Palaeeoecological reconstructions of the Bed I and Bed II lacustrine basins of Olduvai Gorge (Tanzania) and insights into early human behavior

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The archaeological record of Olduvai Gorge has played a pivotal role in reconstructions of early human behavior. Classical Oldowan sites (from Middle Bed I), and the extensive archaeological record from Bed II (including the earliest Acheulian at 1.7 Ma), enable the reconstruction of early human behavior throughout its evolution from almost 1.9 Ma to 1.3 Ma. How such behavioral evolution was influenced by ecological factors is still an object of debate. This special issue presents a detailed meso-scale reconstruction of the paleoecology and paleogeography of the environments where some of these sites were formed, including extensive reconstructions of the paleobotany of the sites and the areas surrounding them. This provides, for the first time, a contextual ecological information framed in a scale large enough to understand human behavioral variability as determined by the exceptional ecological conditions of the Olduvai paleo-lake basin for almost one-and-a-half million years. This information is crucial to understand site functionality and the behaviors exhibited by hominins at each of the anthropogenic sites from Olduvai Gorge during the earliest stages of the evolution of the genus Homo.

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1. Introduction

One of the main objectives of paleoanthropology is the identification of the socio-reproductive organization and subsistence strategies that created human behavior. During the 1970s and 1980s several models emerged to interpret socio-economic behaviors of early hominins through the analysis of the Early Pleistocene archaeological record in Africa. Some models emphasized socio-economic behaviors that resembled those of some modern foraging populations (e.g., Leakey's (1971) "living-floors"; Isaac's (1978) "home base" or "food-sharing" models). Subsequent revisionist models (with a concern for site formation processes) during the 1980s produced ethological models in which hominins had social behaviors that were more similar to those of other non-human primates, such as the marginal or obligate scavenger (Binford, 1981) or the passive scavenger (Blumenschine, 1986) models, the stone-cache model (Potts, 1988), the "chimpanzee-nesting" model (Sept, 1992), or the "refuge" model (Blumenschine, 1991; Blumenschine et al., 1994).
The information gap between the reconstruction of site formation (through taphonomic analysis of materials preserved at sites) and the hominin socio-economic organization required to sustain any of the above models led scholars to abandon social and functional interpretations based on modeling of early sites. Isaac’s (1983) “central-place foraging” model de-emphasized social aspects of his previous model and Cavallo (1998) even managed to reconcile it with passive scavenging models. Schick’s (1987) “favored place” model did not include any significant social components and stressed that sites could simply be created by unintentional re-use of certain spaces, and may have served as secondary sources of raw material (Plummer, 2004). The “near-kill location” model (O’Connell, 1997) or the “male display” (O’Connell et al., 2002) model did not emphasize any specific social organization, despite depicting sites as carcass obtainment loci created through confrontation scavenging to increase male mating fitness. Even though some suggested an evolved version of primate behavior to explain early sites (e.g., the “resource-defense” model (Rose and Marshall, 1996), most models produced during the past three decades have approached Early Pleistocene hominin behavior by making it similar to those of other primates in an increasingly dehumanizing trend. One of the last models produced, the “obligate carnivory” model (Ferraro, 2007) intentionally avoided any interpretation of the social behavior of hominins or of the functionality of sites beyond their reconstruction as places where hominins ate substantial amounts of meat. This avoidance of hominin social organization is surprising, since in ethology it is widely known that subsistence (ecological) behavior is strongly dependent on specific types of social behaviors (Brooks and McLenna, 1991).

In sum, although there is a substantial amount of information available about the subsistence of hominins at a small number of Early Pleistocene sites, it is fair to state that we know very little about early site functionality and about hominins’ general ecological behavior or social organization. In addition, there is potential confusion among the large diversity of interpretations of hominin subsistence, as observed in the array of behavioral models produced. How can their heuristics be empirically tested? This diversity of interpretations may be due to the controversial nature of an insufficient archaeological record and/or to flawed theoretical framing of these models (see critical discussion in Domínguez-Rodrigo, n.d.).

