 equid)			92	8	0
<i>In situ</i> in KS-1 ( <i>n</i> =66; 49 bovid, 14 equid, 3 suid)			74	21	5
<b>Excavation 2</b>					
<i>In situ</i> in KS-3 ( <i>n</i> =13; 2 bovid, 11 hippopotamid)			15	0	0
<i>In situ</i> in KS-2 PS ( <i>n</i> =13; 9 bovid, 3 equid, 1 hippopotamid)			69	23	0
<i>In situ</i> in KS-2 CP ( <i>n</i> =7; 6 bovid, 1 equid)			86	14	0
<i>In situ</i> in KS-1 ( <i>n</i> =9; 8 bovid, 1 equid)			89	11	0
<b>Bed I Olduvai hominid accumulations</b>					
FLK North Level 6 ( <i>n</i> =740, including a partial elephant skeleton)			35	0	10
FLK Level 22 (Zim) ( <i>n</i> =614)			83	6	5
FLK NN Level 3 ( <i>n</i> =390)			65	3	9
DK Level 2 ( <i>n</i> =832)			72	2	14
DK Level 3 ( <i>n</i> =518)			69	4	13

Fossil data given in percent NISP. Game reserve and Olduvai data from Potts (1988: 166–174). Rainfall data and vegetation descriptions from Shipman & Harris (1988: 349–365).



we focus on the implications of this project for understanding Oldowan hominid paleoecology.

A number of studies (e.g., Vrba *et al.*, 1995) have suggested that African climates became colder and more arid during the late Pliocene. This climatic trend has been linked to incursions of large mammals (e.g., *Equus*) into Africa, lineage turnover and morphological changes connected with an increased utilization of tougher and perhaps more abrasive foodstuffs (e.g., Turner & Wood, 1993). Isotopic analyses have suggested an increase in the proportion of C<sub>4</sub> vegetation in East Africa during the late Pliocene and early Pleistocene, with large expanses of pure C<sub>4</sub> grasslands becoming established during the middle Pleistocene (e.g., Cerling, 1992; but see also Kingston *et al.*, 1994). While large-scale environmental change may be documented in the geological and paleontological records, it is difficult to resolve what the relative proportions of specific habitats were at a given place and time, and how the relative proportions of these different habitats may have changed over time. Detailed reconstructions of paleohabitats based on geological and paleontological evidence are necessary in order to better understand hominid habitat usage, particularly whether hominids were using the full spectrum of available habitats or a restricted portion of that spectrum.

While preliminary, results from Kanjera already suggest a novel paleohabitat context for Oldowan hominid activities. As reviewed by Sikes (1994), there is little consensus regarding Plio-Pleistocene hominid habitat preferences in East Africa. Moreover, the depositional context of isolated hominid fossils may not provide a clear indication of habitat preference during life (White, 1988). In contrast, archaeological occurrences can provide evidence of hominid activities in specific paleoecological settings and of the broader paleocommunity that the hominids

were part of (Plummer & Bishop, 1994; Sikes, 1994). Isotopic and faunal methods of reconstructing hominid paleoecology are complementary; isotopic data provide an indication of the paleohabitat in which archaeological accumulations were formed, while archaeological fauna suggest the range of habitats being utilized by hominids and provide information on the broader paleocommunity. Fauna recovered from controlled excavations, which minimize time averaging and provide the most detailed contextual information, are preferable to surface collected material.

