THESE

Pour l'obtention du Grade de

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(Faculté des Sciences Fondamentales et Appliquées)
(Diplôme National - Arrêté du 25 mai 2016)

Ecole Doctorale : Chimie Ecologie Géosciences Agrosciences « *Théodore Monod* »

Secteur de Recherche : Terre solide : géodynamique des enveloppes supérieures, paléobiosphère

Présentée par :

Blade Engda REDAE

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Ecological dynamics of the vertebrate assemblages contemporaneous of the human occupations in the Shungura Formation (Plio-Pleistocene of the lower Omo Valley, Ethiopia)

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Directeur de Thèse : Jean-Renaud Boisserie, Directeur de Recherche
Co-directrice de Thèse : Joséphine Lesur, Maîtresse de Conférences

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Soutenue le 15 Décembre 2022
devant la Commission d'Examen

****

JURY

Briana Pobiner	Research Scientist, Smithsonian Institution	Reviewer
Sally Reynolds	Principal Academic, Bournemouth University	Reviewer
Yohannes Haile-Selassie	Professor, Arizona State University	Reviewer
Sandrine Costamagno	DR, TRACES, CNRS & Université de Toulouse	Examiner
Antoine Souron	MC, PACEA, Université de Bordeaux	Examiner
Gildas Merceron	DR, CNRS & Université de Poitiers	Examiner
Joséphine Lesur	MC, Muséum National d'Histoire Naturelle, Paris	Examiner
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DYNAMIQUES ÉCOLOGIQUES DES ASSEMBLAGES DE VERTÉBRÉS CONTEMPORAINS DES OCCUPATIONS HUMAINES DE LA FORMATION DE SHUNGURA (PLIO-PLÉISTOCÈNE DE LA BASSE VALLÉE DE L'OMO, ÉTHIOPIE)

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Joséphine Lesur	MC, Muséum National d'Histoire Naturelle, Paris	Examinatrice
Jean-Renaud Boisserie	DR, CNRS & Université de Poitiers	Examinateur

Ecological dynamics of the vertebrate assemblages contemporaneous of the human occupations in the Shungura Formation (Plio-Pleistocene of the lower Omo Valley, Ethiopia)

Abstract

The Plio-Pleistocene period provides records of crucial climatic and ecosystem changes that coincide with key events during the course of human evolution, notably in eastern Africa. In this context, while the dietary shift of hominids towards tool-assisted consumption of animal tissue is one of the most significant events, the timing, ecological and behavioral implications of this dietary shift is far from being addressed. In the Turkana region, the record dated from 3.6 Ma to 1 Ma from the Shungura Formation, although rich in faunal and artifacts, it was never investigated from a zooarcheological perspective. This thesis examines the taphonomic and paleoenvironmental contexts of the vertebrate assemblages contemporaneous with the human occupation sites in this formation. My objective was to address the subsistence behaviors of early hominids, and establish the ecological context of the Oldowan and newly discovered Acheulean localities.

The first part focuses on presenting the taphonomic assessments made throughout the Shungura Formation. After preliminary taphonomic analysis, identification and description of various marks were documented. The Shungura Formation provides a perfect testing ground for discriminating various Bone Surface Modification (BSM) agents. Classic zooarcheological methods and Elliptic Fourier-based size analyses were combined to deal with the presence of strong equifinality between anthropogenic and non-anthropogenic BSM. Fossil BSMs were compared with experimental samples including anthropogenic cut marks, trampling marks, as well as crocodilian and carnivoran tooth scores. For the characterization of BSM morphologies, I used an Elliptic Fourier (EF) based approach. In depth analyses of BSMs revealed crocodiles to be active agents in all members of the formation, being particularly abundant in members C and G. Anthropogenic activity is present in members F, G, and L, based on the presence of cut marks as well as hack marks. While some debate still remains on the effective differentiation of BSMs, especially in contexts where both crocodiles and hominids coexist, the present EF based approach was able to confirm the presence of both cut marks, as well as crocodilian tooth marks, while effectively discriminating between the two. Likewise, as a result of my thesis, I was able to effectively identify hominid butchery activities in this area as early as 2.3 Ma. In addition, possible Oldowan bone tools dated to ~2.3 Ma are documented, although to be confirmed through excavation. At Member L bone modifications showing various activities of carcass processing (e.g., defleshing, disarticulation, percussion) from medium to large size mammals as well as fish and turtles indicating exploitation of aquatic resources ~1.2 Ma.

The second part of the dissertation presents paleoenvironmental data surrounding the emergence of the Oldowan in the Member F of the Shungura Formation (at 2.3 Ma) through synthesizing multiple lines of proxies using taphonomy, faunal composition data, as well as 3D dental microwear textural analysis (DMTA). This part examines the faunal assemblages in relation to the archeological occurrences in the lower part of Member F. I have applied DMTA to five bovid

tribes and giraffids from two excavation localities immediately predating the Oldowan occurrence. The DMTA results show inter-locality differences between Aepycerotini and Alcelaphini. DMTA analysis identified grazing dietary behavior at L 398, whereas at OMO 33 these taxa show a tendency towards mixed feeding behavior. Bovid tribes from each unit in Member E and F were also analyzed in order to see if there are faunal indicating change through time, and between localities for spatial analysis within Member F. The overall bovid data at member level indicate that there was a shift towards more arid and open habitats in Member F. The faunal data and DMTA analysis provided additional information on how paleohabitats varied across landscapes at a relatively shorter temporal resolution. At F-0, I have observed both a significant increase in the abundance of Alcelaphini and dietary discrepancies among sympatric taxa. Thus, my results suggest local scale ecological variability in Member F, more prominently than in Member E.

Key words: Plio-Pleistocene, Shungura Formation, Paleoecology, Hominid, Taphonomy, Zooarcheology, Geometric morphometrics, Dental wear

Dynamiques écologiques des assemblages de vertébrés contemporains des occupations humaines de la Formation Shungura (Plio-Pléistocène de la Basse Vallée de l'Omo, Éthiopie)

Résumé

Le Plio-Pléistocène a connu des changements climatiques et écosystémiques cruciaux qui coïncident avec des événements clefs au cours de l'évolution humaine, notamment en Afrique orientale. Dans ce contexte, les implications temporelles, écologiques et comportementales de la transition de l'alimentation des hominidés vers une consommation de tissus animaux assistée par des outils peuvent être étudiées plus avant. Dans la région du Turkana, la formation Shungura, datée entre 3,6 Ma à 1 Ma, bien que riche en faune et en artefacts, n'a jamais été étudiée d'un point de vue zooarchéologique. Cette thèse examine les contextes taphonomiques et paléoenvironnementaux des assemblages de vertébrés contemporains des sites d'occupation humaine dans cette formation. Mon objectif était d'aborder les comportements de subsistance des hominidés anciens, le contexte écologique de l'Oldowayen et de localités acheuléennes récemment découvertes.

La première partie se concentre sur les évaluations taphonomiques réalisées tout au long de la séquence de Shungura. Après une analyse préliminaire, l'identification et la description de diverses marques ont été documentées. La formation de Shungura constitue un terrain d'essai parfait pour discriminer divers agents de modification de la surface des os (BSM). Des méthodes zooarchéologiques classiques et la morphométrie géométrique ont été combinées pour traiter de la forte équifinalité entre les BSM anthropiques et non-anthropiques. Les BSM fossiles ont été comparés à des échantillons expérimentaux comprenant des marques de décarnisation anthropiques, des marques de piétinement et des marques de crocodiliens et de carnivores. Pour la caractérisation des morphologies des BSM, j'ai utilisé une approche basée sur l'analyse de Fourier elliptique (EF). Les analyses approfondies des BSM ont révélé que les crocodiles sont des agents actifs dans tous les membres de la formation, étant particulièrement abondants dans les membres C et G. L'activité anthropogénique a été confirmée dans les membres F, G, et L. Alors qu'un débat subsiste sur la différenciation des BSM, en particulier dans des contextes où coexistent à la fois des crocodiles et des hominidés, l'approche basée sur l'EF a été en mesure de discriminer efficacement les deux. De même, j'ai été en mesure d'identifier efficacement les activités de boucherie des hominidés dès 2,3 Ma.

La deuxième partie de la thèse présente les données paléoenvironnementales entourant l'émergence de l'Oldowan à Shungura (2,3 Ma) en combinant la taphonomie, des données sur la composition de la faune, ainsi que de l'analyse texturale 3D des micro-portraits dentaires (DMTA). Cette partie examine les assemblages fauniques en relation avec les occurrences archéologiques du membre F. J'ai appliqué la DMTA à cinq tribus de bovidés provenant de deux localités fouillées formées immédiatement avant l'apparition de l'Oldowayen. Les résultats de la DMTA montrent des différences intra-locales au sein des Aepycerotini et des Alcelaphini. La DMTA a identifié un

comportement alimentaire de consommation de graminées à L 398, alors qu'à OMO 33 ces taxons tendent vers un comportement alimentaire mixte. Les tribus de bovidés de chaque unité des membres E et F ont également été analysées afin de comparer les signaux fauniques au fil du temps, et spatialement entre localités au sein du membre F. Les données sur les bovidés au niveau du membre indiquent qu'il y a eu une évolution vers plus d'aridité et d'ouverture dans le membre F. Les données sur la faune et la DMTA ont fourni des informations supplémentaires sur la façon dont les paléohabitats ont varié à travers les paysages à une résolution temporelle relativement précise. Pour F-0, j'ai observé à la fois une augmentation significative de l'abondance des Alcelaphini et des divergences alimentaires entre les taxons sympatriques. Ainsi, mes résultats suggèrent une variabilité écologique à l'échelle locale dans le membre F plus marquée que dans le membre E.

Mots clefs: Plio-Pléistocène, Formation de Shungura, Paléoécologie, Hominidés, Taphonomie, Zooarchéologie, Morphométrie géométrique, Usure dentaire.

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Chapter One

Introduction

1.1. Background

Major events in human evolution occurred during the late Cenozoic of Africa, and eastern African Plio-Pleistocene played a key role in this regard. In particular, this period was marked by a significant faunal change dominated by grassland adapted herbivores in the eastern African (Bibi & Kiessling, 2015; Du & Alemseged, 2018; Faith & Behrensmeyer, 2013; Vrba, 1985; Werdelin & Lewid, 2005). This faunal evolution (including hominids) has been linked to environmental changes triggered by global and regional forcers such as climate, tectonics, hydrography, and other biotic and abiotic factors (e.g., Bailey et al., 2011; Bibi et al., 2013b; Boisserie et al., 2008; deMenocal, 1995, 2004; Faith et al., 2018; Foerster et al., 2022; Maslin et al., 2014; Trauth, 2005; Trauth et al., 2010; Vrba, 1985). This change is well marked by hominids speciation and intensive production and use of stone tools starting around the terminal Pliocene (Braun et al., 2019; Harmand et al., 2015; Plummer, 2004; Roche et al., 1999; Semaw et al., 1997; Wood & Strait, 2004).

The effects of these factors on the local or regional biodiversity are, however, far from being fully understood. A focus on ecological dynamics, role of environment and hominids adaptive strategy is critical to address questions regarding human biological and behavioral evolution during the Plio-Pleistocene (e.g., Blumenschine & Peters, 1998; Foley, 2002; Potts, 2013; Reed, 1997).

Previous studies on the Plio-Pleistocene deposits from the Turkana Depression have provided records of environmental changes and major speciation and extinction events that are broadly correlated to global climatic shifts (Behrensmeyer, 2006; Bibi et al., 2013b; Bibi & Kiessling, 2015; Bobe et al., 2002; Bobe & Behrensmeyer, 2004; Bobe & Wood, 2022). For instance, a gradual shift of towards more open and drier environments that starts around 2.8 million years ago (Ma) coincides with the emergence of *Paranthropus* and *Homo* (e.g., Bibi et al., 2013; Bobe et al., 2002), but see (Trauth et al., 2021) for alternative view.

Another important episode was a more abrupt environmental change documented in the Turkana Basin round ~ 2.4 to 2.2 Ma (e.g., Bobe & Behrensmeyer, 2004; Potts, 2007a). This event broadly coincides with the appearance of Oldowan technology from the Nachukui and Shungura formations ~2.3 Ma. Broadly, stone tool production became more common after 2 Ma, and the behavioral adaptation and ecology after this time period is relatively better understood. Furthermore, after 2 Ma, the Oldowan culture also cover a wider geographic range, the use of diverse raw material and production of more diversified tools that involve various techniques and functionality (e.g., Delagnes, 2012). In addition, associated use of these materials including butchery activities are relatively better documented compared to earlier periods (Blumenschine et al., 2012; Bunn, 1981; Domínguez-Rodrigo et al., 2010; Ferraro et al., 2013; Pante et al., 2018; Pobiner et al., 2008). Sites with records of Pliocene hominid behaviors are, however, very rare.

Several Early Pleistocene archeological sites have been found directly or indirect associations with paleontological context (Asfaw et al., 1991; Beyene et al., 2013; Boisserie et al., 2008; Braun et al., 2019; Chavaillon, 1976; Delagnes et al., 2011; Harris, 1983; Howell et al., 1987; Plummer et al., 2009; Roche et al., 1999; Semaw et al., 1997). Various types of environmental settings from open and dry savannah to wooded and forest cover were reconstructed for those archeological sites. However, investigating the extent to which hominids play in the accumulation processes associated to these sites is often hampered by poor preservation, small sample size, or due to the focus of research interests. Thus, the role of hominids in the trophic interaction is not addressed in several early Pleistocene and late Pliocene sites.

Recent palaeoecological studies from archeological contexts at Koobi Fora have linked archeological occurrences associated to certain fauna association (Patterson et al., 2017). In this context, it demonstrates that hominids exploited certain habitat, for instance, archaeological localities were recorded with higher abundance of Alcelaphini than contemporaneous localities but devoid of artifacts or lack of butchery evidence. However, the work by these researchers was on relatively younger archeological sites.

The evolutionary significance of early hominid's carnivory and technological innovations is also linked to hominid-carnivoran interactions or niche partitioning (Lewis, 1997; Pobiner, 2020; Pobiner & Blumenschine, 2003). The encroachment of hominids to the carnivoran guild has been thought to have contributed to the decline of carnivoran, with an impact strongly increased after 2 Ma (Werdelin & Lewis, 2013), although others provide an alternative view (e.g. Faith et al., 2018).

Possible Pliocene cutmarks have been reported from Dikika dated to ~3.4 Ma (McPherron et al., 2010; Thompson et al., 2015), but see Dominguez-Rodrigo et al. (2010) or Sahle et al., (2017) for alternative views. In addition, the earliest lithic artifacts have been reported from ~3,3 Ma site of Lomekwi 3 (Turkana Basin) described as percussive technology (Harmand et al., 2015).

Oldowan sites older than 2 Ma are documented by a very limited number of sites (see table 1.1), and only a few of these sites show associated butchery evidence. Thus, severely limited to our ability to detect what triggered the emergence of the Oldowan lithic industry. In addition, associated faunal remains are few or absent in some sites, and/or most of them lacking taphonomic studies. For instance, associated faunal remains from Nachukui Oldowan sites provide few butchery evidence (Brugal et al., 2003, 2017), but the general faunal composition associated to the Oldowan is poorly preserved (Brugal et al., 2003; Roche et al., 1999).

The other contemporaneous Oldowan site, Ledi-Gerau did not produce faunal assemblages (so far) with cortical preservation suitable for BSM studies (Braun et al., 2019). At Hadar, despite the direct association of artifacts and faunal remains including early *Homo*, no cut marked specimens were identified from this site (Kimbel et al., 1996). In addition, a possible younger age is proposed for this site between 2.4-1.9 Ma (Rowan et al., 2022).

At Gona paleoanthropological site, only few localities show faunal and archaeological association with few cutmark bearing specimens (Domínguez-Rodrigo et al., 2005; Semaw

et al., 2003). At Bouri, a site contemporaneous to Gona in the Middle Awash preserves few specimens with cutmarks while in situ artifacts were not found in direct association (de Heinzelin et al., 1999; Sahle et al., 2017).

The Bouri cutmarks attest disarticulation, defleshing and fracturing of long bone for marrow extraction from large to medium size mammals including on bovids and equids (de Heinzelin et al., 1999). Later re-examination of the modified bones from Bouri confirm the identification of butchery marks, but excludes some specimens previously identified as cut marked (Sahle et al., 2017). Similarly, at Gona, the cut marked specimens including on equids and medium size bovids indicate activities of defleshing, scrapping and percussion (Domínguez-Rodrigo et al., 2005; Semaw et al., 2003). Faunal remains and artifacts from this site shows a strong association (Semaw et al., 2003). However, most of the associated faunal remains from this site are highly fragmented and cortical surfaces are badly preserved (Semaw et al., 2003).

In the Turkana Basin, cut marked specimens Older than 2 Ma are only reported from the Lokalalei sites in the Nachukui Formation (Brugal et al., 2003; Delagnes & Roche, 2005). The modified specimens reported include cut marked specimens from Size-2 (example gazelle size), and size 3 (e.g. wildebeest) mammals, as well as on a turtle carapace indicating exploitation of diverse fauna (Brugal et al., 2003, 2017). However, faunal associations are very few, and bones surfaces are poorly preserved (Brugal et al., 2003, 2017; Delagnes & Roche, 2005; Roche et al., 1999).

Whereas in the Shungura, the faunal remains are not examined from zooarcheological perspective. Therefore, the Shungura Formation, rich in both archaeological and faunal remains, has the potential to be explored from this perspective and could contribute new data from this critical period. The scarcity of such data can be due to factors such as the nature of the preservation and lack of adequate research on this topic.

A summary of pre 2 Ma sites with hominid behavioral record, associated hominids, and reconstructed environmental context is provided in the table below (Table 1.1)

Site	Age/ Ma	Associated hominid/s	Hominid behavior	Habitat settings	Reference:
Dikika	~3.4 Ma	*Au.Afarensis*	Butchery?	Woodland with elements of bushland on a shallow lacustrine	Bonnefille et al., 2004; McPherron et al., 2010; Reed, 2008; Wynn et al., 2006
Lomekwi	~3.33	*Kenyanthropus Platyops*	Lithics	Woodland environment	Harmand et al., 2015
Gona	~2.6	*Homo*	Lithics Butchery	Dominantly woodland (mosaic of open and forest), fluvial setting	López-Sáez & Domínguez-Rodrigo, 2009 ; Quade et al., 2004; Semaw et al., 1997
Ledi-Geraru	~2.6		Lithics	Open grassland, lacustrine	Braun et al., 2019
Bouri	~2.5	*Au. garhi*	Butchery Lithics*	Open grassland, lake margin	Asfaw et al., 1999; de Heinzelin et al., 1999
Hadar	2.4-1.9	*Homo*	Lithics	Dominantly open settings	Kimbel et al., 1996; Rowan et al., 2022
Mille-Logya	~2.44	*Homo*	Lithics*	Open habitat, lacustrine	Alemseged et al., 2020
Nachukui	~2.34	*Homo*	Lithics Butchery	Open, lake coastal occupation	Brugal et al., 2003; Prat et al., 2005; Roche et al., 1999
Shungura	2.32	*Homo Paranthropus*	Lithics	Open dominated, mix habitat, riverbank	Boisserie et al., 2008; Howell et al., 1987; Maurin et al., 2017
Kanjera	~2.0		Lithics Butchery	Open and dry savannah, lake margin	Ferraro et al., 2013; Plummer et al., 2009
Ain Boucherit	~2.4		Lithics Butchery	Fluvial sequence, and shallow lagoons	Sahnouni et al., 2018

Table 1.1: List of Late Pliocene (at 2.6 Ma) and Early Pleistocene sites (dated between 2.58 Ma and 2 Ma) with evidence of artifacts, butchery activity, and/or associated hominid/s. The asterisk (*) indicates scattered artifacts (that do not form archeological assemblages), mostly in surface. Shaded colors correspond to different regions (light green, Afar Rift; light blue, Turkana Basin; gray, Kanjera South (SW Kenya); and light orange, a site outside of the Rift system, i.e., in Algeria).

The Oldowan occurrences at ~2.3 Ma from the Turkana are indicated as spatially restricted to areas where resources are in close proximity, whereas archeological sites after 1.6 Ma are found on a variety of paleogeographic settings (Rogers et al., 1994). The archeological occurrences in the Shungura indicate exploitation of resources across the riverbanks (Maurin

et al., 2017). Thus, it is crucial to first understand the habitat types or ecological contexts associated with hominid activities.

From the perspective of landscape use, important spatial analysis of the Oldowan archeological occurrences have been published, including context and episodes of occupations in the Shungura Formation (Maurin, 2017b; Maurin et al., 2017). Furthermore, the most recent study on use wear analysis shows that artifacts have been used for various purposes, but prominently used for carcass processing in the Shungura Formation (Galland, 2022). In contrast, very little is known concerning bone surface modifications from the Shungura Formation (Maurin; 2017b), despite being crucial for providing direct information about hominid interaction with the rest of the fauna.

The Shungura Formation have provided a wealth of faunal remains including important hominid discoveries dated ca.3.6 Ma to 1 Ma (Alemseged et al., 2002; Boisserie et al., 2008, 2010; Coppens, 1978; Coppens & Howell, 1985; Daver et al., 2018; Eck, 2007; Howell et al., 1987; Suwa et al., 1996). Moreover, the formation also provide records of Oldowan archaeological sites dated to 2.3 Ma (Boisserie et al., 2008; Chavaillon, 1976; Delagnes et al., 2011; Delagnes, 2012; Merrick et al., 1973; Merrick & Merrick, 1976). The vast collection of the faunal remains and the well constrained chronological context has allowed to explore various aspects if paleontological and paleoenvironmental studies (Alemseged, 2003; Alemseged et al., 2007; Bibi et al., 2013a; Blondel et al., 2018; Bobe et al., 2002; Bobe & Behrensmeyer, 2004; Howell et al., 1987; Merceron et al., 2021; Negash et al., 2020; Souron et al., 2012, 2013).

Thus, the Shungura Formation would be an excellent case study to examine early hominid adaptative behaviors such as habitat choices, dietary behaviors, and interaction with the rest of the fauna. Direct evidence about interactions, notably studies of bone surface modification that can document predation by carnivorans and crocodiles as well as possible consumption of animal tissue by early hominids, is not yet explored on the Shungura faunal remains.

With these research gaps in mind, this dissertation seeks to broaden our knowledge of Plio-Pleistocene hominid dietary behavior and the contexts of habitats exploited. This is done by

addressing the ecological context of hominid occupation sites as well as presenting new zooarcheological data from the Shungura Formation dated between ca. 3.75 Ma to ca. 1.09 Ma.

1.2. The Shungura Formation

1.2.1. Historical overview of the Study area

The Shungura Formation is a paleoanthropological site located in the Lower Omo Valley of southwest Ethiopia. The first fossil collection was made by a French physician and naturalist, Emile Brumpt, during Robert Bourg de Bozas' expedition in 1902 (Boisserie et al., 2008). Following this, a first systematic scientific exploration in the site was performed in the 1930s with a French paleontologist, Camille Arambourg, who led the "Mission scientifique de l'Omo" in 1932-1933 (Boisserie et al., 2008).

In 1967, an international team composed of French, American, and Kenyan scientists started an interdisciplinary project in the region. This research program was called the International Omo Research Expedition (IORE; Boisserie et al., 2008; Coppens et al., 1973b; Coppens & Howell, 1985; Howell, 1968). The IORE conducted field works between 1967 and 1976 (see Boisserie et al., 2008 for a more summary of the historical background).

Three decades later, an interdisciplinary research project led by Jean-Renaud Boisserie (CNRS, University of Poitiers) was established as Omo Group Research Expedition (OGRE) and resumed the fieldwork in 2006 (Boisserie et al., 2008). The OGRE has been an ongoing research project since then. The OGRE is a research program that involves paleoanthropological, paleontological, and geological research questions documented in the Omo Group deposits of the Shungura and Usno formations (~4 Ma to younger than 1 Ma). Its amin objectives are understanding the response and adaptations of organisms including hominids to environmental changes throughout this sequence (Boisserie, 2013b; Boisserie et al., 2008, 2010).

1.2.2. Geology of the Shungura Formation

The Shungura Formation is found in the Lower Omo Valley, a northern extension of the Turkana Depression. It is among the few well-documented paleoanthropological sites, which is best known for the rich fossil faunal remains including hominid remains and Oldowan stone tools.

The Turkana Depression is a vast lowland depression consisting in a series of basins accommodating the lake Turkana in northern Kenya and the Lower Omo Valley in southern Ethiopia (Butzer, 1971a). Most of the correlating Plio-Pleistocene sediments in the Turkana Depression were designated as the Omo Group (Feibel, 2011). These include the Mursi Formation, Usno Formation, Shungura Formation, Koobi Fora Formation, and Nachukui Formation. The first three formations are found in the lower Omo Valley, whereas the Nachukui and Koobi Fora formations are situated in western and eastern banks of the Lake Turkana, respectively (Feibel, 2011; Feibel et al., 1989; McDougall & Brown, 2008).

From the Omo Group deposits, the Shungura Formation is the richest in fossils (more than 58,000 specimens so far discovered), and provides the most continuous Plio-Pleistocene faunal record (Feibel et al., 1989; Heinzelin, 1983; McDougall & Brown, 2008). Detailed information on lithology and sedimentary environments is provided by Heinzelin (1983), and see below.

The Shungura Formation is divided into 12 members, each named after the underlying tuffs except the bottom-most, including from bottom to top Basal Member followed by members A to L (excluding I) in alphabetical order (Heinzelin, 1983; Heinzelin & Haesaerts, 1983). Members are then subdivided in units based on the sedimentary cycles as graded from coarser to finer depositional facies (Heinzelin, 1983). Similarly, Heinzelin and Haesaerts demonstrated that units are subdivided into sub-units whenever there are recognizable interfaces within unit sections (Heinzelin, 1983).

Interbedded volcanic ash layers allowed radiometric dating for at least 16 marker levels. Radiometric results were correlated with paleomagnetic polarity to estimate the depositional times of the different members. Relatively continuous sedimentation allowed proposing estimated ages based on sedimentation rate and calibrated by radiometric and paleomagnetic ages. The age model used here is the most recent produced by the OGRE (Boisserie, Pers. comm.). A map describing the location of the study area with the geological members is provided below (Figure 1. 1)

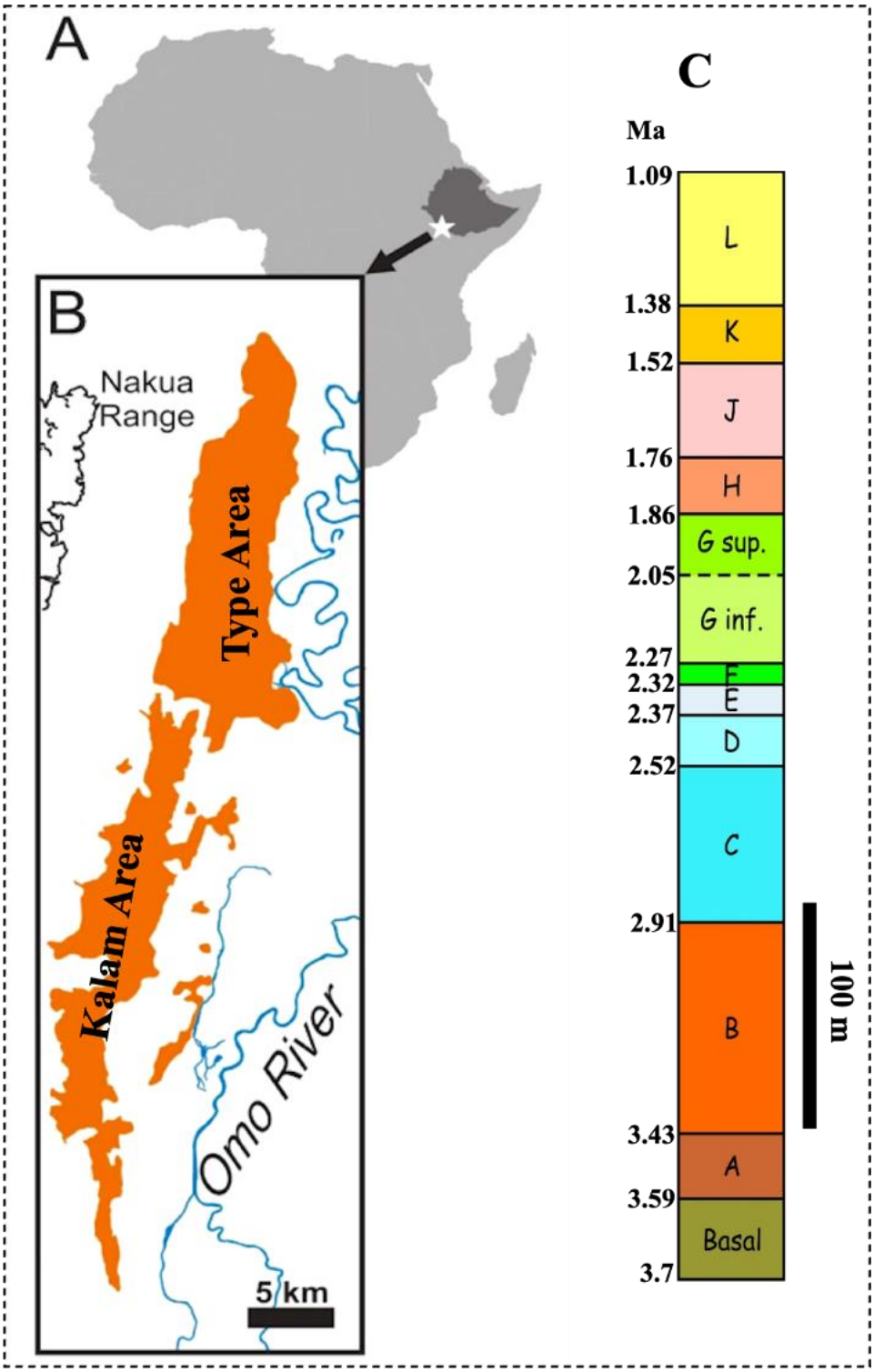

Figure 1. 1: Map of the Shungura Formation showing A) location of Shungura Formation in Ethiopia, B) main geographical (arbitrary) divisions of the Shungura Formation ("Type area" and "Kalam area"), and C) major age models. Map provided by the OGRE.

The depositional environments of the Shungura Formation were described and interpreted by various researchers. The taphocoenoses related to the fossil occurrences of the Shungura were initially described (Arambourg, 1943; Butzer, 1971b; Chavaillon, 1979) later detailed by several by Heinzelin (1983).

Through various studies on geological, fossil fauna remains including mollusks and ostracods, three main types of depositional environments were reconstructed in the sedimentary sequences of the Shungura Formation. These include fluviatile, deltaic, and lacustrine environments. The composition and construction of these Plio-Pleistocene sedimentary deposits are comparable to the extant meandering Omo River (Butzer, 1971a). Five main phases of depositional environments were recorded in the Shungura: three lacustrine phases were interrupted by two fluviatile phases.

The first lacustrine phase at the Basal Member (BAS-1-1) is correlated with the upper parts of the Usno Formation (U-2, and U-3). Fluviatile phases from the Basal Member (BAS-2) to the end of lower G (G-11 to G-13) are characterized by successive flood plains of the Plio-Pleistocene River Omo. The third phase, lacustrine from the base of upper G (G-14) to its peak at G-27, is characterized by shallow lacustrine to littoral (lake shore) and lagoon deposits. The fourth phase is a fluviatile sedimentary deposit from upper Member G (at G-28) to Member L-6. The first level of G-28 to Member H are transitional deltaic lakeshore. The last phase, from Member L-7 to L-9, represents deeper and sharper lacustrine transgression than the other known lacustrine environments in the Shungura (Haesaerts, 1983; Heinzelin & Haesaerts, 1983).

1.2.3. Fossil fauna of the Shungura Formation

The systematic study of the Shungura fossil fauna began with the work of C. Arambourg in the early 1930s and continued with the IORE in the 1960s and 1970s (Arambourg, 1943; Boisserie et al., 2008). During the IORE field campaigns, both paleontological and archeological surveys and excavations were made and resulted in the largest faunal and

artifact collections. During these field seasons, various small to large mammalian taxa, micromammals, reptiles, fish and amphibians were recovered. The Shungura faunal collection consists of more than 50,000 remains representing the largest collection from Plio-Pleistocene Africa (Bobe, 2011; Bobe & Eck, 2001; Boisserie et al., 2010).

The exposure of members J, K, L in the Shungura are not well explored by the IORE producing less faunal collections than those of members B to lower G (LG) (Alemseged, 2003; Alemseged et al., 2007; Eck, 2007). There are extensive exposures of these three members in the southern part of the Shungura Formation and are currently under investigation by the OGRE (Boisserie Pers.com, 2021). Member A provided relatively few specimens due to small outcrop exposure, whereas for upper members (J, K and L) it is due to insufficient survey during the IORE missions (Eck, 2007). More recently, additional faunal remains with a more collection from B and C Members were provided (Boisserie et al., 2008).

Skeletal profile in relation to depositional environments were provided by Alemseged (2003) from members A to LG show a consistent taphonomic condition due to similar fluviatile depositional events. Eck (2007) examined taphonomic bias for the Shungura faunal remains emanating from the exposure of localities (fossil rich sediments), field work efforts, the collection strategy and protocol (e.g., what to collect), and efforts made on surface collection (versus excavations).

Cranial elements (teeth, maxilla, mandibles, and horncores) hold the largest portion of the faunal assemblage from the Shungura (Alemseged, 2003; Eck, 2007). It has been suggested that other agents such as carnivorans could also affect the skeletal elements ratio between the fossil and the original taxa (Alemseged, 2003). However, the degree of carnivoran incidence was not assessed.

Common ungulate remains found throughout the Shungura deposits identified including various species of bovids, hippopotamids, equids, suids, giraffids, rhinocerotids and proboscideans. Among these Bovidae represent the most in the Shungura Formation, while Camelidae are among the least represented. Some of these taxa are briefly presented below.

Megaherbivores such as Proboscideans, Hippopotmidae, Rhinocerotidae, Giraffidae and Camilidae are also well represented in the Shungura Formation (Alemseged et al., 2007; Beden, 1975, 1980; Bobe et al., 2002; Boisserie et al., 2008; Coillot et al., 2013; Eisenmann, 1976; Geraads & Coppens, 1995; Guérin, 1976, 1985; Rowan et al., 2019). Hippopotamidae are the most common of all, and are the second-most abundant mammalian family in the Shungura Formation. Both the IORE and OGRE sampled a large number of this taxa (Boisserie et al., 2008, 2010; Boisserie, 2013; Coppens & Howell, 1985; Coryndon, 1976; Coryndon & Coppens, 1973; Souron et al., 2012).

Bovidae: Bovids represent the largest taxa throughout the Shungura Formation (Bobe & Eck, 2001; Eck, 2007). The most common bovid tribes include Aepycerotini, Alcelaphini, Bovini, Reduncini, and Tragelaphini, whereas Antilopini, Hippotragini, and Neotragini are also present although sparce (Alemseged, 2003; Bobe & Eck, 2001; Eck, 2007). Faunal data particularly based on bovid abundance indicates an increase of aridity from Early Pliocene towards Late Pliocene at ~2.8 Ma (Bobe, 2006; Bobe & Behrensmeyer, 2004; Bobe & Eck, 2001). Other studies also demonstrate that species abundance turnover at ca. 2.3 Ma, which possibly coincided with the emergence of *Paranthropus boisei* (Alemseged, 2003; Alemseged et al., 2007).

Suidae: the family Suidae in the Shungura Formation is represented by specimens that include genera *Nyanzachoerus*, *Notochoerus*, *Metridichoerus* and *Kolpochoerus*. However, *Phacochoerus* is not known with certainty from the Shungura. Suids are useful bio-chronological markers, and they have been used to reconstruct taxonomic, paleoenvironment and biostratigraphic correlations in the Shungura (Bibi et al., 2013b; Cooke, 2007; J. M. Harris & Cerling, 2002; Souron, 2012; Souron et al., 2012). The evolution of the Plio-Pleistocene African Suidae is detailed in Harris and White (1979), among other contributions.

Cercopithecidae: Although they are found throughout the Shungura deposits, cercopithecids are particularly abundant in the lower members (B and C). These primates are among the

largest represented faunal materials in the Shungura deposits (Boisserie et al., 2008; Eck, 2007).

Hominidae: Hominid specimens were recovered throughout the Shungura Formations from 3.4 Ma to 1 Ma (Alemseged et al., 2002; Boisserie et al., 2008; Coppens, 1978; Eck, 2007; Howell et al., 1987). The 1960s and 1970s IORE expedition have yielded more than 250 specimens (Coppens, 1978). Robust and gracile *Australopithecus* as well as early *Homo* were found in lower members, and *Homo erectus*, at Member K (Boisserie et al., 2008; Coppens, 1978; Howell et al., 1987). *Homo habilis* was recovered in members E to G at ~2.4 to 2 Ma whereas *Paranthropus boisei* in members G to K, ca. 2.33 Ma to 1.38 Ma (Suwa et al., 1996; Wood & Leakey, 2011). *Paranthropus aethiopicus* (type) was found in members C to F from ~2.8 Ma to 2.33 Ma (Bobe, 2011; Boisserie et al., 2008; Coppens, 1977; Howell et al., 1987). The OGRE has uncovered five more hominid localities at Member C dated from 2.74 to 2.58 Ma (Boisserie et al., 2008).