A site’s functionality is tightly linked to the ecology of its surroundings: hominins selected specific spots on the landscape for certain activities because particular ecological characteristics enabled these activities. A better understanding of paleoecological conditions is crucial to uncovering site functionality and hominin behavior. Although some attempts have been made to characterize the surroundings of specific sites according to broad ecosystemic categories, (e.g., open grassland versus wooded habitats) (e.g., Plummer et al., 2009), in only a few cases has the ecological nature of a site been described at the local scale level (e.g., what geological features, plants and animals existed at the site and how did these vary according to distance from the site?) (e.g., Ashley et al., 2010; Barboni et al., 2010).

With this ecological framework in mind, there is an inferential chain that should be followed prior to framing scientifically testable behavioral models:

A. A site’s functionality cannot be understood without knowing its paleoecological context. There is virtually no early site where the local ecological characteristics have been accurately reconstructed, beyond general and rather ambiguous interpretations of location (e.g., lacustrine plain or riverine setting). The FLK Zinj site from Olduvai Gorge (Fig. 1) exemplifies how interpretations of site functionality have been linked to interpretations of the paleoecological placement of the site. Initial passive scavenging models situated the site in the middle of a barren lacustrine floodplain (Blumenschine and Masao, 1991). Subsequent research emphasizing the role of the site as a “central-place foraging” spot reconstructed it on a topographic high point within a wooded habitat overlooking a wetland (Ashley et al., 2010; Domínguez-Rodrigo et al., 2010). Recent reconstructions of the site (e.g., Blumenschine et al., 2012) place it in a peninsula surrounded by the water of a braided Okavango-like deltaic system. The hypothesis here is that locus selection by hominins is not random but conditioned by landscape ecology. Traditional archaeology focusing on the micro-scale analysis (the site) gave way to landscape archaeology projects focusing on the macro-scale, in which landscape reconstruction was targeted at kilometric or even regional ecosystems (e.g., Peters and Blumenschine, 1995). However, we argue that the crucial approach to reconstruct site functionality is the meso-scale, where efforts should concentrate on reconstructing in as much detail as possible the landscape surrounding a site in an approximately 1–5 km² area, integrating this subsequently within a broader and more general ecosystemic reconstruction. Sites must be geologically and topographically studied to analyze their physical setting’s morphology and the physical processes operating on them. This type of analysis should start at the site and expand laterally as far as the geological deposit allows. Geochemical (e.g., carbon isotope or organic geochemistry indicators) and paleobotanical (e.g., phytoliths) analyses should also be performed across paleolandscape to determine former in situ local vegetation. Landscape archaeology in the form of systematic test trenches across the landscape will provide information on density and diversity of materials when compared with the dense concentrations documented at sites.

B. A site’s functionality is better understood when compared to other pene-contemporaneous sites. Diversity or homogeneity of sites, preferably those found on the same paleosurface, can be used to study the relationship between site locations and ecological variables. The testing hypothesis is that functionally different types of sites should be located in ecologically different spots. No archaeological approach exists for the Early Pleistocene in which two or more sites located on the exact same paleosurface are compared according to a detailed reconstruction of the physiognomy of their landscape, let alone of the trophic dynamics inferred from the paleobiocoenoses present in it.

C. No site can be understood in terms of human behavior without knowing its formation history, and no selective pressures can be heuristically reconstructed from the landscape without knowing the processes and agents operating on that landscape. Taphonomy is a crucial part of the understanding of site formation. There are abundant taphonomic tools, which, if used in a multivariate format, can be heuristically powerful to discern agents and processes intervening at any given site (see summary in Domínguez-Rodrigo et al., 2007). If the same approach is used at a landscape taphonomic level, successful reconstructions can be made regarding the degree of competition by carnivores in any given habitat within a landscape and their impact on hominin adaptability (see application at the meso-scale in Peninj, Tanzania; Domínguez-Rodrigo et al., 2009a). For example, preliminary landscape taphonomic information derived from the complete sequence of Olduvai Bed I supports the idea that the creation of FLK Zinj coincided with a moment of minimal carnivore impact in the surrounding landscape (Domínguez-Rodrigo et al., 2010).

