

# Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya

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**The manufacture of stone tools and their use to access animal tissues by Pliocene hominins marks the origin of a key adaptation in human evolutionary history. Here we report an in situ archaeological assemblage from the Koobi Fora Formation in northern Kenya that provides a unique combination of faunal remains, some with direct evidence of butchery, and Oldowan artifacts, which are well dated to 1.95 Ma. This site provides the oldest in situ evidence that hominins, predating *Homo erectus*, enjoyed access to carcasses of terrestrial and aquatic animals that they butchered in a well-watered habitat. It also provides the earliest definitive evidence of the incorporation into the hominin diet of various aquatic animals including turtles, crocodiles, and fish, which are rich sources of specific nutrients needed in human brain growth. The evidence here shows that these critical brain-growth compounds were part of the diets of hominins before the appearance of *Homo ergaster/erectus* and could have played an important role in the evolution of larger brains in the early history of our lineage.**

Oldowan | Paleolithic | stone tools | paleomagnetism

Stone artifact production has long been considered a hallmark of human behavior and is often associated with brain expansion and changing patterns of hominin diet (1). The incorporation of animal tissue into the diet of late Pliocene (we refer here to previous definitions of the Pliocene to be consistent with previous descriptions of the paleoanthropological record) hominins is widely considered to be key to the suite of adaptations (e.g., enlarged brain, tooth size reduction, smaller gut, and increased body size) that began to set the earliest members of our genus apart from their ancestors and relatives. Much debate surrounds the diet of hominins, specifically regarding the dietary requirements of hominins with increasingly larger brains at the end of the Pliocene (2). However, remarkably little is known about what resources were important in the diets of hominins before *Homo erectus/ergaster* or how they acquired nutrient-dense resources. A few Pliocene localities display evidence of large accumulations of stone tools (3, 4), but procurement of animal resources before 2 Ma is documented at only a handful of localities in Ethiopia (5, 6) where the evidence of the use of stone tools to access large mammal carcasses is limited to ephemeral occupations and isolated events of hominin carnivory (4, 6) with few, or no, associated tools found in situ (5). The risks associated with increased reliance on large mammal tissue have suggested to some that alternative resources may have been more viable (7). Archaeological assemblages of tools and modified bones are key to our understanding of the food acquisition strategies of later hominin taxa as observed at several Pleistocene localities (8, 9). The large accumulations (Table 1) from the late Pliocene at FwJj20 presented here provides the oldest evidence that the hominin diet included a broad array of high-quality food items, including numerous aquatic resources.

The Turkana Basin in northern Kenya preserves one of the most comprehensive records of late Pliocene hominin behaviors. Early evidence of artifact manufacture can be found in the Shungura Formation (Fm) (10) at the site of Fejej in the northern Turkana Basin (11) and on the western side of the Turkana Basin in the Nachukui Fm (3). To date, however, large, in situ assemblages with associated artifacts, fauna, and hominin-modified bones are absent from the Pliocene archaeological record.

The Koobi Fora Fm on the eastern shores of Lake Turkana has previously yielded evidence of hominin behavior from 1.87 to 1.39 Ma (12, 13). Here we present data from a new locality, FwJj20, which is unique in its high concentration of terrestrial and aquatic faunal remains, some of which indicate modification by hominins in association with numerous artifacts. FwJj20 is located in the II Dura subregion of the Turkana Basin (14) ~10 km north of previously known archaeological sites in the Koobi Fora Formation (Fig. 1).

## Results and Discussion

The Plio-Pleistocene sediments of the II Dura region represent a complex interaction between a rapidly fluctuating lake and a series of fluvial systems (14, 15). These river systems were likely a combination of the dominant large axial river system (Proto-Omo) and ephemeral marginal river systems (Proto-II Eriet). The FwJj20 artifacts and fossil fauna were found in a 6- to 15-cm thick clay lens that is overlain by a fossil-bearing sand and pebble conglomerate unit, which is a laterally extensive feature within the upper Burgi Member (Mbr) in the II Dura subregion (14). A series of fining upward sequences and paleosols cap this sand and represent a transition from lacustrine to fluvial deposition, characteristic of the upper Burgi Mbr in the Koobi Fora Fm (16). The FwJj20 artifact horizon is an incipient soil that developed on the floodplain of a quickly aggrading deltaic system that was fed by either the proto-Omo River or a major tributary river system draining the Surgei Highlands (14).

