Oldest Evidence of Toolmaking Hominins in a Grassland-Dominated Ecosystem

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Abstract

Background: Major biological and cultural innovations in late Pliocene hominin evolution are frequently linked to the spread or fluctuating presence of C4 grass in African ecosystems. Whereas the deep sea record of global climatic change provides indirect evidence for an increase in C4 vegetation with a shift towards a cooler, drier and more variable global climatic regime beginning approximately 3 million years ago (Ma), evidence for grassland-dominated ecosystems in continental Africa and hominin activities within such ecosystems have been lacking.

Methodology/Principal Findings: We report stable isotopic analyses of pedogenic carbonates and unglulate enamel, as well as faunal data from ~2.0 Ma archeological occurrences at Kanjera South, Kenya. These document repeated hominin activities within a grassland-dominated ecosystem.

Conclusions/Significance: These data demonstrate what hitherto had been speculated based on indirect evidence: that grassland-dominated ecosystems did in fact exist during the Plio-Pleistocene, and that early Homo was active in open settings. Comparison with other Oldowan occurrences indicates that by 2.0 Ma hominins, almost certainly of the genus Homo, used a broad spectrum of habitats in East Africa, from open grassland to riparian forest. This strongly contrasts with the habitat usage of Australopithecus, and may signal an important shift in hominin landscape usage.

Introduction

The hominin fossil and archeological records of Africa exhibit substantial anatomical and behavioral change during the Plio-Pleistocene (~1.5–3.0 Ma), including the evolution of Homo and Paranthropus, the origin of lithic technology and archeological sites, the first evidence of large mammal butchery, lower limb elongation and selection for endurance running, and thermoregulatory adaptations to hot, dry environments [1]. These evolutionary innovations have been linked consistently to novel selective pressures encountered as early hominins foraged increasingly in more open, arid woodland and grassland habitats that were replacing wooded biomes. However, the most finely resolved evidence for environmental change is not from the fossil and archeological sites themselves, but from deep sea core records that indicate drier and more variable conditions in tropical and subtropical Africa [2–8]. An increase in arid-adapted vegetation is also reflected by morphological changes across many African large mammal lineages and by the dispersal of the Eurasian grazer Equus across Africa ~2.3 Ma [9,10]. Although these data suggest that grassland-dominated ecosystems (defined here as having >75% C4 plants and a graze-dependent fauna) should be present as one extreme of the continental habitat spectrum, actual documentation of both Pliocene grasslands and of hominin activities in open habitats has until now eluded paleoanthropologists. Here we use faunal and stable isotopic evidence to demonstrate the earliest presence of a grassland-dominated ecosystem, and archeological evidence for hominin activities within this setting from the late Pliocene locality of Kanjera South, Kenya (Fig. 1). At least one species of tool-making hominin, almost certainly of the genus Homo [1], was repeatedly using this open setting. In contrast, most other Oldowan occurrences are situated in more wooded settings. These findings indicate that by ~2.0 Ma tool-making hominins, probably early Homo, accessed and used a broad spectrum of East African habitats, from open grassland to riparian forest.
The late Pliocene Oldowan occurrences at Kanjera South are found on the northern margins of the Homa Mountain Carbonatite Complex, Homa Peninsula, southwestern Kenya (Fig. 1). The Homa Peninsula lies within the Nyanza Rift, which presented a depositional low to the north of the site. The lithological sequence at Kanjera South consists of 6 beds of the Southern Member of the Kanjera Formation, from oldest to youngest KS-1 to KS-6 [11,12]. Only KS-1 to KS-4 is described here since archeological occurrences are known only within this interval, from the top of Bed KS-1 through Bed KS-3.

KS-1 deposition began as a flow of pyroclastic material, possibly as a lahar, from the Homa Mountain complex in the south towards the depocenter in the Nyanza Rift graben. Lower KS-1 shows little internal stratification and no pedogenic development. In contrast, the well-bedded, better sorted and pedogenically modified upper parts of KS-1 represent reworking of the deposits by ephemeral streams running across the fan of the original pyroclastic flows. KS-2 represents a continuation of this environmental setting, with deposition by anastomosing channels flowing with intermittent, diffuse, generally low energy flow regimes and better-developed pedogenesis than KS-1.

KS-3 sees the transition to a wetter depositional environment, as evidenced by soft sediment deformation and the presence of a small channel, though stable land surfaces with pedogenesis...