In sum, micro-scale analysis provides information on how a site was formed and what hominins did in it. Meso-scale analysis provides detailed information regarding why a location was selected and how it enabled or restricted the activities inferred from the micro-scale analysis. Macro-scale analysis (reconstruction of the ecosystem) contextualizes information derived from micro- and meso-scale approaches within a specific framework of trophic dynamics and natural selection. It is only via the combination of three levels of analysis (with special emphasis on the meso-scale) that hypotheses addressing site functionality and hominin behavior can be successfully tested.
2. Application of the meso-scale approach to the archaeological record of Olduvai Gorge (Tanzania): modeling the evolution of Oldowan and Acheulian hominin behavior

Over the past half-century, most of the behavioral models described above have been “tested” or applied primarily to sites discovered in Bed I at Olduvai Gorge, the best-preserved archaeological record for the East African Early Pleistocene. The reasons for this are:

1. Only in Olduvai are there extensively excavated sites with good preservation of materials deposited on vertically discrete layers, which have enabled taphonomists to understand hominin interaction with other site formation agents.

2. At Olduvai, these anthropogenic sites and their landscapes can be extensively traced horizontally on paleosols and paleosurfaces (Fig. 1).

3. Abundant paleobotanical information has recently been uncovered at these sites and their landscapes (e.g., Ashley et al., 2010; Barboni et al., 2010; Bamford, 2012).

4. Olduvai Gorge is situated within the active ecosystem of Serengeti, providing an observable example of trophic dynamics within biocenoses similar to those of the Early Pleistocene Olduvai basin.

This renders the Olduvai record of great value for a meso-scale approach as described above. In the Olduvai Paleanthropological and Palaeoecological Project (TOPPP), we have adopted an evolutionary approach and selected three specific time frames associated with two crucial stages of early hominin behavior. First, we have targeted the only time slice in Bed I where true anthropogenic sites have been identified, as opposed to palimpsests or sites with marginal hominin inputs (Domínguez-Rodrigo et al., 2007). Secondly, we have selected two other time slices where anthropogenic sites are abundant at the gorge, in lower and upper Bed II, which coincides with the co-existence of Acheulian and Oldowan lithic assemblages (Fig. 2). In both cases, an extensive archaeological record exists with associated paleolandslapes, which can be traced laterally over distances of several kilometers.

2.1. In pursuit of hominin behavior during the Oldowan

The paleosol underlying Tuff IC in Bed I contains a thin clay stratum (~20 cm) which can be traced laterally on a good portion of the gorge at the junction and beyond. The stratum can also be traced on both sides of the side gorge for over one-third of its northernmost trajectory. This provides an extensive paleolandscape. This stratum contains the oldest taphonomically-secure anthropogenic site: FLK Zinj (Domínguez-Rodrigo et al., 2007, 2010), which is contemporaneous with a palimpsest (FLK North North 1) representing a fresh water spring (Ashley et al., 2010). In 2012, some 700 m south of FLK Zinj on exactly the same paleosurface, a new equally-dense site was found: Philip Tobi-as Korongo (PTK). In 2014, in a similar distance south east of FLK Zinj, an even denser site was found: David’s site (DS) (Fig. 3). Preliminary analyses of the materials uncovered at both sites support a similarly anthropogenic agency to FLK Zinj. The reconstruction of the landscape around and between FLK Zinj, FLK North North 1, DS and PTK is a good testing background to the activities performed by hominins at the four sites. This is the first time that multiple sites documented not only in the same thin stratum, but also on the same paleosurface will be simultaneously analyzed within their respective ecological contexts and with consideration of the trophic dynamics of their surrounding landscapes. Previous work has focused on detailed reconstruction of a very small portion of the paleolandscape preserved north of FLK Zinj (Ashley et al., 2010) and work to reconstruct the much larger exposure of paleolandscape to the south is yielding very positive results (Uribelarrea et al., 2014). This involved systematic geological and paleobotanical sampling across the landscape, in combination with dozens of archaeological trenches, which is what is required before the paleolandscape can be properly understood. Recent paleobotanical and paleoecological information of this Oldowan paleolandscape will be presented in this special issue.