The FwJj20 locality lies 14 m below a light gray tuffaceous horizon (Fig. 2) and ~40 m above the upper Burgi unconformity surface, which is estimated to 2.0 Ma (14). Geochemical compo-

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**Table 1. Comparison of FwJ20 finds and other Pliocene and Pleistocene localities that have described assemblages of modified bone associated with artifacts**

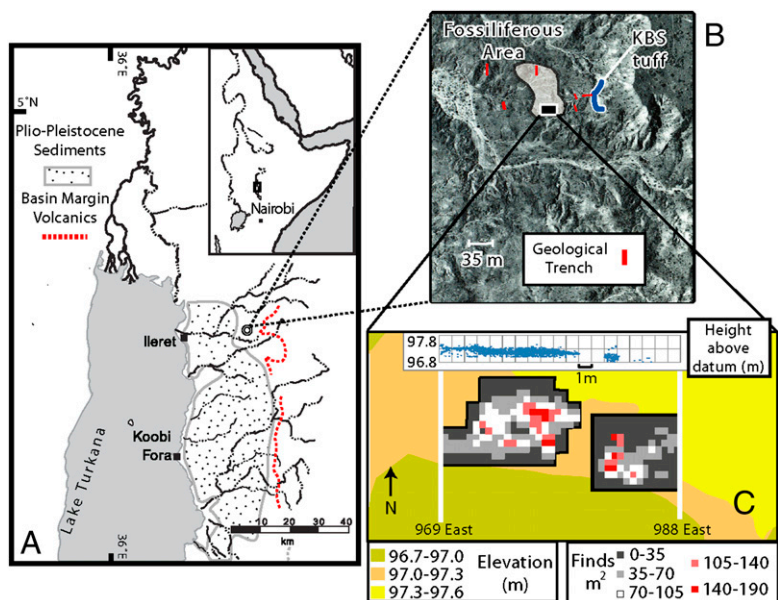
Locality	Age (Ma)	No. of artifacts	No. of identifiable mammal specimens (NISP)*	Minimum no. of individuals	Hominin-modified bones (% NISP) <sup>†</sup>
FxJ 50 (Koobi Fora, Kenya) (36)	1.57	1438	762	20	1.3
FLK "Zinj" (Olduvai Gorge, Tanzania) (36–38)	1.84	2647	699–1467	36	8.6–14.7
DK-2 (Olduvai Gorge, Tanzania) (39)	1.85	1163	832	41	1.2
FwJ20 (Koobi Fora, Kenya)	~1.95	2633	405	48	5.9
Lokalalei 2C (West Turkana, Kenya) (3)	2.34	2067	390	NR <sup>‡</sup>	<0.1 <sup>§</sup>
A.L. 666 (Makaamitalu, Ethiopia) (4)	2.34	34	~50 <sup>§</sup>	NR <sup>‡</sup>	Some specimens <sup>§</sup>
DAN-2(-D) (Gona, Ethiopia) (6)	2.5	Hundreds	>100 <sup>¶</sup>	NR <sup>‡</sup>	5 modified bones <sup>¶</sup>
Hata Mbr, Bouri Formation (Middle Awash, Ethiopia) (5)	2.5	0	NR <sup>‡</sup>	NR <sup>‡</sup>	Several modified bones
OGS 6–7 (Gona, Ethiopia) (6)	2.6	>700	>50 <sup>¶</sup>	NR <sup>‡</sup>	1 modified bone <sup>¶</sup>

NISP, number of identifiable specimens.  
 \*NISP values do not include nonmammalian remains.  
<sup>†</sup>Based on total NISP; values vary depending on inclusion of specimens with varying surface preservation.  
<sup>‡</sup>Values not reported.  
<sup>§</sup>Actual number of specimens not reported (3).  
<sup>¶</sup>NISP values are estimates from surface collections (5).