Olduvai Gorge, Tanzania is the best known locality in which the paleoenvironmental context of Oldowan archaeological occurrences can be assessed using both *in situ* archaeological fauna and stable isotopic data documenting the habitats present during site formation. Stable isotopic analyses of paleosol carbonates and associated organics from Bed I (1.75–1.98 Ma) and lower Bed II (c. 1.74 Ma) Olduvai, for example, have documented archaeological occurrences in habitats ranging from riverine forest to grassy woodland (Sikes, 1994). Sikes' carbon isotopic values on paleosol carbonates agree well with those obtained by Cerling (Cerling & Hay, 1986; Cerling, 1992) from paleosol carbonates from Bed I and Bed II (excluding the Lemuta Member). In contrast to modern East African ecosystems with a large C<sub>4</sub> component, suids are consistently more abundant than equids at the Bed I hominid sites. In fact, suids generally made up more than 10%, and equids less than 10%, of the large mammal fauna in these assemblages (Table 6) (Potts, 1988). It is possible that Bed I hominids were preferentially utilizing wooded habitats over more open ones (Blumeschne, 1987; Sikes, 1994). However, isotopic studies have yet to identify areas of open grassland in Bed I and lower Bed II Olduvai, even though its local presence is clearly indicated by the

habitat-specific morphology of fossil antelopes (Plummer & Bishop, 1994; Kappelman *et al.*, 1997). Hominid foraging through a broad spectrum of habitats, rather than a single habitat, is suggested by the high taxonomic diversity of the Bed I archeological fauna (Potts, 1988), as well as the range of antelope and suid ecomorphologies present in faunal accumulations formed by hominids (Plummer & Bishop, 1994; Bishop & Plummer, in prep.). Therefore, while hominids at Olduvai were undoubtedly utilizing wooded habitats, the question of whether and how they used more open habitats has been difficult to assess.

The depositional setting at Kanjera appears broadly similar to that during Bed I and Bed II Olduvai deposition; deposition of the Kanjera Fm (S) occurred at the margin of a basin which at least periodically contained a small lake (Behrensmeyer *et al.*, 1995). The taxonomically diverse fauna from KS-1 and KS-2 (Table 1) suggests that a variety of habitats existed in the vicinity of Kanjera South, including edaphic grasslands and woodlands. However, unlike Olduvai, stable isotopic analysis of KS-1, KS-2 and lower KS-4 indicate that C<sub>4</sub> grass was the dominant vegetation in this portion of the basin during much of Kanjera Fm (S) deposition (Figure 6). The greater abundance of fossil equids relative to suids in the faunas from Excavations 1 and 2 is similar to the relative abundance of these families in modern East African savannas and contrasts with data from Bed I Olduvai hominid accumulations (Table 6). Moreover, alcelaphines comprise more than 50% of the taxonomically identifiable antelope remains from both KS-1 and KS-2 PS in our excavations. These various lines of evidence suggest that C<sub>4</sub> grass made up a larger component of the overall plant paleocommunity during lower Kanjera Fm (S) deposition than it did at Olduvai. The evidence from Kanjera South complements that from Olduvai, in providing evidence for Oldowan hominid activities

in a paleocommunity that may have been more broadly similar to those existing in East Africa today, as well as documenting Oldowan hominid activities in a more open context than has been noted previously. Kanjera provides an expanded geographical and ecological context for the earliest archaeological hominids and may ultimately broaden our view of their capabilities and behavioral ecology.