Arráz et al. (2017a) introduce the most updated reconstruction of the paleobotany in the paleolandscape surrounding the FLK Zinj-AMK-PTK-DS pene-contemporary complex. Contrary to previous interpretations, the alluvial plain on the Eastern side of the paleolake showed a mosaic nature with abundant wooded vegetation. Along the platform spanning from FLK NN (wetland) to AMK-PTK-DS (fluvial inputs), a forested cover was continuously spread (as in a lacustrine forest) mottled with open patches corresponding to the wettest parts of this paleolandscape. This shows that hominins selected locations not far from potable water sources (as modern hunter-gatherers do), avoiding the prolonged use of focal loci at the bodies of water, where carnivores could be more conspicuous (as documented at FLK NN, by the spring system). This paleobotanical reconstruction also underscores the lack of vegetational restrictions in the selection of activity areas by hominins. Rather than being constrained by focal patches of arboreal vegetation, hominins may have enjoyed similar types of wooded vegetation along the alluvial habitat represented by the Zinj-AMK-PTK-DS complex. This forested and mosaic habitat spanning linearly hundreds of meters suggests that factors other than the presence or absence of closed-vegetation must have determined the selection of activity places. Palm trees seemed abundant in this wooded landscape, as well as the presence of ferns, which indicate a closed canopy keeping the understory shaded conditions of humid forests.

In this wooded landscape, anthropogenic sites like Zinj, PTK and DS co-exist with natural paleontological locations, such as AMK, which provides a good indication of the densest concentrations of fossils that natural background clusters and scatters could afford in the Zinj paleolandscape. These remain in stark contrast with the significantly higher densities of materials uncovered in the other anthropogenic sites, as the work of Arrández et al. (2017a) shows. This contrast further stresses the dynamic accumulative nature of the anthropogenic processes transporting and processing carcasses at Zinj, PTK and DS.

Domínguez-Rodrigo and Cobo-Sánchez (2017a) spatial analysis of FLK Zinj and PTK show a common single-cluster pattern in this type of Oldowan sites, revealing a common hominin behavior for both sites. Given that modern foragers reside in multi-household social structures, which are reflected in the multi-cluster nature of modern home bases, as the work of Domínguez-Rodrigo and Cobo-Sánchez (2017b) shows, the single-cluster nature of the two Oldowan sites suggest a non-nucleated social structure for those early hominins. This enables approaching the social behavior of hominins from a new perspective never tried before and shows that the typical social structure of modern humans differs substantially from that reflected in the use of space by Oldowan hominins.

2.2. In pursuit of hominin behavior during the Acheulian

Lower Bed II has proved to be the best part of the stratigraphic sequence to document the “transition” of Oldowan to Acheulian technologies and their typological co-existence. An extensive stratigraphic overlying tuff IIA can be laterally traced for several km providing an opportunity to document different types of sites and behaviors on this paleolandscape. The stratum targeted in this part of the sequence by TOPPP starts at FLK West (the oldest recorded Acheulian in Olduvai Gorge and one of the three oldest in the world) (Díez-Martín et al., 2015) and ends up in Long Korongo, including sites like HKWE in between. This paleolandscape contains evidence of where hominins were using Acheulian and Oldowan tools according to site functionality. This paleolandscape has been reconstructed using a meso-scale approach by Uribelarrea et al. (2017). In their paper, Uribelarrea et al. show how hominins were alternating the use of Acheulian and Oldowan industries in connection with the fluvial system where FLK West is located, whereas they were using more Oldowan tools as they
Fig. 1. Location of Olduvai Gorge in Tanzania (insert) and distribution of the sites studied by TOPPP in Bed I and Bed II (by D. Uribelarrea).
moved away from this fluvial system into the wetland situated further away. Habitat type, thus, seemed related to lithic assemblage type and site functionality, with butchery widely documented at FLK West and very marginally so at locations like HWK-E (Egeland and Domínguez-Rodrigo, 2008).