Carnivorans: Various species of large carnivorans including hyaenids, felids (such as *Megantereon, Dinofelis* and panthers as well as smaller *Felis*) were also uncovered from Shungura (Boisserie et al., 2008; Coppens & Howell, 1985; Howell & Petter, 1980; Werdelin & Lewid, 2005). Small carnivores known from this site also include viverrids and mustelids (Boaz et al., 1982). A rare otter fossil is also represented by *Enhydriodon sp* (Lewis & Werdelin, 2007; Werdelin & Lewis, 2005). Carnivores are represented by cranial and postcranial remains from various taxa. More recently, additional large carnivores of felids, hyaenids and mustelids as well as small to medium size carnivores of cf. Lutrinae and cf. Vivrridae were recovered from Member C (Boisserie et al., 2008). No canid has been reported so far from the Shungura Formation.

Reptilians, in particular crocodilians and chelonians are common in the Shungura Formation. However, except some works on crocodiles and tortoise (de Broin, 1979; Tchernov, 1976), studies on these taxa are not as fully described as the other mammalian groups. Fossil specimens of crocodiles are common throughout the Shungura Formation and about three possible species were noticed (Tchernov, 1976, 1986). While crocodylians and

Chelonia are abundant, squamates are relatively less represented in the sequence. Arambourg reported six species of reptiles and described the two species of crocodile as *Euthecodon brumpti*, *Crocodylus niloticus* (Arambourg & Coppens, 1967). Butzer (1971) also explained that the overall faunal spectrum is dominated by aquatic reptiles including Crocodiles (*C.niloticus, E.brumpti)*, several chelonians and lizards, as well as various species of amphibians and fish (Butzer, 1971b)

Fish remains are abundant in the Shungura Formation. Arambourg documented nine species of fossil fish in the formation (Arambourg, 1943; Arambourg et al., 1969; Stewart & Murray, 2008a). A diverse fish community is recorded from various members in the Shungura that are dated to 3.4 Ma to 1.8 Ma. It is described that the general taxonomic composition of fish is similar to that of Plio-Pleistocene of eastern Turkana (Stewart & Murray, 2008b). Although are among the most common faunal remains to be found in the Shungura, but, unlike mammalian fauna, they were not consistently collected and studied (Stewart & Murray, 2008b). In addition, the effort and interest towards collecting these taxa was low during the IORE projects (Eck, 2007).

Micromammals: Micromamals are known to be good environmental indicators and have been a focus of paleontological studies. A detailed study of these micromammals from the Shungura was provided by Wesselman (1984). However, due to their small size and various taphonomic agents, these faunal materials are represented in smaller numbers. They are either swallowed by carnivores or easily washed away by water transports (Andrews & Evans, 1983; Wesselman, 1984). Large rodents like porcupines (*Hystrix*) are also present (Butzer, 1971a; Wesselman, 1984). The existence of rodents on a site could also be attested by the traces left on larger well-preserved fossils. Rodents gnaw bone edges, and their incisors leave typical marks (Pokines, 2015).

1.2.4. The Shungura Formation archeological record

Archeological occurrences older than those of Olduvai Gorge with were first reported from the Shungura Formation and currently dated to 2.3 Ma (Boisserie et al., 2008; Chavaillon, 1970, 1976; Coppens et al., 1973b; Delagnes et al., 2011; Howell et al., 1987; Maurin et al., 2017; Merrick et al., 1973; Merrick & Merrick, 1976). Archeological occurrences were recovered both *in situ* and in secondary deposits (Delagnes et al., 2011; Howell et al., 1987; Maurin et al., 2017).

Reassessment of the IORE archeological collections indicate that unambiguous archeological materials come from localities in lower Member F and lower Member G (de la Torre, 2004; Delagnes et al., 2011; Maurin et al., 2017). The OGRE has uncovered more than 22 archeological localities from both surface and in *situ* artifacts from Member F (Boisserie et al., 2008; Delagnes et al., 2011; Maurin et al., 2017).

The lithic assemblage of the Shungura shows distinct technological features (de la Torre, 2004; Delagnes et al., 2011). Analyses on recovered artifacts and archeological age conglomerates indicate the preference of quartz as a main raw material (Delagnes et al., 2011). A similar behavior has been reported from Fejej, another Plio-Pleistocene site from the Omo Valley (Barsky et al., 2011).

Some archeological occurrences of the Shungura yield stone tools directly associated with faunal materials (Delagnes et al., 2011; Maurin, 2017b). However, the functional relationship of the faunal and lithic artifacts at Shungura has not been addressed yet. Recent use wear analysis of the artifacts indicated their potential use mainly for carcass exploitation (Galland, 2022). However, archeological sites are not distributed throughout the sequence and even become absent from upper Member G up to Member L (Delagnes et al., 2011). A study on spatial behavior of these early Oldowan tool makers in Member F and lower Member G showed variations of artifact density that could be due to preferred environmental settings suitable for Oldowan tool makers in the Shungura (Maurin et al., 2014).

In addition, the archeological study of more than one hundred of Oldowan occurrences from Member F indicated a single or limited number of occupation episodes (Maurin et al., 2017). It also suggests that tool knapping activities took place on the paleo-Omo riverine environments (Maurin et al., 2014, 2017). This is congruent with most early Plio-Pleistocene sites occurring in paleoecological contexts associated with riparian and/or lacustrine environments (Blumenschine & Peters, 1998; Plummer & Bishop, 1994; Shipman & Harris, 1988).

Hominid raw material selection and transport could be due to decisions made based on various factors. It is suggested that carcass availability on a landscape scale could vary and influence hominid stone tool dispersal patterns (Blumenschine, 1986; Blumenschine et al., 2008; Peters & Blumenschine, 1995; Pobiner & Blumenschine, 2003). It is thus important to understand why and how hominin behaviors vary according to certain ecological conditions.

The Shungura Formation is a key site for the study of Plio-Pleistocene hominid biological and cultural evolution. Evidence of significant behavioral changes occurred ~2.3 Ma, especially in Member F (Delagnes et al., 2011). To date, no zooarcheological studies have been conducted on the Shungura bone assemblages, despite their paleoanthropological significance. Recent OGRE project aims at investigating this potential (Boisserie et al., 2008). Within the framework of the OGRE project, the main aim of the thesis is thus to provide new taphonomic data, and environmental context of the Oldowan archeological occurrences from the Shungura Formation, Lower Omo Valley.

1.3. Research questions and objectives

The dissertation focuses on reconstructing the ecological context of Oldowan occurrences and identifying the origin of BSM agents from the Shungura Formation through examining the vertebrate faunal data. The aim of this study is to understand the hominid habitat types and hominid-non hominid interactions by integrating the data obtained from faunal composition, dental microwear and zooarcheological assessments.

With this, this dissertation attempted to address the following major questions.

1) Central to this study is the question why there is a sudden appearance of Oldowan lithic artifacts in Member F?

2) What is the ecological context in space and time associated with the appearance of these Oldowan technology? Could faunal distribution and dietary ecology distinguish habitat types at a local scale?

3) What was the purpose of these tools? Can we detect hominid butchery activities in these units and in the Shungura sequence in general? With this, a complementary, but an important question can be asked regarding the ability to correctly identify BSM agents considering the presence of crocodiles, mammalian carnivorans, hominids, and the fluviatile nature of the Shungura deposits.

4) What does this event imply in terms of ecology, behavior and habitats, and comparison at a Shungura scale?

In seeking to address these questions, the thesis is organized into five chapters.

Following the present introductive chapter, Chapter two of this dissertation presents the taphonomic and ecological context associated with the emergence of the Oldowan in the Shungura Formation. This chapter tries to address the question regarding the ecological context in space and time associated to the appearance of the Oldowan technology. Here, faunal distribution and dietary ecology of selected ungulates are studied to track habitat change through time and distinguish habitat types at a local scale. In this chapter I integrate taphonomic history of the vertebrate assemblages, dental microwear on selected ungulates, and faunal abundance distributions from Member E and Member F, between units (temporal), and across space within units, with a specific focus on the basal Member F excavations and its faunal data. I discuss the ecological aspects prior to Oldowan activities contemporary to the Oldowan occurrences of the Shungura Formation.

Chapter three is dedicated to presenting bone surface modifications throughout the Shungura sequence. Here, both classical zooarcheological methods and new 3D geometric morphometric analysis of BSM were applied to identify modification types. The main objective of this part is to identify the agents of bone accumulators in the Shungura faunal assemblages with special emphasis on the role of early hominids.

Once the ecological contexts of those Oldowan sites were reconstructed, and BSM identification methods are studied in the previous chapters, the fourth chapter presents a case study of locality OMO 57. This locality includes several paleontological (faunal) and archeological (lithic) occurrences. This site complex provides rich faunal remains including hominids and associated artifacts at the unit F-1. Here, I have conducted a comprehensive taphonomic study from both surface and excavation samples in order to understand site formation process, assess functional association between the lithic artifacts and faunal remains and over all to provide data on the nature of the assemblages.

The final part of the thesis (Chapter five) presents a short summary of results and research perspectives. Each Chapter, except for Chapters one and five last chapter, has a content with introduction, materials and methods, conclusion, and references.

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Chapter Two

Vertebrate ecology at the onset of Oldowan technology in the Shungura Formation (Lower Omo Valley, Ethiopia)

2.1. Introduction

Environmental changes that occurred during the Plio-Pleistocene have been hypothesized as key drivers of human evolution (Coppens, 1975; deMenocal, 1995, 2004; Maslin et al., 2014; Potts, 2007, 2012; Vrba, 1988). This period is featured by major ecosystem changes that coincide with hominid behavioral and taxonomic diversification and extinctions (Potts, 2012; Reynolds, 2007). In particular, the Early Pleistocene is characterized by high environmental variability following the expansion of open and dry ecosystems during the Pliocene (Levin, 2015; Maslin et al., 2014; Potts, 2013). This environmental shift has been linked to hominid speciation and to important behavioral changes (Foley, 2002; Wood & Leakey, 2011).

Various ecological studies have been conducted on both eastern and southern African Plio-Pleistocene records with an attempt to address the relationship between such paleoecosystem dynamics and human evolution (Bibi et al., 2013; Hernández Fernández & Vrba, 2006; O'Brien et al., 2020; Patterson, Braun, Behrensmeyer, Lehmann, et al., 2017; Patterson et al., 2014; Reed, 1998; Shipman & Harris, 1988; Vrba, 1985). These studies have contributed to our understanding of paleoecosystem changes at rather large spatiotemporal scales.

Yet, local scale biotic and abiotic factors can clearly influence faunal structure (Bailey et al., 2011; Bailey & King, 2011; Boisserie et al., 2008; Fillion & Harrison, 2022; Kingston et al., 2007; Reynolds et al., 2011; Robinson et al., 2017). For example, patterns of faunal change could be influenced by local and regional tectonics as well as other environmental processes (Bailey & King, 2011; Behrensmeyer, 2006; Boisserie et al., 2008). Environmental variability might be increased by the frequent disruption of already heterogeneous landscapes due to volcanic events (Bobe & Carvalho, 2019; Trauth et al., 2010).

At basin scale, the Turkana Basin provided important data regarding Early Pleistocene faunal organization. A landscape heterogeneity across space and through time has been recorded across early Pleistocene sites from the Turkana region (Bobe & Behrensmeyer, 2004; O'Brien et al., 2020; Patterson, Braun, Behrensmeyer, Lehmann, et al., 2017). Within this basin, the Shungura Formation, stretched north-south along the Omo River (Figure 2.1), displays a relatively continuous fossiliferous depositional sequence dated to ca. 3.6 Ma to ca. 1 Ma that seems ideal to explore relationship between faunal evolution and these various factors at local scale.

The Shungura Formation yielded a very rich fossil faunal assemblage including hominids and among the few known archaeological occurrences dated to earlier than 2 Ma, as documented by the International Omo Research Expedition (IORE) between 1967 and 1976 (e.g. (Chavaillon, 1976; Coppens et al., 1973; Coppens, 1977; Heinzelin, 1983; Howell et al., 1987; Merrick et al., 1973), and later by the Omo Group Research Expedition (OGRE) since 2006 (Boisserie, 2013; Daver et al., 2018; Delagnes et al., 2011; Maurin, 2017). Its geological and chronostratigraphic record is well-established, and it possesses a long history of paleontological and archaeological study (Boisserie et al., 2008, 2010; Delagnes et al., 2011; Eck, 2007; Feibel et al., 1989; McDougall et al., 2012; Suwa et al., 1996).

Previous studies of the Shungura record documented faunal turnovers and changes in abundance of bovids, cercopithecids, suids, and hominids through time (Bibi & Kiessling, 2015; Bobe & Behrensmeyer, 2004; Bobe & Eck, 2001). A relative increase in grassland adapted taxa appears to document an environmental change toward more arid and open landscape during the Early Pleistocene (Bobe et al., 2002). This period is also accompanied by an extensive increase in C_4 biomass (Cerling et al., 2015; Levin et al., 2011; Uno et al., 2016).

At the beginning of Pleistocene, the Shungura Fm. indicates more wood cover than eastern and western Turkana sites (Levin et al., 2011). Similar observations have been predicted based on analyses of bovid abundance (e.g., Bobe *et al.,* 2007). Previous work on the Shungura faunal remains explored environmental changes through time with the objective to

identify key driving factors and habitat preferences (Bibi et al., 2013; Bibi & Kiessling, 2015; Blondel et al., 2018, 2022; Martin et al., 2018; Merceron, Kallend, et al., 2021; Negash et al., 2015, 2020; Plummer et al., 2015). Furthermore, a spatial variation of faunal distribution across north and south sectors has been observed in both member G and F (Alemseged et al., 2007; Maurin, 2017b).

The earliest secure record of lithic production in the Shungura Formation so far is from Member F, dated to 2.32-2.27 Ma (Boisserie et al., 2010; Delagnes et al., 2011; Maurin et al., 2014). During the 1970s, the first stratigraphic unit of Member F (Unit F-0) has provided an abundant faunal record including both gracile and robust hominids that shortly predate the production of Oldowan technology. In addition, this period records an increase in grazing ungulates adapted to open habitat marking the expansion of arid landscapes (Bibi & Kiessling, 2015; Bobe & Behrensmeyer, 2004; Bobe & Eck, 2001; Rannikko et al., 2017; Shipman & Harris, 1988).

The largest record of ungulates from Member F prominently came from excavations at two localities sampling the same layer, i.e., F-0, OMO 33 and L 398, separated by ca. 2.0 km. Hence, it could provide a particularly interesting case for investigating a local ecological signal within a short time interval, and its bearing on the overall faunal signal of Member F.

This unit (F-0) immediately predates the development of stone knapping in the Shungura occurrence at F-1. Thus, it would be useful to capture the ecological context on the onset of this important behavior.

This study aims to address the following questions. Is there an abundance distribution difference across the outcrops of Unit F-0, specifically between these two localities (OMO 33 and L 398)?

Does dietary ecology differ among these sympatric communities, and for which possible reasons? It is well known that various taphonomic factors can hamper palaeoecological reconstructions (Behrensmeyer, 1988). Thus, I also aim at evaluating the taphonomic aspects

of the assemblages prior to the ecological study. For tackling these questions, I studied the taphonomy, composition, and dietary ecology of the F-0 ruminants, i.e., bovids and giraffids.

2.2. Materials and Methods

2.2.1. Material

In this study, I used faunal assemblages from members E and F, dated between ~2.38 Ma to 2.271 ± 0.041 Ma (McDougall et al., 2012). I mainly focused on two localities, L 398 and OMO 33, exploited through survey and excavations during the IORE field campaigns from 1970 to 1973 and from 1967 to 1974, respectively. I compared them to other localities from member E and F collected by both the IORE and OGRE research projects. These analyses were performed on the records of the Omo Database managed by the OGRE, which resulted from subsuming into a single relational database the IORE catalogue with the new fossil record constituted by the OGRE in 2006, and regular updates of both IORE and OGRE specimen lists since then. It must be noted that differences in the collection interests and strategies between these two research programs are documented.

L 398 was excavated by the American research team in 1971-1973 (Dechant Boaz, 1994). A total of 178 m^2 was exposed and, although initial report indicates a total of ~2,717 specimens (Dechant Boaz, 1994; Johanson et al., 1976) and 2,642 for Eck (Eck, 2007), the total number of specimens was in fact recounted giving a total of 2,829 specimens following the Omo database. OMO 33 was excavated by the French contingent under the direction of Claude Guillemot in 1973 and 1974 (Alemseged et al., 1996; Johanson et al., 1976). OMO 33 yields the largest faunal assemblage (n=3,386) from Member F. OMO 33 has a total area of 26 square meters (Alemseged et al., 1996). Together, these two localities represent 62.1 % of the total fauna known in Member F. I have removed from the catalogue specimen numbers attributed to indet, stones and coprolites. NISP count of bovids for each unit is provided below (

Table 2. 1).

Both localities situated at the base of Member F (Unit F-0) are defined as channel deposits (Dechant Boaz, 1994; Johanson et al., 1976). Member F is a fluviatile sedimentary deposit comprising of five units (F-0 to F-5). Deposits of Unit F-0 at L 398 and OMO 33 consist of a sandy tuffite correlated and partly coeval to the vitric tuff F observed in other localities (Heinzelin & Haesaerts, 1983), and dated to 2.324 ± 0.020 Ma (McDougall and Brown 2008). Tuff F' has three sedimentary features defined as F'-α, F'-β, and F'-γ subunits. F'-α has a coarse-grained composition lying at the bottom of a channel deposit, F'-β has medium to silty components, and F'-γ is made up of finer silty tuffite at the top (Heinzelin & Haesaerts, 1983). At L 398, the main fossiliferous horizon occurs at F'-α, the richest being at the bottom part. Whereas at OMO 33, the assemblage comes from F'-β, but truncated at F'-α (Heinzelin & Haesaerts, 1983).

Taxa	**E-1**	**E-2**	**E-3**	**E-4**	**E-5**	**F-0**	**F-1**	**F-2**	**F-3**	**F-4**	**F-5**
Aepycerotini	18	13	54	25	17	242	115	2	42	4	2
Alcelaphini	4	0	3	1	5	332	32	0	5	1	0
Bovini	5	1	8	3	13	106	20	0	3	1	0
Reduncini	22	14	41	20	27	76	69	0	33	1	0
Hippotragini	0	0	1	0	1	0	1	0	0	0	0
Neotragini	0	0	3	0	1	2	0	1	0	0	0
Tragelaphini	56	26	79	36	39	104	40	1	24	1	1
T.*nakuae*	45	25	70	33	18	7	6	0	1	0	1
T.*gaudry*	4	1	4	2	20	94	31	1	23	1	0

Table 2. 1: NISP counts of Bovids from IORE from units of Member E (E-1 to E-5) to top of Member F (F-0 to F-5). Counts are based on Cranio-dental elements.

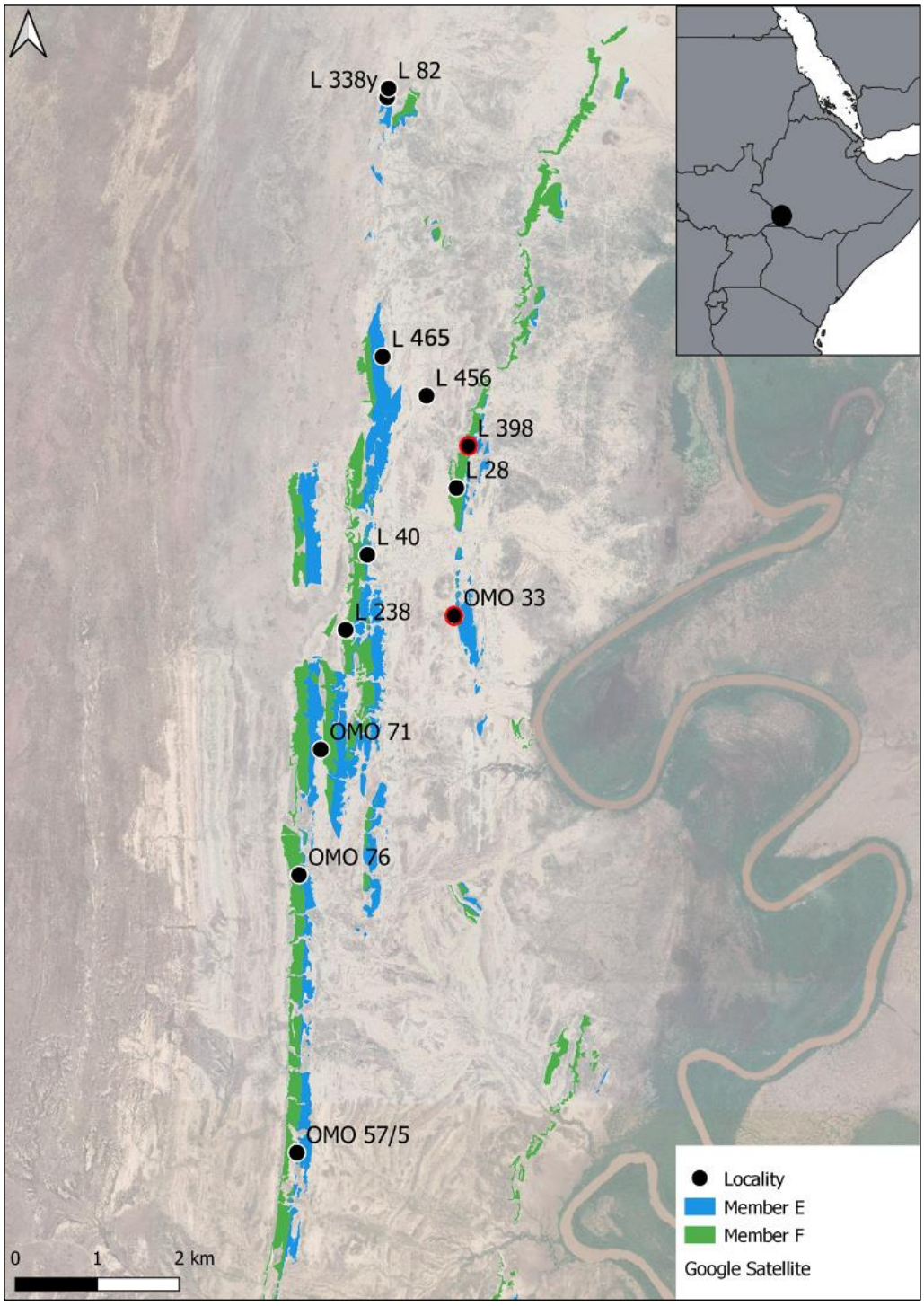


Figure 2. 1: Map showing the location of the Shungura Formation (Type Area), and the localities studied within members E and F. Target localities (OMO 33 and L 398) are circled in red outline.

Thus, the two localities have comparable depositional settings and geographical proximity. In addition, the largest share of the total IORE faunal assemblage in Member F comes from Unit F-0 (73.4%). When I consider only identified mammalian fauna, about 64 % are from this unit, of which bovids represent 24 %. This analysis primarily focuses on bovid taxa with a comparison with other localities of similar temporal resolution. Giraffids, which make up ~4%, are included only in the microwear analysis.

The comparative localities come from members E and F in the Type Area (Figure 2. 1). I first assessed the temporal faunal structure by analyzing units from lower Member E up to the top of F. The main reason I have focused on OMO 33 and L 398 was due to 1) they represent the most significant sample size in unit F-0, and in Member F in general, 2) both are from large scale excavations, and their context is well defined, and 3) predates immediately before the Oldowan lithic production in the Shungura.



Figure 2. 2: Examples of horncores from L 398 bovids. Left to right: *Tragelaphus nakuae* (A), *Tragelaphus gaudryii* (B), and Aepyceros sp. (C). Scale bar is 5 Cm.

I have focused my analysis on the excavation localities because they have huge records at locality scale and makes it interesting to drive a comparison between very local signals. With this, I have targeted bovids because they were well studied in the sequence, abundantly used for environmental reconstructions. Furthermore, to include all groups is beyond the scope and time allocated to this during my PhD.

I have targeted five bovid tribes (Aepycerotini, Alcelaphini, Bovini, Reduncini and Tragelaphini) and on giraffids for paleodietary analyses (at OMO 33 and L 398) and abundance analyses (throughout members E and F). Other bovid tribes, namely Antilopini, Hippotragini, and Neotragini, are rarely occurring and limited to only a few localities; they were therefore excluded from this analysis. All studied specimens are housed at the National Museums of Ethiopia/Ethiopia Heritage Authority at Addis Ababa and were accessed within the framework of the OGRE research permit in Ethiopia.

2.2.2. Methods

I focused on palaeoecological and taphonomic data to examine the lower part of Member F and the lithic bearing units (mostly F-1 to F-3). Analysis of faunal abundance, 3D dental microwear texture analysis (DMTA), and taphonomic investigations have been conducted. Such case studies (at unit and locality levels) could offer a more precise link between the environmental context and the adaptive response of hominids and of the rest of the fauna at a well-defined spatio-temporal temporal resolution.

2.2.2.1. Taphonomic methods

Whether the faunal distribution across these sites is an ecological pattern or the consequence of preferential preservation due to taphonomy was assessed. Here, I examined bone surfaces for taphonomic signals including natural post-depositional impacts (Lyman, 1994a; Madgwick & Broderick, 2016; Thompson, 2005). These include bone damages, breakage and weathering and abrasion patterns. Bone weathering stages were particularly used to compare duration of sub-areal exposure between the two assemblages (OMO 33 and L 398)

following Behrensmeyer (1978). I have used X20 and dino-lite to capture detailed images. I assessed the skeletal element distribution across localities. I used the Kolmogorov-Smirnov test for equal distribution skeletal elements to evaluate differences among localities. In addition, I applied the same statistical test to compare taphonomic differences such bone weathering among localities.

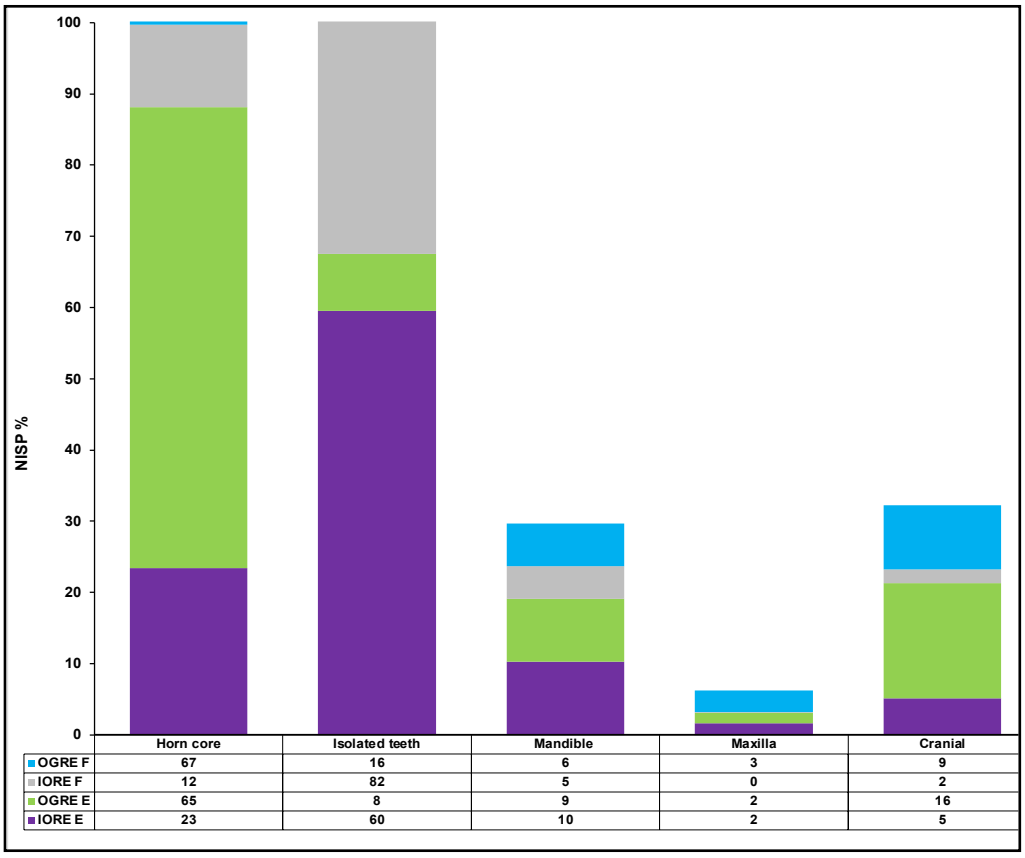
2.2.2.2. Abundance analysis

For abundance analysis, I focused on the family Bovidae, specifically on specimens taxonomically identified at a tribe rank. Bovids are the most common in the eastern African fossil record, known to be ecologically diverse and habitat specific (Bobe & Eck, 2001; Vrba, 1996). They are widely used for reconstructing paleoenvironments through time and across space. It has been suggested that correspondence analysis is a robust method in analyzing samples of nonlinear data (Ludwig & Reynolds, 1988). This method has been useful to graphically compare faunal associations to geographical or geological context (Bobe & Eck, 2001).

Number of identified specimens (NISP) and minimum number of individuals (MNI) are the most common abundance analysis methods (e.g. Lyman, 1994b, 2008). MNI is recommended for assemblages that are less impacted by uneven skeletal distribution (e.g., scattering by transportation), whereas NISP is a better option for fluviatile contexts (Badgley, 1986). In this analysis NISP of each taxon was counted by unit and per locality. For temporal comparisons, I used NISP counts of bovids per unit in members E and F. I applied a similar method on localities from various sectors to determine if there is a difference in bovid distributions across space.

A chi-Square test was used to compare if there is a significant difference between bovid tribes at each unit and locality. Then, I applied SIMPER (similarity percentages) to determine which tribes contributed the most in driving the significance. For taxonomic distance, I used Bray-Curtiss' similarity index in the SIMPER analysis. Statistical tests were applied on R using the vegdist package. For basic quantification and data visualization, Excel and Past

software were also utilized. I chose localities with a diversified composition and a NISP equal or larger than 30.



	Horn core	Isolated teeth	Mandible	Maxilla	Cranial
OGRE F	67	16	6	3	9
IORE F	12	82	5	0	2
OGRE E	65	8	9	2	16
IORE E	23	60	10	2	5

Figure 2. 3:Percentage of counts of bovid cranio-dental elements from Members E and F collected by IORE and OGRE

There is a significant difference in the sample medians between the two projects in both members (P = <0.0001). Within the IORE, both the French and the American team were collecting cranio-dental elements of bovids similarly in both members (Alemseged et al., 2007; Bobe & Eck, 2001; Eck, 2007; Maurin, 2017b). Thus, there was no bias introduced due to the sampling method between the two teams. The collection strategy between the IORE and the OGRE regarding bovids is however different (Figure 2. 3). While the IORE was collecting isolated teeth, the OGRE was not collecting them unless they were found in association or in proximity.

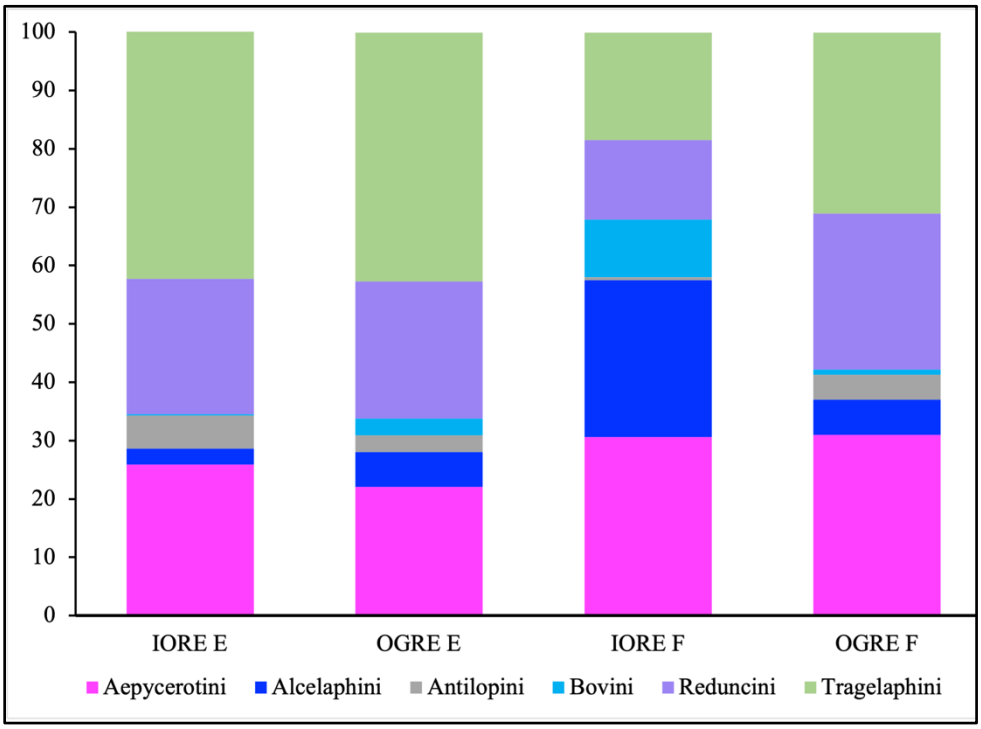


Figure 2. 4: Percentage counts of bovid tribes from members E and F collected by the IORE and the OGRE. The high number of Alcelaphini is visible only in IORE F. This is due to most of the bovid samples for the IORE Member F comes from unit F-0, in particular from large scale excavations carried out at L 398 and OMO 33 by the IORE.

Within the IORE teams, both French and American projects applied similar collection methods regarding bovids (Eck, 2007). Similarly, regardless of the difference in collection protocols, the OGRE and the IORE collected a similar number of bovid taxa.

In Member E, for both projects, Tragelaphini, Aepycerotini, and Reduncini are the most dominant, and similarly distributed (Figure 2. 4). In Member F, while Aepycerotini is equally represented in the collection by both teams (31%), there is difference in the number of Alcelaphini, the second most common in the IORE (27%) but less represented in the OGRE collection. Whereas from the OGRE, Tragelaphini is represented equally as Aepycerotini followed by Reduncini at 27%. However, this variability at Member F likely originates from

the sampling at unit F-0. Unlike the OGRE, the IORE conducted large-scale excavations of F-0 deposits, and Tuff F' proved to be quite rich in Alcelaphini.

2.2.2.3. DMTA

Abundance analysis and ecomorphology based studies provide the general spectrum of habitat categories (e.g., (Barr, 2015; Kovarovic & Andrews, 2007; Plummer et al., 2015; Reed, 1998). However, ecological factors determine the availability of plant resources (e.g., due to climatic or seasonal shift). The study of feeding ecology through DMTA was performed to effectively discriminate between dietary groups within short temporal scale (Merceron et al., 2010, 2016), especially within the context of comparing L 398 and OMO 33 localities, which are close in space and time, and with comparable faunal composition. In such conditions, paleodietary analyses have therefore the potential to capture ecological partitioning at a community scale.

To apply the DMTA method, suitable molars that could be identified at the tribe level were selected (n=176). Initial selection of molars was made based on preservation and wear stage on upper and/or lower molars (M1, M2, M3). Each molar surface was cleaned using cotton swabs soaked in acetone to remove any dirt on their facets. A silicon material (Colten President Jet Regular Body) was applied to capture impressions of the dental occlusal surfaces. Peels of these samples were exported to France to perform the 3D scan at the Laboratory Paleontology Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM), University of Poitiers (Figure 2.5). Each facet was placed on a flat position and scanned using TRIDENT, a surface profilometer white light scanning confocal microscope Leica DCM8 (see Merceron et al., 2017, for protocol).

Generally, the second molar (either upper or lower) was preferred when an individual has a tooth raw (M1-M3). The lingual enamel band of the paracone and protocone for upper molars and the buccal enamel band of the protoconid for lower molars was targeted. For upper molars, in some instances, the metacone was alternatively scanned when the paracone was taphonomically altered since both have the same function (Ramdarshan et al., 2017). Similarly, the protoconid of the lower molar and the protocone of the upper molar have both

shearing function (Ramdarshan et al., 2017), and were therefore treated together. Examples of good quality surfaces are provided below (Figure 2. 5). In a few samples, the hypoconid was considered and grouped with the shearing facets. Thus, for simplicity, all crushing facets were grouped as Par and shearing facets as Ptcd in this study. Finally, there was relatively larger sample of shearing facets (Ptcd) for each taxon, I focused the statistical analysis on this facet.