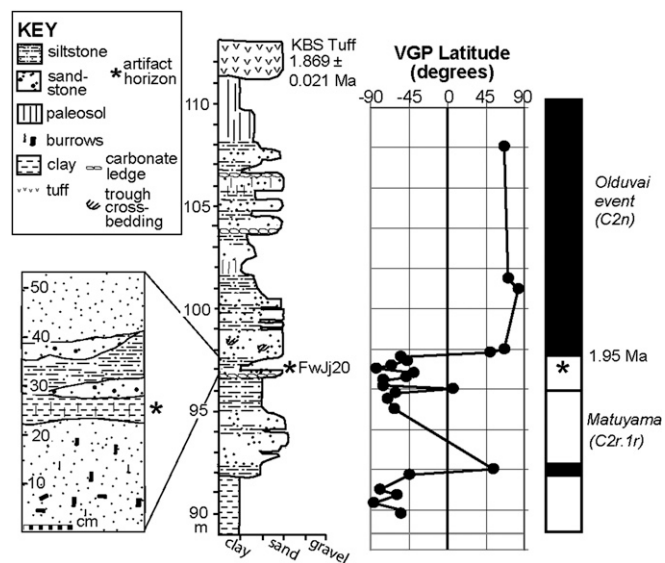
sition of the tuffaceous horizon above the site (Table S1) confirms this as the Kay Behrensmeier Site (KBS) tuff [1.869 ± 0.021 Ma (17)]. Magnetostratigraphic analysis indicates that the top 15 m (Fig. 2) of the section records a stable normal magnetic polarity. The Olduvai normal polarity Subchron is dated to between 1.95 and 1.78 Ma (18). As such, the normal polarity recorded below the KBS tuff is considered to represent the base of this event. A transition from reversed to a period of stable normal polarity occurs 0.9–1.0 m above the archaeological horizon. The artifact layer is associated with a stable reversed polarity and is located just below, or during, the polarity transition, thus placing the site at just older than the beginning of the Olduvai event at ~1.95 Ma (18).

The artifact and fossil-bearing clay horizon at FwJ20 overlies a bioturbated sandstone and may represent an abandoned channel bar or floodplain surface (Fig. 2). The blocky structure, lack of bedding, and oxidized Fe and Mn components of this laterally discontinuous clay horizon indicate incipient soil de-

velopment within the sediment onto which the artifacts were deposited. This surface was ephemeral and quickly buried. This scenario of rapid burial and high depositional rates is typical of the upper Burgi Mbr. Lateral to FwJ20, a pebble conglomerate is devoid of clasts resembling the artifacts at FwJ20, in either size or shape, and represents a high-energy environment adjacent to the FwJ20 soil surface. Higher energy scenarios of site formation at FwJ20 are precluded by (1) the lack of abraded edges on the stone artifacts, (2) the lack of preferred orientation of artifacts or fossils (Fig. S1), and (3) the lack of clasts similar in size or shape to the bones in the near-by pebble conglomerate. The data from FwJ20 point to an in situ assemblage of artifacts that was deposited on a short-lived soil surface by hominins. Although the artifacts may have been rearranged during deposition of the overlying silts and sands, the presence of both small artifacts and fossil bone fragments (<2-cm maximum dimension) reduces the likelihood of site winnowing (19). The vertical dispersion of



**Fig. 1.** Location of the FwJ20 Locality. (A) Map of the lower Omo Valley in Ethiopia and the northern part of Lake Turkana. Note Pliocene and Pleistocene sediments of the Koobi Fora Formation [redrawn from Brown et al. (40)] with location of the FwJ20 site marked as circle. Coordinates based on World Geodetic System 84 datum. (B) Aerial photograph noting lateral geological trenches. (C) Excavation of FwJ20 noting vertical distribution of finds, the elevation relative to a local datum, and the density of finds per square meter.



**Fig. 2.** Composite stratigraphy, virtual geomagnetic pole latitude, and geomagnetic polarity for the section above and below the FwJ20 site horizon and representative microstratigraphy of the artifact horizon. Normal polarity events are represented as a solid blocks. Section height is reported in meters and based on an arbitrary site datum. The microstratigraphy of the artifact horizon is drawn without vertical exaggeration.

artifacts and fossil bones is extremely thin. Over 98% (6,155 artifacts and fossils) of the excavated specimens were recovered within a 15-cm horizon.