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## References

- Behrensmeyer, A. K. (1975). The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bull. Mus. Comp. Zool.* **146**, 473–578.
- Behrensmeyer, A. K., Potts, R., Plummer, T., Tauxe, L., Opdyke, N. & Jorstad, T. (1995). The Pleistocene locality of Kanjera, Western Kenya: stratigraphy, chronology and paleoenvironments. *J. hum. Evol.* **29**, 247–274.
- Bisford, L. (1988). Fact and fiction about the *Zinjanthropus* floor: data, arguments, and interpretations. *Curr. Anthropol.* **29**, 123–149.
- Bishop, L. (1994). Pigs and the ancestors: hominids, suids and environments during the Plio-Pleistocene of East Africa. Ph.D. Dissertation, Yale University.
- Blumenschine, R. (1987). Characteristics of an early hominid scavenging niche. *Curr. Anthropol.* **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. *J. hum. Evol.* **29**, 21–51.
- Bonnefille, R. (1995). A reassessment of the Plio-Pleistocene pollen record of East Africa. In (E. Vrba, G. Denton, T. Partridge & L. Burckle, Eds) *Paleoclimate and Evolution with Emphasis on Human Origins*, pp. 299–320. New Haven: Yale University Press.
- Brown, F. & Feibel, C. (1988). “Robust” hominids and Plio-Pleistocene paleogeography of the Turkana Basin, Kenya and Ethiopia. In (F. Grine, Ed.) *Evolution History of the “Robust” Australopithecines*, pp. 325–341. New York: Aldine de Gruyter.
- Bunn, H., Harris, J. W. K., Isaac, G., Kaufulu, Z., Kroll, E., Schick, K., Toth, N. & Behrensmeyer, A. K. (1980). FxJj 50: an early Pleistocene site in northern Kenya. *World Archaeol.* **12**, 109–136.
- Bunn, H. T. & Kroll, E. M. (1986). Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthropol.* **27**, 431–451.
- Cande, S. C. & Kent, D. V. (1995). Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. *J. Geophys. Res.* **100**, 6093–6095.
- Capaldo, S. D. (1997). Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. *J. hum. Evol.* **33**, 555–597.
- Cavallo, J. & Blumenschine, R. (1989). Tree-stored leopard kills: expanding the hominid scavenging niche. *J. hum. Evol.* **18**, 393–399.
- Cerling, T. E. (1984). The stable isotopic composition of modern soil carbonate and its relationship to climate. *Earth Planet. Sci. Letters* **71**, 229–240.
- Cerling, T. E. (1992). Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeog., Palaeoclimatol. Palaeoecol.* **97**, 241–247.
- Cerling, T. E. & Hay, R. (1986). An isotopic study of carbonates from Olduvai Gorge. *Quat. Res.* **25**, 63–78.
- Cerling, T., Bowman, J. & O’Neil, J. (1988). An isotopic study of a fluvial-lacustrine sequence: The Plio-Pleistocene Koobi Fora sequence, East Africa. *Palaeogeogr., Palaeoclimatol. Palaeoecol.* **63**, 335–356.
- Cerling, T. E., Quade, J., Wang, Y. & Bowman, J. R. (1989). Carbon isotopes in soils as ecology and palaeoecology indicators. *Nature* **341**, 138–139.
- Coppens, Y., Howell, F. C., Isaac, G. L. & Leakey, R. (Eds) (1976). *Earliest Man and Environments in the Lake Rudolf Basin*. Chicago: University of Chicago Press.
- deMenocal, P. & Bloemendal, J. (1995). Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution: a combined data-model approach. In (E. Vrba, G. Denton, T. Partridge & L. Burckle, Eds) *Paleoclimate and Evolution with Emphasis on Human Origins*, pp. 262–288. New Haven: Yale University Press.
- Ditchfield, P., Hicks, J., Plummer, T., Bishop, L. & Potts, R. (1999). Current research on the Late Plio-Pleistocene deposits north of Homa Mountain, southwestern Kenya. *J. hum. Evol.* **36**, 123–150.
- Dominguez-Rodrigo, M. (1997). Meat-eating by early hominids at the FLK 22 *Zinjanthropus* site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. *J. hum. Evol.* **33**, 669–690.
- Foley, R. (1987). *Another Unique Species*. New York: John Wiley & Sons.
- Foster, J. B. & McLaughlin, R. (1968). Nairobi National Park Game Census, 1967. *East African Wildlife Journal* **6**, 152–154.
- Grine, F. (ed.) (1988). *Evolutionary History of the “Robust” Australopithecines*. New York: Aldine de Gruyter.
- Hay, R. L. (1976). *Geology of the Olduvai Gorge: A Study of Sedimentation in a Semiarid Basin*. Berkeley: University of California Press.
- Harris, J. M. (Ed) (1991). *Koobi Fora Research Project*, Vol. 3. Oxford: Clarendon Press.
- Harris, J. M., Brown, F. H. & Leakey, M. G. (1988). *Stratigraphy and Paleontology of Pliocene and Pleistocene Localities West of Lake Turkana, Kenya*. Natural History Museum of Los Angeles County, Contributions in Science, Number 399.
- Harris, J. W. K., Williamson, P. G., Verniers, J., Tappen, M. J., Stewart, K., Helgren, D., de Heinzelin, J., Boqz, N. T. & Bellomo, R. V. (1987). Late Pliocene hominid occupation in Central Africa: the setting, context, and character of the Senga 5A site, Zaire. *J. hum. Evol.* **16**, 701–728.
- Hill, A., Ward, S., Deino, A., Curtis, G. & Drake, R. (1992). Earliest *Homo*. *Nature* **355**, 719–722.
- Houston, D. C. (1979). The Adaptations of scavengers. In (A. Sinclair & M. Norton-Griffiths, Eds) *Serengeti*, pp. 263–286. Chicago: University of Chicago Press.
- Howell, F. C., Haesaerts, P. & de Heinzelin, J. (1987). Depositional environments, archeological occurrences and hominids from Member E and F of the