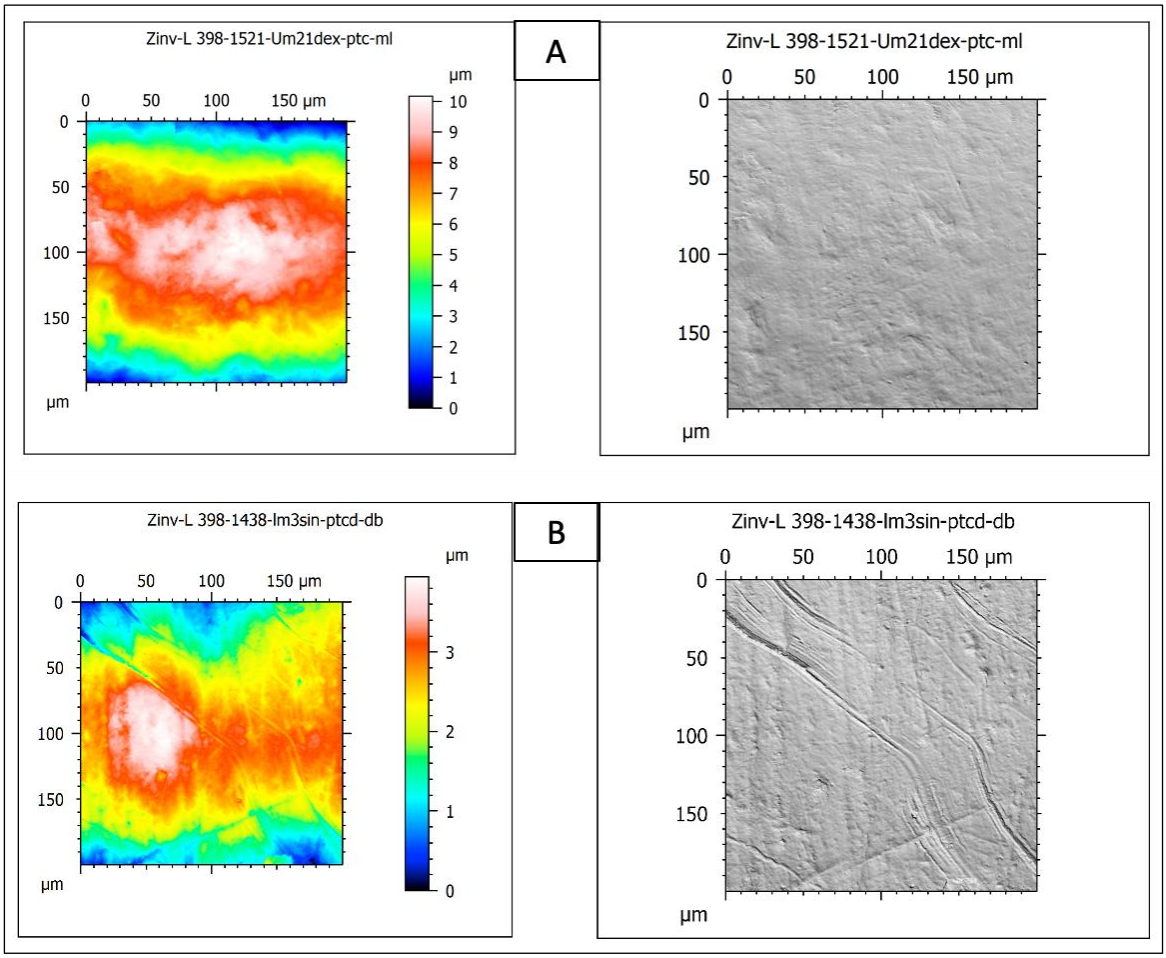


Figure 2. 5: A) Examples of photosimulations, A) Aepycerotini from L 398 (upper molar, protocone facet) and B) Alcelaphini from L 398, a Lower M3-Ptcd (protoconid) facet.

Each scan (plux file) was processed using LeicaMap v8.0 software. Within the extracted area, a surface of a 200X200 µm was selected for each specimen and, in case of artifacts, the filling of non-measured points was executed. Details regarding such data treatment can be found in Merceron et al (2016).

Once this data treatment was completed, a Scale Sensitive Fractal Analysis (SSFA) template was applied to generate the four SSFA parameters. A detailed description of these variables is provided by Scott et al (2006). Once the parameters with their respective measured values were generated, r^2 (regression coefficient) was checked, and all values below 0.97 were deleted. This was applied to avoid any abnormal values that might have been by taphonomy, bad scanning or any error during treatments.

To identify the most discriminant parameter, bar plots and statistical tests were conducted for each facet (per taxa and site) separately. Statistical analyses were performed using R statistical software (Version 3.6). The data were box-cox transformed before using analysis of variance (ANOVA). Differences between the two localities and among taxa were then assessed using ANOVA. To test the homogeneity of variance, both Bartlett test and diagnostic plots were performed first. In addition, both Kruskal Wallis and Dunn's non-parametric tests were made to cross-check the variance homogeneity. To determine the source of significant variation, both post hoc (HSD) and Fisher's LSD tests were applied. One-way ANOVA was applied to specify the interaction between the variables (site and taxa). The R packages (Agricole, ggplot2) were used to perform this analysis and visualize results.

In addition, to better detect dietary-related behavior, an analysis of dispersion was also carried out with a larger sample size. Behaviors related to mobility, seasonality, and mechanical property of the food are among the most important factors to consider in DMTA studies (Merceron, Berlioz, et al., 2021). Results were also discussed in comparison to the microwear of extant fauna and published paleoenvironmental data from the Shungura Formation, mainly isotopic study of ungulates (e.g. Bibi et al., 2013; Blondel et al., 2018, 2022; Negash et al., 2015, 2020).

2.3. Results

2.3.1. Taphonomy

2.3.1.1. Skeletal element representation

In both localities, cranial elements constitute the largest number of skeletal elements with slight variations in the extent. Compared to L 398, cranio-dental parts are more represented at OMO 33, with teeth constituting 83 % of the assemblage. Despite a significant proportion of cranio-dental material, L 398 also has more postcranial elements (27 %) preserved than at OMO 33. Postcranial elements at OMO 33 represent only 11.6 % of the total assemblage. Kologorov-Smirnov test for equal distribution indicates that distributions are not significantly different between the two localities (D: 0.18182; *p*-value = .98517). This is considering animals of similar size (all bovids). This indicates the effect of hydraulic sorting is high and affects both localities in more or less the same way. The sorting is clearly indicated by high number of cranio-dental (

Table 2. 1), i.e., elements constant with high energy water flow (Alemseged, 2003; Alemseged et al., 1996; Behrensmeyer, 1988; Dechant Boaz, 1994; Voorhies, 1969) . This is also evident by the high number of abraded specimens.

	Elements (Bovidae)	L 398 NISP (%)	OMO 33 NISP (%)
Cranio-dental	Teeth	176 (**62**)	965(**83**)
	Horncores	12(4.2)	27(2.3)
	Crania	3(1.1)	4(0)
	Mandibles	12(4.2)	31(2.7)
	Maxilla	1(0.4)	0(0)
Post-crania	Vertebrae	6(2.1)	3(0.3)
	Scapulae	2(0.7)	5(0.4)
	Phalange	7(2.5)	6(0.5)
	Pelvis	2(0.7)	0(0)
	Compact bones*	29(**10.2**)	51(4.4)
	Long bones	34(**12**)	70(**6**)
	Total	284(100)	1162(100)

Table 2. 2: Skeletal element representation of L 398 and OMO 33, NISP counts and % are in brackets. Compact bones* include basipodials, calcaneus and astragalus.

2.3.1.2. Weathering and abrasion

Both excavation localities (OMO 33 and L 398) have overall comparable taphonomic history. Weathering, with particular focus on medium to large size ungulates indicates short durations of surface exposure in both assemblages.

The majority of the bovid postcranial specimens from L 398 (n=29) show early-stage weathering, stage 1 (55.2%) followed by weathering stage 0 (n=31%). Similarly weathering stage 1 (55.6%) dominates at OMO 33, although followed by weathering stage 2(22.2%). No weathering stages 4 and 5 are observed in both assemblages (Table 2. 3).

Weathering Stages	OMO 33 (%)	L 398 (%)
Stage 0	6(11)	56 (**48**)
Stage 1	31(**56**)	50(42)
Stage 2	13(24)	8(7)
Stage 3	5(9)	4(3)
Stage 4	0(0)	0(0)
Stage 5	0(0)	0(0)
Total	**55(100)**	**118(100)**

Table 2. 3: Large to medium size mammals post crania used for weathering category (81% Bovidae for OMO 33, and 47% for L 398 identified as Bovidae).

Dechant Boaz (1994) also noted that only few samples from L 338y show weathered specimens beyond stages 0 and 1 due to rapid burial. I observed similar weathering at OMO 33 and L 398. This less weathering effect could be associated to rapid burial of the skeletal elements (Behrensmeyer, 1978).

2.3.1.3. Bone surface Modifications

At L 398, one possible insect damage, featured with star shaped marks (Backwell et al., 2012) is observed. The specimen is a long bone shaft comparable to size of Leporidae, however, both epiphyses are missing (Figure 2. 6). A small number of remains from L 398 (n=5) shows signs of carnivore damage. Notably, an avian long bone shaft displays toothmarks, and both ends were chewed off. In addition, moderately abraded rodent gnaw marks were observed on one shaft frag from a medium size mammal. The size of the gnaw marks are bigger, similar to those produced by porcupines (Fernández-Jalvo & Andrews, 2016). A single tooth of hyrax is present within this assemblage.



Figure 2. 6: A small mammal (Leporidae?) long bone shaft showing star-shaped marks, possibly related to termite damage (Backwell et al., 2012). Scale bar 1 cm.

Abrasion caused smoothing of breakage edges causing difficulty to categorize observations into Bone Breakage patterns (Blumenschine, 1995; Lyman, 1994a; Thompson, 2005). Although green fractures are common, a single long bone flake shows a fracture with wider percussion notch resembling of a hammerstone percussion (Blumenschine, 1995). However, the fact that it lacks additional marks, despite a well-preserved cortex, makes it difficult to conclude about human activity. At L 398, two specimens show linear marks, but are attributed to preparation marks.

At OMO 33, no definitive mark is observed that can be attributed to bone surface modification; the high abrasion of surfaces due to hydraulic abrasion makes it difficult to

detect. However green fractured specimens with some that seem to show “percussion notches” are observed (Figure 2. 7). Linear marks are observed on two bovid’s long bones, though difficult to characterize due to heavy abrasion.

Corrosion and effects of acid attack are also observed on both localities. This impact is observed on few dental remains, thus could not be attributed to digestion. Furthermore, abrasion water transport and post-depositional breakages could probably be responsible for the lose traces of bone surface modifications in both assemblages (Thompson, 2005).

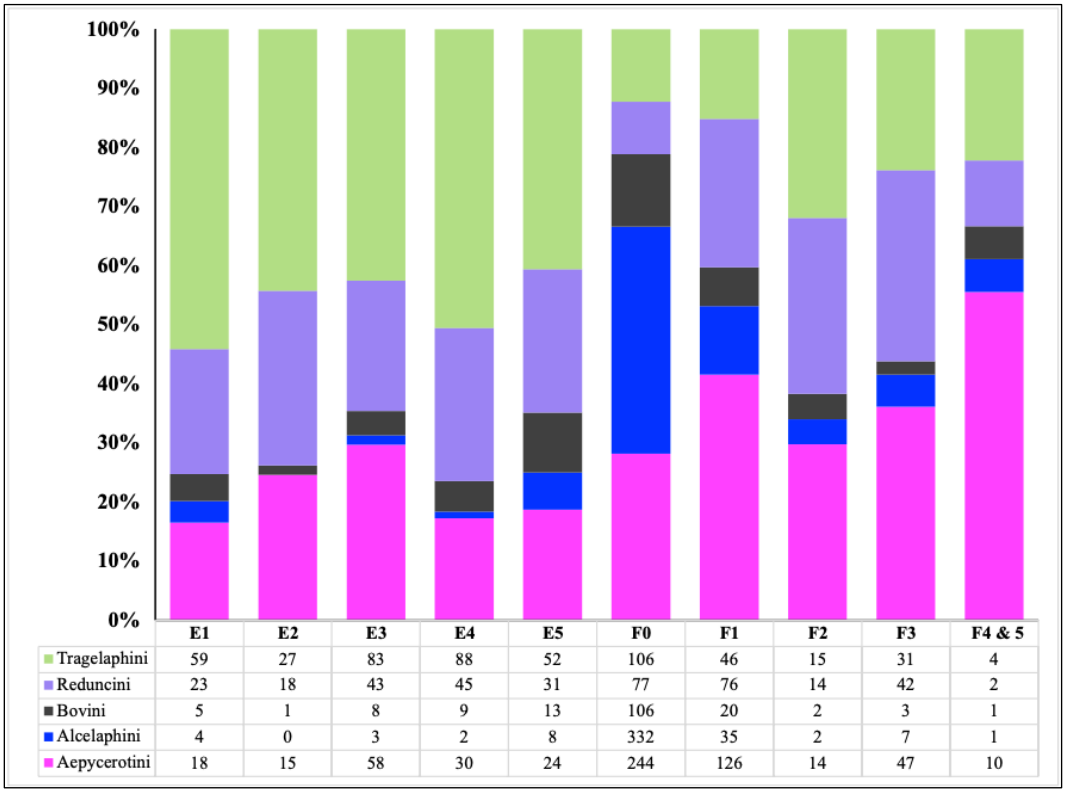


Figure 2. 7: Distal femur of a large size bovid from OMO 33 (A), and shaft bone flake from a medium size mammal L 398 (B), show examples of green fractured specimens from OMO 33 (A) and from L 398 (B). scale bars 2 cm.

2.3.2. Abundance

For temporal comparison, I first compared all units from lower Member E to upper Member F. Each unit was first compared using the IORE database. A second test was made by integrating both the IORE and the OGRE database.

There is a clear difference between Member E and Member F. When considered at a member level, Aepycerotini, Tragelaphini and Reduncini are the most common tribes and remain relatively constant throughout these sequences. The results indicate that Tragelaphini dominate in Member E followed by Aepycerotini and Reduncini. Member F however is dominated by Aepycerotini and Alcelaphini (Figure 2. 8). At a unit level, Alcelaphini show an abrupt appearance.



	E1	E2	E3	E4	E5	F0	F1	F2	F3	F4 & 5
Tragelaphini	59	27	83	88	52	106	46	15	31	4
Reduncini	23	18	43	45	31	77	76	14	42	2
Bovini	5	1	8	9	13	106	20	2	3	1
Alcelaphini	4	0	3	2	8	332	35	2	7	1
Aepycerotini	18	15	58	30	24	244	126	14	47	10

Figure 2. 8: Percentage distribution of bovids across units in Member E and F. Note that there is an increase in both Aepycerotini, Alcelaphini and Bovini from Member E to Member F. However, the most significant is the peak of Alcelaphini at F-0.

An increase of Alcelaphini, Bovini and Tragelaphini (in particular, *T. gaudryi)* from Member E to F is evident. However, the most significant increase is seen on Alcelaphini, a spike by 27 %. When I compare compositional differences of bovid tribes between units in Member E, there are no significant differences among units, except for the upper units (E-4 and E-5).

Pearson's Chi-square test between Unit E-4 and Unit E-5 show significant differences (X-squared=10.303, df =4, *p*-value = 0.03562).

I have also compared the top Unit E-5 and the base of F (F-0). It indicated significant differences (*p*-value < 2.2e-16). The base of Member F shows differences between unit F-0 and unit F-1. Chi-square test between these two units indicate significant differences (*p*-value <2.2e-16). Unit F-1 is also different from Unit F-3 (*p*-value = 0.03475), but no difference is observed between F-3 and the top F units (F-4 and F-5). As indicated in Figure 2. 9 , the cluster analysis differentiates both members.

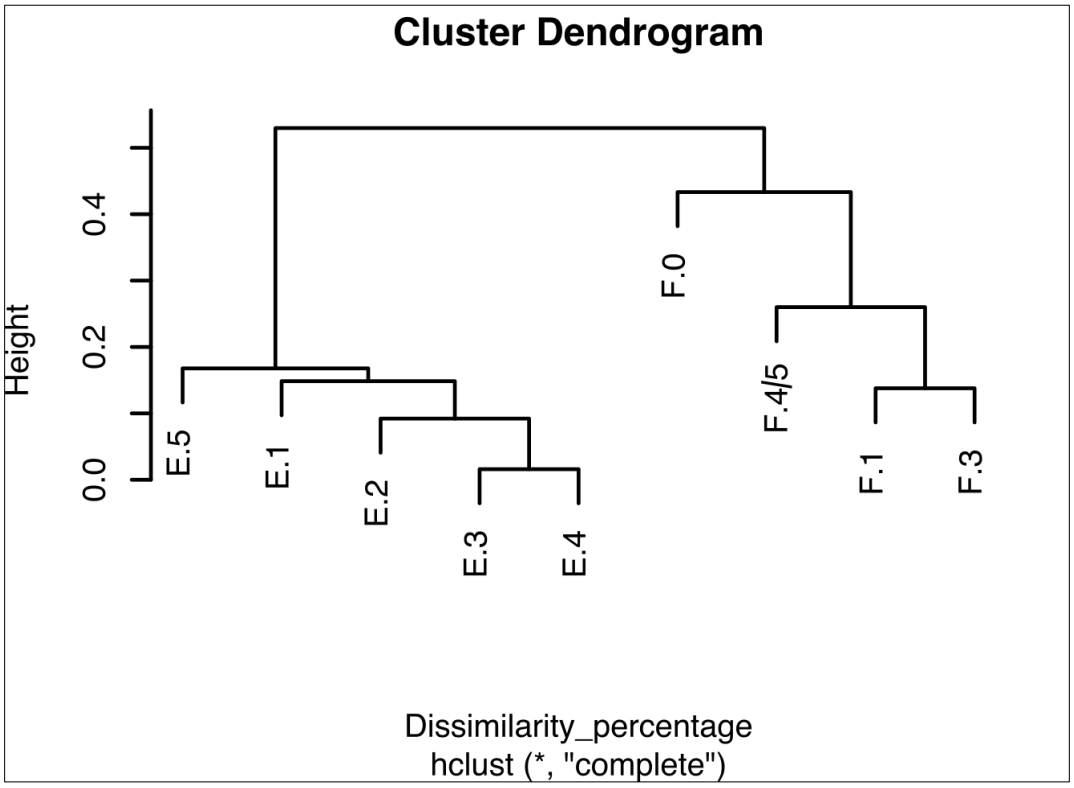


Figure 2. 9: Both cluster analysis and correspondence analysis showing compositional differences. The most contributing taxa between units within Member E and F are Tragelaphini (37.997%) followed by Aepycerotini (23 %) and Alcelaphini (20 %), whereas Reduncini (~13%) and Bovini (~ 7 %) contribute the least. I removed Unit F-2 due to smaller sample size.

Unit F-0 generally shows a relatively homogeneous bovid distribution between L 398 and OMO 33 (Figure 2. 10). When I considered the complete faunal assemblage, locality L 398 has more aquatic remains such as fish, crocodiles, and Chelonia than OMO 33. However, no significant difference is observed regarding terrestrial faunal assemblages, except for micromammals (common in OMO 33, absent in L 398). Considering their similar condition, this difference in rodents might not be related to taphonomy.

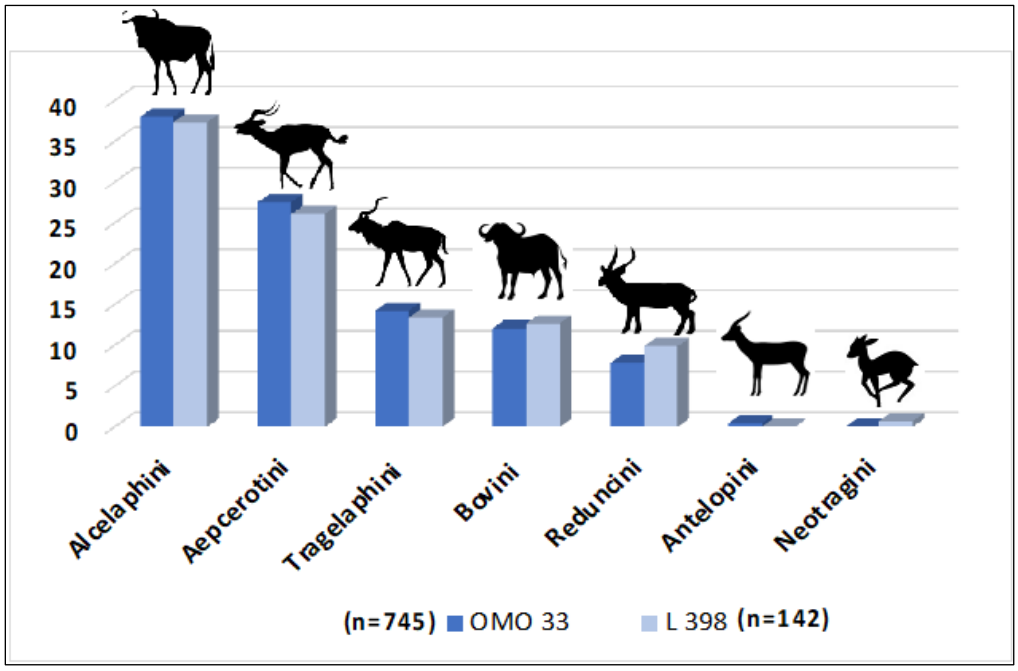


Figure 2. 10: Percentage counts of bovid compositional differences have been also tested between localities. This allows to test disparities among localities within a unit.

Bray-Curtis compositional dissimilarity identifies Aepycerotini and Alcelaphini as the main contributing factors followed by Reduncini, whereas Bovini contributed the lowest.

At the top of Member E, I compared bovid abundance between OMO 57/4 and OMO 57/5, and I observed no significant difference (p-value = 0.4432). In addition, Pearson's Chi-square test between L 398 and OMO 33 localities at Unit F-0 indicates no significant difference (p-values = 0.0657). However, within Unit F-1, where archaeological occurrences are common,

I have tested bovid composition comparison between two localities. These localities, OMO 76 and L 28 shows significant differences (*p*-value = 0 .0002). In addition, the localities are unit F-1 are significantly different from those at F-0. The reason that F-0 is different from the unit at E and at F, could be mainly the Alcelaphini spike at this unit.

2.3.3. DMTA

The DMTA results indicate that complexity (Asfc), epLsar (anisotropy) and HAsfc (heterogeneity of complexity) variables are the most discriminant parameters. This is clearly demonstrated among tribes Aepycerotini and Alcelaphini which show a significant variation.

Anisotropy and complexity discriminate within dietary groups on some taxa between L 398 and OMO 33. The bivariate plot of anisotropy and complexity shows that both Aepycerotini and Alcelaphini from OMO 33 are plotted very close to each other within the range of mixed feeders. Whereas at L 398, both taxa are plotted together, with higher values of epLsar and low values of Asfc. A summary table of the DMTA and taxa analyzed is provided (Table 2. 4).

			Asfc		***epLsar* (10^{-3})**		**HAsfc81 cells**	
Taxa	Loc	N	Mean	Sd	Mean	Sd	Mean	Sd
Aepycerotini	L 398	33	1.68	1.06	2.54E-03	2.94E-03	0.51	0.16
	OMO 33	19	2.14	0.93	2.91E-03	1.71E-03	0.43	0.15
Alcelaphini	L 398	10	1.32	0.40	4.41E-03	2.18E-03	0.50	0.18
	OMO 33	50	2.25	1.28	2.96E-03	1.54E-03	0.445	0.15
Bovini	L 398	11	2.13	1.49	4.05E.03	2.07E-03	0.64	0.23
	OMO 33	6	1.92	0.60	2.78E-03	2.38-03	0.61	0.17
Giraffidae	L 398	5	1.51	0.39	2.55E-03	1.84E-03	0.39	0.06
	OMO 33	14	2.75	2.13	1.92E-03	1.48E-03	0.67	0.28
Reduncini	L 398	5	1.91	0.36	3.12E-03	1.68E-03	0.49	0.11
	OMO 33	8	2.11	1.06	3.78E-03	2.02E-03	0.44	0.17
Tragelaphini	L 398	10	1.80	0.31	2.42E-03	2.45E-03	0.47	0.13
	OMO 33	5	1.91	1.32	2.35E-03	1.90E-03	0.45	0.16

Table 2. 4: Descriptive statistics (Mean and standard deviation (Sd)) of dental microwear texture parameters for L 398 and OMO 33.

Post hoc LSD test of complexity (Asfc) significantly distinguished Aepycerotini between these localities (P = 0.021), although HSD test of Asfc failed to differentiate (p = 0.19). Anisotropy (epLsar) shows the most significant variation between Aepycerotini on both HSD (p = 0.002) and LSD (p = 0.000), discriminating from both localities effectively. LSD test on HAsfc81 variable also weakly differentiates Aepycerotini between L 398 and OMO 33 (p = 0.051).

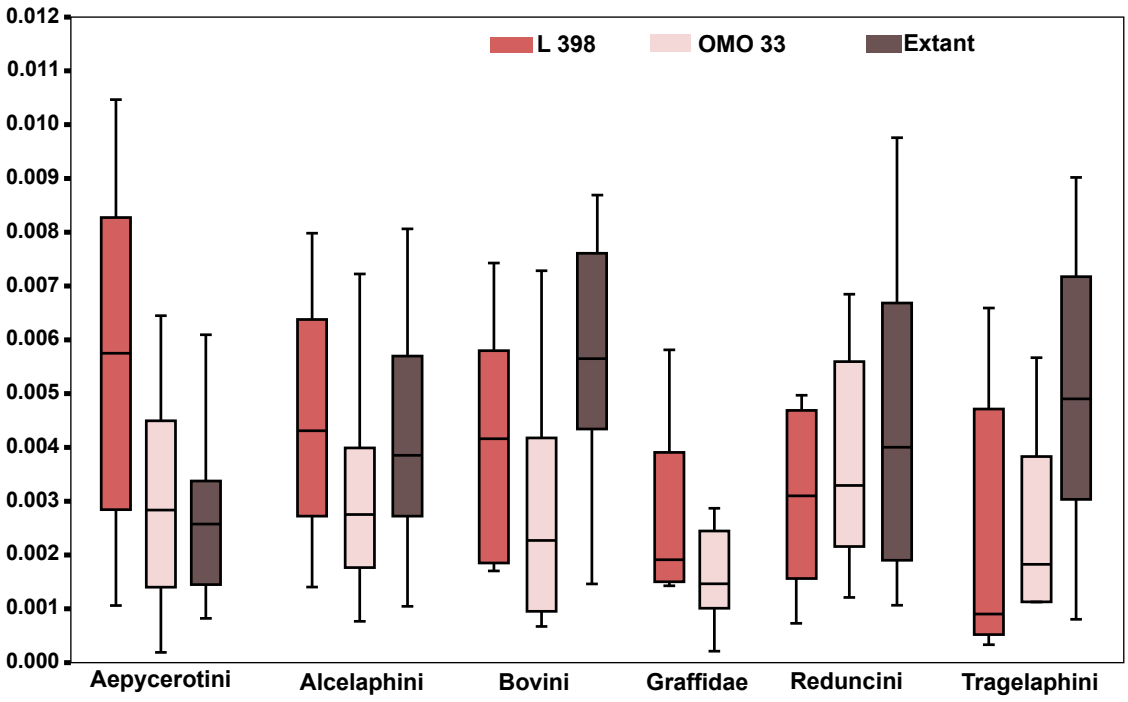


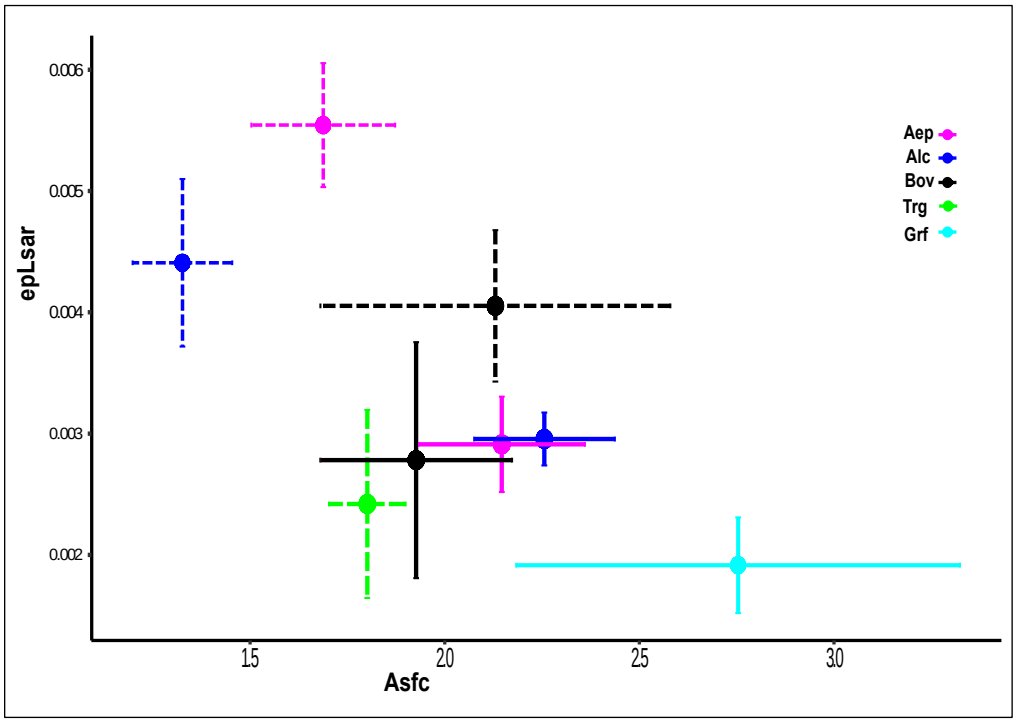
Figure 2. 11:Boxplots of epLsar (anisotropy) values for L 398, OMO 33, compared to extant bovid tribes. Note that the anisotropy values for OMO 33 are low.

OMO 33 shows low values of anisotropy compared to L 398 and extant taxa (Figure 2. 11). This could be explained either due to the effect of taphonomy (King et al., 1999; Uzunidis et al., 2021), the presence of more than one species of Alcelaphini, or assemblages the two

localities are from different seasonal deposits. However, the effect of taphonomy does not seem to explain well, as the values are still within the normal dietary range. This could be better addressed with future experimental studies and is beyond the scope of this thesis.

The other intriguing difference comes from Alcelaphini. The most abundant taxa in both localities, do not exhibit similar dietary category in both localities. Alcelaphines at L 398 shows higher epLsar values and very low Asfc value. This high anisotropy and low Asfc values, though an expected value for grazer taxa, at OMO 33 the ranges fall within the mixed feeders. LSD test of complexity significantly separates Alcelaphini between the localities ($p = 0.008$), although they are not strongly differentiated in anisotropy ($p = 0.054$). At L 398, anisotropy values for Aepycerotini are significantly different from the rest of the taxa, except with Alcelaphini ($p = 0.133$).

At OMO 33, I observed differences in HAsfc among mixed feeders, for instance, between Bovini and Reduncini ($p = 0.037$). Giraffids are easily distinguished from the rest of the bovid tribes. Bovini, a taxon categorized as wider mixed feeder is within the expected range in both localities, except higher values epLsar at L 398. Tragelaphines overlap with giraffids and bovines from OMO 33 in showing low value of anisotropy. This could be related to browsing on soft leaves. Tragelaphini differs from giraffids due to the lower values of Asfc.


epLsar
0.006
0.005
0.004
0.003
0.002
15
20
25
30
Asfc
Aep
Alc
Bov
Trg
Grf

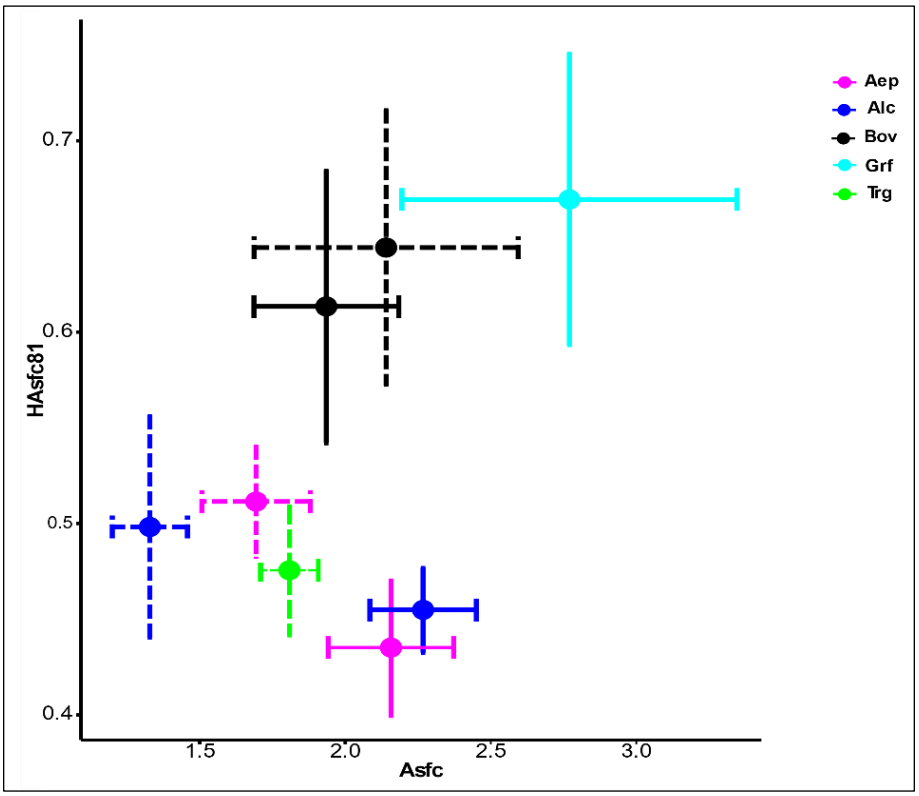

HAsfc81
0.7
0.6
0.5
0.4
1.5
2.0
2.5
3.0
Asfc
Aep
Alc
Bov
Grf
Trg

Figure 2. 12: Biplots, based on standard error of the mean showing anisotropy (top panel), and heterogeneity of complexity (bottom panel), both plotted against complexity. Taxa names are written in abbreviations as (Aep=Aepycerotini, Alc=Alcelaphini, Bov=Bovini, Grf=Giraffidae, and Trg=Tragelaphini. Plots are based on standard error of the mean. Plots with dashed outlines represent L 398, continuous lines represent OMO 33. Biplots only include samples larger than five.

Giraffids, commonly interpreted as browsers, show the lowest epLsar and highest Asfc Values. Giraffids at L 398 have lower HAsfc, which is expected for browsers. LSD test on HAsfc significantly distinguishes between giraffids from L 398 and OMO 33 ($p = 0.007$). Bovini from both localities also exhibits higher values of HAsfc. Aepycerotini and Alcelaphini from L 398 have lower value of HAsfc. However, both these taxa manifest the lowest HAsfc values at OMO 33, Aepycerotini being the lowest. An unexpected value from this parameter is the low value for Tragelaphini, that significantly differs from Bovini and Giraffidae (Figure 2. 12).

2.4. Discussion

The aim was to assess the pattern of faunal distribution, particularly across the lower units of Member F by integrating the taphonomic features of the assemblages. In addition, I examined local scale dietary variation among sympatric large herbivores, i.e., bovids and giraffids. This time interval covers from 2.38 Ma to 2.27 Ma, comprising from slightly before to after the first appearance of Oldowan lithic assemblages in the Shungura sequence, at 2.32 Ma. My analysis of integrating those three factors has identified a subtle difference in bovid distribution across times of members E and F deposition, as well as in dietary variation among local herbivore community. The DMTA results slightly differ from previous dietary interpretations based on broader spatial and temporal scales, i.e. at member level (Blondel et al., 2018, 2022; Negash et al., 2015, 2020).

2.4.1. Assemblage composition

The results from the taphonomic analysis indicate that there is a general similarity considering subarea weathering and hydraulic transportation between L 398 and OMO 33. Mammalian assemblages from both localities show early stages of weathering. However, majority of the postcranial remains suffered from hydraulic transportation causing surface abrasions. Thus, the bone surface abrasions make it difficult to detect traces of hominid butchery activity.

Both assemblages seem to have been affected by moderate to heavy hydraulic transportation. Despite this, I believe that the faunal composition is not significantly impacted to cause preferential preservation. This is in general agreement with Dechant Boaz (1994)'s description of L 398 and Alemseged et al. (1996)'s study on OMO 33, as well as with the general fluvial contexts at Shungura (Alemeseged, 2003). Although both localities document similar trends of mammalian abundance, there is obvious difference in the overall faunal composition. While L 398 has more fish and reptiles, OMO 33 has preserved relatively abundant micromammals while these are almost absent in the former.