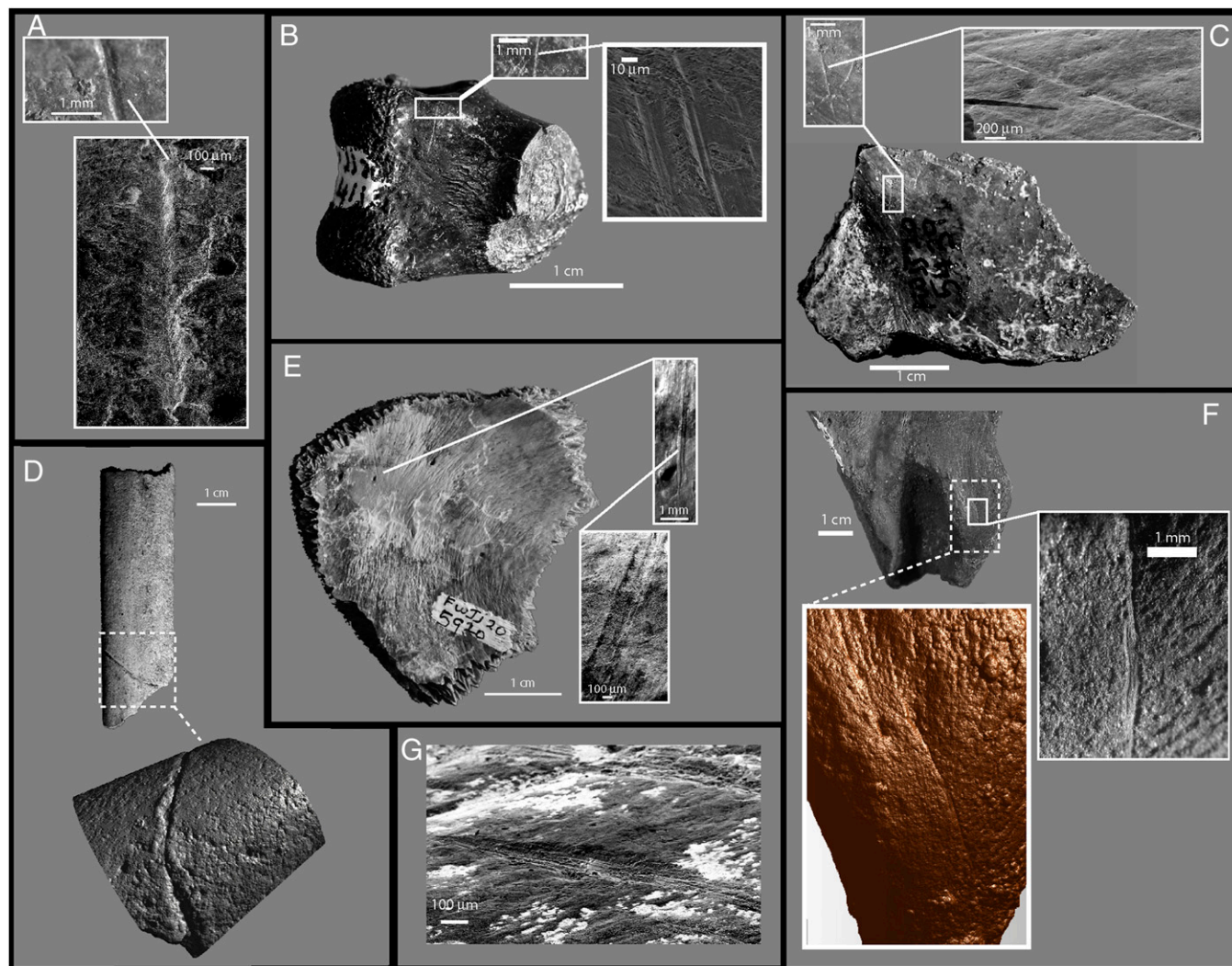
FwJ20 represents one of the largest Pliocene accumulations of stone artifacts from a single horizon associated with a large fossil assemblage (artifacts: 2,633; fossils: 3,648; Table S2). River systems draining the nearby Surgei-Asille highlands would have provided abundant access to large basalt cobbles. Although the smaller debitage portion of the assemblage is made on a variety of raw materials (e.g., chert, jasper, quartz), core forms are almost exclusively produced on basalt (91% of cores). This suggests variable artifact discard patterns mediated by raw material availability.