Figure 1. Placement map and stratigraphic diagram showing the location of Kanjera in southwestern Kenya and of the Southern Exposures at Kanjera. The composite stratigraphic log shows the basal three beds of the Southern Member (KS-1 to KS-3) and the base of KS-4. Spatially associated artifacts and fossils are found as diffuse scatters and also in more vertically discrete concentrations from the top of KS-1 through KS-3, with KS-2 providing the bulk of the archeological sample.
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continued to be found. KS-4 represents a continuation of this moister trend, with clays being deposited either during the transgression of a lake out of the depocenter to the north or during the formation of a wetland system. The homogeneity of the KS-4 clays favors the former interpretation, and the paleosol layers interbedded in KS-4 indicate intervals of lake regression sufficiently long for pedogenesis to take place.

A combination of biostratigraphy (co-occurrence of the equid Equus sp., the suids Metrodorcas andrewsi and M. modestus, and the proboscidean Dinotherium sp.) as well as magnetostratigraphy (a reversed sequence in Beds KS-1 to KS-4 with the presence of the Olduvai subchron (1.95–1.77 Ma) in Beds KS-5 and KS-6) indicate that the KS-1 to KS-3 archeological occurrences date between ~2.3 Ma (the dispersal of Equus across Africa, first occurrence of M. modestus) and 1.95 Ma (the base of the Olduvai subchron) [1,11]. Given the apparent rapidity of deposition, an age of ~2 Ma for the archeological occurrences seems most likely.

Except for artifacts and fauna found in thin, discontinuous conglomerate lenses, hominin activity was the primary agent of accumulation of the majority of archeological materials at this site [11,13]. Discussion here focuses on KS-2 materials from the 169 m² Excavation 1, which has yielded 2190 fossils and over 2471 artifacts with three dimensional coordinates from several levels within the 1.5-m-thick sequence. KS-2 accumulated rapidly and, based on the limited development of pedogenic features, likely represents decades to centuries of deposition.

Results and Discussion

Habitats rich in plants using the C₃ photosynthetic pathway, such as woodland and dry forests, are well-documented between 10 and 2 Ma in East Africa (Fig. 2). Stable isotopic analysis of pedogenic carbonates and occluded palcosol organic matter across an 130 m transect of the Kanjera South locality provide the first clear evidence of a grassland setting (>75% C₄ vegetation) in this 10 million year sequence (Fig. 2, Tables S1 and S2). Evidence that grassland habitats dominated the regional ecosystem beyond the confines of our excavations is provided by large mammal frequencies, particularly of the family Bovidae, as well as the stable isotopic composition of tooth enamel from a suite of herbivorous mammals. Large mammals often range extensively during the course of a season or year [14,15] and so can provide a sense of regional vegetation structure [16]. Predicted habitat and dietary preferences of primates, ungulates and proboscideans from Kanjera (Table S3) are based primarily on analogy with extant relatives, degree of hypsodonty, functional analysis of limbs and masticatory morphology, and stable isotopic analyses of South and East African fossil and modern fauna [9,17–27]. Several taxa (crocodile, Phalacrocoracidae [cormorant], hippopotamid) reflect East African fossil and modern fauna [9,17–27]. Several taxa (crocodile, Phalacrocoracidae [cormorant], hippopotamid) reflect East African fossil and modern fauna [9,17–27].

Paleosol carbonate isotopic chemistry from the most informative Bed I archeological occurrence, FLK I Level 22 (FLK Zinj), suggests that artifacts and fossils were deposited in a grassy woodland (Fig. 2). Stable isotopic analysis of enamel samples from the extinct gazelle Antidorcas recki document an increasing amount of grass and a decreasing amount of browse in their diet through the Bed I sequence (Fig. 3b), consistent with a drying trend noted by other lines of paleontological and geological evidence [24,28,32]. Enamel samples of A. recki from FLK Zinj suggest a mixed diet of browse and grass, whereas Kanjera A. recki was predominantly grazing. Antidorcas recki individuals from the relatively arid, upper portion of the Bed I sequence have more negative δ¹³C values than those in the Kanjera KS-2 sample, suggesting that there was a greater proportion of open habitat at Kanjera than at any time during the deposition of Bed I Olduvai.