Dechant Boaz (1982, 1994) reported both L 338y and L 398 assemblages are very fragmentary, with many spirally fractured shaft pieces and suggested that the high degree of fragmentation of the L 338y sample could be due to trampling, whereas for the L 398 assemblage it occurred due to transport in a channel environment, coupled with carnivore chewing, weathering, trampling and post-depositional damage. This is evidenced by the presence of "polished" bone pebbles and fragments that are common in the L 398 assemblage (Dechant Boaz, 1994)

There is, however, an overall similarity in skeletal element representation in both localities. The patterns documented in the faunal abundance is mainly on cranio-dental elements (Alemseged, 2003; Eck, 2007), which are the most common elements in these fluviatile depositional systems (Bobe & Eck, 2001). L 398 has a relatively higher number of postcranial than OMO 33, though displaying a higher level of fragmentation.

I have indicated in the results section that there is a discrepancy between units in Members E and F. Furthermore, differences among localities are more noticeable in Member F than in Member E. Compared to F-0, unit F-1 seems to show a partial return to wooded and edaphic habitats with Tragelaphini and Aepycerotini becoming dominant again. When I include other grazing taxa of suids and equid, Units F-1 to F-3 are distributed across axis-1 (Figure 2. 13) closer to these taxa. F-0 is clearly different from units at E and at F, driven mainly by Alcelaphini. Previous interpretations of Member F as dry and arid condition (Bobe & Behrensmeyer, 2004; Bobe & Eck, 2001), could probably be due this high incursion of Alcelaphini at F-0.

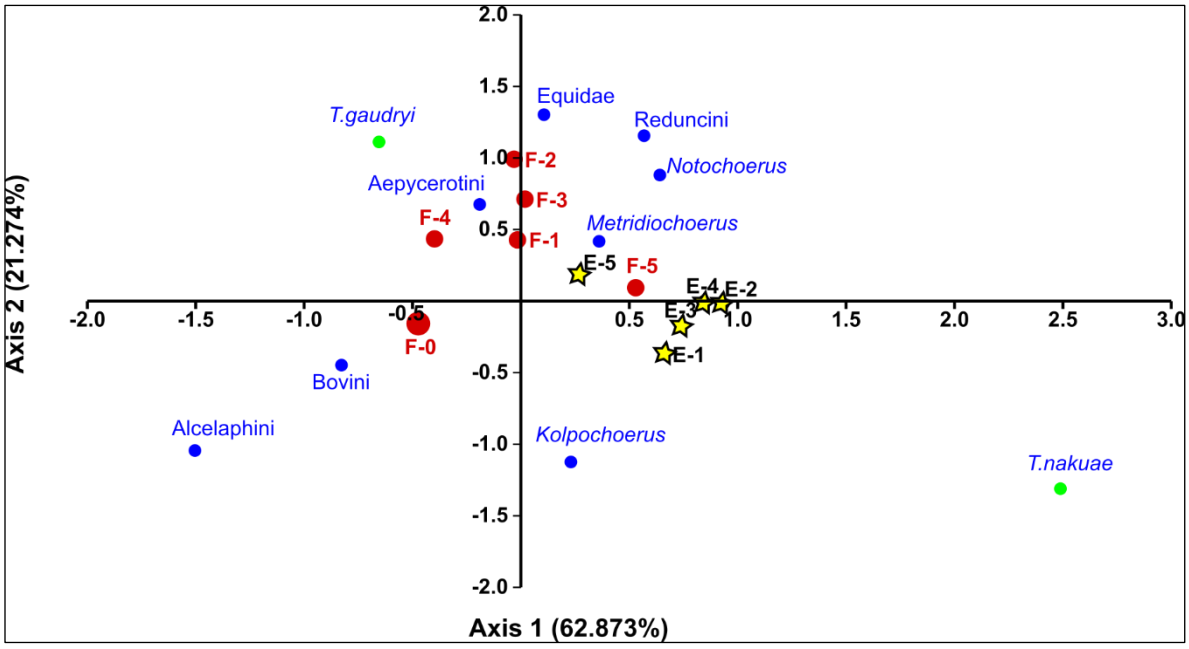


Figure 2. 13: Correspondence analysis of bovids, suids and equid across units in E and F. All units in Member E are represented in a yellow with black outline star, whereas units in F are shown in red filled circles.

However, although there is a general increase in Alcelaphini at a Member scale, units above F-0 show both open/dry and wet conditions are present. This clearly indicates that heterogeneous landscapes are common in these units where the Oldowan archaeological

occurrences are abundant. For instance, at OMO 76 (unit F-1), where bovids constitute 32 % (n=93) of the total assemblage, I observed a relatively balanced distribution of bovid tribes, reduncines being slighly more abundant (at 26 %) than aepycerotines (24 %) and tragelpahines (23 %), alcelaphines and bovines being only slightly less abundant (16 % and 12 %, respectively). I noted a similar distribution at localities L 465 and L 28.

The spatio-temporal variation among bovids in Members E is also interesting mainly, due to the significant increase in abundance within *Tragelaphus* at top E. Tragelaphines are particularly abundant in Member E and remain common in Member F, but *T. gaudryi* which was less common than *T. nakuae* at lower units become more abundant at upper Member E and F units (Figure 2.12). As seen in the plot above (Figure 2.12), *T.gaudryi* is plotted above axis-2 with units F, whereas *T. nakuae* is driven by units at Member E. Thus, the dynamic observed at the base of unit F, probably started at top E.

The micro mammals from OMO 33 were identified as indicators of mesic environment where as xeric for L 398 (Wesselman, 1984). Thus, despite similarities in bovid distribution, other faunal remains such as micro-mammals and the composition of aquatic remains indicate difference between these localities. This clearly indicates, a multi-proxy approach rather than on bovid composition only is more viable way to reconstruct paleohabitats at least, when study at spatio-temporally restricted contexts. This is where dental wear proxies such microwear could be useful.

2.4.2. Comparison of other dietary proxies

Though there is temporal disparity between the two proxies (i.e. short term and long term dietary signals), isotope data on OMO 33 can be compared to the microwear data. Based on isotope data, aepycerotines and alcelaphines from OMO 33 are grouped into C-4 plant eaters, likely herbaceous monocots (Negash et al., 2015, 2020). Besides, dental microwear textures for OMO 33 suggest that these two taxa do not indicate obligate grazing, but mixed feeding habits. Thus, the long-term dietary behavior (isotope data) of these two taxa from OMO 33

is comparable to the microwear textures from locality L 398. The discrepancy between the two localities could be interpreted due to seasonal availabilities of the vegetal resources (Merceron et al., 2010). Regarding L 398, there is a lack of isotope data at this stage to create a direct comparison.

Aepycerotini is the most abundant taxon in Member F, and show C_4 dominated diet (Negash et al., 2015). Extant *Aepyceros* (impala) has a flexible dietary behavior depend on regional and seasonality (Vrba, 1984). This is supported by isotopic analysis of *A.* melampus showing a dietary range from intermediate and mixed to C_4 grazers (Cerling et al., 2015). This taxon tends to graze on fresh grasses during rainy season switches to browsing when conditions are dry (Sponheimer et al., 1999). In Shungura members E and F, only one species was identified, *Aepyceros shungurae*.

Although fossil Alcelaphini might differ, the extant genera of this tribe are characterized by pure either obligate (>90% grass) or variable (60-90% of grass) grazers, meaning they mostly include C-4 plants. Habitat preference of extant alcelaphines is known to be mainly open savanna landscapes with short grasses although few species preferred woodlands (Vrba, 1996). This behavior could probably explain the different results observed in the microwear textures from the two assemblages.

Reduncini, also generally identified as grazing bovids, are more common in members B and G than in E and F (Blondel et al., 2022; Bobe & Eck, 2001). Isotope values indicate a dietary shift from C_3/C_4 mixed feeding to C_4 grazing (Negash et al., 2020). Dental wear analysis of reduncines from the Shungura sequence shows a dietary shift from browsing during the Late Pliocene to a range of mixed feeding and grazing at the beginning of Pleistocene (Blondel et al., 2022). The DMTA analysis for this taxon similarly shows mixed feeding, and no difference between the two localities. Extant reduncines are known grazers with preference for wetlands and edaphic grasslands (Sponheimer et al., 1999).

The Tragelaphini is common throughout the lower part of the Shungura Formation. Isotope values from the Shungura indicates a diet characterized by a mixed C_3-C_4 signal (Negash et

al., 2020). Dental wear analysis by Blondel *et al*., (2018) found no significant difference between tragelaphines in members E, F and G, with diet most likely covering a spectrum from browsing to mixed C3/C4 diet. Similarly, in both my study cases, the DMTA supports mixed feeding habits Tragelaphini.

A change in cranial morphology of *Tragelaphus nakuae* is observed during this period, ca. 2.3 Ma (Bibi 2011). The faunal data indicated that whereas *T. nakuae* is common in both Member E and Member F, there is an increase in *T. gaudryi* which become more abundant starting top E and throughout Member F. Yet, both taxa do not contrast in diet (Blondel *et al*; 2018). The habitat category for Tragelaphini is reconstructed as heavy cover dwellers (Kappelman, 1997).

Tragelaphini shows a similar diet in Member E and F in the Shungura (Blondel et al., 2018). The expansion of C_4 grasses and increase in abundance of grazing herbivores in the Plio-Pleistocene eastern Africa could be due to change in seasonality (Blumenthal et al., 2017).

Giraffids are predominantly browsers throughout the Plio-Pleistocene and nowadays (Cerling et al., 2015), and are indicated by C_3 resources throughout the Shungura sequence (Negash et al., 2015, 2020). Unsurprisingly, the DMTA data for this taxon falls within the range of soft/no-tough foliage browsers.

2.4.3. Intra- and Inter- Member ecological Variations

Previous studies demonstrated that although major shifts towards open environments started to occur at Member E, and even earlier, Member F has recorded more open and drier landscapes (Geraads & Coppens, 1995; Maurin, 2017b). Later studies also found spatial differences within members, i.e., between northern and southern sectors in Member F (Maurin, 2017b), and Lower G (Alemseged et al., 2007).

Member F is characterized by predominantly open and drier environments. Others also documented an increase in relative bovid abundance from E to Member F is represented by

increasing Alcelaphini, Aepycerotini and Antilopini (Bobe & Behrensmeyer, 2004; Bobe & Eck, 2001; Maurin, 2017b). In addition, studies on pollen and micromammals also demonstrated an open and arid conditions in Member F (Wesselman, 1984).

Previous work also shows faunal distribution differences, and particularly bovids indicate differences between the two members. In particular, bovid distribution across north and south sectors are different in Member F, but not observed in Member E (Maurin, 2017b). Although Aepycerotini and Reduncini are represented, Tragelaphini dominates in Member E. However, Alcelaphini and Aepycerotini become more dominant in Member F. The high proportions of these in Member F assemblages clearly indicate an open and lightly wooded environment (Vrba 1988).

The two ecomorphological studies indicate that there is an increase of open environments when I compare between members E and F (Barr, 2015; Plummer et al., 2015). However, Barr (2015) sampled only from the northern sector (IORE's American team) and only two samples from L 398. The habitat category for these two specimens were identified each as forest and light cover (Barr, 2015).

However, Plummer et al. (2015) incorporated materials from both the French and American team, that include localities from north and south parts. Samples from OMO 33 include all habitat categories including wetland (Plummer et al., 2015). Their data indicate that forest environments are more common in the southern zone than the northern parts of Member F (Plummer et al., 2015). This could be another factor that explains differences in DMTA between the two localities, and notably the low differences between species in OMO 33.

While this supports for the OMO 33 microwear data, it contrasts to the overall signals from faunal composition and dietary behaviors reconstructed through isotope and dental wear. The data based on the ecomorphology data and the Reduncini distribution across north and south sectors in the Shungura thus could explain the presence of wetlands albeit to a smaller extent.

2.4.4. Member F habitat heterogeneity and its relevance to the archaeological occurrences

The high proportion of grazing taxa, but diverse habitats in Member F, particularly units F-1 to F-3 could be tempting to interpret that archaeological sites are distributed across heterogeneous habitats dominated by open environmental settings.

Isotope data from Turkana basin herbivores show C_4 dietary signals dominated after 2.35 Ma for Nachukui and Koobi Fora Formations (Cerling et al., 2015). At ~2 Ma, faunal studies from the Kanjera South archaeological sites indicate early hominids exploited open savannah landscapes (Plummer et al., 2009). In younger sites from Okote and Koobi Fora Members, an increase of Alcelaphini (which are all engaged in grazing) among fossil assemblages is observed, and most notably in archaeological localities with lithic assemblages (Patterson, Braun, Behrensmeyer, Merritt, et al., 2017) (Paterson *et al*., 2017). Similar association has been inferred at Lokalalei sites from Nachuki where Oldowan sites are comparable to the Shungua (~2.3 Ma). This supports the idea that archaeological sites are more frequent in open settings.

Oldest Oldowan occurrences dated to ~2.6 Ma come from localities at Gona and Ledi-Geraru, both in the Afar rift (Braun et al., 2019; Semaw et al., 1997). Pollen data from Gona indicates woodland dominated riverine settings (López-Sáez & Domínguez-Rodrigo, 2009), whereas open landscape close to water source is inferred through faunal data for Ledi-Geraru (DiMaggio et al., 2015; Braun et al., 2019). At a similar temporal scale, the Bouri site in Middle Awash where butchery evidences were found associated to scattered artifacts document an open condition nearby a lake margin (de Heinzelin et al., 1999).

The environmental dynamics of the rift valley could contribute to fragmented patchy habitats within close proximity (Kingston, 2007; Bibi and Kiessling, 2015). Thus, heterogeneous habitat types could occurred due to physical changes such as volcanic and hydraulic changes in the Turkana basin (Bailey et al., 2011; Bailey & King, 2011; Lepre, 2014; Trauth et al., 2010). The degree to which the volcanic events and hydraulic changes is documented in the

Shungura Formation (Heinzelin & Haesaerts, 1983), and it seems to occur in relatively short intervals in Member F.

Various research linked early human adaptability to environmental variability at a wider sense (e.g., (Potts, 2013; Potts & Faith, 2015)), and microhabitat variability at a local scale (Kingston et al., 2007; Patalano et al., 2021) as key factors. The difference detected between localities in member F therefore indicates a wide diversity of habitats suitable for early hominids. Differences between units with archaeological context and those devoid of artifacts could thus be tentatively inferred.

Similarly, the literature for the lower sequence of Member G indicates an increase in grazing bovids dominated by Reduncini in a context of open woodlands, edaphic grasslands, and flood plains in lower G (Alemseged, 2003; Reed, 1997). It is also indicated that differences in bovid abundances particularly within Reduncini between north and south sectors (Alemseged et al., 2007). This member shows similar aspects of faunal structure, spatially among bovids and is interpreted as an extended form of Member F (Maurin, 2017b; Reed, 1997). Archaeological occurrences are so far known only from these two members; Member F and Member Lower G (Delagnes et al., 2011; Maurin et al., 2014).

In conclusion, from the perspective of dietary preferences using DMTA, OMO 33 has less abundance of grazers than L 398. Thus shows a slight contrast between the wet land reconstruction based on the ecomorphology and the presence of Reduncini in both localities. Although the abundance shows both localities have depicted an open dominated with slightly wooded habitat types, the inclusion of wetland habitats could be related to flood plains along the paleo-Omo River or proximity to the Turkana paleolake. The difference based on DMTA could be related to a short-term dietary choice inflicted by seasonal drought.

Overall, unit F-0 is distinct in bovid composition, mainly indicated by the disproportional abundance of Alcelaphini not documented anywhere in the Shungura sequence. The main localities from this unit record an exceptional abundance of this taxa. Whereas the units at F1 and above document more or less proportional bovid diversity, are associated to high

intensity of lithic production. Thus, it seems that the archaeological occurrences coincide to the landscapes with heterogeneous settings.

2.5. Conclusions

This study documented ecological patterns between 2.38-2.28 Ma based on faunal abundance and DMTA, and contextualize Member F at a local scale. This provides additional information on how paleohabitats could vary across landscapes in a relatively shorter temporal resolution, even within geological units. I show that the taxonomic composition of bovid tribes varies across localities, which a major shift at F-0, but probably started at the top of Member E. While there is little change in the presence/absence of taxa in both members, the top of E and basal F is featured by a strong increase in of *T. gaudryi*.

The base of Member F is characterized by faunal distribution dominated by Alcelaphini and Aepycerotini. At F-0, I have observed both a significant increase in the abundance of Alcelaphini and dietary discrepancies among sympatric population, particularly within Alcelaphini and Aepycerotini. DMTA analysis shows that Alcelaphini and Aepycerotini at L 398 present grazing dietary behavior whereas, at OMO 33 these taxa show a tendency towards mixed feeding behavior. Thus, the results in this study also confirm the previous proposals suggesting local scale ecological variability during Member F times, more importantly prominent differences between units with archaeological context and those without.

2.6. References:

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Chapter Three

Methods for BSM Identification and new data from the Shungura Formation

3.1. Introduction

Zooarcheology, as a discipline, examines subsistence patterns and reconstruct the behavioral ecology of hominids as well as their interaction with the rest of the faunal community. However, the current knowledge on the evidence of tool-assisted animal butchery of early hominids is very scant. The zooarcheological records become remarkably rare in earlier periods of human evolution particularly prior to 2 Ma. Archeological sites and associated evidence of animal consumption by early hominids are apparent only from very few Plio-Pleistocene sites (e.g., Braun et al., 2019; Dominguez-Rodrigo et al., 2005; Ferraro et al., 2013; Heinzelin et al., 1999; Kimbel et al., 1996).

Regardless, there is a strong debate about bone surface modifications indicators of early hominid activities. Recent discoveries of marks on bone surfaces suggested the use of stone tools at ca. 3.4 Ma by australopithecines in the Afar (McPherron *et al*., 2010). Experimental studies have questioned these interpretations (Dominguez-Rodrigo et al., 2010; Domínguez-Rodrigo et al., 2012; Sahle et al., 2017).

So far, the oldest known plausible evidence of hominid meat consumption come from Pliocene sites in Ethiopia (de Heinzelin et al., 1999; Dominguez-Rodrigo et al., 2005; Sahle et al., 2017; Semaw et al., 2003). The first reports on evidence of stone-tool-assisted butchery activities at ~ 2 Ma come from the Olduvai Gorge and Koobi Fora (Bunn, 1981; Bunn et al., 1986; Potts & Shipman, 1981). Until recently, the majority of zooarcheological and taphonomic reports and debates on hominin meat-eating in eastern Africa were based on a single site, FLK22, Zinj, Tanzania (Binford, 1981, 1985; Blumenschine, 1986, 1995; Blumenschine & Selvaggio, 1988; Bunn, 1981; Bunn et al., 1986; Domínguez-Rodrigo &

Barba, 2006, 2007; Domínguez-Rodrigo, 1997, 1997; Lupo, 2012; Potts & Shipman, 1981; Selvaggio, 1994; Yravedra, Diez-Martín, et al., 2017).

Very recent collections from early Pleistocene sites of Turkana and Kanjera South formations provided larger assemblages of modified bones (Archer & Braun, 2013; Braun et al., 2010; Bunn, 1994; Ferraro et al., 2013; Parkinson et al., 2022; Pobiner et al., 2008; Pobiner *et al.*, 2008; Braun *et al.*, 2010; Braun, 2013; Ferraro *et al.*, 2013). However, these sites, yet extensively studied, are younger than the oldest known archeological/zooarcheological sites in the Turkana Depression and in the Afar Depression.

However, for the Oldowan archeological sites from the Turkana Depression, their taphonomic and zooarcheological interest is the least investigated. These archeological occurrences dated to ~2.32 Ma come from two neighboring formations of the Omo Group, the Shungura Formation at 2.3 Ma (Boisserie et al., 2008; Chavaillon, 1976; Delagnes et al., 2011; Merrick et al., 1973) and Nachukui at about 2.34 Ma from Kenya (Kibunjia, 1994; Roche et al., 1999; Tiercelin et al., 2010).

In general, archeological, and paleontological studies revealed that sites in the rift valley of Ethiopia and Kenya are crucial with earlier evidence of human biological and behavioral records. However, early evidence (prior to 2 Ma) of meat consumption in this region comes from only a few of these sites in the Afar rift. Furthermore, despite the Turkana sites such as the Shungura and Nachukui providing potential evidence of early hominid faunal exploitation, the study of archeofauna from these sites is unfortunately rare.

Instead, faunal analyses in Turkana have been conducted almost exclusively to reconstruct paleoenvironments. Similarly, archeological studies were focusing on lithic analyses to reconstruct hominid behavior (e.g., raw material use, source of raw material, etc.). Bone surface modifications are useful to retrace trophic interactions, habitat exploitations, and to understand the taphonomic processes. However, fossil materials collected from the Shungura Formation remained unstudied in that regard. Thus, unlike the other Plio-Pleistocene sites, a zooarcheological work on this important Plio-Pleistocene site is yet to be documented.

Its rich fossil record forms a continuous sequence, and the presence of defined stratigraphic units at a refined spatio-temporal scale make it an excellent place to examine Plio-Pleistocene bone modifications (anthropic or not) for comparisons with other eastern African sites. This has stimulated new interests in conducting research within this faunal rich, yet taphonomically poorly understood, Shungura deposits. The well curated museum collections from this site coupled with the ongoing research by the OGRE are therefore important to examine and prospect its potential in addressing the above-mentioned research gaps.

Taphonomic assessment conducted for this study aimed at identifying assemblage history and agents of bone accumulation, at tracing potential hominid induced marks, and documenting the inter-community interactions such as predation.

Debates whether Pliocene hominids used tools to access meat (Dominguez-Rodrigo et al., 2010; McPherron et al., 2010; Sahle et al., 2017; Thompson et al., 2015), or the debate surrounding early access to meat (hunting vs scavenging) during Pleistocene (Binford et al., 1988; Blumenschine, 1986, 1995; Bunn, 1981; Bunn et al., 1986; Domínguez-Rodrigo & Barba, 2006; Pante et al., 2012; Parkinson, 2018; Pickering & Bunn, 2012; Selvaggio, 1994) lies on the correct identification of cutmarks.

The disagreements on the identifications and interpretations of BSMs among taphonomists and zooarcheologists has been, related strongly to the problem of equifinality i.e., morphological similarity of marks (Njau & Gilbert, 2016). With the goal to contribute on the methodology and increase new zooarchaeological data from this time period, this part of the thesis tries to address these aspects through integrating Elliptic Fourier (EF) based analysis.

This part of the thesis aims at documenting various taphonomic traces, particularly those that are useful for the study of hominid behavioral ecology. This is accomplished through the assessment of bone surface modifications with emphasis on identifying traces of hominid activities. These include identification and quantification of tooth marks, breakage patterns and possible percussion or cut marks left on the bone surfaces.

3.2. An overview to the classical methods of bone surface modifications

Analysis of bone surface modifications are among the most widely used approaches to study interactions between humans and other animals throughout human evolution. For instance, taphonomic study of faunal assemblage provide information on the agents and processes of the accumulation (Fernández-Jalvo & Andrews, 2016). Furthermore, identifying assemblages altered by hominids or other animals would reflect behavior, interactions as well as environmental context (de Heinzelin et al., 1999).

Stone tool assisted animal butchery leaves distinct traces on bone surfaces including percussion grooves, percussion pits and cut marks with micro-striations in all these marks (Blumenschine, 1995; Bunn et al., 1986; Domínguez-Rodrigo et al., 2009; Fisher, 1995; Olsen & Shipman, 1988; Pickering & Egeland, 2006; Pobiner et al., 2008). These marks are identified as linear grooves with V-shaped in cross section and internal micro-striations (Bunn, 1981; Domínguez-Rodrigo et al., 2009; Olsen & Shipman, 1988; Potts & Shipman, 1981).

Similarly, animal bites on other animals leave definite tooth marks on bone surfaces. These include tooth pits, punctures, scores, furrows, and gnawing/chewing marks as well as escalloped marks on bone margins (Andrews & Evans, 1983; Binford, 1981; Haynes, 1980; Pickering et al., 2004; Selvaggio, 1994).

However, subsequent research noted that similar marks can be produced by different agents and could confuse correct identifications of stone tools inflicted marks. This condition is referred by as equifinality, i.e., when different agents produce similar features (Njau & Gilbert, 2016). For instance, sediment abrasion and trampling marks (Behrensmeyer et al., 1986; Domínguez-Rodrigo et al., 2009; Fiorello, 1989; Haynes et al., 2020; Olsen & Shipman, 1988), crocodile bite marks (Njau & Blumenschine, 2006; Sahle et al., 2017), mammalian carnivore bite marks (Binford, 1981; Egeland et al., n.d.; Haynes, 1980; Hill,

1989; Pickering et al., 2003; Selvaggio, 1994) can produce marks that are very similar to butchery marks.

Some mammalian carnivores such as hyenas have a great potential in accumulating large faunal assemblages or in modifying already existing hominid or felid accumulated assemblages (Haynes et al., 2020; Haynes & Hutson, 2020; Villa & Bartram, 1996). Felids such as lions and leopards as bone accumulators are also evident from archeological sites (Arriaza et al., 2019; Pickering et al., 2004). Research on carnivore predations documented that some carnivores are specialized in meat slicing, while others are both meat eaters and bone crushers (Cruz-Uribe & Klein, 1994; Klein & Cruz-Uribe, 1984). The size and availability of fauna as a food resource could have an influence on carnivore predation and selection (Vrba, 1980). The existence of extensive furrows and scalloped edges on bone surfaces have been associated to mammalian carnivore chewing (Binford, 1981; Cruz-Uribe & Klein, 1994; Hill, 1989).

However, reptilian carnivores such as crocodylians are less considered in the taphonomic studies, although they are abundant within paleoanthropological sites (Njau & Blumenschine, 2006). Crocodylians are not only considered as an important bone modifier but also as bone accumulators useful for paleolandscape interpretations (Njau & Blumenschine, 2012; Westaway et al., 2011). In addition, their interaction with hominids has been documented either as sources of food for Early Pleistocene hominids (Braun et al., 2010), and possibly also predators of hominids (Njau & Blumenschine, 2012; Westaway et al., 2011)

However, correctly identifying the traces between crocodylians and carnivores, in particular felids, has also been a challenge. Research based on experimental methods were significant to recognize and infer the relevance of bite marks on prehistoric materials (Baquedano et al., 2012; Njau & Blumenschine, 2006; Njau & Gilbert, 2016; Noto et al., 2012). Njau and Gilber (2016) provided detailed illustrations of types of crocdylian bite marks (Figure 3. 1)

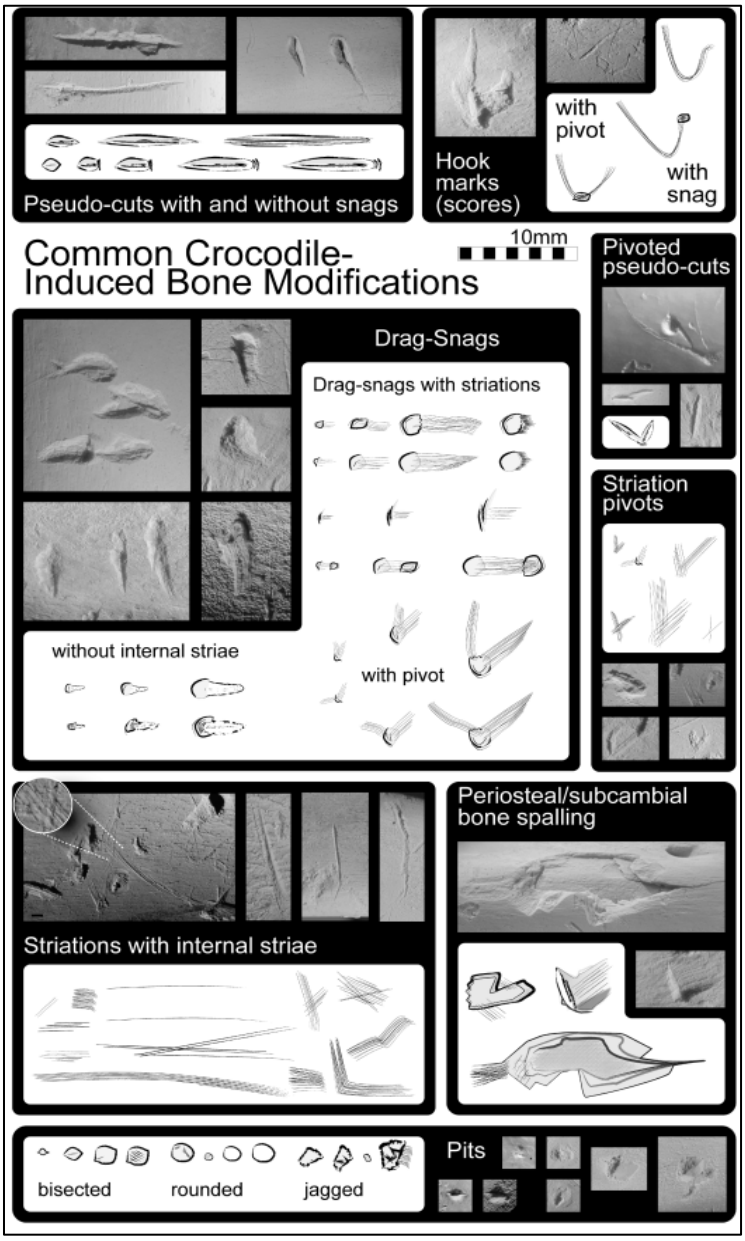


Figure 3. 1: Types of crocodylians bite marks, figures and illustrations from Njau and Gilbert (2016)

The lack of mammalian carnivore features and the presence of hook scores, which are 'L-or J- shaped' structures, are associated with crocodyliform feeding behaviors (D'Amore & Blumensehine, 2009; Drumheller & Brochu, 2014; Njau & Blumenschine, 2006; Noto et al., 2012). Tooth scores made by crocodylians could also be differentiated by the continuous and discontinuous microstriations with either curvy or straight forms (Njau & Blumenschine,

2006). However, experimental works also cautions that some carnivores such as lions and wolves, as well as modified hammerstones could produce similar bisected pits (Baquedano et al., 2012), despite the lack of 'bicarinated' teeth in mammalian carnivores (Njau & Blumenschine, 2006). In general both experiments consent that more than 80 % of crocodylians tooth marked bones show carinated marks compared to carnivorans (Baquedano et al., 2012; Njau & Blumenschine, 2006).

Various methods and experimental studies have been made to differentiate sediment abrasions and trampling marks from cut marks. Trampling is created when a bone surface contacts on stony or abrasive ground surfaces creating linear marks on the bone surfaces (Behrensmeyer et al., 1986; Olsen & Shipman, 1988). The effect of trampling has also been described as a major cause of bone fragmentation (Lyman, 1994b). Trampling marks are characterized by shallow, fine striations of various width and orientations (Domínguez-Rodrigo et al., 2009; Fernández-Jalvo & Andrews, 2016). Striations due to sedimentary abrasion may be distinguished from cut marks by their more frequent occurrence over bone shafts, and generally form numerous closely spaced shallow striations with considerable variation in depth, width and direction (Olsen & Shipman, 1988).

Bone abrasion is a gradual erosion of bone surfaces characterized by smoothness and polishing due to the removal of external lamellar bone (Gümrükçü & Pante, 2018; Thompson, 2005). It is manly produced due to hydraulic transportation, trampling (animal movement), carnivore leaking, exposure to acidic conditions and the use of bone as a tool (Behrensmeyer, 1988; Dechant Boaz, 1994; Haynes, 1980; Pante & Blumenschine, 2010; Selvaggio, 1994; Villa & Bartram, 1996).

Behrensmeyer (1978) defined weathering as the processes when organic and inorganic components of a bone are destroyed or disintegrated by physical and chemical agents in a sub-areal exposure. The effect of these process on bone surfaces is characterized by cracking, exfoliation, splitting and disintegrating (Behrensmeyer, 1978; Fisher, 1995; Hill, 1979; Lyman, 1994a). However, when skeletal materials can be rapidly buried and a very short-term exposure may not leave weathering evidences (Behrensmeyer, 1978; Lyman, 1994a).

Other aspects of taphonomy in zooarcheological context is related to bone breakage patterns, such as spiral and longitudinal fractures are indicative of fresh bone breakages. These can be caused by butchery for marrow extraction, carnivoran damage and trampling by large size animals (Villa & Bartram, 1996; Villa & Mahieu, 1991). However, the analysis of bone breakage pattern goes beyond the limit of this study. Thus, unless otherwise associated to specimens with BSMs, further elaboration of these samples is not aimed/intended.

It is documented that the presence and location of cut marks on bone surfaces is highly variable (Domínguez-Rodrigo et al., 2009; Domínguez-Rodrigo & Yravedra, 2009). It is also stated that shape and morphology could be affected by the hardness of both the stone tools used and bone properties (Braun et al., 2016). The inconsistency of cut marks could also be due to factors such as when tool edges reduce sharpness, butchery actions, carcass size and bone density could also affect cut mark size and shape (Bello et al., 2009; Braun et al., 2008, 2016; Merritt, 2012).

Throughout the Shungura sequence, crocodilians, mammalian carnivorans and hominids are all components of the faunal assemblages. With this, most of the assemblages occur on fluviatile context. As explained above, taphonomic processes from these agents could result in producing a strong equifinality, often difficult to decipher despite the various methods that have been developed. It will be thus interesting to test if we can differentiate/discriminate these with comparative experimental data before further interpretations of the cutmarks can be made.

3.3. Materials and Methods

Cut marks are linear grooves that penetrate the surface of the bone through the displacement of organic tissue. They are typically described by a deep \/ shaped cross-section, with several associated characteristics such as shoulder flaking, and small micro-striae both on the base of the mark and parallel to the main groove (Domínguez-Rodrigo et al., 2009). Trampling marks are superficial, _/ shaped grooves, that can be associated with internal microstriations,

and present a variety of different length-width ratios (Domínguez-Rodrigo et al., 2009). Thus, one can expect similarity or overlaps between trampling and cutmarks when analyzing these two.

Those macrostrains, however, are not common on carnivore tooth scores, and are thus different from both cut and trampling marks and are commonly represented as shallower depressions. In addition, tooth scores exhibit irregular features with more U-shaped cross-sections, commonly associated with crushed irregular edges (Binford, 1981; Blumenschine, 1995; Cruz-Uribe, 1991; Haynes, 1980). Crocodylian tooth scores feature a possible mix between cut marks and tooth scores, with deeper \/ shaped cross-sections, and associated internal micro-striations are common (Drumheller & Brochu, 2014; Njau & Gilbert, 2016; Njau & Blumenschine, 2006). Similarly, either overlaps or similarity between some crocodylian tooth scores and cutmarks could be expected when shape analysis is performed.

In order to tackle these and assess butchery evidence in the Shungura in general, large samples were collected, but unfortunately not all materials were studied due to reasons explained in the perspective part. The initial aim was to study the whole spectrum of the fauna with regard to ecology and behavior of the newly discovered Acheulean site. I had a plan to study the behavior of *Homo erectus* from the Shungura instead I used portion of the samples to 1) report the potential significance, 2) to test the use of shape analysis develop methodology for future analysis, in particular to apply to the Shungura collections.

The objective of this part is now 1) to investigate morphological similarity between BSM morphologies to characterize and overcome equifinality, and 2) identify the origin of the BSM agents in the Shungura Formation.

3.3.1. Fossil material

I have assessed numerous specimens (n>6000) targeting on documenting bone surface modifications, yet the studied sample is only a small portion of the materials recovered from

this site. Nevertheless, the studied sample allows us to get an idea of bone modification agents, of predation, and of the ecology of early hominids in the Plio-Pleistocene Shungura.

An assessment on the IORE specimens was made from all Members. From the IORE ~ 2,200 specimens were analyzed. Samples from OGRE were mainly from 2019 field season from OMO 57 and Member L, both obtained through total collection of bulk samples and surface survey. For the bulk samples and part of the OGRE collections, not all samples were studied due to time constraints during the covid crises.

Specimens for the IORE come from various members and geological units from Shungura and Usno (most Usno fossils come from levels correlated to lower part of Shungura Member B). Among this sample, 557 are from Member G (440 from GL, 111 from GU, and six more specimens from unknown localities in Member G). Member C is the second largest represented member with 361 specimens, followed by members F (189), B (163), E (139), H (48), D (47), J (23), K or L (13), L (8), and A (7). The rest, a few specimens, either have unrecognized specimen number (specimen number lost) or come from unknown members.

Generally, IORE collections from the lowermost members (Basal and A), and uppermost members (H, J and K) are smaller and could be impacted by the variability of assemblage richness or research efforts bias in these members (Eck, 2007). Thus, available samples from these Members are generally small for this study.

More than 80% of the collections belong to cranio-dental remains. This is due to two main reasons; 1) the nature of the Shungura deposits, dominantly fluviatile deposits (Heinzelin, 1983), which favor cranio-dental preservation (Behrensmeyer, 1988; Dechant Boaz, 1994), and 2) the preferential collection by researchers focused on most diagnostic specimens only. Thus, it is important to keep in mind that the samples available for this study in particular from the IORE are affected by the afro mentioned biases. For this, as part of the OGRE, I have decided to conduct a total collection (100% sampling) from sites in particular associated to archaeological occurrences (discussed later).