- Shungura Formation (Omo basin, Ethiopia). *J. hum. Evol.* **16**, 665–700.
- Kappelman, J. K. (1984). Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeog., Paleoclimatol. Palaeoecol.* **48**, 171–196.
- Kappelman, J., Plummer, T., Bishop, L., Duncan, A. & Appleton, S. (1997). Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *J. hum. Evol.* **32**, 229–256.
- Kibunja, M. (1994). Pliocene archaeological occurrences in the Lake Turkana basin. *J. hum. Evol.* **27**, 159–171.
- Kimbel, W. G., Walter, R. C., Johanson, D. C., Reed, K. E., Aronson, J. L., Assefa, Z., Marean, C. W., Eck, G. G., Bobe, R., Hovers, E., Rak, Y., Vondra, C., Yemane, T., York, D., Chen, Y., Evensen, N. M. & Smith, P. E. (1996). Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *J. hum. Evol.* **31**, 549–561.
- Kingston, J. D., Marino, B. D. & Hill, A. P. (1994). Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. *Science* **264**, 955–959.
- Kruuk, H. (1972). *The Spotted Hyena*. Chicago: University of Chicago Press.
- Lamprey, H. F. (1964). Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. *East African Wildlife Journal* **2**, 1–46.
- Leakey, M. D. (1971). *Olduvai Gorge*, vol. 3. Cambridge: Cambridge University Press.
- Leakey, M. G., Feibel, C. S., McDougall, I. & Walker, A. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* **376**, 565–571.
- Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press.
- McHenry, H. (1994). Behavioral ecological implications of early hominid body size. *J. hum. Evol.* **27**, 77–87.
- Milligan, K., Ajayi, S. S. & Hall, J. B. (1982). Density and biomass of the large herbivore community in Kainji Lake National Park, Nigeria. *Afr. J. Ecol.* **20**, 1–12.
- Morgan, M. E., Kingston, J. D. & Marino, B. D. (1994). Carbon isotopic evidence for the emergence of C<sub>4</sub> plants in the Neogene from Pakistan and Kenya. *Nature* **367**, 162–165.
- Oliver, J. (1994). Estimates of hominid and carnivore involvement in the FLK Zinjanthropus fossil assemblage: some socioecological implications. *J. hum. Evol.* **27**, 267–294.
- Partridge, T., Bond, G., Hartnady, J., deMenocal, P. & Ruddiman, W. (1995). Climatic effects of late Neogene tectonism and volcanism. In (E. Vrba, G. Denton, T. Partridge & L. Burckle, Eds) *Paleoclimate and Evolution with Emphasis on Human Origins*, pp. 8–23. New Haven: Yale University Press.
- Plummer, T. W. & Bishop, L. (1994). Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *J. hum. Evol.* **27**, 47–75.
- Plummer, T. W. & Potts, R. (1989). Excavations and new findings at Kanjera, Kenya. *J. hum. Evol.* **18**, 269–276.
- Plummer, T. W. & Potts, R. (1995). The hominid fossil sample from Kanjera, Kenya: description, provenance and implications of new and earlier discoveries. *Am. J. phys. Anthrop.* **96**, 7–23.
- Potts, R. (1988). *Early Hominid Activities at Olduvai*. New York: Aldine de Gruyter.
- Potts, R. (1994). Variables versus models of early Pleistocene hominid land use. *J. hum. Evol.* **27**, 7–24.