Isotopic data at or in the vicinity of other Oldowan occurrences, including the oldest archeological sites (2.5–2.6 Ma) at Gona, Ethiopia [33] and 1.75–2.0 Ma occurrences at Koobi Fora, Kenya [34] indicate hominin activities in habitat mosaics that on average had 50% C₃ vegetation (Fig. 2). Pollen data from Gona is concordant with a well-wooded setting for hominin site activities [35]. Vegetation mosaics including substantive woodland components are also suggested for Pioene and early Pleistocene Oldowan sites in West Turkana, Kenya, and the Shungura Formation, Ethiopia [36,37]. Finally, Oldowan hominin activities in a riparian forest setting are suggested by paleoenvironmental evidence from the Koobi Fora Formation in the Turkana basin, Kenya, at ~2.0 Ma [38].

These findings indicate that by ~2.0 Ma Oldowan hominins had access to and used a broad spectrum of East African habitats, from open grassland to riparian forest. Stone tool manufacture and archeological site formation at this time is most likely attributable to the genus Homo. Associations between H. habilis sensu lato (here including *H. habilis* and *H. rudolfensis*) and stone tools
are known in the geological record by 2.3 Ma [39,40]. The single definitive stone tool user in the Plio-Pleistocene, *H. erectus* (here including *H. ergaster*), appears in Africa by 1.8 Ma [41]. Overlap in size, cranial morphology, and cranial scaling between *H. habilis* and *H. erectus* suggest a close phylogenetic relationship between the two species [42–44], and support the idea that late Pliocene stone tool use was part of the behavioral repertoire of the evolving *Homo* lineage. Brain size expansion and masticatory changes in the *Homo* lineage have plausibly been linked to stone tool-dependent foraging [1].

*Paranthropus*, also known prior to 2.0 Ma, has been argued to have made stone tools based on hand bone morphology, and its

Figure 2. Stable carbon isotopic composition of paleosol carbonates from the late Miocene through Pleistocene of East Africa [7,11,30,33,51–59]. Shaded intervals represent pedogenic nodules forming in *C*₃ dominated and *C*₄ dominated environments. Paleosol carbonate δ¹³C values of -2 or greater are approximately equivalent to floral communities with 75% or more *C*₄ plants [31]. Intermediate values represent a mix of *C*₃ and *C*₄ vegetation. Plant root systems associated with KS-2 archeological site formation could have extended into the top of KS-1, so paleosol carbonate data from both KS-2 and the top of KS-1 are presented.

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Figure 3. Stable carbon isotopic data of enamel from Kanjera South and other African localities. A. Stable carbon isotopic composition of fossil mammal tooth enamel from KS-2 in Excavation 1. The KS-2 fauna is supplemented by several taxa unique to KS-1 or KS-3, or found on the surface of the KS-1 to KS-3 sequence, to provide a more complete sense of the diet of the mammalian community during the deposition of the archeological levels. The shading reflects the relative importance of C3 browse versus C4 grass in the diet, with δ13C values greater than -1 reflecting a diet with more than 75% C4 vegetation. Isotopic dietary classification follows others [23]. A probable ostrich (cf. Struthio) eggshell fragment was also analyzed. B. Box and whiskers plots of the stable carbon isotopic composition of modern and fossil gazelles from Kanjera, Bed I Olduvai Gorge, Tanzania, and Sterkfontein and Swartkrans, South Africa [60,61]. Like many modern antilopines, Antidorcas recki was able to switch between browse and graze as necessary [9]. Numbers in parentheses after site name represent number of samples analyzed. Bed I localities are presented in stratigraphic order, from oldest (DK I, ~1.87 Ma) to youngest (FLK Nl, ~1.78 Ma) [3].

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stratigraphic association with Oldowan artifacts in eastern and southern Africa [43]. However, the developmental investment in very large jaws and cheek teeth seen in Paranthropus would have been unnecessary if a stone tool kit allowing extra-oral processing of food was in use. Moreover, there is no perceptible change in the archeological record after Paranthropus goes extinct, as might be expected if two parallel tool traditions, one formed by Homo, the other by Paranthropus, were in place during the late Pliocene and early Pleistocene [1]. While Paranthropus may have used a non-lithic technology [46], it is unlikely to have formed the Oldowan occurrences under consideration here.

The breadth of habitat use inferred for early Homo by 2.0 Ma contrasts strongly with that of Australopithecus, a precursor to Homo, for which heterogeneous environments, all with significant woodland or forest components, are documented consistently [23,47]. The ~1.5 Ma H. erectus skeleton from Nariokotome, Kenya, signals adaptive shifts in hominin mobility, foraging, and thermoregulation towards the increased use of open, hot, and dry environments [48–50]. These shifts are anticipated by the recurrent use of open habitats by early Homo at Kanjera. The Kanjera data do not, however, necessarily indicate that early Homo used open habitats in preference to wooded ones. Combined evidence from Oldowan sites suggests that early Homo was flexible in its habitat use, and that the capacity to extract resources from a range of open and more wooded environments was a vital component of its adaptation.