3.3.1.1. Comparative reference material for 3D reconstruction methods for morphometric study

Prior to applying to the fossil data, a preliminary case study using experimental samples from different research projects (Barisic, 2006; Castel, 2004; Cusimano, 2015; Drumheller & Brochu, 2014; Parkinson et al., 2014; Rozada et al., 2018; Soulier & Costamagno, 2017), previously published by Souron et al. (2019). High-resolution silicon molds of a chosen sample of 787 cross-section profiles taken from 79 marks representing 11 different types of BSMs were for comparative study (

Table 3. 1).

Mark type	Number of Profiles	Number of Marks
Cut Marks (CM)	288	29
Crocodilia tooth marks (Croc)	153	15
Carnivore tooth marks (TM)	299	30
Trampling	27	3
Trampling with flint	20	2
Total	**787**	**79**

Table 3. 1: Description and number of the comparative experimental samples used for morphometric analysis.

For the fossil data, more than 300 BSMs from well preserved 90 specimens were sampled initially. About 3,300 profiles were extracted. These include pits, scores, linear marks of various types including identified cut marks. The profiles from pits were excluded from analysis as the experimental data were not readily available, and it requires a longer time for the software to process these profiles than linear marks. About 2200 profiles of the linear BMS samples were analyzed. List of specimens with identified cutmarks are provided in the appendix (Appendix).

3.3.2. Methods

3.3.2.2. Identification and casting of marks

Mark identification and characterization were made on the original fossil specimens. Bone surface modifications were identified first with naked eye, handheld lenses with 10 X and 20 X magnifying power. Selected specimens were photographed using dino-lite and Canon type cameras depending on the size of the mark. Stereomicroscope imaging was used to capture images when the visibility of marks is affected due to colorization of the bone by, e.g., manganese coating of bone surfaces. This is particularly useful for Member L samples, where most of the specimens are blackish. Finally, mold samples of the BSMs were made using a silicon impression material (polyvinylsiloxane elastomers, Coltone President) to acquire high resolution surface topography of the linear marks. These molds were exported to France and each surface was scanned using confocal microscope used for scanning the surfaces for the 3D profilometry required for the morphometric analysis.

3.3.2.3. An overview to the geometric-morphometrics

Geometric morphometric is a growing approach in the study of taphonomy, and in particular to the study of Bone Surface Modifications (e.g., Aramendi et al., 2017; Bello et al., 2011; Bello & Soligo, 2008; Courtenay et al., 2019; Souron et al., 2019; Yravedra, García-Vargas, et al., 2017). The objective of this chapter is to apply these, contribute to develop new methods of BSMs supported with experimental data, and provide new taphonomic information on the Shungura Plio-Pleistocene assemblages.

Various researchers have used different types of techniques and tools to capture 3D BSM (Arriaza et al., 2019; Bello et al., 2009; Bello & Soligo, 2008; Courtenay et al., 2019; Maté-González et al., 2017; Souron et al., 2019; Yravedra et al., 2018). The high resolution of the confocal microscope allows capturing most microstriations (Figure 3. 2) that are clearly visible in the final cross-sections (Souron et al., 2019). Thus, confocal microscopy could be

a powerful tool to compare morphologies of cut marks, tooth scores, and trampling and differentiate them.

3.3.2.4. The application of Confocal Microscopy and Elliptic Fourier analysis

The 3D model of each mark was made using a Sensofar S Neox Confocal Microscope from Bordeaux University with a 20x objective producing a lateral resolution of 0.645 µm, a vertical reproducibility of 8 nm, and an optical resolution of 0.31 µm (Souron et al., 2019). Then, the SensoMap 7.4 Software was used to process the models, filling in the missing points using the nearest neighbor algorithm, followed by outlier detection and nose measurements. Next, a least-square plane algorithm was used to level the models, which the Z axis was then inverted to obtain the topography of the replica of the original BSM.

The analyses are based on 30 landmarks (LM) on each cross-section of a profile. Generalized Procrustes analysis (GPAs) of the LM coordinates and principal component analysis (PCA) of the resulting shape coordinates were performed using the package library to load the Morphologika file containing profile coordinates. The resulting PCA plots provide shape differences among the experimental and fossil data.

However, as the heterogeneity of BSM profiles is much greater which makes it problematic to control size and shape analysis using geometric morphometric analysis (Courtenay et al., In Prep.), the use of Elliptic Fourier (EP) based analysis become useful overcome these limitations. Fourier Analysis is used to describe shape as a series of periodic functions along the curvature of an outline (Ferson et al., 1985). Once Fourier coefficients are used as opposed to Procrustes coordinates, Procrustes Distances with Mahalanobis Distances are used to classify new samples (Courtenay et al., In Prep.). For Mahalanobis classification, an R function has been provided in (Coutrenay et al., In Prep.) to predict classes of samples.

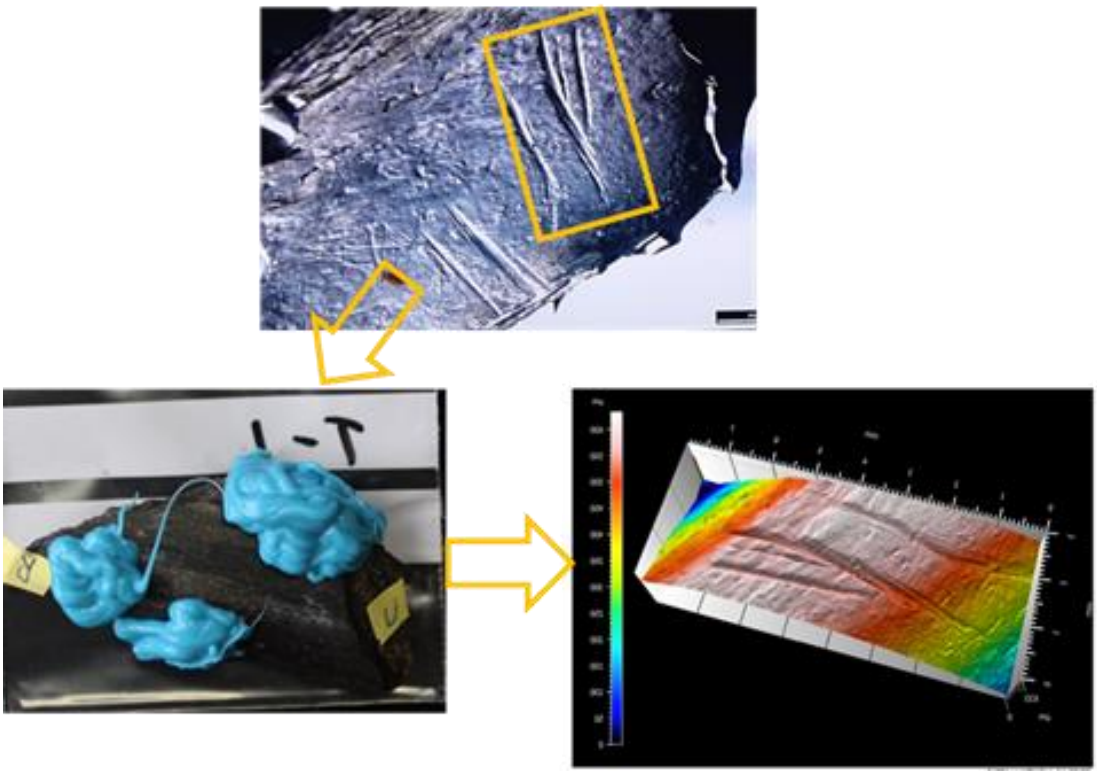


Figure 3. 2: Picture showing part of the pre-analysis procedures (fossil specimen, molding and 3D surface of the scanned BSM).

To get the micro-topography of each BSM from the 3D models, a series of 2D cross-section profiles along the total length of the mark were extracted. A total of 11 profiles were initially extracted (10 cross sections per profile, plus one automatically generated mean profile) see (Souron et al., 2019) for detail, and illustration below (Figure 3. 3). The cross sections are placed equally at every 10 % of the whole BMS length from 5% to 95%. However, these can be manually adjusted to avoid automatic placing them on altered surface within the mark.

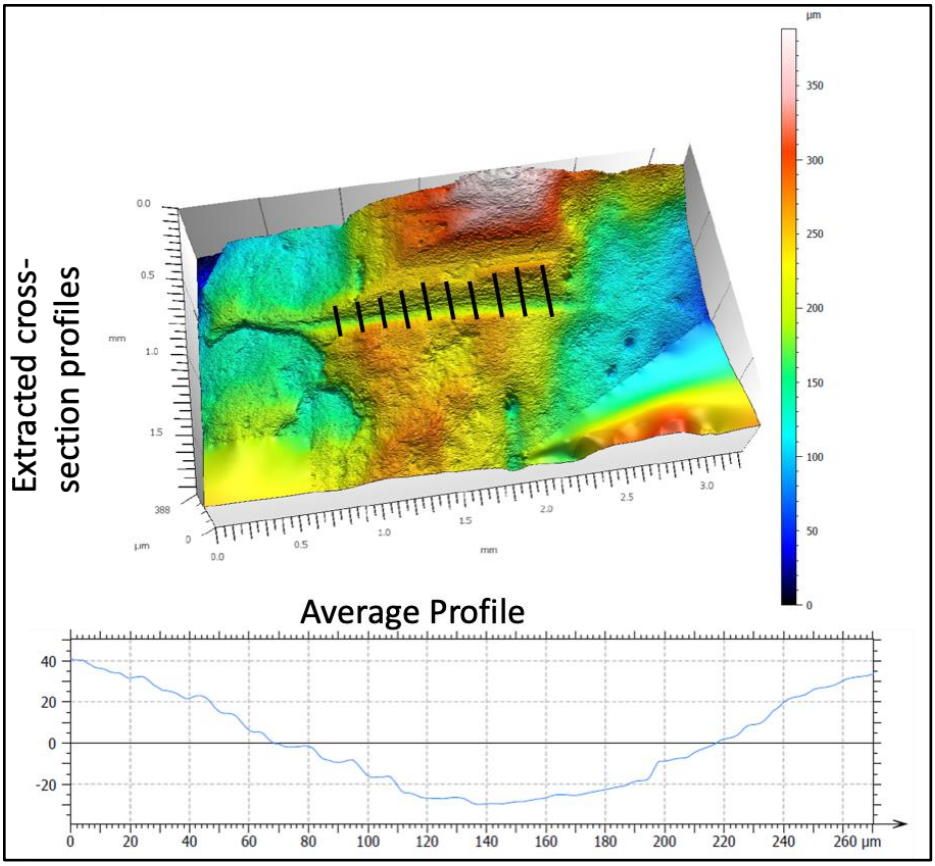


Figure 3. 3: Example of 3D model of a cutmark from a fossil specimen (OMO 377-T004) showing the position of the 10 cross sections (in black vertical lines), and an average profile of the extracted surfaces.

Souron et al. (2019) used 2 landmarks (LM)and 58 semi-landmarks for each profile. However, 30 LMs capture enough morphological information useful to statistically differentiate experimental samples while avoiding noises (Courtenay et al., In Prep). The R code for calculation of the optimal number of landmarks was programmed by L.A. Courtenay (Courtenay Pers. comm).

A preliminary study calculating the Mean of each profile proved to present a large amount of noise (Courtenay et al., In Prep.), therefore all subsequent analyses were performed on each of the profiles separately. The extracted profiles were saved in ".txt" format. All analysis were then conducted using the R Software using packages (geomorph, shapes, abind, sf, MASS, dplyr, car, ramify, rgl, Rvcg).

Elliptic Fourier coefficients were applied as descriptors of the morphology, i.e., profile shapes and outline. A cumulated Harmonic Fourier power calculated for BSM profiles described by 30 computational equidistant points along the profile on the experimental data by Courtenay L.A (Courtenay et al., In Prep). Then a principal component analysis can be derived from scaled and non-scaled Fourier Coefficients.

The experimental data indicate that when PC scores are analyzed, the relative position of the median sample profiles reveals a pattern with crocodilian bite marks approximating cut marks, whereas trampling marks are frequently grouped together (Souron et al., 2019); Courtenay et al., In Prep, and Pers.comm.). With this assumption, a new R function has been provided for the calculation of Interquartile and Interquantile PCA plots (Souron et al., 2019; Courtenay et al., 2021a).

3.4. Results

3.4.1. Evidence of Bite Marks in the Shungura vertebrate assemblages

In this section, the results are based on visual survey following qualitative descriptions.
The taphonomic samples with significance to behavioral ecology, mainly presenting the presence of carnivoran and crocodylian bite marks as well as traces of possible butchery marks, in the Shungura sequence are presented. Bone breakage patterns are not detailed in this chapter as this part focuses on BSMs only. Tooth marks are first dealt with in this section, with examples and descriptions of the marks. The traces of possible human activity are reported in a separate section below.

From the IORE samples, only 520 (26 %) specimens of the whole surveyed samples show bone surface modifications, including tooth marks form crocodylian and carnivorans, green fracture patterns, potential percussion pits, possible cut marks, and modifications that are not surely identified and confidently not attributed to a certain agent. Out of the total modified long bones (n=520), 42% of these specimens show tooth marks of various types. These include rodent gnaw, crocodilian bite marks, and carnivoran tooth marks (Figure 3. 4).

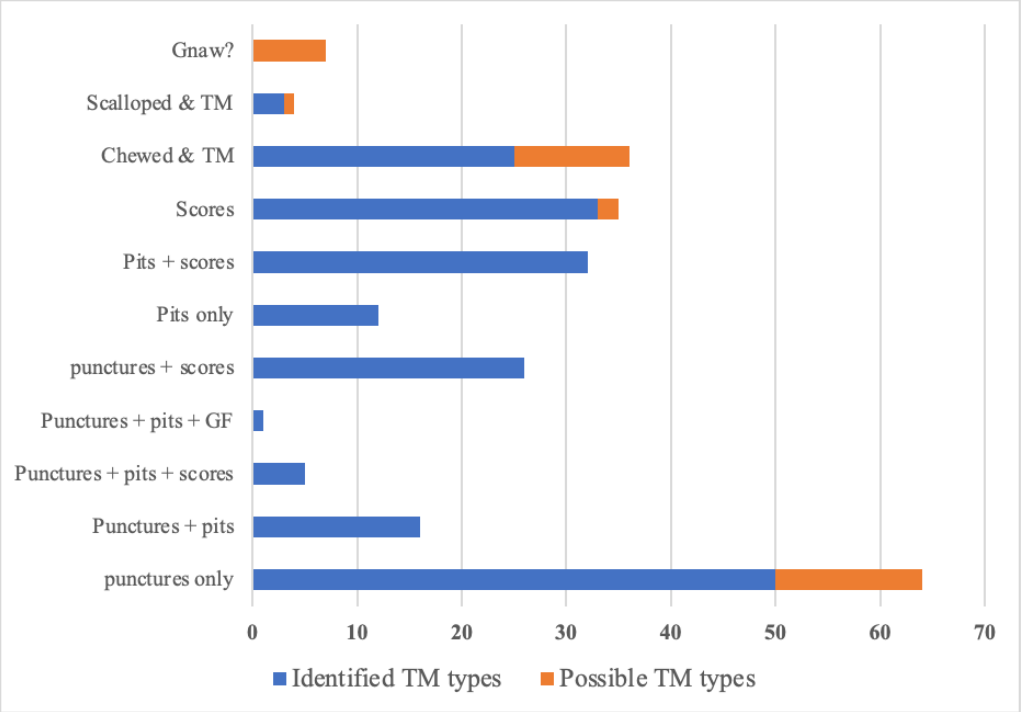


Figure 3. 4: Types of identified tooth marks (TM) and their association/co-occurrence to each other within a specimen (IORE samples only). All in blue are identified tooth marked specimens, whereas all in orange (possible tooth marks).

Bite marks were documented on more than 220 elements that shows different types of clearly identified tooth marks. Marks are distributed into different postcranial elements. More than 60 % of the tooth marks were identified as crocodylians bite marks based in qualitative observations. The fact that specimens with crocodilian bite marks are more common than mammalian carnivorans could be related to the depositional context, where crocodylians are more active near water bodies (Njau & Blumenschine, 2012; Westaway et al., 2011).

Identified tooth marks are categorized as punctures, pits, scores, chewed, and scalloped tooth marks. However, when two or more types of marks are found together (associated) on a single specimen, these marks are documented as punctures with pits, punctures with scores, punctures with pits and scores, pits with scores, chewed and scalloped marks.

Other marks are identified with less confidence such as ‘punctures?’, ‘Scores?’, and ‘chew marks?’ and ‘rodent gnaw?’ are recorded but not included for the analysis. Tooth marks are also encountered on green fractured bones and are present in 13 specimens associated with either pits, scores, or with both types of marks. Some exemplary pictures are provided below (Figure 3. 5; Figure 3. 6; Figure 3. 7).



Figure 3. 5: A medium size bovid ulna (OMO 1/C-1967-684) from Member F showing typical tooth punctures by mammalian carnivoran. The specimen has tooth punctures on both medial and lateral sides. Scale bar is 2 cm.



Figure 3. 6: Cercopithecoid pelvis fragment (L 551-5) showing both tooth scores and associated chewed edges (indicated by white arrows). The shallow and wider tooth scores associated with scalloped edges are typical of mammalian carnivoran tooth marks. Scale bar is 1 Cm.



Figure 3. 7: Cercopithecoid distal tibia (L 32-235, Member C (C-8) showing two bisected punctures typical of crocodilian bite marks. Scale bar is 2 cm.

In general, crocodile bite marked specimens are documented more than carnivoran in the sequence. The distribution of carnivoran activities are higher only in upper G, with slightly higher than crocdilians at Member F (Figure 3. 8).

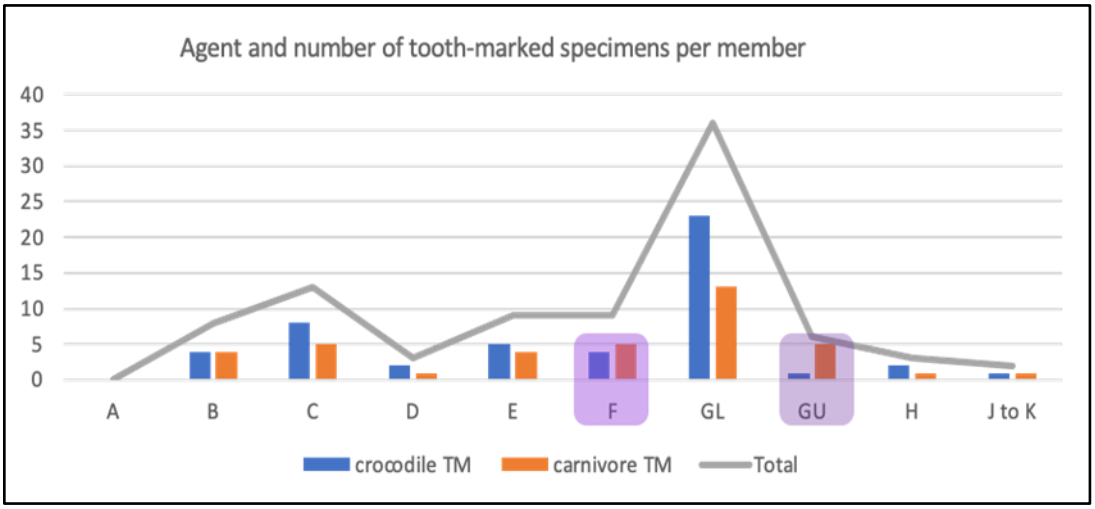


Figure 3. 8: Percentage distribution of tooth marked samples showing number of observed bones with marks per stratigraphy (IORE samples only). Carnivoran activity is dominant in Member F and upper G.

Hominid interaction with carnivores and crocodiles were observed, but in a limited extent. Few specimens (n=3), at lower G, were identified (not definitive) as marks overlapped by more than one agent. Two specimens show overlap of possible cutmark with tooth marks; one specimen cutmark with carnivoran tooth mark and ctmarked specimen with with crocodile bite marks, both in lower G.

In addition a complete hominid phalanx from OMO 323, lower part of Member G (Daver et al., 2018) displays small bite marks on both palmar and dorsal sides. The marks include both pits and score (Figure 3. 9).



Figure 3. 9: OMO 323-10069, a hominid hand phalanx with small pits and scores. The bite marks are on both palmar and dorsal sides. Scale bar 1 cm.

The pits and scores, on this specimen are very small in size, and some of the pits show bisected edges similar discritpion to the crocodile pits (Njau & Blumenschine, 2012). However, none of the scores show definitive crocodile marks dicussed above. The phalanx has more than 10 marks. Five of the scores were further analysed using the confocal microscopy.

Bite marks on carnivores and crocdiles are rare. A single speimen of hyena femure show tooth puncture and score probably belong to crocodile bit marks.

3.4.2. Possible hominid induced marks in the Shungura sequence

At lower members, C, D and E each has single specimen with linear marks that can be classified within the range of equifinality (crocodile bite marks or cut marks). At Member E, only a single specimen (L 26-5a, distal metapodial of a medium size bovid shows a deep V-shaped mark associated with microstriation.

Counting the number of specimens with cutmarks, Member F has the most (n>8, possibly 10), followed by Member G (n=5 in the lower sequence, n=4 in the upper sequence). This, however, is simply due to the fact that I have sampled more specimens from Member F than the rest of the Members. The samples studied from OMO 57 contribute the most. Results for OMO 57 and Member F in general are provided in Chapter Four. Cut marked specimens

were found mainly associated with green fractures, particularly in Member F. Few specimens showing scarp marks associated with fractures and percussion pits (Figure 3. 10) were also found in Member F, mainly at OMO 57 (n=3).

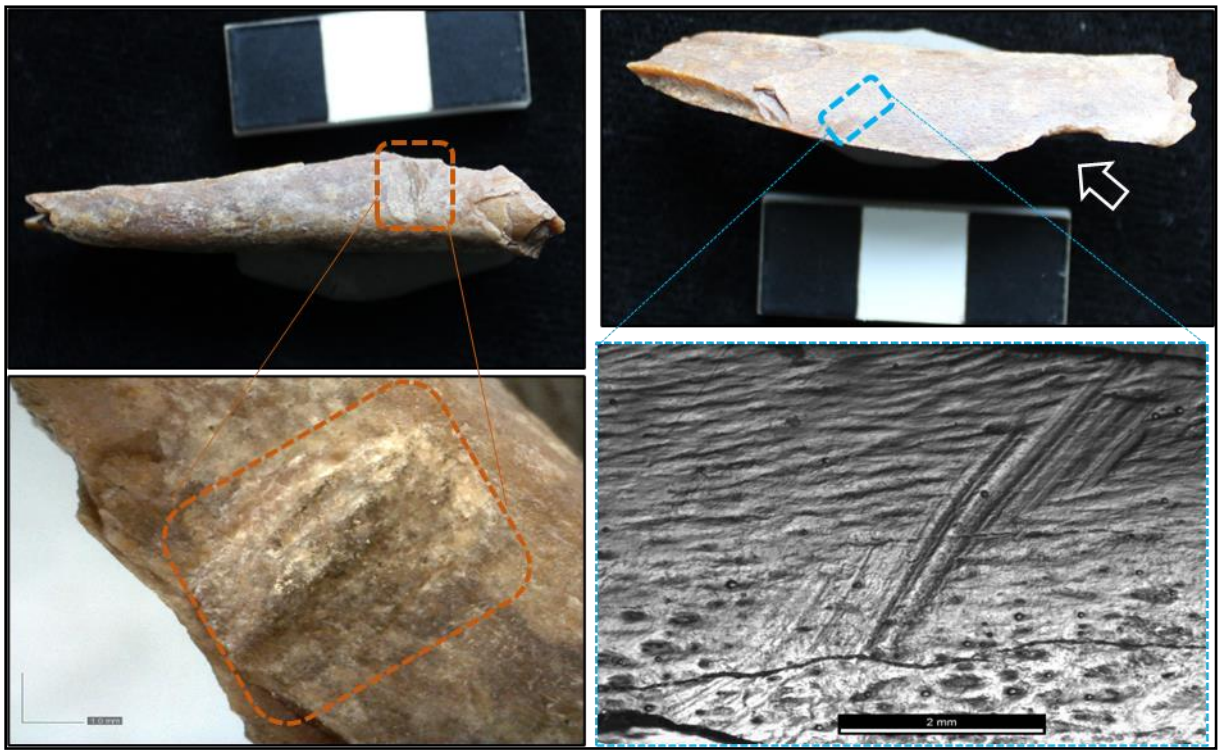


Figure 3. 10: A long bone flake from OMO 57/5 (Mb F) probably belong to size-1 ungulate. It shows a percussion pit with internal micro striation (orange rectangle) and scraping mark and a percussion striation at a breakage angle (blue rectangle), and a percussion notch (white arrow). It was collected during the 2019 OGRE mission.

Green fractured postcranial specimens are common in the Shungura Formation. However, significant of these specimens with such fractures are without associated diagnostic features such as cut mark or tooth marks. For consistency, considering the IORE sample only 42% show fractures without other marks, 22% with notches, 16 % with linear marks, 10% with tooth marks and 10% linear marks identified as possible cut marks. Thus, could be interpreted that bone crushing carnivores might be less active in the Shungura sequence. However, this

could be related to the sampling problem as mentioned above. This is due to samples were mainly collected preferentially to taxonomically diagnostic specimens by paleontologists.

Percussion marks associated with cutmarks are present in both Member F and Member G. However, some of the specimens are affected by other taphonomic agents such as weathering and root marks (Figure 3. 11).



Figure 3. 11: A distal tibia of a medium size bovid (OMO 322-1976-1016) from LG (unit G-11) showing percussion pits on both lateral and medial sides. The pits and the specimen in general is highly affected by root marks. The specimen also has two parallel possible cut marks within the medial depression (not shown here).

At lower G, OMO 50, specimens are better preserved and the least affected by weathering and abrasion. However, only a few (n=2) specimens show marks with hominid induced modification. An example from this locality is provided in (Figure 3. 12) below. An additional specimen was noted in the field (but not collected as it was part of a nearly

complete elephant remain) that shows possible cutmarks on one rib, where other recognizable crocodilian bite marks on other parts of the specimen.



Figure 3. 12: OMO 50-T1 (LG) A tibia shaft flake from a large size ungulate (size 4-5?). The specimen has two cut marks (lower right panel), and percussion stria (upper right panel). The specimen was found during the 2019 OGRE field mission.

Most of the samples for this study, however, are from Member L. Localities from this member produce numerous specimens with possible cutmark (n > 38). Three localities (Figure 3. 13) were surveyed from this Member : OMO 377, OMO 388, and OMO 395 in 2019.In Member L, only a single specimen (F-357, proximal metatarsal) that belong to a large size bovid with percussion mark was found from the IORE collection.

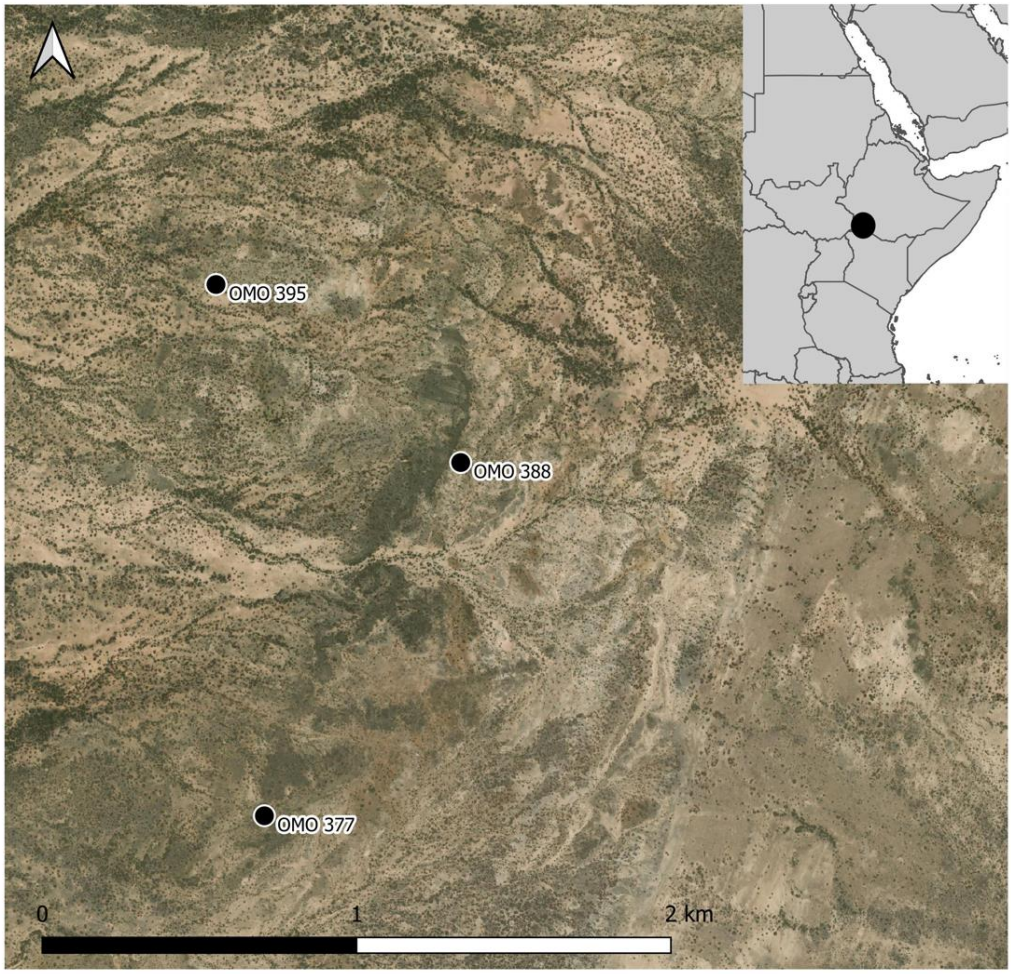


Figure 3. 13: Map showing the location of Shungura Formation, and the three localities from Member L where zooarchaeological survey and collection was conducted in 2019 (map provided by Tiphaine Maurin).

At OMO 395, 11 specimens were collected with definitive cut marks. However, the total assemblage collected by the OGRE paleontology team was not studied due to reasons explained in the summary and perspective chapter. Within the collected samples, bovid, a suid and possible proboscidean postcranial fragments were documented. The indeterminate (Indet.) samples were tentatively recorded as small, medium, and large size mammal remains. A single fish specimen shows a potential cut mark.

At OMO 377, bones and artifacts are accumulated within braccia type sediment associated with carbonate and root casts on the top. At the base of the of the assemblages is a fine sand and silty deposit. Two freshly eroding outcrops rich in lithic and faunal assemblages indicate a very recent erosion exposed those materials. In 2016, the OGRE project found two specimens with potential butchery marks from OMO 377. Following this, in 2019, I have surveyed and collected more samples. The area where there is concentration of fauna was intensively surveyed and samples with potential cutmarks were collected. I have collected more than 2,000 specimens using both transect (bone walk) and total collections by setting grids on freshly eroded outcrops. From this locality more than 20 specimens with potential butchery marks were identified from bovids, hippopotamids, fish, turtles and other undetermined taxa and skeletal elements from small to large size classes of mammals.

Two outcrops exposed numerous fossil fauna and artifacts are selected for a total collection using a grid system. For a reason not to mix with the paleontological samples collected from this locality, I have named OMO 377-T1 and OMO 377-T2. OMO 377 being the locality, and T1 and T2 represent outcrops 1 and 2. Outcrop T2, exceptionally preserved fauna and artifacts intact creating a mound of braccia. The density and faunal association from this outcrop is provided in (Figure 3. 14). Similarly, T1 is associated with root casts and sandstones at the top and, underlying is a fine silty sandstone.

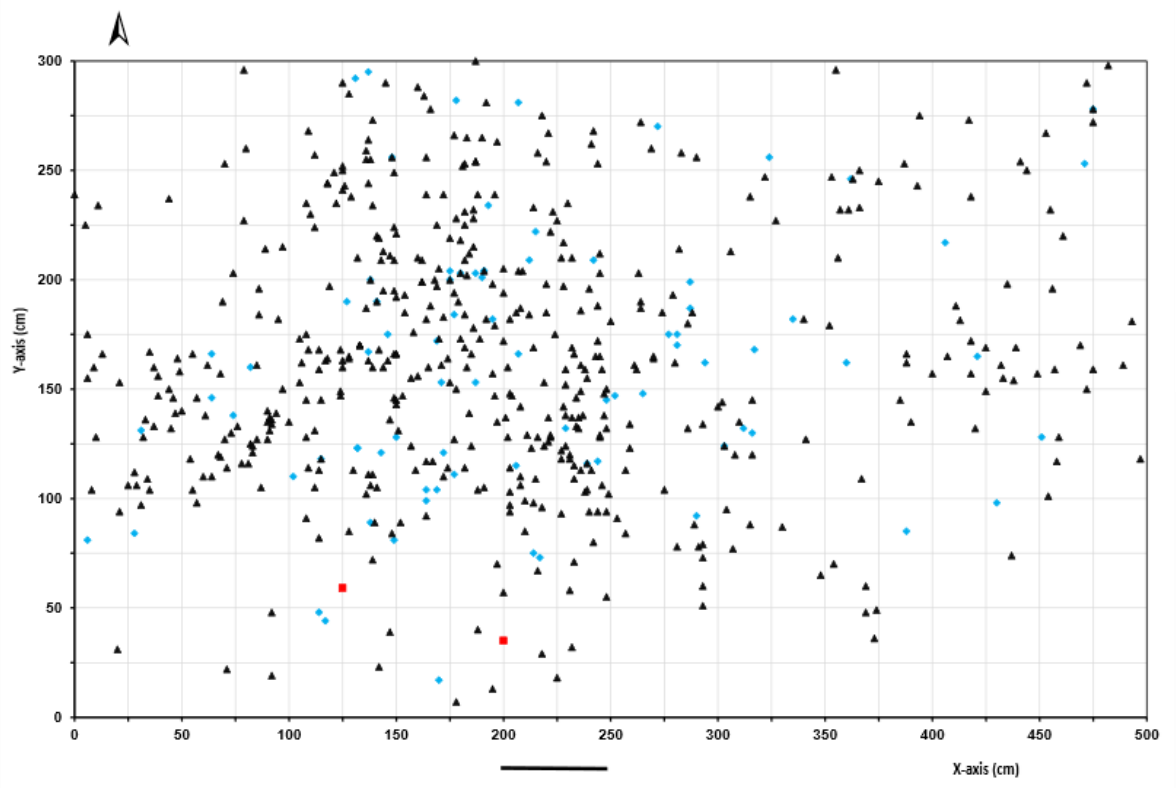


Figure 3. 14: A 3X5 meter grid was set for a 100% collection. This grid is from OMO 377-T1, showing density and distribution of samples collected; bones (black triangles), teeth (blue rectangles) and horncores (red rectangles). Each square represents 25 square centimeters. Scale bar 50 Cm.

Outcrop 1 was named OMO 377-T1, where the first cut marks were found by the OGRE in 2016. Three specimens are so far identified as definitive cutmarks, no tooth mark was found on site, a single specimen shows randomly oriented linear marks identified as trampling. The second outcrop (OMO 377-T1) has produced five specimens within the grid, all hippos and one fish. The remaining assemblages are yet to be studied.

In Member L, aquatic exploitation is evident. This was documented on fish (n=3) and turtle (n =2) specimens that show clear evidence of cut marks. Two other specimens were also observed, but not surely identified. In addition, both large hippopotamid and aff. *Hippopotamus aethiopicus* were represented well (n=7). One of the turtle specimens with modifications (Figure 3. 15) shows both percussion pit, a cut, and a possible hack mark.

Examples of fish bones with cut marks from OMO 377 locality are also provided below (Figure 3. 16).