Excavations yielded 740 identifiable fossil bones of which 506 were suitable for the investigation of bone surface modifications [i.e., fracture patterns, surface preservation (20, 21)]. Investigations of the sediments above and below the archaeological site strongly suggest an association between surface and in situ fossils, however; all environmental and behavioral interpretations described here derive from analysis of the in situ materials. The high frequency of epiphyseal elements (36%; 98 epiphyses: 172 shaft fragments), especially of size class 1–2 animals (30 epiphyses: 29 shaft fragments, including examples of avifauna) suggest that the assemblage is markedly different from the patterns of bone accumulation documented for carnivores that crush and digest bone (22). Moreover, the percentage of carnivore tooth marks on limb bone fragments at FwJ20 (1.9%) is well below experimentally determined thresholds (~67%) associated with carnivore-only accumulations (22) and even lower than the frequency expected for assemblages ravaged by carnivores after hominin processing of carcasses (~20%) (23). Of the identifiable bone specimens that exhibited bone preservation that allowed surface modification investigation, 5.9% exhibit evidence of hominin modification (26 cutmarks, 4 percussion marks). Examples of percussion-fractured shaft fragments and bones with cut marks indicate that hominins at this site exploited terrestrial and aquatic mammals for meat and marrow, as well as the flesh of reptiles and fish (Fig. 3). The animals that these early tool users were accessing

range from size class 2 (e.g., impala, suids) to size class 5 (e.g., hippopotamus, rhinoceros) animals (13) and also include crocodiles, turtles, and catfish (Tables 2 and 3). Evidence of marrow extraction is present but lower than experimental expectations (FwJ20: percussion damage = 13% of all modifications). This is partially attributable to the prevalence of reptiles, which do not have marrow cavities that are appropriate for marrow extraction. Yet excluding reptile and fish bones does not increase this percentage to within experimental frequencies [1% of mammalian number of identifiable specimens (NISP)]. Evidence for hominin modifications at FwJ20 indicates that at least 10 separate animals were butchered at that site. Cut-mark locations are consistent with the disarticulation of large animals (e.g., cut marks on the astragalus of a hippopotamus and the glenoid of a bovid scapula). In addition, cut marks suggest evisceration (e.g., ventral surface of the costal shield of a turtle (24) as well as the medial side of the rib of a rhinoceros) and flesh removal (e.g., cut marks on the palmar surface of a phalanx of a crocodile severing the tendons of the muscle mass on the palmar surface of the manus).

Postfossilization fracture of limb bones during diagenesis and taphonomic degradation of the bone surfaces makes it difficult to quantitatively compare frequencies of bone surface modifications from FwJ20 with those determined in tightly controlled actualistic experiments. Experimental and archaeological evidence suggests that butchery of smaller animals (i.e., fish, reptiles) is less likely to leave characteristic evidence of butchery (25, 26). Therefore, the location and frequency of modifications at FwJ20 is not sufficient to address whether or not this collection represents the result of passive or confrontational scavenging from large carnivores. Hominins may have collected these elements from carcasses of natural death accumulations. However, hominins were clearly capable of accessing flesh from multiple carcasses. The percentage of hominin modifications at FwJ20 is lower than some experimental models of hominin butchery (27), indicating that hominins may not have been the only accumulating agent. However, the virtual absence of carnivore activity suggests that hominins were substantial actors of accumulation. The recovery of large numbers of individual animals [minimum number of individuals (MNI) = 48] from a discrete horizon suggests that at least some of the fragmentary specimens lacking clear evidence of modification may also be reflective of a Pliocene hominin diet. The skeletal representation of fish bones [over-abundance of cranial fragments: 64% of fish NISP (28)] and turtle/tortoise bones [over-abundance of carapace and plastron fragments: 90% of turtle/tortoise NISP (29)] corresponds to ethnographic and archaeological distributions associated with hominin foraging. The number and taxonomic diversity of hominin-modified bones imply that hominins used the FwJ20 locality for the acquisition of meat from several different carcasses of terrestrial and aquatic animals as well as marrow from mammalian bones. This provides strong evidence of a diverse animal component in the diets of hominins before the appearance of *H. ergaster/erectus*.