An extensive anthropogenic archaeological record identified in uppermost Bed II (ca. 1.3 Ma), comprising sites like BK and TK, provides an exceptional opportunity to understand hominin behavior during the Acheulian period. At this time there is a higher diversity of sites, and probably behavior, as reflected in sites with Acheulian implements without clear association with faunal exploitation (e.g., TK) and sites with Oldowan tools used for butchery purposes, such as BK (Domínguez-Rodrigo et al., 2009b). This period also shows more frequent exploitation of megafaunal remains, such as at SHK (Domínguez-Rodrigo et al., 2014) or BK or even later sites such as WK (Leakey, 1971) or VEB (Stollhofen and Stanistreet, 2012), which must have been of adaptive importance for hominins. The deposit spanning uppermost Bed II is widespread both in the main and the side gorges. The abundance of megafauna in some parts of this landscape (such as at BK) and its virtual absence in others (such as at RHC or closer to the former lake) also poses stimulating questions as to whether faunal migratory processes were more influenced by altitude (up and down the slopes of the Lemagrut volcano) than by the Serengeti ecosystem. How this may have impacted hominin behavior remains to be studied. Here, a detailed reconstruction of the paleolandscape at BK will be carried out. Arraiz et al. (2017b) show how BK, despite being surrounded by a fairly open landscape, which prevented the preservation of carcass remains in most of it, exhibited a gallery forest associated with the river where the site was formed. This slightly wooded habitat was one (but surely not the only) factor that attracted a substantial amount of megafaunal remains to the area, which hominins exploited systematically over vast periods of time. Organista et al.’s (2017) work shows a careful reconstruction of site formation and the impact of fluvial processes in the modification and preservation of the assemblage of BK4c. This still enigmatic redundancy in the use of the space and the exploitation of megafauna and large game across such a large stratigraphic sequence indicates that, despite ecological factors enabling this situation, hominins seemed to have sought repeated access to such large animals. When single carcass butchery processes are identified, they show thorough consumption of these animals by hominins, hinting that social hominin groups at this time may have been substantially bigger than commonly assumed.

Uribelarrea and Domínguez-Rodrigo (2017) provide in their paper a detailed geological reconstruction of BK and its surrounding context, which accounts in part for the uniqueness of the site. They show how a riverine setting with a gallery wooded/forested habitat in the middle of a very dry and open landscape provided access to water to mammal faunas for a very prolonged period of time, enabling the formation of an archaeological sequence spanning more than three meters of sediments.

In addition, this special issue contains three methodological papers of different nature. Arriaza et al.’s (2017) paper is a methodological contribution that uses geometric morphometric analyses for the first time for the adscription of tooth mark scores to specific carnivore types. This method is applied to a modern carnivore assemblage discovered at Olduvai and previously interpreted as caused by large felids, namely, lions. The results of this study concur with previous taphonomic work by showing how these tooth marks most closely resemble those of lions as opposed to other carnivore types. A different 3D morphometric analysis of tooth marks is described in Aramendi et al. (2017b). These authors apply the 3D morphometric method to the interpretation of the crocodile tooth marks from OH8. This methodology, based on the 3D reconstruction and Geometric Morphometric analysis of carnivore tooth marks, enables for the first time the differentiation of carnivores beyond size groups.

The third methodological paper by Domínguez-Rodrigo and Cobo-Sánchez (2017b) focuses on the social use of space by modern foragers and how it reflects social structure. By selecting a
few modern sites with short and prolonged occupations, with anthropo- 
genic modification of the space by cleaning of activity areas or with- 
out any post-depositional disturbance by humans, these authors show 
how multiple-household social structure of modern humans is reflected 
in the multi-cluster nature of their assemblages. This opens the door to 
multiple types of spatial analyses (e.g., of taphonomic nature) that can 
address these and other contextual behaviors in the formation of the ar-
chaeological record. Multiple reoccupations at archaeological open-air 
sites do not have to mask this pattern as documented in modern 
camps if it existed in the past if hominins had a similar social structure. 
More extensive occupations would have resulted in denser assemblages 
and even more multi-clustered records. The presence of dense 

assemblages with single-clusters at some Olduvai sites indicates that 
the social structure behind Oldowan hominins was more cohesive and 
different from that of modern humans (Domínguez-Rodrigo and 
Cobo-Sánchez, 2017a).

3. Conclusions

The two time periods selected cover a crucial period of human evo-

lution spanning over half a million years (from 1.9 Ma to 1.3 Ma). The 
latter period is terra incognita regarding behavioral inferences. The be-

havioral models described earlier have been proposed for the Oldowan 
record of Bed I and for pene-contemporaneous sites from Koobi Fora
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