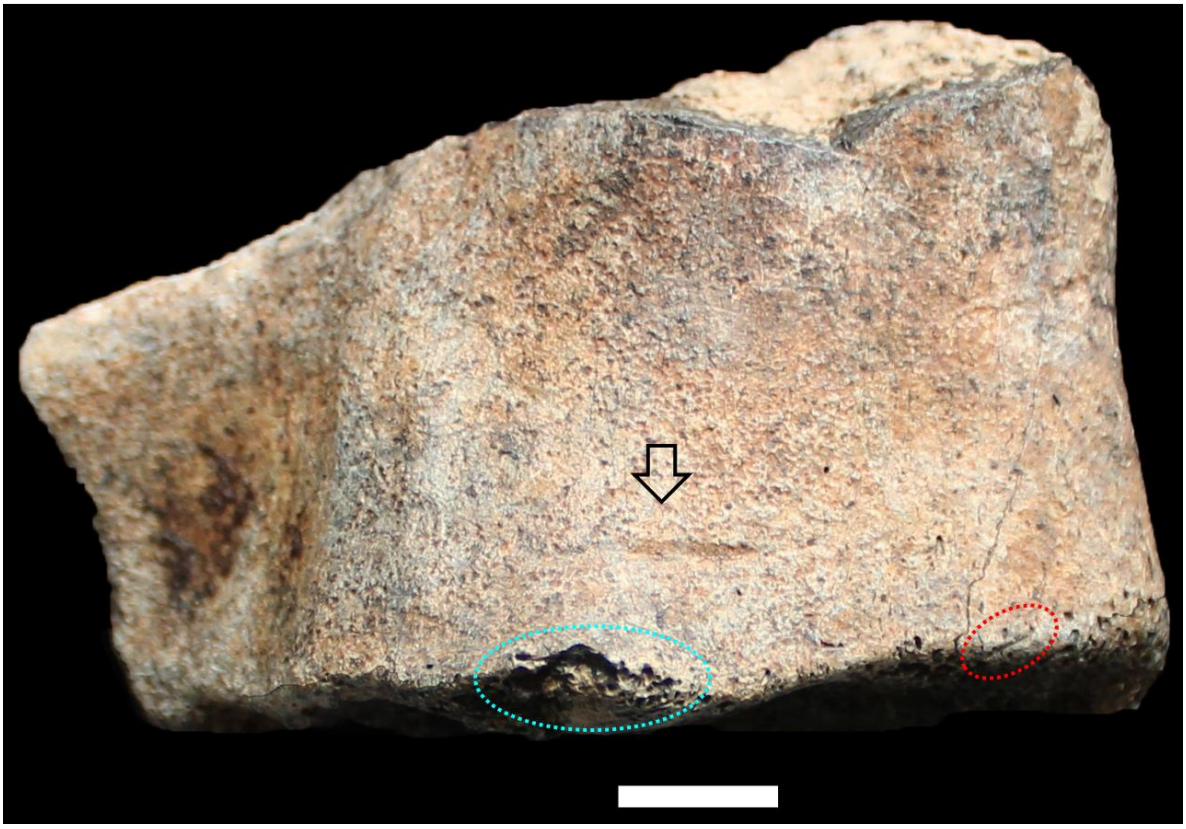


Figure 3. 15: A turtle carapace fragment (probably large terrestrial taxon) from OMO 377-surface collection. The arrows indicate a hack mark nearby percussion notch (blue circle), and a cut mark on the edge carapace (red circle). Scale bar 1 Cm.

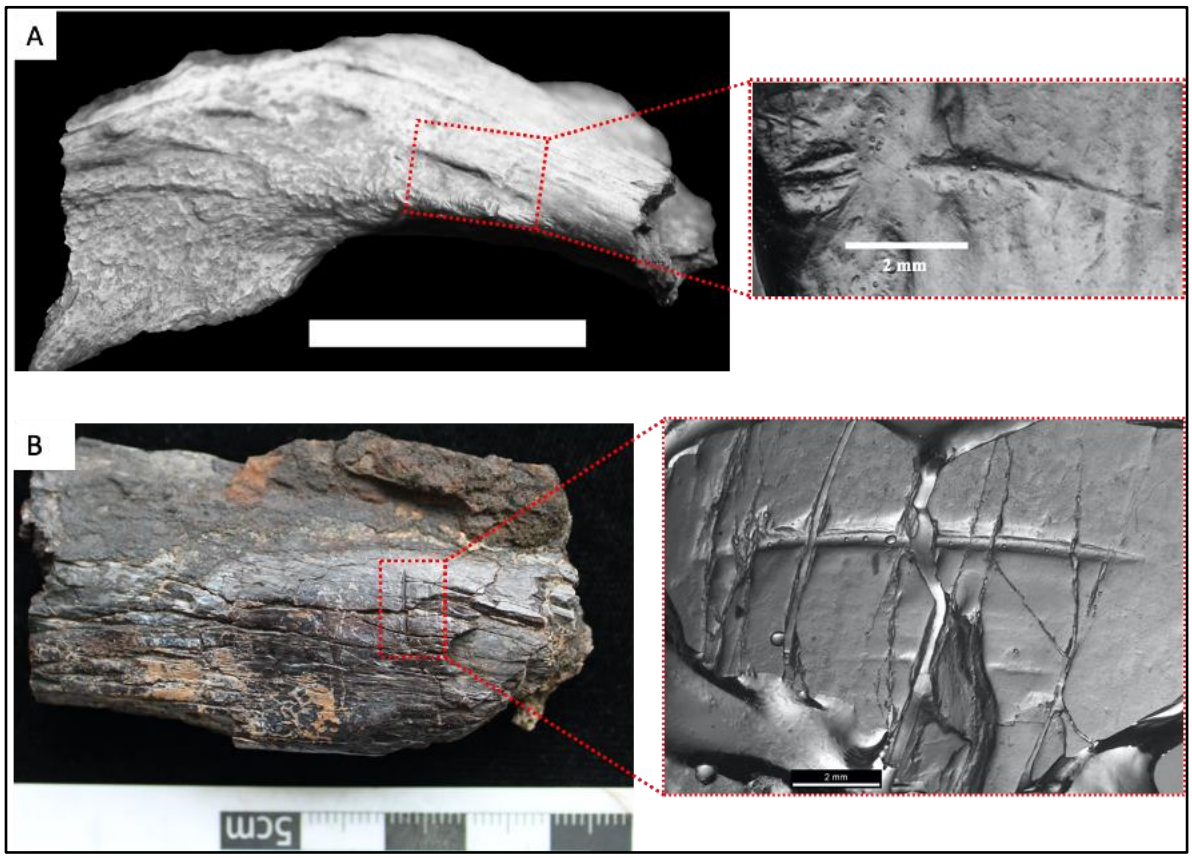


Figure 3. 16: Fish bones with cutmarks from OMO 377 surface collection. A) a fish bone (probably Cleithrum fragment, OMO 377-T033 showing percussion and cut marks. The percussion and the main cut are enlarged and indicated in blue outline. Scale bar 2 Cm. B) A large fish bone fragment showing cutmarks. The specimen has cracking and slight abrasion impacts affecting the visibility of the striations that are associated to the main cutmark.

Percussion marks on large mammals (n=11) were also observed in this member. While all were on long bone shafts, two were on one rib (Figure 3. 17) of a large size mammal.

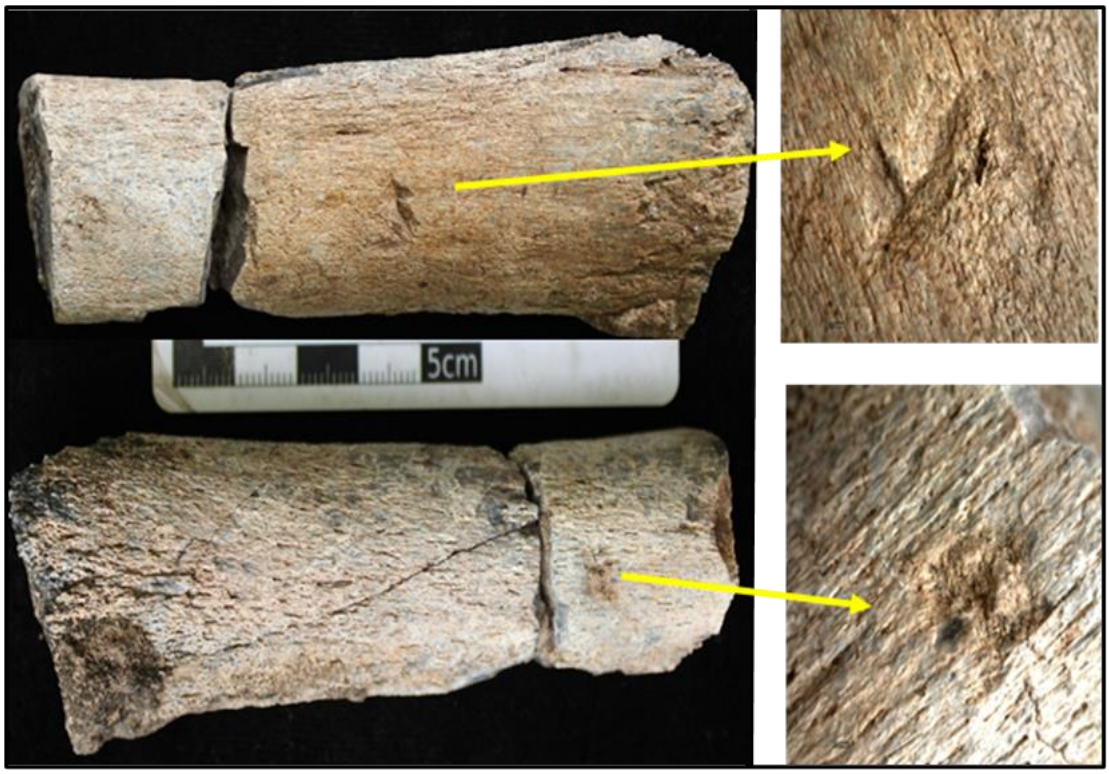


Figure 3. 17: Rib fragment of a large size mammal (size 4 to 5?), from OMO 377 (Member L). Two percussion pits (indicated by yellow arrow) on both lateral and medial sides of the specimen. In addition, the specimen has two cut marks on both anterior and posterior edges.

3.4.3. Geometric morphometric data

The objective was to investigate morphological differences between BSM morphologies and develop methods to characterize and overcome equifinality. It characterizes what is "real" equifinality (similar morphology of BSM that are not distinguishable regardless of the methods used) from "apparent" equifinality (BSM that look overall similar when studied with classic methods but are in fact morphologically distinguishable). With this, the work tries to address the origin of these linear BSM marks in the Shungura Formation.

In the lower members, the marks from Member C and E were initially identified as cutmarks qualitatively through the classical descriptions of marks (e.g. Domínguez-Rodrigo et al., 2009; Olsen & Shipman, 1988), but with low confidence. In addition, the morphological

analysis of the profiles is plotted not within the range of the experimental data. Thus, for now are not considered as definitive cutmarks. At Member E, a single specimen identified (L 26-6a) from unit E-1 as potential cutmark using qualitative methods were also classified as cutmark using the Mahalanobis classification. In addition, a plot based on centroid size discriminates the fossil cutmarks from the experimental ones.

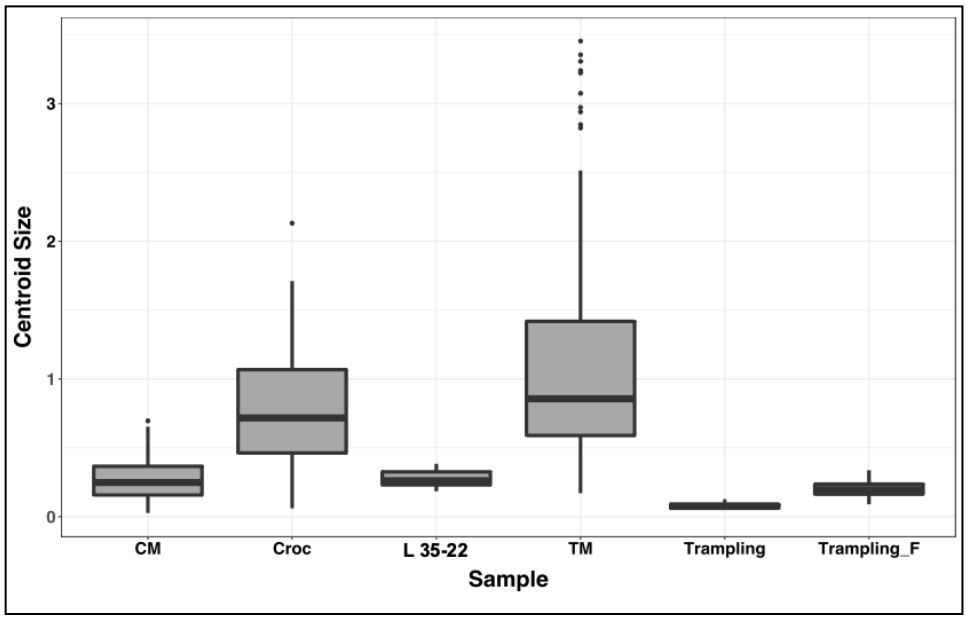


Figure 3. 18: Centroid size plot of BSM from L 35-22 (lower G) compared to experimental BSMs; cutmarks (CM), crocodile tooth scores (Croc), carnivoran tooth mark (TM), Trampling and trampling with flint (Trampling-F).

L 35-22 is distal metapod of medium size bovid. It has two clusters linear marks associated to green fractured bone breakage (Figure 3. 18). The marks were initially identified as cutmarks with low confidence (Appendix). Both marks (Cut A and Cut B) were classified as cutmarks using Mahalanobis at mean classification 83 %. Descriptive statistics for Cut A: Kruskal-Wallis chi-squared (X^2= 0.61085, df = 1, p-value = 0.4345), while strongly discriminated from both bite marks and trampling marks at ($p < 0.000$).

Three specimens at OMO 377 show high density of cutmarks relative to bone surface. Three of the specimens belong to juvenile aff. *Hippopotamus aethiopicus*, OMO 377-10051a (femur), OMO 377-10051b (tibia), and OMO 377-10091 (tibia). Additional specimen (fourth) of a femur head with two cutmarks attributed to the same taxa was also recovered from the same locality. The complete femur (OMO 377-10051a) has exceptional density of marks (n >30), with various size and depth, as well as overlapping of marks. ten of the marks were analyzed (by randomly selecting the main grooves) and all identified as cutmarks with mean average classification of more than 83% (Figure 3. 19).

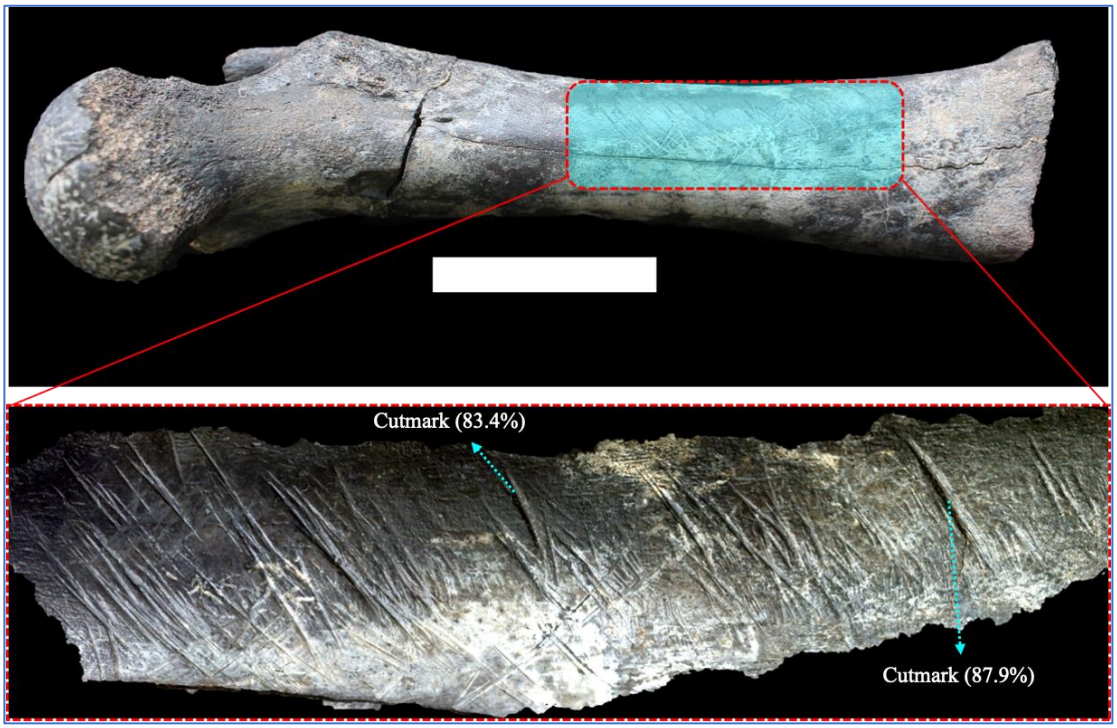


Figure 3. 19: BSMs observed on fossil femur of a juvenile aff. *Hippopotamus aethiopicus*, (OMO 377-10051a) from Member L. The highest concentration of marks is on the shaft of the femur (highlighted in blue) and enlarged below (red outline). Percentage values indicate average Mahalanobis classification of marks compared to the experimental data. Scale bar is 5 Cm.

Overall, I have observed similar results on all specimens from this individual, except only a single mark identified as trampling, and one as tooth score. Tooth marks are very rare in these assemblages. Only a single specimen which was found outside of the collection area shows a tooth mark. Few specimens however were observed with trampling marks with shallow and randomly oriented on exposed cortical surfaces.

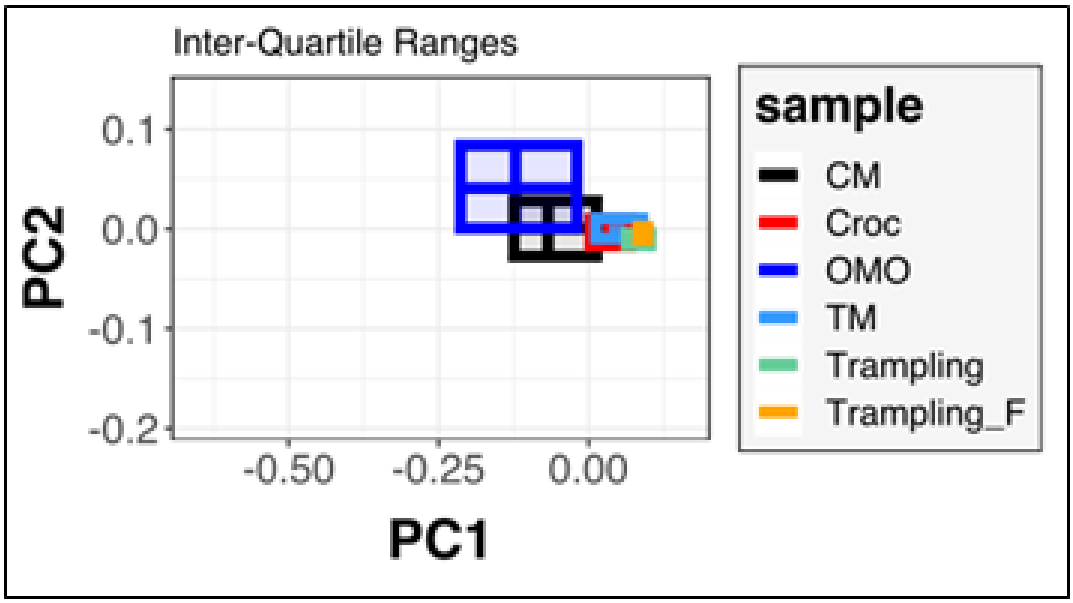


Figure 3. 20: PCA plot of a cut mark from OMO 377-10051b (mark E2) compared to experimental data. Mark E-2 is the second mark within a cluster mark E found at the proximal end of OMO 377-10051b tibia. The specimen has five clusters of cut marks placed on different locations and are named clusters A to G. It has also a flake scar on the posterior side of its proximal end.

Descriptive statistics from OMO 377-10051b (mark E2) using Kruskal-Wallis test (chi-squared = 1.5732, df = 1, p-value = 0.2097) did not discriminate the mark from cutmark, but it discriminated it from the other types of marks (p = < 0.000) (Figure 3. 20).

Morphometric analysis of the hominid phalanx (OMO 323-10069) identified the scores as mammalian carnivore. Descriptive robust statistics did not discriminate it from experimental carnivore tooth scores, while significantly differ from crocodile bite marks and cutmarks (p = 0.0001).

3.5. Discussions

Analysis of BSM a tool to explore predator-prey relations at large, including the place of humans within trophic networks (Blumenschine, 1995; Njau & Blumenschine, 2012; Pobiner, 2016; Pobiner, 2020). In the Shungura Formation, crocodylian and mammalian carnivore tooth marks, as well as trampling or abrasion due to the fluvial nature of the deposits, are the most common taphonomic agents. Anthropogenic activities have been confirmed in Members F, G and L through both qualitative and morphometric analysis using confocal and Fourier analysis.

However, cut marks are characterized by a high intra-mark variability (Domínguez-Rodrigo & Yravedra, 2009). As seen in the figure below (Figure 3. 21) the marks differ in size, shape and morphology. This emanates from the diversity of stone tool uses, from the type and carcass size, and from the skeletal element exploited. These factors such as the type of raw material and carcass processing behaviors could greatly influence morphometric analysis of BSM.

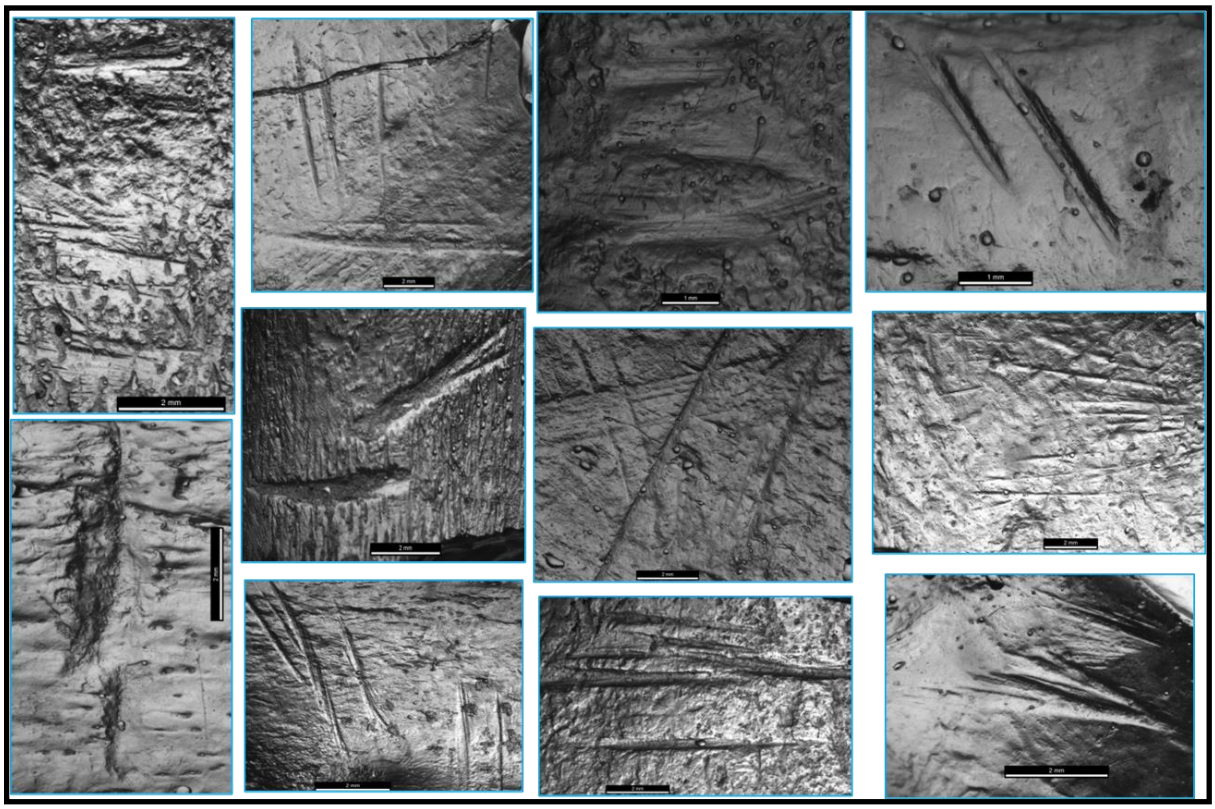
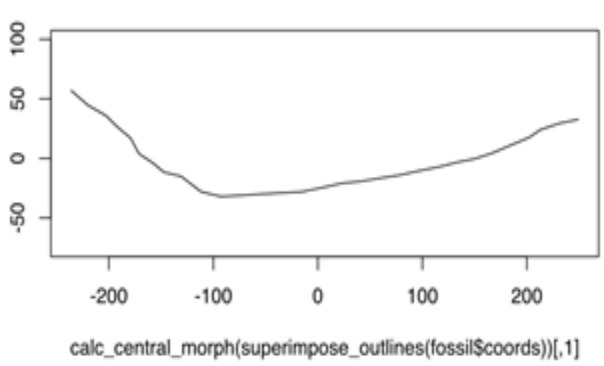


Figure 3. 21: Stereomicroscopic images showing examples of cutmark variability at single locality, OMO 377. Marks are from various skeletal elements and taxon.

Although these morphological irregularities were better discriminated using the elliptic Fourier analysis than geometric morphometric analysis. The main strength of this method is that it has the advantage of capturing and analyzing more than one profile per mark. Previous works have been used only single profile (e.g., (Archer & Braun, 2013; Courtenay, Yravedra, Huguet, et al., 2019; Moretti et al., 2015; Otárola-Castillo et al., 2018; Sahle et al., 2017), ignoring intra-mark variability. Focusing only a single profile with the whole range of marks could cause erroneous identifications. The set of 10 profiles per mark with 30 landmarks helps to capture detailed morphology of the marks. With this, the Mahalanobis offers an identification probability for each profile, where a mean profile of the marks can be calculated.



	Classification	Probability	Distance
OMO1	CM	78.60964	2.9400170
OMO2	CM	82.76413	1.0213272
OMO3	CM	83.11477	0.9721094
OMO4	CM	85.25581	0.7350219
OMO5	CM	82.40580	1.0762440
OMO6	CM	80.16378	1.7269150
OMO7	CM	80.02545	1.8892880
OMO8	CM	79.82067	2.3140128
OMO9	Croc	89.94138	0.4025120
OMO10	TM	97.85986	0.0665398

Figure 3. 22: An example showing variation within a mark. The mark has an outline that is deeper on one side (right panel), and the two last cross-sections were mis classified as bite marks (right panel).

In the figures above (Figure 3. 22), 10 of the profiles on a single cutmark indicate that while eight of the cross section were identified as cut marks, the remaining two cross sections were classified as crocodile and carnivore tooth score.

This method is particularly useful on specimens that show intra-mark variability. Despite this, the work is preliminary, and it has its own limitations. The main drawback comes from the smaller set of experimental data, in particular with trampling. In addition, the experiment lacks the diversity of raw materials found in eastern Africa archeological assemblages. Thus, it is in my future plan to diversify and increase the experimental samples. This will be particularly useful to apply on experimental samples of cutmarks made using quartz (Moclán et al., 2018), and basalts raw materials.

3.6. Summary and future directions

An assessment of the bone surface modification from the Shungura sequence revealed crocodylians to be active agents in all members of the Shungura Formation, while being dominant in members C and G. Carnivoran tooth marks have also been noted on all members, although more common in Member F and upper part of Member G. Similarly, anthropogenic

activity has been confirmed in members F, G (both lower and upper parts), and L, based on the presence of butchery cut marks as well as hack marks. Most traces are attributable to crocodylian activities.

For the characterization of BSM morphologies, I have used an Elliptic Fourier (EF)-based approach. This analysis has proved to be a valuable tool in BSM classification, as shown through notable statistical between experimental samples, and Mahalanobis classification results differentiating between cut marks and crocodylian tooth scores with up to ≈ 87% accuracy. While some debate still remains on the effective differentiation of BSMs, especially in contexts where both crocodylians and hominids coexisted, the present EF-based approach was able to identify and discriminate between cut marks and crocodylian tooth marks. This method is able to effectively identify hominid butchery activities in this area as early as 2.3 Ma.

3.7. References

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Chapter Four

Taphonomy and faunal analysis of OMO 57, Shungura Formation (lower Omo Valley, Ethiopia)

4.1. Introduction

During the Late Pliocene and Early Pleistocene transition, a significant shift in hominid evolution has been recorded. Major events include the appearance of *Paranthropus* and early *Homo* and the later morphological transitions, and/or divergence from other hominids as well as disappearance in the fossil record (Boisserie et al., 2008; Coppens, 1977; Kimbel et al., 1997; Suwa et al., 1996; Villmoare et al., 2015; Wood & Leakey, 2011). The emergence of stone tools is another important event that marks a change in hominid behavior, and which likely impact on ecology and other behaviors (Braun et al., 2019; Harmand et al., 2015; Harris, 1983; Plummer, 2004; Roche et al., 1999; Semaw et al., 1997).

Those evolutionary trends were generally linked to global environmental and climatic changes, and further associated with expansion of grasslands and mammalian turnovers (deMenocal, 2004; Maslin et al., 2014; Potts, 2007; Potts & Faith, 2015; Trauth et al., 2021; Vrba, 1985). However, the impact of local environmental conditions is generally not well integrated, as these processes are often gradual and regionally distinct (Bibi et al., 2013; Bibi & Kiessling, 2015; Boisserie et al., 2010). In addition, intra- and inter-biotic interaction play an important role in ecology that could greatly shape an ecosystem (Boisserie et al., 2008; Brantingham, 1998; Domínguez-Rodrigo, 2001; Ferraro et al., 2013; Kingston, 2007; Pobiner, 2020; Pobiner & Blumenschine, 2003; Shipman, 1986; Vrba, 1980). Besides, the paleoenvironmental data used to link these key events are often hampered by taphonomic processes, as well as scale and type of data employed (Behrensmeyer, 1988; Patterson et al., 2017). Particularly, evidences of early hominid behavior prior to 2 Ma are limited to a handful of archeological sites (Plummer, 2004; Pobiner, 2020).

The oldest known Oldowan sites from the terminal Pliocene thus far are Ledi-Geraru and Gona from the lower Awash Valley, both dated ~2.6 Ma (Braun et al., 2019; Semaw et al., 1997). Slightly younger sites dated to ~2.3 Ma such as Lokalalei of the Nachukui Formation and Member F of the Shungura Formation (Arroyo et al., 2020; Boisserie et al., 2008; Chavaillon, 1970, 1976; Coppens et al., 1973b; Delagnes et al., 2011; Delagnes & Roche, 2005; Merrick et al., 1973; Merrick & Merrick, 1976; Roche et al., 1999, 1999). New sites from Mille-Logya remains of Homo and few lithic artifacts from ~2.4 Ma (Alemseged et al., 2020). Other sites like Hadar dated to 2.34-1.9 Ma include Oldowan artifacts directly associated to remains early *Homo* (Johanson et al., 1980; Kimbel et al., 1996; Rowan et al., 2022). Outside the Rift, the site of Aïn Boucherit, in north Africa (Algeria) is known for its Oldowan artifacts associated with cut marked bones dated to ~2.4-1.9 Ma (Sahnouni et al., 2018).

The function of these tools has been mainly associated to butchery (Dominguez-Rodrigo et al., 2005; Ferraro et al., 2013; Heinzelin et al., 1999; Thompson et al., 2019), although they can be used to process plant food or wood (Plummer, 2004; Galland, 2022). Regardless, the behavioral shift towards stone tool assisted meat eating by early hominids has a significant evolutionary consequence (Bunn, 1982; Plummer, 2004; Pobiner, 2020). In addition, this carnivory behavior put early hominids in direct competition with large carnivores (Blumenschine, 1995; Lewis, 1997; Pobiner, 2020; Pobiner & Blumenschine, 2003; Werdelin & Lewis, 2013), but see also (Faith et al., 2018). Thus, the cooccurrence of artifacts or hominids associated to carnivores in a faunal assemblage requires careful analysis and interpretations.

With this, however, the record of butchery evidence contemporaneous to Oldowan is poorly documented, particularly from the Turkana Depression assemblages. Outside the Afar Depression, Shungura and Nachukui Formations are the only two sites with published Oldowan artifacts older than 2 Ma in the eastern African record. The fossil fauna associations with the Lokalalei sites of the Nachukui Formation are few and poorly preserved. Furthermore, a zooarcheological study has never been performed on the faunal assemblages

from the Shungura Formation. This limited our knowledge and interpretations regarding the subsistence behaviors of Oldowan hominids from the lower Omo valley.

The Shungura Formation of the Lower Omo Valley provides particularly rich paleontological and among the oldest Oldowan archeological sites. The artifact assemblages are restricted between lower Member F to lower Member G dated to 3.319 Ma to 2.062 Ma (Boisserie et al., 2010; Chavaillon, 1970, 1976; Coppens et al., 1973b; de la Torre, 2004; Delagnes et al., 2011; Howell et al., 1987; Maurin et al., 2014, 2017; Merrick et al., 1973; Merrick & Merrick, 1976). The oldest occurrences and richest in assemblages are those from Member F dated to 2.319 to 2.271 Ma (Delagnes et al., 2011; Maurin et al., 2014).

Despite a long history of faunal study and archeological investigations in the Shungura, early taphonomic studies (Alemseged, 2003; Alemseged et al., 1996, 2007; Dechant Boaz, 1982, 1994; Eck, 2007; Maurin, 2017b) have never been made from a zooarcheological perspective. The vast majority of the studies on the Shungura Oldowan hominid behavior have focused on artifact technology and the context of these assemblages (Chavaillon, 1970, 1976; Coppens et al., 1973b; de la Torre, 2004; Delagnes et al., 2011; Howell et al., 1987; Maurin et al., 2014, 2017; Merrick et al., 1973).

In this study, I present the taphonomy and faunal data at OMO 57, a locality that is constituted from both Oldowan lithic assemblages (~2.3 Ma) and faunal remains associated with or contemporaneous to the archeological occurrences. This complex also includes units from Member E that are devoid of archeological assemblages.

The taphonomic and palaeoecological study of OMO 57 therefore could offer new data regarding the subsistence behaviors of lower Omo Valley hominids during the Early Pleistocene. In a broader sense, the zooarcheological data from these Oldowan assemblages could contribute to an additional knowledge to the behavioral ecology of early hominids.

4.1.1. Context and historical overview of OMO 57

Jean Chavaillon discovered the OMO 57 archeological occurrences in 1968. This area of 300 m x 200 m is located in the southern part of the "Type Area." There are no major faults crossing the complex but the presence of many gullies are associated with many changes in lithofacies (Coppens et al., 1973a). In 1968, a mandible (OMO 57-1968-41) and an isolated tooth (right M_3, OMO 57-1968-42) were discovered and attributed to australopithecines (Coppens et al., 1973a). In 1972, a sieving operation at the same spot led to the discovery of additional hominid teeth fragments, a right upper molar and premolar (OMO 57-1972-147 and OMO 57-1972-148). During the same year, Chavaillon opened an excavation to the north-west of this hominid locality.

Within this complex, the collection of artifacts occurred in nine points called Point 1, 2, 3, 4, 5, 6, 7, 7Ginf (Lower G) and 8. Point 5 and Point 7 underwent extensive excavation, with the discovery of in situ material. All the occurrences in this complex are found in secondary position in sand and coarse sand deposits with surface and in situ material. The lithic assemblages from OMO 57 along with those from OMO 123 are what led Chavaillon to propose the existence of a "Shungura facies" (Chavaillon, 1976) distinct from the Oldowan assemblages described at Olduvai (Leakey, 1971).

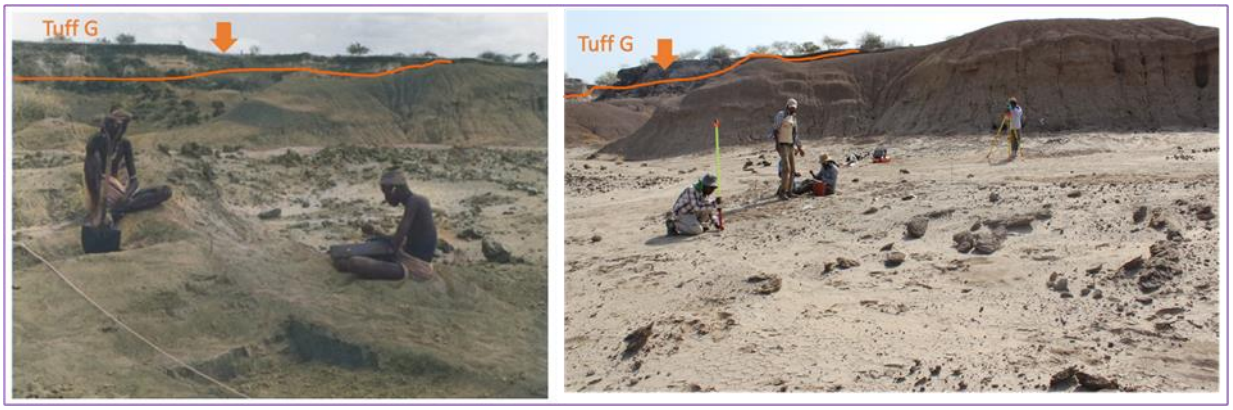

Figure 4. 1: OMO 57/5 collection area. Left, 1972 excavation (from Chavaillon's archives), and right, 2019 surface collection using theodolite.

The main exposures of OMO 57 are from units E-3 to F-1 with Tuff E missing and Tuff F in channel (Heinzelin, 1983). However, others described OMO 57 including Tuff G (Howell et al 1987), and unpublished data from Chavaillon shows a drawing of the whole sequence up to tuff G. Important units with abundant faunal remains are however E-4, E-5, and F-1, the later also including artifact remains (Chavaillon, 1976; Heinzelin, 1983; Howell et al., 1987). The area was shaped by a paleochannel of a braided network cutting into Tuff F from the base of Member G (Howell et al., 1987). This depositional environment was interpreted as a floodplain associated with breaded streams. Important archeological excavation areas, points 5 and 7, are in proximity to each other (Figure 4. 2).