The butchery activities at FwJ20 occurred in a well-watered environment. The dominant taxonomic families among the 347 excavated specimens identifiable to family level include Hippopotamidae, Bovidae, Suidae, and Equidae (Tables 2 and 3). The FwJ20 bovid assemblage is dominated by more water-dependent tribes such as reduncines and tragelaphines (42% of the bovid NISP). Of the suids, the brachyodont form *Kolpochoerus* (cf. *heseloni*) is the most abundant genus. These fauna, in addition to other water-dependent genera (e.g., *Hippopotamus*, *Hexaprotodon*, and *Crocodylus*), indicate a well-watered environment at FwJ20. The mesic nature of the site is further supported by oxygen isotopic data of tooth enamel from FwJ20 (Figs. S2 and S3 and Table S3), which indicate an environment with low environmental aridity. The well-watered context of the FwJ20 is further supported by the recovery of plant macrofossils that are indicative of a lack of water stress on the surrounding vegetation (Figs. S4 and S5 and Table S4) (30).



**Fig. 3.** Hominin-modified bones from FwJ20. (A) Photograph and SEM image of a cut mark on a rib of a size 2 bovid; note internal striations and v-shaped mark. (B) Phalanx of a large reptile (Crocodylidae?) with a transverse cut mark; note the multiple striations and shoulder marks in the SEM image. (C) Internal surface of turtle carapace with two subparallel marks. SEM image shows v-shape of this mark. (D) Rib of a rhinocerotid with large v-shaped mark. (Lower) A 3D reconstruction of this mark created using a Roland MDX-40 scanner. (E) Turtle entoplastron with a single linear cut mark on the internal surface. SEM image shows internal striations of this mark. (F) Cranial fragment of *Clarias* with a single linear striation showing internal striations. Three-dimensional reconstruction created as in D. (G) SEM image showing scraping on the internal surface of a plastron fragment of a turtle/tortoise.

Generic-level identification of floral communities at FwJ20 indicated that *Drypetes* (Euphorbiaceae/Putranjivaceae), a palm tree, was the most common genus. Modern members of this genus occur mainly in low-altitude riverine forests.

The technological organization and artifact-mediated extraction of high-quality food resources found in the upper Burgi Mbr suggests that stone artifact manufacture was a significant part of the adaptive complex for hominins before *H. erectus/ergaster*. These data support inferences that suggest an increase in the diversity of dietary adaptations in Pliocene hominins (31, 32). The scale of butchery activities at FwJ20 contrasts with the isolated incidents of hominin carnivory recorded at other late Pliocene localities. The evidence from FwJ 20 indicates that hominins were very effective at securing access to a wider variety of high-quality animal tissues than has been previously documented. Some of these resources would have provided necessary dietary resources without the added predation risks associated with interactions with large mammalian carnivores that are sometimes involved with the acquisition of elements of large mammal carcasses (28, 33). In addition, although animal tissues provide

nutrient-rich fuel for a growing brain, aquatic resources (e.g., fish, crocodiles, turtles) are especially rich sources of the long-chain polyunsaturated fatty acids and docosahexaenoic acid that are so critical to human brain growth (2). Therefore, the incorporation of diverse animals, especially those in the lacustrine food chain, provided critical nutritional components to the diets of hominins before the appearance of *H. ergaster/erectus* that could have fueled the evolution of larger brains in late Pliocene hominins.

### Materials and Methods

**Paleomagnetic Analysis.** Seventy-two independently oriented samples were taken from two sections that were used to create a composite stratigraphic sequence (Fig. 2). Standard mineral magnetic measurements were undertaken on sister subsamples to determine the remanence-carrying minerals (34). Measurements were made using a cryogenic, superconducting quantum interference device based, spinner magnetometer. Sister samples from each layer were subjected to a 10- to 16-point alternating field, thermal and hybrid demagnetization. This indicated a strong viscous overprint in many samples, typically removed by 8 mT to reveal stable characteristic remanent magnetizations (ChRM). After magnetic cleaning, ChRMs were determined using principal component analysis. Fisher statistics were used to determine

**Table 2. Faunal remains associated with the excavation at FwJj20 locality**

Taxon	NISP	Hominin modification*	Carnivore modification
Aves	1		
Mammalia indeterminate	21	3 (2)	
Size class 1	39		
Size class 2	130	5	5
Size class 3	109	3 (1)	
Size class 4	79	1	
Size class 5	30		
Bovidae	1		
Size class 1	4		
Size class 2	41	1 (1)	2
Size class 3	6	2	1
Size class 4	5		
Giraffidae	8		
Hippopotamidae	23	2	
Suidae	8	1	
Equidae	8		
Rhinocerotidae	1	1	
Cercopithecidae	1		
Elephantidae	1		
Osteichthyes	15		
Clariidae	41	1	
Crocodylidae	85	2	
Chelonia	83	4	
Total	740	26 (4)	8

Number of identifiable specimens (NISP) and number of hominin- and carnivore-modified bones associated with the FwJj20 excavation. This table includes all specimens regardless of surface preservation.