Methods

Excavation 1 was carried out within a grid of 169 1m×1m squares, excavated in 5 cm spits following site stratigraphy. Fossil and artifact-bearing horizons were dug with awls and dental picks. A Topcon total station was used for the precise determination of specimen N, E, and Z coordinates and in contour mapping. Object dip and orientation was measured with a Brunton compass. Sediments were dry sieved through 1 mm mesh. Sedimentary, taphonomic, and zooarchaeological analyses indicate that the site assemblages formed predominantly through hominin activity [11,13]. In KS-1, KS-2 PS, and KS-3 there is a clear spatial relationship between the artifacts and fauna. Many objects are outsized clasts relative to grain size; a diverse array of skeletal parts exhibiting a range of hydraulic transport potentials have been recovered; artifact and fossil refits have been made; and both percussion marks and cut marks have been found on bones.

Isotopic Analysis of Paleosol Carbonates

Pedogenic carbonates used in this analysis exhibited microstructure consistent with in situ formation without subsequent recrystallization. The difference in the δ 13C of occluded organic matter and pedogenic carbonate fits theoretical predictions for diagenetically unaltered materials. Diagenetic carbonate cements from the Kanjera Formation have negative δ 13C values (Table S1), so that the positive signal reported here is unlikely to have resulted through diagenetic alteration.

Paleosol carbonate samples were washed in double distilled water and dried. The outer layers of the carbonate nodules were removed using a dental burr and discarded. The inner part of each carbonate nodule was crushed in an agate mortar and each sample was split into two aliquots, the first treated with 2% NaOHCl solution at 60°C for 24 hours to remove any organic contamination. The second aliquot was treated with 1M HCl until no reaction was resulted through diagenetic alteration.

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Isotopic Analysis of Enamel

Tooth enamel samples were carefully cleaned using an aluminium oxide air abrasive system to remove any adhering sediment and cementum. The outer surface of the enamel was abraded further, removing the outermost portion that was most likely to be diagenetically altered. Samples were then extracted from the cleaned enamel using a 0.5 mm diamond dental burr. Samples were ground and homogenized using an agate mortar. Powdered enamel samples were treated with 2% NaOHCl solution at 60°C for 24 hours to remove any organic contamination. Samples were then washed with double distilled water and treated with 0.1M CH3COOH at 25°C for 6 hours under vacuum to remove any secondary carbonate contamination. Samples were rinsed to neutrality and dried. All enamel samples for isotopic analysis were reacted with 100% phosphoric acid at 90°C in a common acid bath system. The evolved CO2 was pre-concentrated using a cold finger system and was analyzed at the University of Oxford using a VG Prism gas source isotope ratio mass spectrometer running in dual inlet mode. Results are reported using the standard delta per mil (%o) notation relative to the VPDB international standard. International and in-house standards analyzed along with the enamel samples gave standard deviations of ±0.08‰ for carbon and ±0.12‰ for oxygen.

Supporting Information

Table S1 Isotopic data from diagenetic sparry, pendant and poikilotopic calcite cements from KS-1 and KS-2, and from samples of carbonatite from the Homa Mountain carbonatite complex. Found at: doi:10.1371/journal.pone.0007199.s001 (0.03 MB DOC)

Table S2 Paleosol Carbonate Isotopic Data. Found at: doi:10.1371/journal.pone.0007199.s002 (0.04 MB DOC)

Table S3 Vertebrate taxon list from KS-2, Excavation 1. Isotopic dietary classification of Kanjera mammalian fossils follows others [23] using the isotopic data presented in Table S4. Obligate grazers and obligate browsers consume an almost exclusive (>95%) C4 or C3 diet, respectively. Variable grazers and variable browsers consume a predominantly (75–95%) C4 or C3 diet, respectively. Brower-grazer intermediate refers to taxa consuming a mix of C4 and C3 vegetation. Found at: doi:10.1371/journal.pone.0007199.s003 (0.04 MB DOC)

Table S4 Stable isotopic composition of fossil eggshell and tooth enamel from Excavation 1. Found at: doi:10.1371/journal.pone.0007199.s004 (0.13 MB DOC)

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