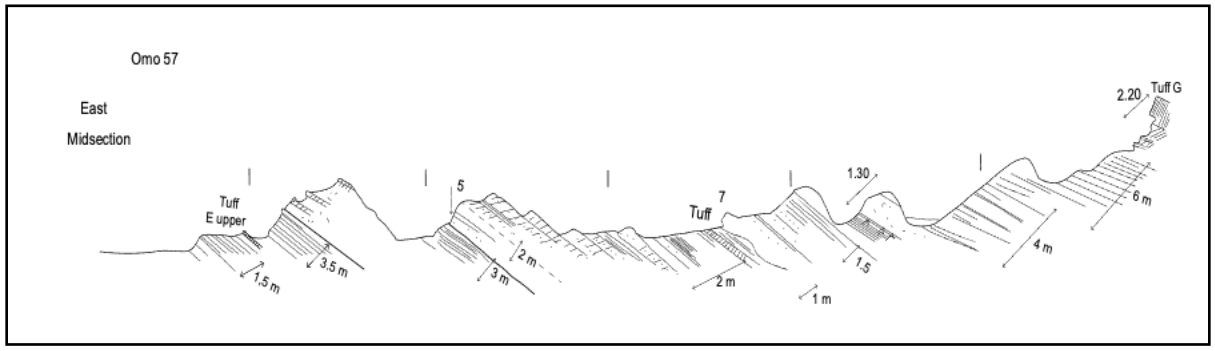

Figure 4. 2: OMO 57, section east, and positions of points 5 and 7 excavation areas. Redrawn from Chavaillon's 1972 notebook.

OMO 57/5 is positioned slightly above OMO 57/4 and has a sedimentary composition of gravels at the base followed by a silt concretion, fine sand and silty components at the top (Coppens et al., 1973b; Heinzelin, 1983). The hominid fragments and associated quartz artifacts come from the basal part (Chavaillon, 1976; Howell et al., 1987). The archeological remains from this site complex come from unit F-1-2. The context of the artifact and the faunal concentration are indicated in the figure below (Figure 4. 3).

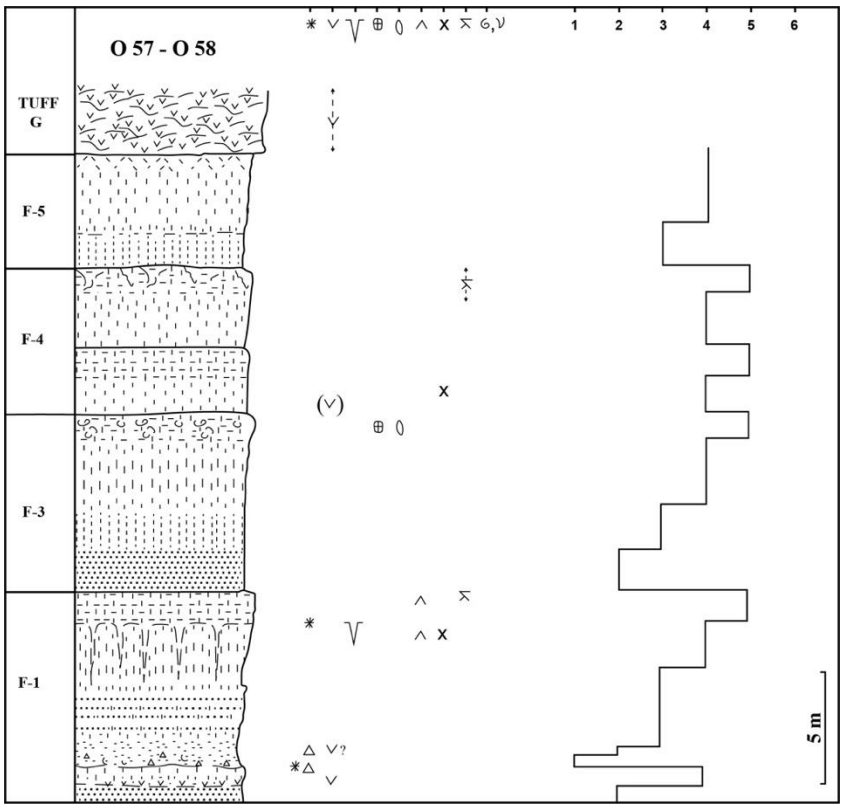

Figure 4. 3: Map showing Member F and Tuff G at OMO 57 and OMO 58 (sector 23 (redrawn from (Heinzelin, 1983)). Concentration of artifacts is indicated at the base of F-1 (Δ), and the symbol ∗ indicates bone concentration. Numbers 1 to 6 symbolize estimated textural classes from coarser sand to clay.

The assemblage in this study comes from Member E and Member F units. Member E is dated to 2.378 Ma to 2.319 Ma, and Member F to 2.319 to 2.271 Ma (McDougall et al., 2012; McDougall & Brown, 2008).

4.2. Materials and methods

4.2.1. Materials

I have used the paleontological database from the IORE and OGRE to highlight the ecological context. For taphonomy, I have made a total (100%) collection from a freshly eroded outcrop at OMO 57/5 during the 2019 OGRE mission. I have then compared it to the

faunal collections from the 1972 excavations by J. Chavaillon, described with similar context. The faunal remains from the excavation are not published and were analyzed for the first time in this thesis.

Every specimen collected from the 2019 mission were analyzed and stored in the collections of the Ethiopian Heritage Authority (National Museum of Ethiopia). The fossil samples from Chavaillon's excavation were analyzed in PACEA (University of Bordeaux) where they were initially stored. These materials were repatriated to the National Museum of Ethiopia in December 2022 and are now stored there.

The 2019 taphonomic assemblage involves a total collection of specimens, regardless of their completeness that are >2 centimeters (except for micromammals and dental remains). A total of 1,192 faunal remains and 64 artifacts were collected using theodolite. Despite the significant number of paleontological samples, a 100% surface collection is preferred to capture a more detailed information (Su, 2016). This method has the advantage of avoiding collection bias by researchers.

The faunal data from Member F are primarily targeted in this study as they are either directly associated or penecontemporaneous to the Oldowan assemblages. Member F provides a unique density of Oldowan occurrences (Delagnes et al., 2011; Maurin, 2017b).

The richest archeological assemblages come from FtJi1, FtJi2, OMO 57, OMO 84, and OMO 124. The first two occurrences (FtJi) were excavated by Merrick and Merrick (1976), and the OMO occurrences were excavated by J. Chavaillon (Chavaillon, 1976; Coppens et al., 1973a). Archeological specimens from OMO 57, FtJi1, and FtJi5 are considered as secondary position, but close to their initial deposition (Coppens et al., 1973a; Maurin, 2017b; Merrick & Merrick, 1976). OMO 123 and FtJi2 constitute artifacts in primary position (Delagnes et al., 2011). A map of the main archeological occurrences including OMO 57 is provided below (Figure 4. 4).

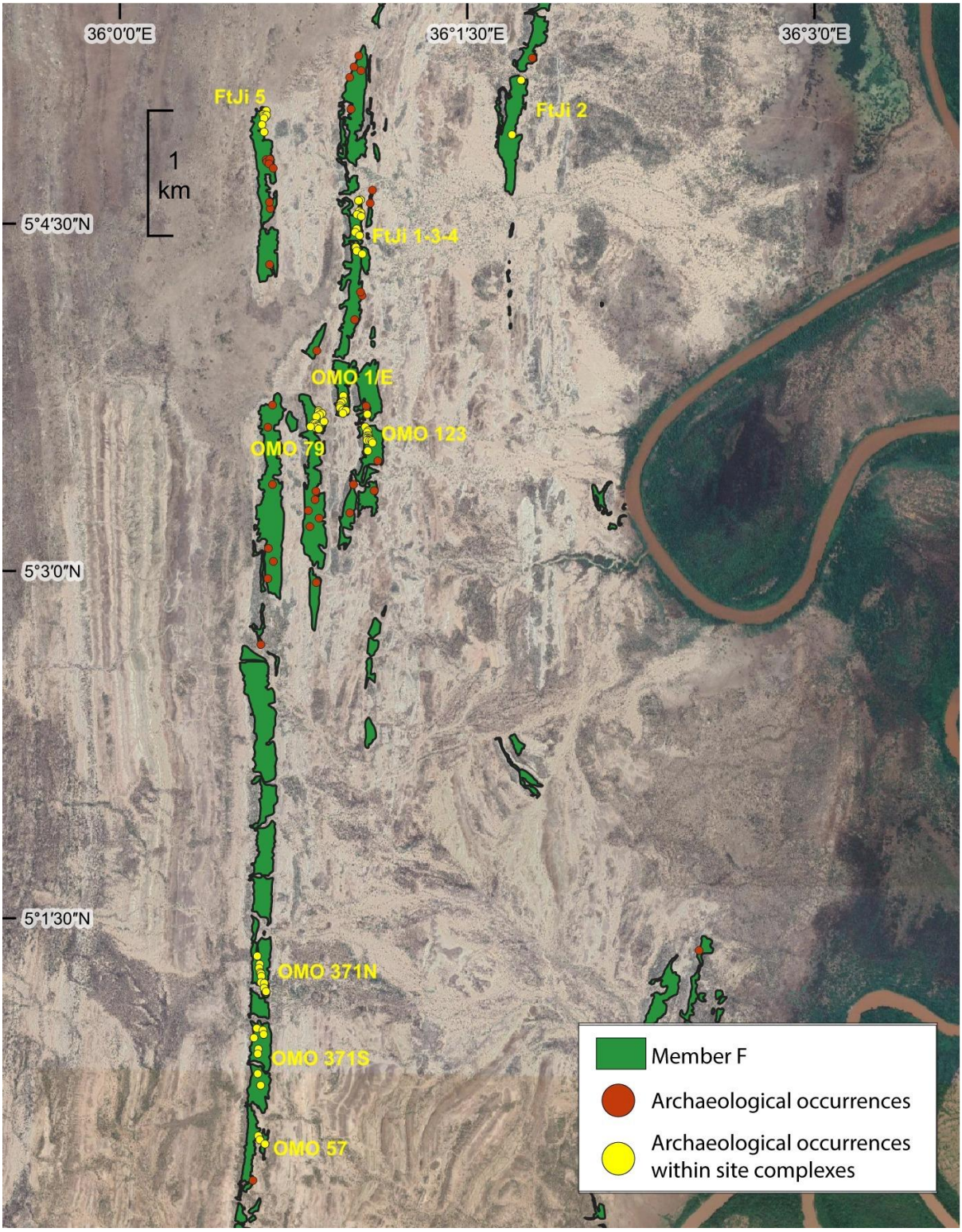

Figure 4. 4: Map showing Oldowan archeological occurrences in Member F (Galland, 2022).

The IORE first reported occurrences of Oldowan archeological occurrences from Member E and F of the Shungura Formation. However, later investigations by the OGRE indicate that unquestionable Oldowan assemblages at the Shungura are so far from lower Member F to Lower G (Delagnes et al., 2011; Maurin, 2017b). Beside refining the context of the IORE localities, the OGRE has significantly increased the number of Oldowan occurrences (Boisserie et al., 2008, 2010; Delagnes et al., 2011; Maurin et al., 2017).

4.2.2. Methods

This study uses field data, IORE and OGRE database and collections from the 1970s archeological excavations. It involves the taphonomic assessment of the fauna assemblages, the quantification of the faunal composition with an emphasis on bovid distribution as well as a brief study of the artifacts found in association with the faunal remains.

4.2.2.1 Surface survey and total collection

In 2019, I have made a survey in the OMO 57 site complex as part of the OGRE field mission. After prospecting the areas where the 1970's archeological excavations took place, I made a collection from an outcrop of the same context. The total collection strategy was applied using Leica theodolite geosystems to precisely plot each fossil and artifact collected in 2019. X, Y and Z coordinates were measured to piece plot and show distribution and density of the collected samples. The collection area (stratigraphic position within unit F-1) is approximately 20 meters northeast of the Chavaillon's Point 5 excavation area. I have targeted a freshly eroded outcrop where faunal and artifacts were associated, and the faunal remains were not homogenous to avoid collecting samples that could belong to an individual or few individuals. Most importantly, I observed bones with distinct breakage patterns and surface modifications from this outcrop.

4.2.2.2. Bone surface Modifications

Traditional zooarcheological criteria for the identification of linear marks were used for qualitative descriptions and initial identification (Behrensmeyer et al., 1986; H. T. Bunn, 1981; Domínguez-Rodrigo et al., 2009; Fisher, 1995; Njau & Blumenschine, 2012; Olsen & Shipman, 1988). In addition, we followed previous works on the identification of percussion marks which are among important traces during butchering activities (Blasco et al., 2014; Blumenschine, 1995; Blumenschine & Selvaggio, 1988; Haynes et al., 2020; Pickering & Egeland, 2006; Villa & Mahieu, 1991).

Identification of skeletal elements, taxonomic classification when possible, and taphonomic evaluations were recorded. The taphonomic assessments include extents of abrasion, exposure to weathering, fragmentation as well as tracing of other biotic and non-biotic agents. I compared between the surface collections and excavations based on NISP and MNI counts as well as the overall assemblage compositions and taphonomy. Lithic assemblages were classified by typology with the help of Anne Delagnes and Aline Galland. The latter also studied the artifacts for potential use wear (Galland, 2022).

I used a hand lens with X10 and X40 magnification both in the field and laboratory for the initial observation of BSM. When specimens were observed with linear marks, further examination was performed and photographed using both a standard digital Camera as well as a Dino-lite for close-up pictures. I performed a 3D morphometric analysis of the BSM surfaces using a Confocal Microscope. The fossil data were compared to the experimental data.

I used both Principal Component Analysis (PCA) and the Elliptic Fourier analysis to investigate morphological differences and developed methods to tackle equifinality [It is ok here to not detailed because you explained in the previous paragraph, but eventually for a paper you'll need to explain it all]. Mahalanobis distances were used to assign fossil BSMs to the experimental samples. Identifying the origin of the linear BSMs from the Shungura formation can be challenging due to the existence of carnivore bite marks (both crocodilian

and mammalian), abrasion/trampling as well as potential butchery marks. See Methodology part (Chapter 3 from this thesis) for details.

4.2.2.3. Taxonomic composition

Analysis of faunal composition are among the most commonly used to reconstruct hominid environments whether at a wider regional or basin scale (Bibi et al., 2013; Bibi & Kiessling, 2015; Bobe et al., 2002; Bobe & Behrensmeyer, 2004; Bobe & Eck, 2001) or at a shorter spatial scale (Alemseged, 2003; Brugal et al., 2003; Maurin, 2017b; Patterson et al., 2017; Plummer et al., 2009).

Due to the methodological differences introduced in the collection strategy by the American and French research teams (Alemseged et al., 2007; Eck, 2007; Maurin, 2017b), I based my study on bovid cranio-dental counts. Bovids were not only similarly collected by both teams but are also among the most common and taxonomically diverse throughout the Plio-Pleistocene, and the abundant literature indicates that their ecological behavior is relatively well understood.

The location of OMO 57 in the southern part of the "Type area" is also important to consider, to compare with localities from the northern part. Thus, localities with a relatively larger sample size are compared to localities with the same temporal framework, but different geographic position. This could allow us to draw an assessment of the distribution of the archeological occurrences. The objective is to test if assemblages from units that yield archeological artifacts exhibit similar ecological patterns. Chapter two of this thesis addressed the spatio-temporal variability, particularly at the base of Member F (pre-Oldowan context). It indicates differences within units and between localities. Here, I focus on spatial comparisons at a locality level, mainly within units from lower F, where Oldowan occurrences are abundant.

4.3. Results

The 100% collection of both the fauna and artifacts uncovered 1,192 specimens (725 bones, 398 teeth and 64 artifacts). The distribution of these specimens clearly shows a high number of bone fragments followed by tooth then quartz. The association and distribution of the samples on the outcrop is indicated on the density map below (Figure 4. 5).

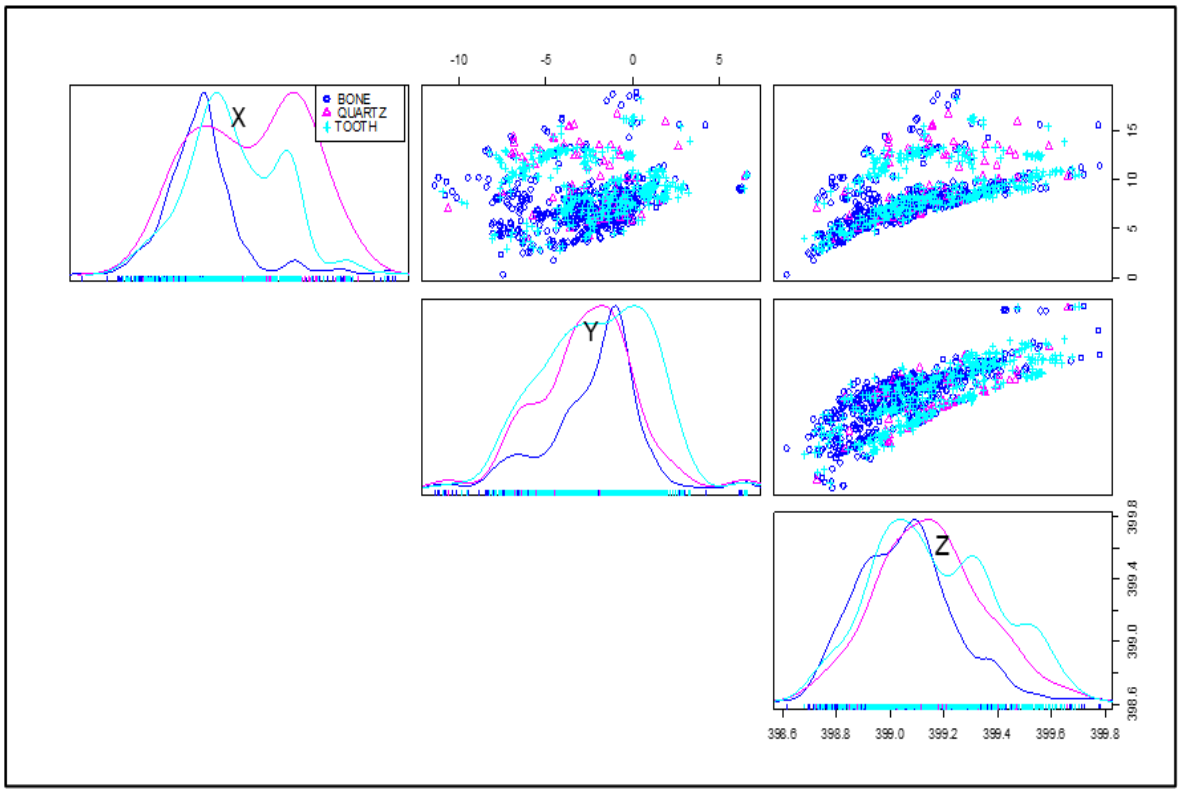

Figure 4. 5: Distribution of bones (dark blue squares), dental remains (light blue crosses) and artifacts (red triangles) across the outcrop across X, Y and Z points.

4.3.1. Taphonomic Data

Bone surfaces from OMO 57 had been strongly subjected to subaerial weathering, exfoliation, and sedimentary abrasion, making visibility and definitive identification of linear marks difficult. Despite that, few specimens with cut marks, and fractured long bone

diaphysis indicate, hominids had access to meat and marrow, although the degree to which extent involved is difficult to determine due to the above stated taphonomic factors. The faunal data and taphonomic assessments from both surface and excavations are presented below.

4.3.1.1 Skeletal element representation

The number of remains was counted for all faunal remains. For large mammals (except for dental remains), specimens less than 2 cm were not collected. These were compared with faunal collections from the 1972 excavation by Chavaillon.

Although there is a difference on the 2019 and 1972 NISP counts, the faunal composition does not differ significantly if we consider the MNI counts of mammals (

Table 4. 1). Except for giraffids, that is present in the surface collection only, the difference comes from the two small mammals. Teeth remains of two Rodentia and a Leporidae are represented in the excavation, whereas micromammals were absent from the surface. The main difference comes from non-mammal taxa which are common in the excavation than surface collection. However, the difference could be simply related to the methodology applied rather than a real composition difference.

Considering the mammal remains only, both samples constitute undetermined bones, 44 % for the surface and 65 % for the excavation. Surface collection includes more mammalian long bone fragments (36 %) than that of excavation (only 9 %), whereas cranio-dental elements are slightly more abundant from the excavation (20 %) compared to the surface (13 %). Axial skeletons are represented equally in both at 7 %. Thus, the samples from excavation probably experienced a relatively faster flow than those from the surface. Judging from the soil bulk sample (sediment piles from excavation), and examination of stratigraphic section at excavation points, the excavated deposits are constituted of smoothed and rounded pebbles

as large as ~2 cm. Whereas the surface collections were mainly on silty condition or possibly surface lag.

	Excavation 1972			**Survey-2019**		
OMO 57/5	NISP	MNE	MNI	NISP	MNE	MNI
Bovidae	35	2	2	13	4	1
Cercopithecoidea	7	4	1	2	2	1
Giraffidae	0	0	0	2	2	1
Hippopotamidae	12	4	1	35	3	1
Suidae	8	1	1	1?	-	-
Proboscidea	7	2	1	201	2	1
Leporidae	1	1	1	0	0	0
Rodentia	2	1	1	0	0	0
Mammalia	170*	6	-	156	9	-
Total Mammalia	***>240***	***21***	***8***	***458***	***22***	***5***
Crocodylia	14	-	-	229	-	-
Chelonia	9	-	-	46	-	-
Actinopterygii	49	-	-	37	-	-
Reptilia indet.	27	-	-	166	-	-
Indet*	77+	-	-	256	-	-
Total	***>416***			***1192***		

Table 4. 1: Counts of faunal remains from the 1972 excavation and 2019 surface collections. Specimens difficult to assign to skeletal element and lower taxonomic level are indicated with *

Both terrestrial and aquatic fauna is common. Within the bovids, a single lower molar (M_1 or M_2) belonging to Reduncini was identified from the excavation. Similarly, one upper molar (M^1/M^2) from the surface belongs to Reduncini. The rest of bovid tooth fragments from both assemblages are difficult to identify confidently at tribe level. The high number of proboscideans and crocodile tooth fragments from the surface indicated here could belong to probably a single cranio-dental element of an individual. Generally, the high proportion of MNI/NISP seen in these assemblages could indicate a high fragmentation rate (Lyman, 1994) on both assemblages.

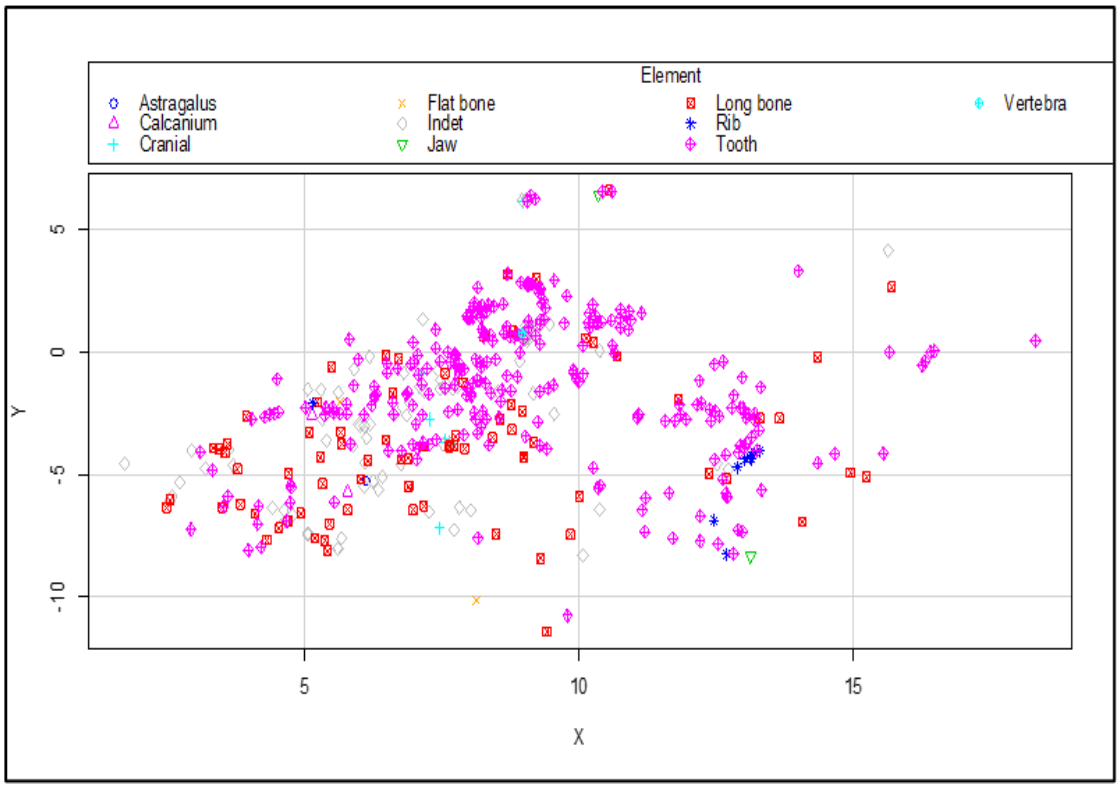

Figure 4. 6: Skeletal element distribution of mammalian only. Isolated teeth are tightly distributed likely due to fragmentation (including after exposure), whereas long bones are relatively sparsely distributed with almost no recent (post-fossilization) breakage.

It is likely that most of the fragmentation of these skeletal elements occurred pre-burial and during hydraulic transportation. Despite this, long bones are represented well in both collections. The 1972 Chavaillon's excavation points are interesting as they provide a relatively direct association with the artifacts. Although there is clear evidence of fluvial disturbances indicated by some rolled specimens, well-preserved surfaces are common.

This variation in preservation is possible due to the recurrent intervals of floodplain (Howell et al., 1987) and thus affected by the occasional (seasonal) water flow. Similar observations on lithic artifacts are also confirmed with both fresh and slightly abraded surfaces from similar context (de la Torre, 2004). Thus, I assessed the bone remains whether to conclude their association is accidental or there is functional association where evidence of butchery could be pointed out.

4.3.1.2 Post-depositional alterations

Assessment of mammal bones from both assemblages show early stages of weathering (stages 0 to 1). Kolmogorov-Smirnov test for equal distribution indicates there is no significant difference between these two samples (D: 0.4, P = 0.71). Only few specimens are noted at stage 3 and 4 from the surface collection (Figure 4. 7). This indicates both samples had relatively shorter sub-areal exposure (Behrensmeyer, 1978).

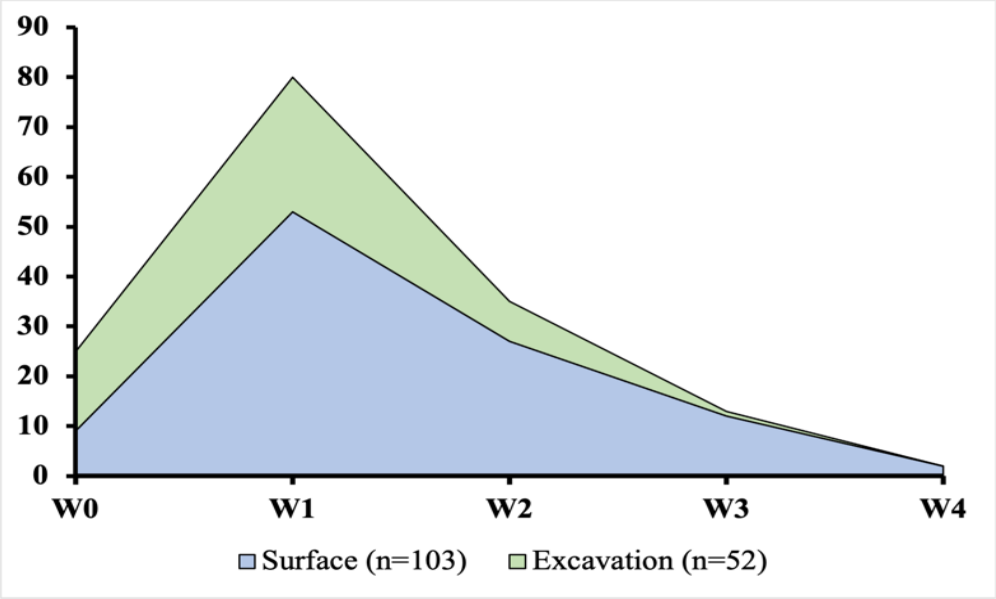

Figure 4. 7: Bone weathering data from both surface (2019) and Excavation (1972). Both samples show early weathering stages (W0 and W1).

About 80% of the samples studied for abrasion (n=922) show moderate to heavy abrasion. Only 3%, however, show rolled and smoothed edges related to long distance transportation by water. Other natural modifications such as exfoliation and pitting were observed on bone surfaces. About 4% also exhibit leached and corroded surfaces probably due to soil chemistry.

Surface samples show an overall higher abrasion and weathering than the excavation samples. Surface assemblages have specimens from well preserved to abraded specimens. This could be due to various episodes of depositions, as proposed by Howell for this locality (Howell et al., 1987). It compromises light bones with no or less abrasion (deposited by low energy water transport), and bones with heavily abrasion indicating of high energy deposits. Specimens also show weathering and exfoliation indicating the variability of the length of sub-areal exposure (quick burial to years of surface exposure or re-exposure due to erosion).

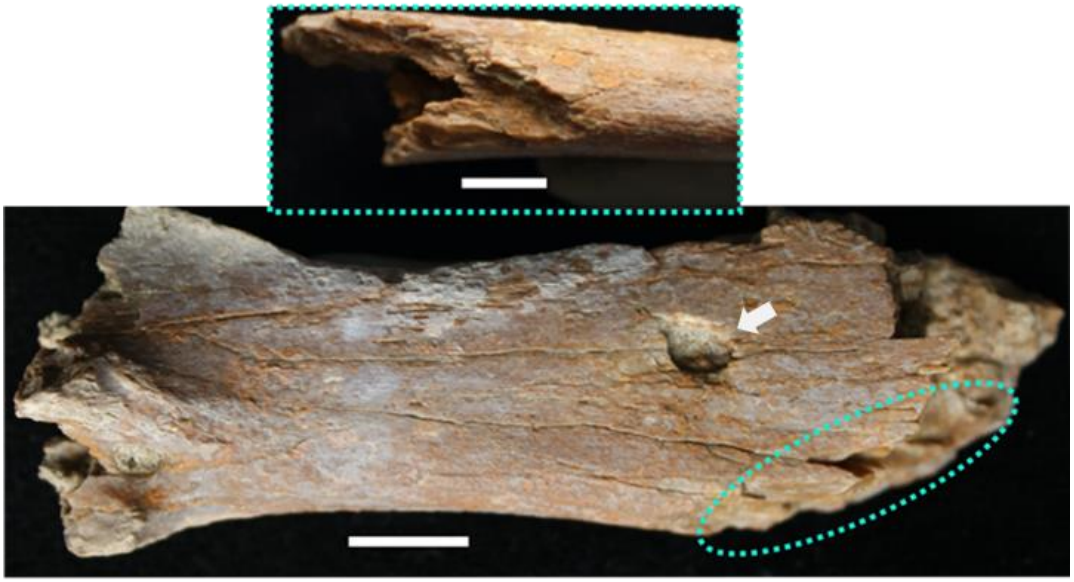

Figure 4. 8: Bovid fragmentary mandibular corpus (edentulous) from OMO 57/5 surface collection. The specimen shows a carnivore tooth puncture and a breakage edge indicated by white arrow and blue circle, respectively. The specimen also exhibits an example of weathering stage 2. Scale bar is 1 cm.

From the excavation, only one specimen has a pit, but it is heavily abraded to distinguish from tooth pit. The specimen above (Figure 4. 8) shows a puncture commonly observed on mammalian carnivore (Binford, 1981; Hill, 1989). The reduction of the size of an element is often associated to hyena activity (Binford, 1981; Cruz-Uribe, 1991; Hill, 1989). Although weathered and slightly abraded, the specimen has scalloped edges on both ends probably related to chewing by bone-ravaging carnivores. While fossil hyaena are present throughout the Shungura, canids are absent. Hammerstone breakage, hyaena ravaging and trampling by

large animals could cause various breakage patterns (Cruz-Uribe, 1991; Haynes et al., 2020; Hill, 1989; Marean, 1991; Villa & Mahieu, 1991). Thus, the damage to this specimen could possibly be assigned due to hyaena feeding.

From the collection area, no single specimen was found with traces of crocodile tooth mark despite abundant crocodile teeth remains. Only one specimen of turtle carapace with crocodile bite marks was noted in the field (Figure 4. 9). But the location of the specimen is outside the collection area and is close to the top E collection (probably E-5?). On the paleontological specimens collected from E5-F1 (OMO 58 and OMO 56/bis), however, there were two specimens identified as crocodile-induced bite marks.

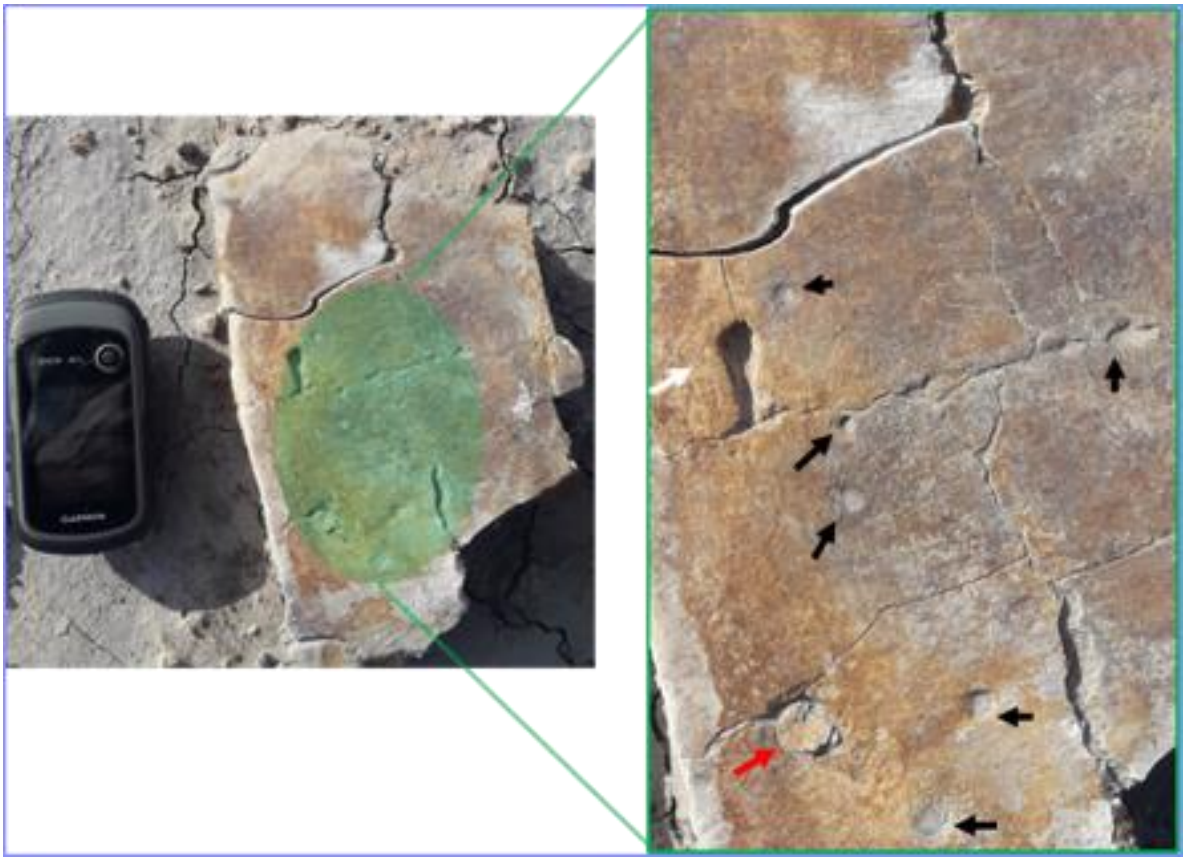

Figure 4. 9: A turtle shell with crocodile bite marks-puncture and pits (indicated with white and black arrows), and a crocodile tooth stuck inside the shell (indicated by red arrow). The specimen is outside the collection area, and thus noted and left on site.

4.3.1.3. Traces of hominid activities

At OMO 57, bone modifications attributed to possible human activity are relatively more abundant than those induced by carnivores. Limb bones associated with distinct breakage patterns, linear marks and percussion pits were observed in both assemblages.

Postcranial remains constitute 80 % (excavation) and 87 % (surface) of the mammalian remains. Out of the mammalian postcranial from the surface (n=130), 12 % show various forms of fracture modifications. Three specimens show associated percussion stria, percussion with wider notch (n=1), and associated linear marks(n=3). One small flake (~1.2 cm x 0.5 cm) has percussion scars on two sides with buttering point visible. Four of the specimens could belong to smaller size (size 1), while the rest belong to medium to large mammal taxa (2 to 3).