\*Percussion marks are in parentheses.

virtual geomagnetic pole latitude for each sample location or group of statistically different samples within these sample locations (Fig. 2). Detailed methodology is described in *SI Materials and Methods*.

**Tephrostratigraphic Analysis.** The tuff sample, K83-1562, was collected by F. H. Brown in 1983 from an outcrop of the tuff  $\approx$ 400 m south of the FwJj20 site. The tuff forms a prominent ledge and is continuous in outcrop between FwJj20 and the location of sampling. The sample K83-1562 was analyzed by x-ray fluorescence techniques using the preparatory methods and analytical conditions described in Brown and Cerling (35). The trace and minor element chemistry of K83-1562 is a match for the KBS Tuff sampled at its type locality (Table S2).

**Stable Isotopic Analysis.** Sixty-one fossil teeth were sampled from the FwJj20 locality, including most mammalian taxa at the site, except primates, micro-mammals, and carnivores. Tooth enamel was analyzed using an on-line carbonate device, the Finnigan Carboflo, and analyzed on a Finnigan MAT 252 mass spectrometer at the University of Utah. Corrections were based on internal Carrara marble and tooth enamel reference materials calibrated to the NBS-19 calcite standard. Enamel reference materials have a standard deviation of 0.15‰, for both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ , over the course of the analyses performed for this study. Carrara marble reference material yielded standard deviations of 0.07‰ and 0.09‰ for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ , respectively. All isotope values are reported in reference to the isotopic standard Vienna Pee Dee Belemnite using standard  $\delta$ -notation. See *SI Materials and Methods* for additional information.

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**Table 3. Faunal remains associated with the excavation at FwJj20 locality**

Taxon		MNI in situ	MNI surface
Aves		1	
Bovidae			2
	Aepycerotini	1	2
	Alcelaphini		1
	<i>Alcelaphus</i> sp.		
	cf. <i>Connochaetes</i> sp.	3	
	cf. <i>Damaliscus</i> sp.	3	
	Antilopini	1	
	<i>Antidorcas</i> cf. <i>recki</i>		
	<i>Gazella</i> sp.	1	5
	Hippotragini	1	
	cf. <i>Oryx</i> sp.	1	
	Reduncini	1	
	<i>Kobus kob</i>	1	
	<i>Kobus sigmoidalis</i>	2	
	<i>Kobus</i> sp.		1
	cf. <i>Menelikia</i> sp.	2	
	<i>Redunca</i> sp.		3
	Tragelaphini	1	
	cf. <i>Tragelaphus strepsiceros</i>		
	<i>Tragelaphus</i> sp.		4
Giraffidae	cf. <i>Giraffa</i> sp.	1	1
	<i>Giraffa pygmaeus</i>	1	
	<i>Giraffa stillei</i>		1
Hippopotamidae	<i>Hippopotamus</i>	3	
	<i>gorgops</i>		
	<i>Hexaprotodon</i> sp.	1	
	<i>Hippopotamus karumensis</i>	7	
Suidae	<i>Kolpochoerus heseloni</i>	3	4
	<i>Metridiochoerus andrewsi</i>	2	2
	<i>Notochoerus scotti</i>	1	3
Carnivora			3
Equidae			1
	<i>Eurygnathohippus</i> sp.	2	2
	<i>Equus</i> sp.	1	1
Rhinocerotidae	<i>Ceratotherium</i> sp.	1	1
	<i>Diceros bicornis</i>	1	
Cercopithecidae	<i>Theropithecus oswaldi</i>	1	2
Colobinae			1
	<i>Rhinocolobus</i> sp.		1
Elephantidae	<i>Elephas recki</i>	1	1
	<i>Loxodonta adaurora</i>		1
Rodentia		1	1
Clariidae		1	1
Crocodylidae		1	1
Chelonia		1	1
Total		48	47

MNI animals collected in association with the excavations and surface collections at FwJj20.

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