- Prentice, M. & Denton, G. (1988). The deep-sea oxygen isotope record, the global ice sheet system and hominid evolution. In (F. Grine, Ed.) *Evolutionary History of the "Robust" Australopithecines*, pp. 383–403. New York: Aldine de Gruyter.
- Reed, K. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. hum. Evol.* **32**, 289–322.
- Roche, H. (1989). Technological evolution in the early hominids. *OSSA* **14**, 97–98.
- Rogers, J., Harris, J. W. K. & Feibel, C. (1994). Changing patterns of land use by Plio-Pleistocene hominids in the Lake Turkana basin. *J. hum. Evol.* **27**, 139–158.
- Schaller, G. B. (1972). *The Serengeti Lion*. Chicago: University of Chicago Press.
- 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. *Nature* **385**, 333–336.
- Sikes, N. (1994). Early hominid habitat preferences in East Africa: paleosol carbon isotopic evidence. *J. hum. Evol.* **27**, 25–45.
- Swan, A. R. H. & Sandilands, M. (1995). *Introduction to Data Analysis*. Oxford: Blackwell Scientific.
- Tobias, P. V. (1991). *Olduvai Gorge IV: The Skulls, Endocasts and Teeth of Homo habilis*. Cambridge: Cambridge University Press.
- Toth, N. (1987). Behavioral inferences from early stone artifact assemblages: an experimental model. *J. hum. Evol.* **16**, 763–787.
- Turner, A. & Wood, B. (1993). Comparative paleontological context for the evolution of the early hominid masticatory system. *J. hum. Evol.* **24**, 301–318.
- Turner, M. & Watson, M. (1964). A census in Ngorongoro Crater. *East African Wildlife Journal* **2**, 165–169.
- Voorhies, M. (1969). *Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska*. University of Wyoming Contributions to Geology Special Paper No. 1. Laramie.
- Vrba, E. S. (1985). Ecological and adaptive changes associated with early hominid evolution. In (E. Delson, Ed.) *Ancestors: the Hard Evidence*, pp. 63–71. New York: Alan R. Liss.
- Vrba, E. S. (1995). The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In (E. Vrba, G. Denton, T. Partridge & L. Burckle, Eds) *Paleoclimate and Evolution with Emphasis on Human Origins*, pp. 385–424. New Haven: Yale University Press.

- Wesselman, H. (1995). Of mice and almost-men: regional paleoecology and human evolution in the Turkana Basin. In (E. Vrba, G. Denton, T. Partridge & L. Burckle, Eds) *Paleoclimate and Evolution with Emphasis on Human Origins*, pp. 356–368. New Haven: Yale University Press.
- White, T. D. (1988). The comparative biology of “robust” *Australopithecus*: Clues from context. In (Grine, F. Ed) *Evolutionary History of the “Robust” Australopithecines*, pp. 449–483. New York: Aldine de Gruyter.
- WoldeGabriel, G., White, T. D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W. K. & Heiken, G. (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* **371**, 330–333.
- Wood, B. (1991). *Koobi Fora Research Project, Volume 4. Hominid Cranial Remains*. Oxford: Clarendon Press.
- Wood, B. (1992). Origin and evolution of the genus *Homo*. *Nature* **355**, 783–790.