From the surface collection, only 5 % (n=9) of the total mammalian postcranial (n=173) show a clear modification. Most of these long bone fractures could belong to medium to large size taxa, except one could belong to size 1, Percussion with cut (n=1), percussion with pit and scrapping marks (n=1), and other percussion with notches and pits (Table 4. 2) have been recorded. The most characteristic specimens are OMO 57/5-T1 and OMO 57-639 (Figure 4. 10): both display series of large flake removals on the main cortex associated with small (retouches) removals on both distal and proximal ends. Interesting OMO 57/5-T1 has an associated percussion stria and a linear mark that can be tested and compared to the experimental data.

Specimen inventory	Ungulate long bone fractures	Associated marks
OMO 57/5-T1	Near epiphysis (size 3) WS-0	1 cut, serious of flake removal, Pc pit, Pc striation, and wide notch
OMO 57/5-T102	Near epiphysis (Size 1), WS-0	Scrapping marks, Pc striation, Pc pit, wide notch
OMO 57/5-T657	Shaft flake (size 3-4), WS-1	Pc pit, wider notch
OMO 57/5-T878	Shaft flake (Size 4-5), WS-2	Flake removal, pc notches,
OMO 57/5-T639	Shaft flake (size 3-4), WS-1	Serious of flake removal, Pc notch
OMO 57/5-T933	Shaft flake (size 3-4), WS-2	Pc notch
OMO 57/5-T542	Shaft flake (size 3-4), WS-1	Pc pit, Pc notch
OMO 57/5-T568	Shaft flake (size 3), WS-2	Pc notch, spiral fracture
OMO 57/5-T649	Shaft flake (size 3-4), WS-1	Pc notch, spiral fracture

Table 4. 2: Description of OMO 57/5 (surface collection) green fractured long bones and associated marks. WS-is for weathering stage, and Pc stands for Percussion.



Figure 4. 10: Two specimens from OMO 57 surface collection: OMO 57/5-T1 (right panel) and OMO 57/5-T639 (left panel), both showing removal of several flakes, cutmark (white arrow) and percussion striation (black circle). Scale 1 cm.

4.4. Discussion

4.4.1. Bone tools as old as the Oldowan? A case study of OMO 57/5-T1

The specimen belongs to a shaft flake near epiphysis, possibly proximal humerus of a large size bovid, although this identification remains tentative. It has at least eight major negative flake scares on its cortical beside the small bending fractures on both proximal and distal ends (Fig. 4.10). Those small series of fractures are probably related to retouching. Although I have observed two linear marks visible using X20 hand lens and dino-lite, one is too shallow and difficult to visualize. The other mark, however, shows a slightly deeper incised is further analyzed here.

First the linear marks were compared to the experimental data (provided in Chapter two) to identify the origin of the linear mark. Kruskal-Wallis rank-sum test shows that OMO 57/5-Cut 1 is significantly different from both crocodile (Croc) and mammalian carnivore tooth

marks (TM) (df = 1, p = <0.000). Even though the test failed to differentiate it from between trampling with flint (Trampling_F) and cutmark (CM), inter-quartile range of the PCA plot shows a strong overlap with cutmark. Interestingly, Mahalanobis classification categorized nine out of the 10 profiles as cutmark with mean value of 86%. A summary table of the descriptive statistics is provided below (Table 4. 3)

OMO 57/5-Cut 1 compared to Experimental	Robust descriptive statistics (Kruskal-Wallis rank sum test)
OMO Vs Cutmarks	X^2=1.8906, df=1, p-value = 0.159
OMO Vs Croc	X^2=22.375, df=1, p-value = 2.243e-06
OMO Vs TM	X^2 = 27.2227df=1, p-value = 1.816e-07
OMO Vs Trampling	X^2 =21.339 df=1, p-value = 3.8493-06
OMO Vs Trampling_F	X^2=0.048387 df=1, p-value = 0.8259

Table 4. 3: OMO 57/5 Mark Cut 1 compared to experimental data and descriptive statistics.

The mark is generally shallow. When we consider size, only two out of eight profiles of the mark are identified as trampling using Mahalanobis classification. Not only that only two profiles are identified as trampling with flint, associated local pebbles are dominated by quartz and rounded river pebbles. Furthermore, the specimen is also associated with percussion pit and green fractured with wider percussion notch.

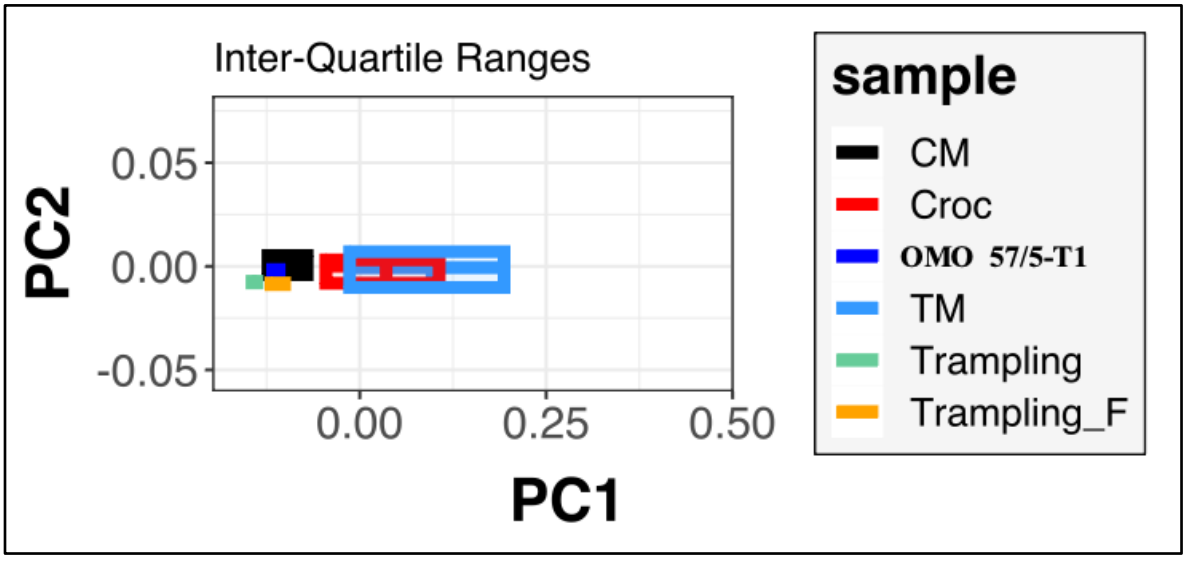

Figure 4. 11: PCA plots of Inter-Quartile Ranges shows OMO 57/5T1 overlap with the experimental cutmarks. CM (cutmark), Croc (crocodile bite mark), TM (Carnivoran tooth score), Trampling_F (trampling with flint).

The figure above (Figure 4. 11) shows that cutmarks (CM) and the OMO 57 sample plotted closer to PC2 than to PC1. While cutmarks generally have high PC1and PC2 values, tooth scores are characterized by lower PC2 values. This is mainly related to the high intra-mark variability of cutmarks (Souron et al., 2019).

In addition, analysis based on size of the profiles using centroid size classified the mark within experimental cutmarks (CM) overlapping with trampling with flint (Trampling_F) (Figure 4. 12).

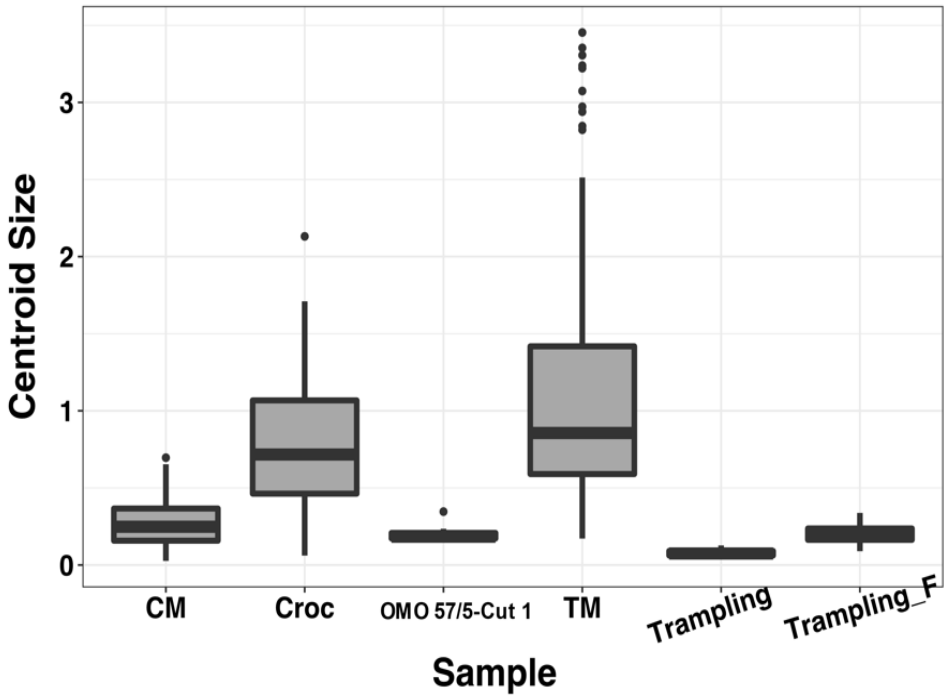

Figure 4. 12: PCA plot based on centroid size indicates OMO 57/5-cut1 fall within the range of Cutmark and trampling with flint. The specimen has two parallel linear marks (cuts 1 and 2). The main cut (cut 1) is compared to the experimental data, whereas cut 2 is a small striation associated to it, likely a shoulder effect.

With the linear mark identified as cut mark and the patterns of such flake removals could be due to human agency. I have conducted a similar analysis on the OMO 57/5-T102 specimen and reached similar result. The scrap mark from this specimen was identified as cut mark and trampling with flint, although the inter-quartile ranges overlap close to the cutmark. In addition, Mahalanobis classification identified nine out of the 10 profiles as cutmarks with mean value of 85%.

In addition, excavations at OMO 123 produced in situ artifacts and associated bones. Unfortunately, the bone remains are very few and poorly preserved. However, one definitive

cutmark with percussion fracture and another specimen with percussion notch and stria are observed. At least one has a well-preserved cortical surface with two clusters of cut marks, and a bulb of percussion. It is a long bone shaft flake and, based on the cortical thickness, the specimen could belong to a medium size mammal (size 2 to 3).

The presence of linear marks in Member F have been recently recognized, although were not further identified (Maurin, 2017b). The first report of bone modification and its relevance to hominid activity from the Shungura was made by Chavaillon (Chavaillon, 1970). He reported three possible bone tools associated with a few lithic artifacts from locality OMO 71, Member E. However, the diagnostic features of these specimens and the context of the site was later questioned and interpreted as natural (de la Torre, 2004).

4.4.2. Modified bones and hominid behavior

Bone tools are generally rare in the archeological record, and thus far, there is no report of bone tools older than 2 Ma in the eastern African. So far, the Oldest bone tools come from the Kromdraai B, South Africa dated ~2.3 (Stammers et al., 2018). Other identified bone tools from the southern African early Pleistocene (e.g. Backwell & d'Errico, 2001) are discussed below.

The findings are consistent with observations made for bone tools features, such as serious of flake removal, bending fractures and in some cases polished edges due to use wear (Pante et al., 2020; Romandini et al., 2015; Sano et al., 2020). I therefore conclude that the two OMO 57/5 above described, modified bone shafts could probably represent bone tools dated ~2.3 Ma in eastern Africa. However, to reach a definitive conclusion, this must be confirmed by further investigations to find in situ (from excavation). In addition, the function of these possible bone tools should be further investigated by comparing them to experimental data. Further, a detailed microscopic analysis and wear patterns are to be conducted.

From the excavation sample, two small pieces (a flaked bone and task fragment) with traces of common technological features are identified. At Gona, a small bone flake with platform

(butt) and a bulb of percussion was found associated with artifacts and cut marked specimens, and was identified as a possible flake from a limb bone shaft (Semaw et al., 2003). The two specimens from the OMO 57 archeological excavation, in particular the flaked bone, shows similar features but are probably smaller in size (~1.2 cm x 0.5 cm). Although recent experimental studies suggest bone flakes could have been used as cutting tools (Gürbüz & Lycett, 2021a) , they could have also been produced during percussion activities.

Breakage patterns of limb bones from large size animals including proboscideans could cause modifications similar to human-induced flakes (Haynes et al., 2020). However, breaking open bones when fresh show distinctive features that can be distinguished from other post-depositional impacts (Blasco et al., 2014; Cruz-Uribe, 1991; Villa & Mahieu, 1991). Furthermore, unlike breaking for accessing marrow, producing bone tools requires even more modifications that could create identifiable patterns (Pante et al., 2020; Sano et al., 2020). A growing research on bone tools is proposing a probably older origin to the antiquity of bone tools (Backwell & d'Errico, 2005; Gürbüz & Lycett, 2021a; Pante et al., 2020; Sano et al., 2020).

Bone tools were discovered from Bed I to Bed IV at Olduvai Gorge (Backwell & d'Errico, 2005; Leakey, 1971, 1994; Shipman, 1989). Re-evaluation of bone tools from Bed I (~2.04-1.8 Ma) and Bed II (~1.8-1.2 Ma) confirm their identification as tools (Backwell & d'Errico, 2005; Pante et al., 2020). The bone tools are characterized as similar morphotype to stone tool manufacturing technique featured by either intentional knapped resulting in series of flake removals or used as anvils/hammers (Backwell & d'Errico, 2005; d'Errico & Backwell, 2009; Leakey, 1994; Pante et al., 2020; Shipman & Rose, 1988). Another bone tool from eastern African context with similar morphology to the Olduvai materials including hand-axe shaped bone tools are these from Konso date to ~1.4 Ma (Echassoux, 2012; Sano et al., 2020).

The oldest known bone tools from Early Stone Age (ESA) context in south Africa were reported from Sterkfontein, Swartkrans, Drimolen and Kromdraai dated between ~2.3 and 1.0 Ma (Backwell & d'Errico, 2001, 2008; Backwell & D'Errico, 2003; Barham et al., 2002;

d'Errico & Backwell, 2009; Stammers et al., 2018). The morphology of these tools is different from those of eastern Africa. The tools are characterized by unmodified weathered bone splinters, and are shaped through time as they are used (Backwell & d'Errico, 2001, 2008). The functional purpose of these South African bone tools are attributed to termite foraging and/or digging activity (Backwell & d'Errico, 2008; d'Errico & Backwell, 2009; Stammers et al., 2018).

Whereas the bone tools from eastern Africa were described as anvils, barbed points, as well as used as in a similar fashion to the Oldowan stone tools (Pante et al., 2020), or probably used for cutting activities (Gürbüz & Lycett, 2021b). On two specimens from OMO 57, I observed similar features to those from eastern Africa exhibiting series of flake removals, one in particular has various flake scars with small bending fractures on both ends.

Bone tools from younger Pleistocene sites elsewhere might have different function such as processing leather and fur (e.g. Hallett et al., 2021).

At OMO 71 (unit E-1), a side chopper and 3 bone tools were reported by Chavaillon. In addition, excavation in 1969 and 1970 uncovered side pebbles broken transversely broken and some with signs of percussion marks. However, these specimens were found associated with gravel, and later reassessment discarded the archeological authenticity of this site (Torre, 2004).

Instead, one interesting specimen was collected in 1968 by Chavaillon. It shows a clear pattern of bone tool with percussion and flake removals as well as a polished end similar to the ones I collected at OMO 57/5. The specimen is intentionally flaked off from a proboscidean tusk and has multiple percussion impacts and polished tip. Unfortunately, its context could not be retrieved except for the fact that it has been collected from Member F in 1968 as it was written on the specimen itself. His notes indicate that in 1967 and 1968, he was mainly prospecting, and mapping identified sites. Thus, it is likely that he collected the specimen during survey before assigning locality names. Furthermore, the attribution to members from these early surveys may be uncertain or correspond to a different member.

Use wear analysis from the Shungura Oldowan stone tools provides evidences of carcass processing (defleshing, scrapping and a cutting) and few cutting movement of undetermined materials (Galland, 2022). Almost all the data comes from localities in unit F-1, except for OMO 123, which is situated within F-3.

This locality has no significant faunal remains except a specimen that belongs to aff. *Homo* (Howell et al., 1987). Similarly, archeological excavations also produced only a few fragmented specimens. Interestingly however, there are at least two long bone shaft fragments that show bone surface modifications. One has percussion scar associated with series of cuts (Figure 4. 13). Parts of the marks are however slightly affected by recent breakage.

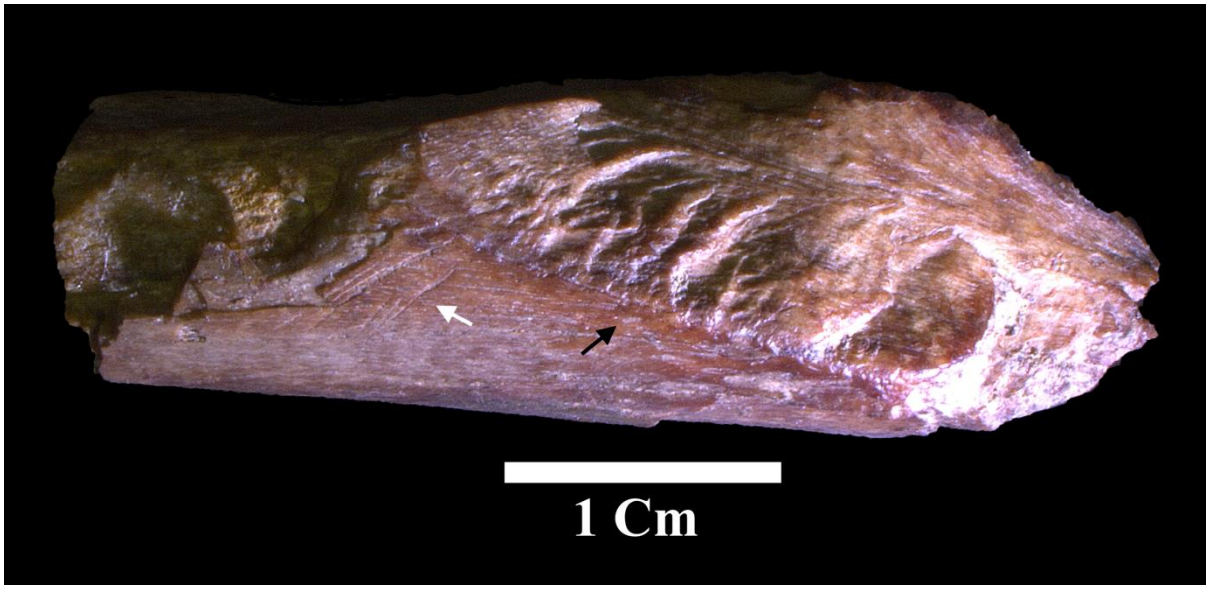

Figure 4. 13: A long bone shaft frag from OMO 123-1973-1976 (Unit F-3) of the IORE. The specimen is from excavation context. The specimen is probably a metapodial shaft from a possible size 3 ungulate. Both cut marks (white arrow) and percussion scar (black arrow) are present.

Another specimen from this locality is also a shaft fragment probably medium size ungulate. It has one shallow percussion pit and percussion stria. It has also a breakage with wide percussion notch with inner conchoidal scar, probably inflicted for marrow extraction (Pickering & Egeland, 2006; Vettese et al., 2020). The specimen is slightly abraded, most likely due to water transport.

4.4.3. Implications for hominid behavioral ecology

In the Turkana Depression, butchery marks are rare, even though Oldowan sites dated to ~2.3 Ma are well documented. The Lokalalei assemblages from the Nachukui Formation also provides some evidence of carcass exploitations (Brugal et al., 2017; Delagnes & Roche, 2005). The marks from Lokalalei 1 are described as percussion and cutting on size 2 and 3 bovids and on a turtle shell (Brugal et al., 2017). Delagnes and Roche (2005) also reported a single cutmark on a mammalian bone fragment from Localalei 2C. Brugal and colleagues concluded that meat consumption was still very limited, and mainly supplemented by a substantial vegetal part for the Lokalalei Oldowan (Brugal et al., 2017). The interpretation is because specimens with cutmarks are few and parts of the bones have been destroyed by carnivores (Brugal et al., 2017).

Linear marks from sediments dated to ~3.4 Ma at Dikika were interpreted as cut marks induced by early hominids (McPheron et al., 2010; Thompson et al., 2015). However, others opposed this identification and attributed it to trampling (Dominguez-Rodrigo et al 2012; 2014), and crocodile bite marks (Sahle et al 2017). Undisputed human induced cutmarks thus far are those from Bouri and Gona at ~ 2.5 Ma (de Heinzelin et al., 1999; Dominguez-Rodrigo et al., 2005; Sahle et al., 2017; Semaw et al., 2003).

The environmental context indicates that these behaviors are recorded at different environmental settings from forest like to open landscapes. At Gona, pollen data indicate a forest dominated riverine landscape (López-Sáez & Domínguez-Rodrigo, 2009). Compared to Nachuiki, the Shungura for the same period has less alcelaphines and antilopinies. Whereas

Tragelaphini and Reduncini are more common in the Shungura members E and F than at Lokalalei (Bobe & Behrensmeyer, 2004; Bobe & Eck, 2001; Brugal et al., 2003) suggesting wet and forest like conditions are common in the Shungura paleolandscapes.

Based on the faunal and taphonomic data (although few and poorly represented), the behavioral ecology for Lokalalei Oldowan hominids was interpreted as an opportunistic scavenging (passive scavenging) on a relatively wooded area along a river or lake side (Brugal et al 2017). For the Shungura, access to large carcass by hominids is evident as indicated with the presence of cutmarks and percussion activities, and possibly modifying bones for tool use. Based on the sedimentary context (Howell et al 1987; Maurin, 2017b), and the abundance of aquatic fauna, butchery activity possibly took place on a flood plain close to a riverbank.

The two ecomorphological studies at the Shungura Formation (Barr, 2015; Plummer et al., 2015) indicated unit F-1 is represented by all habitat categories more or less proportionally represented. Thus, based on this method, unit F-1 where Oldowan archeological occurrences are common is reconstructed as heterogenous habitat type.

I have observed a shift in abundance of bovids between E and F, while the general taxonomic composition remains similar. Chapter two of this thesis also demonstrate that except for a short event at unit F-0 which shows a pick in Alcelaphini, units F-1 to F-3 accommodate diverse habitat types. Similar results were also observed by comparing faunal distribution pattern across north and south sectors in Member F (Maurin, 2017b). Within these dynamics, the most important changes include a significant increase in the abundance of Alcelaphini at the base F.

4.5. Conclusion

Despite the high impact of bone surface preservations and fragmentation, some pieces of mammalian bones showed traces of cut marks and percussion marks from both surface and excavation localities. At a slightly higher stratigraphic position (F-3), OMO 123 also provided evidence of cutmarks and percussion marks, thus increased the number of specimens with cutmarks within the Oldowan archeological context. Few specimens, although surface collected, also indicated the shaping of bones probably as tools.

Overall, the bone modifications indicate that medium to large mammal tissues were processed, presumably for meat consumption, marrow and possibly as tools at ~ 2.3 Ma. However, the percussion activities and shaping of those large bones contrasting to the very small size of the associated stone tools left us ponder regarding the functional relationship. Recent usewear analysis on these tools indicate the use of carcass processing such as defleshing with some samples compared to wood work (Galland, 2022). For the percussion activities, one possible scenario could be that the hominids might be using fewer larger hummer stones but preserving them for longer time as opposed to use and discard?

Based on these data, along with additional specimens from other contemporaneous localities, I believe that early hominids had access to both meat and marrow from large mammal carcasses. In addition, the associated large bone flakes (at least the two specimens) shaped to form as tools suggest bone tool antiquity tracing back to ~2.3 Ma.

Based on the faunal data, the environmental settings where these activities took place seem to be near aquatic associated with open settings. This is confirmed by the dominant presence of grazing taxa, semi-aquatic and aquatic faunal remains. However, as indicated in chapter two of this thesis, localities from other archeological units in Member F indicate variety of fauna composition across localities.

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Chapter Five

Conclusion and Future directions

The dissertation attempts to address questions surrounding the ecological contexts associated to the emergence of Oldowan culture in the Shungura Formation, and hominid butchery activities throughout the sequence as well as correct identification of such traces. To do so, I have used 3D dental microwear texture analysis (DMTA), faunal abundance analysis, and bone surface modifications (BSM) on the vertebrate assemblages from the Shungura Formation (3.6-1 Ma). The first two proxies are used to study the dietary behavior of herbivores (particularly bovids), and their habitat distribution across space and time within the context of the emergence of the Oldowan technology in the Shungura Formation. Whereas BSM study was used as a tool to explore predator-prey relations, including the place of hominids within the trophic network in the Shungura sequence. This study also marks the first use of Elliptic Fourier based analysis of cut mark morphology.

This dissertation is the first attempt to systematically document zooarcheological data from the Shungura Formation. The result of this study indicates that the units immediately predating the Oldowan occurrences at the Shungura show relatively dry settings associated with high abundance of hyper-grazer taxa, notably Alcelaphini. This study detects that microwear analysis coupled with faunal abundance at a locality scale provides a more precise ecological context. Heavy cover and wet habitats might have been less common than reported using ecomorphology methods. The results in this study are in general accordance with previous faunal abundance and dietary ecology studies. Oldowan archeological occurrences in Member F (units 1 to 3) from the Shungura are distributed across heterogeneous landscapes rather than in units immediately predating them.

Taphonomic investigations on the portions of the Shungura faunal remains indicate that most specimens were predominantly altered by fluvial transportation. The assessment of these bone surface modification (BSM) studies shows that crocodilians to be active agents in all members, especially in Members C and LG.

Definitive butchery evidence was found as old as ~2.3 Ma. Evidence for carcass exploitations were found regardless of their association with archeological occurrences. The largest samples with cut marked specimens however come from Member L, dated to 1.2 Ma.

The study of linear BSM using confocal microscopy and Elliptic Fourier analysis in comparison with experimental data proves to overcome equifinality. Mahalanobis-based classifications had an average of 86.2 % confidence when classifying fossil BSM from bite marks and trampling marks.

The thesis provides new information regarding hominid behavioral ecology during the early Pleistocene in the Shungura Formation. However, the past two years have been challenging in accomplishing the initial proposal of the thesis mainly due to the covid pandemic, and the conflict that broke out in November 2020 in Ethiopia. These severely affected my study which preventing me from travelling to Ethiopia to complete data gathering. With this, the psychological stress due to the war in Tigray which also cause loss of contact with my family for nearly two years is beyond what I can express here.

This crisis has specifically impacted my research objective for Member L. The initial plan of this part was to conduct a zooarcheological study with the aim to reconstruct the ecological context and dietary behavior of Early-Middle Pleistocene *Homo erectus*. To accomplish this, I have collected numerous faunal samples during the 2019 field mission from three localities, two attributed to new Acheulean sites. The OGRE has also collected numerous faunal remains from this Member, and the materials were to be integrated for taphonomic and ecological (taxonomic composition) studies. But, due to the sanitary crisis, laboratory work was not possible to study the whole assemblages. Only partial samples with BSM were studied from these localities. These data were used mainly for methodological improvement of BSM marks analysis, not for behavioral and ecological interpretations.

A future study should look at the whole assemblage of the collected samples, and notably assemblages from Member G to Member L. The faunal compositions should be compared between units and localities, in members L, G and other upper members (H, J and K). For instance, a quick Survey at OMO 50 (Member Lower G) in 2019 produces stone tool modified

bones including a shaft flake with percussion pit and cutmarks. Thus, it can be anticipated that further fieldwork will yield additional samples in this area, and in the Shungura sequence in general. As zooarcheological data gathering was not within the objectives of IORE research missions in the 1960s and 1970s, such samples were excluded from collection protocols unless from excavations. It is within the OGRE's commitment in integrating multidisciplinary research approaches including zooarchaeology that this thesis was designed.

The new geometric morphometric method applied here could be expanded by increasing the experimental data that are relevant to eastern African Plio-Pleistocene sites. Given the large number of quartz artifacts in the Shungura Oldowan record, it would be useful to extend the experimental samples. This will help tackle and further explore issues regarding cutmark variabilities, in particular due to the use of different raw materials.

Furthermore, this study has been limited to linear BSM analysis, though tooth punctures and pits were also collected. But this part is not included in this thesis due to time constraint. The measurements of punctures and pits (tooth and percussion induced) with known experimental data is ongoing. The aim was to test differences between tooth pits and punctures between carnivorans and crocodilians as well as stone tool induced percussion pits. This will allow interpretations regarding the mode and intensity of carcass exploitation hominids and other carnivores in the Shungura.

Finally, plans are underway to fully investigate the Member L faunal assemblages as well as to increase and diversify experimental samples to strengthen the BSM methods applied in this study.

This thesis does not only provide clue to the paleoenvironmental background surrounding the emergence of the Oldowan in Member F, but also poses new questions. For instance, what caused the Alcelaphini peak at unit F-0 (?) is yet to be addressed. Integrating isotope data on F-0 are in progress. Isotope sampling for OMO 33 and L 398 bovids is already made at the National Museum of Ethiopia, but sample treatment and analysis is yet to be performed.

Furthermore, possible bone tools are identified in this study from Member F (~2.3 Ma) and possibly from Member L ~1.2 Ma. These materials very few and are all from surface context. Despite such samples show the great potential, further field work is planned to be performed for additional samples.

Beside the studies in Member F, general faunal evolution at local scales (in space and time) lack of stone tool assemblages from G-14 (2.057 Ma) to L-7 (1.206) Ma. Despite this, hominid remains and traces of butchery activities were documented in this study on some specimens from parts of these units. Thus, BSM samples could offer alternative explanations regarding human activities/behavior in particular on units devoid of lithic artifacts.

In this study, faunal remains from OMO 57 was used as a case study of site formation from the Shungura Oldowan occurrences. Other Oldowan archeological localities from the Member F of the Shungura Formation such as OMO 1/E, OMO 79 has been reported to have fauna associations by previous workers. However, although initially planned, the trip to access these collections was not possible due to the sanitary crises. These should be assessed in the future as they are associated with archeological occurrences.

Overall, to better understand the role of hominids in Shungura ecosystem from 3.75 Ma to 1 Ma, a full assessment of the Shungura BSM on all taxa and through the sequence is planned.

Appendix

List of possible stone tool modified bones from the Shungura Formation

Specimen #	Member	Unit	Mark type	Element	Taxa	Cutmark# (cluster)	Size class
L 26-5a	E	E-2	Cut?	Metatarsal, distal	Bovidae	1	2
OMO 57-7-exc-1-A	F	F-1	Cut	Indet	Mammal	2	
OMO 57-7-exc-1-B	F	F-1	Cut	Indet	Mammal	2	
OMO 57-7-exc-1-C	F	F-1	Cut?	Indet	Mammal	1	
OMO 57-7-exc-24-A	F	F-1	Cut	Indet	Mammal	1	
OMO 57-7-exc-C	F	F-1	Cut?	Indet	Mammal	1	
OMO 57-T1	F	F-1	Cut, bone tool?	long bone	Mammal	1	3?
OMO 57-T102	F	F-1	Cut	long bone	Mammal	2	1-2
OMO 57-T639	F	F-1	bone tool?	long bone flake	Mammal		3-5?
OMO 123-1973-1976	F	F-3	Cuts	long bone flake	Mammal	1	3
OMO 123-1976-33	F	F-3	percussion	long bone flake	Mammal		3?
OMO 123K-1973-1976	F	F-3	Cut?	long bone flake	Mammal	1	2-3
P 774	F	F-3	Cut?	long bone flake	Mammal	2	2-3
OMO 136-1972-69	GL	G-1	Cuts	Tibia, distal	Bovidae	1	1
OMO 136-1972-780	GL	G-1	percussion	Metatarsal	Giraffidae		
OMO 253-1973-5113	GL	G-11-G-12	Cuts	Humerus, distal	Bovidae	2	2
OMO 322-1976-1016	GL	G-11-G-13	Cuts	Tibia, distal	Bovidae	1	
L 422-5	GL	G-4	Cuts?	Rib fragment	Mammal	8	4?
L 35-22	GL	G-4-G-5	Cut	Metatarsal, distal	Bovidae	3	2
OMO 50-T1	GL	G-7-G-10	Cuts	long bone	Mammal		
OMO-50	GL	G-7-G-10	Cuts?	Rib fragment	Proboscidea	3	
OMO 323-1976-1446	GL	G-8	Cut?	MT, juvenile	Bovidae	1	
OMO 323-1976-1531	GL	G-8	Cut?	Radius, distal	Bovidae	1	
OMO 47-1972-2	GL	G-8	percussion	Tibia	Bovidae		
OMO 269-1974-1257	GU	G-19	Cut?	Tibia, distal	Bovidae	1	1
OMO 270-1974-1098	GU	G-19-G-20	percussion	Humerus, distal	Bovidae		2

OMO 215-1974-17	GU	G-24	percussion	Tibia, distal	Bovidae		1
OMO 316-1976-751	GU	G-26	percussion	Radius, proximal	Bovidae		2
F 356-7	L	L	percussion	Metatarsal, proximal	Bovidae	1	2-3
OMO 377-10051a	L	L-6	Cuts	Femur, Complete	*Hip. aethiopicus*	>10	
OMO 377-10051b	L	L-6	Cuts	Tibia, complete	*Hip. aethiopicus*	6	
OMO 377-10091	L	L-6	Cuts	Femur, complete	*Hip. aethiopicus*	8	
OMO 377-T002	L	L-6	Cuts, bone tool?	long bone/ shaft	*Hip. aethiopicus?*	1	
OMO 377-T004	L	L-6	Cut	Scapula, distal	*Hip. aethiopicus*	5	
OMO 377-T005A&B	L	L-6	Cut	Rib, frag	large mammal	4	
OMO 377-T006	L	L-6	Cut	long bone	large mammal	1	3?
OMO 377-T008	L	L-6	Cut?	Carapace	Testudinidae	2	
OMO 377-T009	L	L-6	Cuts	Jaw fragment	Suidae?	3	2
OMO 377-T010	L	L-6	Cut	Ulna, proximal	*Hip. aethiopicus*?	3	
OMO 377-T011	L	L-6	Cuts	Indet	Mammal	1	
OMO 377-T012	L	L-6	Cuts	Pelvis? fragment	Mammal	1	1-2
OMO 377-T013	L	L-6	percussion	long bone	Mammal		2-4
OMO 377-T014	L	L-6	Cuts	Ulna, distal	*Hip.aethiopicus?*	2	
OMO 377-T016	L	L-6	Cuts	Humerus, proximal	Bovidae	2	2
OMO 377-T017	L	L-6	Cuts	Indet	Mammal	2	2-4
OMO 377-T018	L	L-6	Cuts	Indet	Reptile	2	
OMO 377-T020	L	L-6	Cuts	Indet	Mammal	1	3?
OMO 377-T022	L	L-6	Cuts	long bone, fragment	Mammal	2	2-3
OMO 377-T024	L	L-6	Cut	Cranial? fragment	Mammal	5	
OMO 377-T025	L	L-6	percussion	long bone	Mammal		3-4?
OMO 377-T026	L	L-6	Cuts	Femur, proximal end	*Hip. aethiopicus*	1	
OMO 377-T028	L	L-6	Cuts?	Rib, frag	Mammal	2	2
OMO 377-T029	L	L-6	Cuts	Radius? /Shaft	*Hip. aethiopicus?*	2	
OMO 377-T030	L	L-6	Cut	Indet	Fish	2	
OMO 377-T031A	L	L-6	Cuts	Indet	Fish	1	
OMO 377-T031B	L	L-6	Cuts	Indet	Fish	1	
OMO 377-T033	L	L-6	Cuts	Cleithrum	Fish	2	
OMO 377-T034	L	L-6	Cuts	Rib, fragment	Mammal	1	4-6
OMO 377-T035	L	L-6	Cuts	Plastron/Carapace	Testudinidae	2	
OMO 377-T036	L	L-6	Cuts	Rib? Frag	Mammal	3	5-6

OMO 377-T054	L	L-6	Cuts	long bone	Mammal	2	4-5
OMO 377-T2-G10	L	L-6	Cut	Metapodial	Hippopotamidae	3	large
OMO 377-T2-H6	L	L-6	Cut	Metapodial, distal	Hippopotamidae	1	large
OMO 395-T1	L	L-7-L-8	Cuts	long bone	Mammal	3	1-2
OMO 395-T10	L	L-7-L-8	Cut	Indet	Mammal	1	3-5
OMO 395-T11	L	L-7-L-8	Cuts, bone tool?	long bone	Proboscidea?	2	6
OMO 395-T2	L	L-7-L-8	Cut	scapula?	Mammal	2	1-2
OMO 395-T3	L	L-7-L-8	Cut	Rib, fragment	Mammal	1	1-3
OMO 395-T4A&B	L	L-7-L-8	Cuts	long bone flakes (5)	Mammal	4	1
OMO 395-T5	L	L-7-L-8	Cut	long bone	Mammal	3	2?
OMO 395-T6	L	L-7-L-8	Cut	Indet	Mammal	1	3-5
OMO 395-T9	L	L-7-L-8	Cuts	long bone, fragment	Mammal	2	1-2